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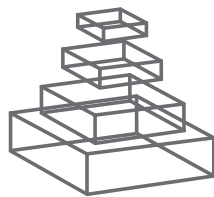
ATTENTION AND CONSCIOUSNESS IN DIFFERENT SENSES

Topic Editors

Naotsugu Tsuchiya and Jeroen J. Van Boxtel



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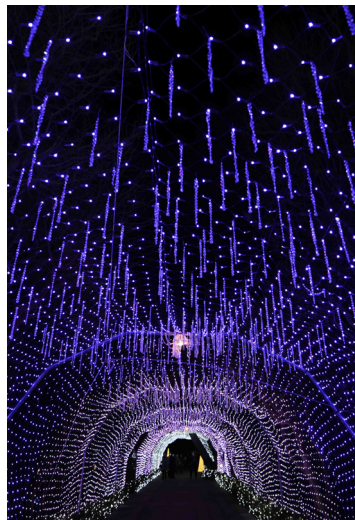
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ATTENTION AND CONSCIOUSNESS IN DIFFERENT SENSES

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Although often used in everyday speech and in the scholarly literature, “selective attention” and “consciousness” lack clear, undisputed definitions. Partly because of this deficit there exists a lively debate on the relationship between the two. Nevertheless, attention has been studied scientifically for a long time, because a variety of tasks allow researchers to control several of its aspects (e.g. focused and feature-based attention).

Consciousness as a scientific subject of study has emerged more recently, but is now rapidly gaining traction. Scientific studies of consciousness concern the state or level of consciousness (e.g., awake as opposed to in coma, dreamless sleep or under anaesthesia) as well as the contents of consciousness or the phenomenology of perception.

With the increase in consciousness-focused research, there is a concomitant surge in research examining the relationship between attention and consciousness. This relationship between attention and consciousness is the topic of this Research Topic. Contributions related to or focused solely on attention or on consciousness will not be considered.

It had long been assumed that attention and consciousness are inextricably intertwined: two sides of the same coin. However, recently substantial evidence has emerged that attention and consciousness are interacting, but separable processes. It is however debated how tight the interactions are, and what the exact nature of the relationship is.

Therefore, we invite researchers from different “camps” to provide opinionated but balanced literature reviews. Different groups will interpret the same data in different ways. We feel

that combining these views in one Research Topic is immensely valuable to researchers from different fields. Apart from reviews we also invite potential contributors to provide new and exciting evidence in the form of original contributions that may support any of the different views. Even though attention and consciousness are critical aspects of many different cognitive processes, they are mainly studied (though not exclusively) in the domain of visual perception. In other sensory modalities, e.g. olfaction or audition, it is currently not clear whether distinctions between attention and consciousness exist, which is even more true for other cognitive processes such as memory. Therefore, we specifically invite contributions covering the auditory, somatosensory, olfactory, and memory domain.

We ask all contributors to provide discussions on the relationship between attention and consciousness, and focus on (1) the influence of attention on sensory processing; (2) the formation of conscious perception, (3) the evidence for unconscious processing and its modulation by attention; (4) potential indications for dissociations between attention and consciousness (e.g. does paying attention to a stimulus decrease performance on e.g. a discrimination task?); (5) neuroimaging and neurophysiology data pertaining to these questions.

Often, one is caught in one's own research field and lacks the time or the knowledge to delve into another field. This Research Topic should provide a great overview in great breadth of the current state of knowledge on the links between attention and consciousness, and their interactions, in several different sensory modalities.

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Introduction to research topic: attention and consciousness in different senses

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The question of the origin of consciousness has engaged scientists and philosophers for centuries. Early scholars relied on introspection, leading some to conclude that attention is necessary for consciousness, and in some cases equating attention and consciousness. Such a tight relationship between attention and consciousness has also been proposed by many modern theorists (Posner, 1994; Merikle and Joordens, 1997; Mack and Rock, 1998; Chun and Wolfe, 2000; O'Regan and Noe, 2001; Mole, 2008; De Brigard and Prinz, 2010; Prinz, 2011; Cohen et al., 2012). The relationship between attention and consciousness has come under increasing scrutiny with the development of neuroscientific methods. In modern neuroscience, the effects of attention are often objectively defined and measured as reduced reaction time and improved performance. Similarly, conscious awareness of an object is established by a subjective report in combination with objective forced-choice performance (Seth et al., 2008; Sandberg et al., 2011). With these measures in place, a variety of methods has been used to manipulate attention (e.g., cueing, divided attention, etc.) and consciousness [e.g., masking, crowding, and binocular rivalry (Kim and Blake, 2005)]. These empirical studies have culminated in recent proposals that attention and consciousness are supported by different neuronal processes and they are not necessarily correlated all the time (Iwasaki, 1993; Baars, 1997; Hardcastle, 1997; Kentridge et al., 1999; Naccache et al., 2002; Lamme, 2003; Woodman and Luck, 2003; Bachmann, 2006; Koch and Tsuchiya, 2007; van Boxtel et al., 2010).

Our original motivation to edit this Research Topic was three-fold: (1) to gather and collect current, diverse views on the relationship between consciousness and attention, (2) to invite reviews on consciousness and attention in non-vision modalities, (3) and to invite empirical studies of consciousness and attention. As summarized below, our goals are largely achieved thanks to 17 contributions to this issue.

CURRENT PERSPECTIVES ON THE RELATIONSHIP BETWEEN CONSCIOUSNESS AND ATTENTION

Posner (2012) sets the stage for the discussion by distinguishing different ways in which “consciousness” and “attention” are used colloquially. Clarifying the three senses of consciousness, namely, the level or state of consciousness (as in coma, sleep, or awake), sensory awareness (or contents of consciousness), and

voluntary control, Posner claims that the neuronal mechanisms that support each type of consciousness overlap with those for a distinct type of attention: alerting, orienting, and executive attention, respectively. Chennu and Bekinschtein (2012) investigate the workings of attention at different levels or states of consciousness. Reviewing the mismatch negativity in the auditory oddball paradigm, they survey evidence for dissociations and parallels between bottom-up and top-down attention and the level of consciousness. Marchetti (2012) largely agrees with Posner (2012), emphasizing the variety in types of attention and consciousness. By considering each type, Marchetti argues that consciousness is always associated with some kind of attention and attention is always associated with some kind of conscious perception. Chica and Bartolomeo (2012) dissect attention into endogenous/top-down and exogenous/bottom-up components, considering their relation with consciousness. They claim that endogenous attention is neither necessary nor sufficient for consciousness agreeing with some views (e.g., Koch and Tsuchiya, 2007; van Boxtel et al., 2010) while exogenous attention is necessary (but not sufficient) for consciousness (also see Hsu et al., 2011). They note the prefrontal parietal network (PPN) as central for both exogenous spatial attention and conscious perception. The importance of the PPN is also stressed by Bor and Seth (2012), who review recent empirical studies for identifying potential neuronal correlates of consciousness (NCCs). Based on the fact that the PPN has been commonly identified as the neuronal correlate for both attention and consciousness (Rees and Lavie, 2001), they suggest that attention is an important and necessary aspect of consciousness. As the PPN is also associated with working memory, executive control, and chunking, they argue that these cognitive functions, including attention, make up the core psychological components of consciousness. A contrasting view on the role of the PPN is provided by Tallon-Baudry (2011), who argues against the tight relationship between consciousness and attention. She raises several issues about the interpretation of previous results with respect to the PPN. For example, many previous experiments did not independently manipulate both attention and consciousness. To explain recent neural findings pointing to a dissociation of attention and consciousness, she proposes “a cumulative influence model,” where both attention and consciousness contribute to the final stage of decision making through independent paths.

Two novel theoretical ideas are put forward in this Research Topic. Hohwy (2012) proposes a framework based on predictive coding (Rao, 2005; Friston, 2009), where attention optimizes expectations about perceptual precisions, while conscious perception is a result of the prediction error minimization. Bachmann (2011) proposes to broaden the research view from focusing on modality-specific and feature-specific effects of attention to inter-modal effects of attention on consciousness. He concludes that attention and consciousness are separable and that consciousness can come about without selective attention. As Bachmann points out, the articles introduced so far build their theories mostly on the experimental evidence obtained in the visual modality. Next we will overview the articles looking outside the visual modality.

CONSCIOUSNESS AND ATTENTION IN NON-VISION FIELDS

Snyder et al. (2012) review recent experiments in auditory neuroscience, which investigated how conscious auditory perception is influenced by various high-level factors, including attention. They also review a variety of methods, including multistable stimuli and masking phenomena in the auditory domain, which will allow future research to shed a new light on the overlap in the neuronal mechanisms of attention and consciousness in audition and vision.

Keller (2011) explores the potential law-like relation between attention and consciousness in olfaction. As olfaction is very different from vision in several aspects (e.g., lack of spatial specificity, no object as a unit for selection, etc.), the concept of attention is clarified in comparison with that in vision. Then, Keller goes on to speculate about possible neuronal loci for attentional selection and conscious processing for olfaction. He concludes that attention is necessary for olfactory consciousness.

Lou et al. (2011) and De Brigard (2012) extend the discussion into non-sensory modalities. Lou et al. (2011) examine the role of the brain regions that locate around the midline, (i.e., paralimbic, resting-state, or default-mode network) in self-awareness and self-control, concluding that the network integrates attention, awareness and emotion to allocate brain resources. Looking at memory research, De Brigard (2012) dissect the kinds of attention important for memories. De Brigard follows the recent proposal for a distinction between internal and external attention (Chun et al., 2011) and argues that internal attention is necessary, but probably not sufficient, for conscious retrieval of memories.

EMPIRICAL STUDIES ON ATTENTION AND CONSCIOUSNESS

The Research Topic concludes with several empirical studies. While top-down selective attention is commonly assumed to be required to bind features into objects, Rosenholtz et al. (2012) argue that recent changes in the understanding of peripheral vision provides an alternative view. Their texture tiling model [also see perceptual metamers (Freeman and Simoncelli, 2011)] successfully explains why complex tasks, such as pop-out in visual search and natural scene categorization (Li et al., 2002), can be performed well in the periphery where the accuracy of information is severely impaired. Their model does not resort to top-down attention in accomplishing the complex visual tasks. Moutoussis (2012) reviews the findings on perceptual timing

and binding of visual features, concluding that misbinding illusions are due to differences in neural processing times as well as exogenous attention. Perry and Fallah (2012) conducted a psychophysics study to investigate the influence of bottom-up and top-down attention on a visual illusion called “motion direction repulsion.” They found that attentional manipulation via color affects processing speed without changing the conscious perception of motion. Delevoeye-Turrell and Bobineau (2012) investigated the effects of lowered and heightened attention on motor consciousness using a metacognitive approach (e.g., reproduction of a motion trajectory) for reflex-like stimulus-based and deliberate intention-based actions. Reproduction quality depended on how skillful subjects were in meditation, presumably reflecting the effectiveness of attentional control on the body. Finally, Willenbockel et al. (2012) recorded intracranial neuronal activity from the insula and amygdala of awake human patients to characterize the effects of visibility using continuous flash suppression (Tsuchiya and Koch, 2005) as well as using spatial-frequency “bubbles” (Willenbockel et al., 2010). They found that low spatial frequency information of invisible faces distinctively activated these regions and that activation by invisible faces precedes those evoked by visible faces.

QUESTIONS FOR FUTURE STUDIES

Over all the articles collected here, the most recurring issue is whether attention is necessary for conscious perception (Bachmann, 2011; Keller, 2011; Tallon-Baudry, 2011; Bor and Seth, 2012; Chennu and Bekinschtein, 2012; Chica and Bartolomeo, 2012; De Brigard, 2012; Marchetti, 2012; Posner, 2012; Rosenholtz et al., 2012). There are two aspects in this debate.

First, the role of the PPN for attention and consciousness is disputed (Tallon-Baudry, 2011; Bor and Seth, 2012; Chica and Bartolomeo, 2012). While meta-analyses of studies on consciousness and (exogenous) attention (Bor and Seth, 2012; Chica and Bartolomeo, 2012) point to a large overlap in the PPN for both attention and consciousness, Tallon-Baudry (2011) argues that not all the experiments have shown consciousness-related activation in the PPN (e.g., Tse et al., 2005), that some of the PPN activation may be related to a confound related to report or resolution of conflict (Knapen et al., 2011; van Boxtel and Tsuchiya, 2013), and that most studies did not independently manipulate attention and consciousness. These are all empirical issues, which can be relatively easy to address in the future studies.

The second issue is a bit trickier. Some claim that attention is always necessary, not only for vision but also for olfaction (Keller, 2011) and memory (De Brigard, 2012). Such an argument could be countered by everyday examples, such as peripheral vision (Rosenholtz et al., 2012), unexpected strong olfactory stimuli (Keller, 2011), and the feeling of familiarity (De Brigard, 2012), all of which appear to give rise to conscious experience without deliberate attentional amplification. This view is also supported by conscious perception of an isolated stimulus, because top-down attention can function when only the sensory inputs are competing with each other (Koch and Tsuchiya, 2007; van Boxtel et al., 2010). However, it is possible to argue that even these cases require some amount of attention, because attention is present

everywhere in some diffuse way (De Brigard and Prinz, 2010; Keller, 2011; Cohen et al., 2012; Marchetti, 2012).

Currently, no psychophysical experimentation in humans can prove or disprove such a hypothesis, as it seems impossible to induce the state of no attention in humans. However, the advent of optogenetics in animal research might allow us to create a situation where no attentional activation, fed back from the PPN, arrives at the visual cortex (Tsuchiya et al., 2012). It remains to be seen if such animals without (top-down) attention can consciously see an isolated object or not.

Even if it turns out animals can visually perceive an isolated object without top-down attention, it remains unclear if inter-modal attention is required for conscious perception in a non-dominant modality, such as olfaction and memory. It is plausible that regardless of the inputs, there may be always competition between modalities (e.g., dominant vision vs. non-dominant olfaction) and between times (e.g., dominant present

vs. non-dominant past memory or future planning). By default, the dominant modality may be a winning coalition (i.e., present visual input) requiring nearly no top-down attentional amplification to be consciously experienced while non-dominant modalities might require some level of attentional amplification to reach consciousness.

We hope these articles will inspire the readers for further conceptual and empirical work on the issue of the relationship between consciousness and attention. Untangling this relation is the necessary step toward uncovering the neuronal basis of consciousness.

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Attentional networks and consciousness

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The term consciousness is an important one in the vernacular of the western literature in many fields. It is no wonder that scientists have assumed that consciousness will be found as a component of the human brain and that we will come to understand its neural basis. However, there is rather little in common between consciousness as the neurologist would use it to diagnose the vegetative state, how the feminist would use it to support raising male consciousness of the economic plight of women and as the philosopher would use it when defining the really hard question of the subjective state of awareness induced by sensory qualities. When faced with this kind of problem it is usual to subdivide the term into more manageable perhaps partly operational definitions. Three meanings that capture aspects of consciousness are: (1) the neurology of the state of mind allowing coherent orientation to time and place (2) the selection of sensory or memorial information for awareness and (3) the voluntary control over overt responses. In each of these cases the mechanisms of consciousness overlap with one or more of the attentional networks that have been studied with the methods of cognitive neuroscience. In this paper we explore the overlap and discuss how to exploit the growing knowledge of attentional networks to constrain ideas of consciousness.

Keywords: attention networks, alerting, orienting, executive

INTRODUCTION

A previous paper on this topic Posner (1994) argued that the mechanisms of attention form the basis for an understanding of consciousness. Since that time the study of attention has greatly advanced (Petersen and Posner, 2012; Posner, 2012). While the intervening years have provided evidence of dissociations between brain networks involved in attention and aspects of consciousness (Koch and Tsuchiya, 2007), I still believe that much can be learned about consciousness from an understanding of attention.

As many have pointed out there are dissociations between attention and consciousness, however, there are also dissociations between various aspects of attention and some of the latter may help account for the former.

In this paper I first summarize the relation of attention and consciousness and illustrate how the study of attentional networks might help illuminate dissociations. Because attention involves different brain networks (Posner and Petersen, 1990; Posner and Rothbart, 2007) and because consciousness has a wide variety of definitions it is necessary to illustrate their constraints and inter-relations rather than provide a single unified account. I try to do this by dealing first with the conscious state, second with consciousness of sensory qualities and finally with volition. The distinction between conscious state and content is one that has been frequently made (Laureys, 2005). The idea that there is a level of voluntary control or will that reflects conscious control of behavior is also a common idea (Baumeister et al., 2007). It turns out that each of these definitions is predominantly associated with a different attentional network. I then turn more briefly to the issue of the most important unsolved questions and the methods that their solution might require.

STATE

Within neurology consciousness often refers to a brain state in which the person is capable of responding to external events and relate them to the self (Posner et al., 2007a). This state is closely associated with the concept of arousal and to the diurnal cycle of sleep and wake. Clearly during sleep we are unable to respond appropriately to many external events and patients with lesions of the arousal system are often unable to determine their current location or the time of day or year.

Recent fMRI studies have revealed that the resting brain involves activity in two oscillating brain networks (Raichle, 2009). In experiments it is possible to provide a warning signal that a target is about to occur. The participant relaxes between trials into a state which is toward that obtained during continued rest, the warning signal alters this state. These studies have revealed the importance of the brain's norepinephrine system arising in the brain stem locus coeruleus and involving both frontal and parietal brain areas. In the posterior part of the brain this system influences more dorsal areas involved in orienting of attention toward sensory stimuli and has little direct input into strictly sensory areas of vision. A warning signal too fleeting to be conscious can still induce the alert state. Here is one of the places where a state change related to attention provides a critical bridge for awareness. If being alert is called paying attention than one can say attention can occur without consciousness of the signal that caused it.

By having a person to participate in a long and somewhat dull task one can measure their vigilance over time (Posner and Petersen, 1990; Posner, 2008, 2012). The right cerebral hemisphere is most involved in maintaining the alert state over long periods of time (tonic alertness), while the left cerebral hemisphere responds more to phasic changes induced by warning signals. Support for

this link between the mechanisms of alertness and the conscious state comes from a recent finding showing that the conscious state of rats can be eliminated by injecting anesthetic into the midpontine tegmental system which has close connections to the locus coeruleus, the anterior cingulate, and other frontal structures (Sukhotinsky et al., 2007). Thus detailed findings about the physiology of the alert state provide a background for the study of consciousness.

Even in the absence of the alert state we can be conscious of internal events as in dreams. In the vegetative state there is evidence of arousal but no evidence of consciousness, showing that while the alert state clearly influences consciousness it is not sufficient for awareness of external events.

SENSORY AWARENESS

An important distinction in studies of awareness (Iwasaki, 1993) is between general knowledge of our environment (ambient awareness) and detailed focal knowledge of a scene (focal awareness). We generally believe that we have full conscious awareness of our environment, even when our focal attention is upon our own internal thoughts. Experimental studies (Rensink et al., 1997), show us how much this opinion is in error. In the study of “change blindness” when cues that normally lead orienting of attention are suppressed, we have only a small focus for which we have full knowledge and even major semantic changes in the remainder of the environment are not reported.

Change blindness is closely related to studies of visual search which have been prominent in the field of attention and are known to involve an interaction between information in the ventral visual pathway about the object identity and information in the dorsal visual pathway that controls orienting to sensory information (for a review, see Driver et al., 2004). Visual search tasks have been important for examining what constraints attention provides to the nature of our awareness of a target event. There is clear evidence that attention to a visual event increases the brain activity associated with it. Most evidence arises from studies using event related electrical potentials with visual stimuli and these have clearly shown that early sensory components of the visual evoked potential P1 and N2 (80–150 ms) are enlarged by the presence of attention (Hillyard et al., 2004).

If attention can serve to constrain conscious experience its presence indicated by enhanced P1 should increase the perceived luminance of a visual target and lead to the judgment that it is brighter than would otherwise been reported. Indeed Yeshurun and Carrasco (1999) found that a cue that causes orienting to a target can serve to changes its contrast function. Moreover, the increased P1 found in the EEG studies would support also support this prediction. However, this shift in visibility when orienting to a visual stimulus apparently does not occur, at least for stimuli that are sufficiently bright to be conscious. In an extensive series of experiments Prinzmetal et al. (1997) have shown that being able to pay attention to a stimulus or directing attention to a stimulus location reduces the variability of judgments about luminance or other stimulus dimensions but does not produce a subjective brightening of the stimulus. This suggests an important dissociation between luminance increases and attention on subjective experience even when they influence the same component of the scalp recorded ERP. While it is possible that a previously unseen

stimulus will become conscious when attended, it appears generally that top down influence on sensory systems can usually be distinguished from sensory changes even when they involve the same general neural systems.

In a review of the literature Koch and Tsuchiya (2007) argued that attention and consciousness of external stimuli are two distinct brain processes. They produce a fourfold table that distinguishes between non-conscious and conscious processes and between attended and non-attended. They argue that all four possibilities are possible. Two of them, attention without consciousness and consciousness without attention, are dissociations. For example, they argue that the pop out effect in visual search, or the ability to provide the gist of a scene are examples of conscious processes that can occur without attention. This idea seems to confuse orienting of attention to items in the display, which is often not reported, with focal attention involved in processing the target. Duncan (1980) showed that multiple locations can be monitored simultaneously, but that the detection of one target drastically reduces the ability to detect another target. This reflects the important distinction that orienting can be summoned very efficiently to a target if it is not currently engaged but once engaged it is difficult to disengage. Corbetta and Shulman (2002) have shown that the temporal parietal junction of the right hemisphere is critical brain area for disengaging the orienting mechanism. This mechanism imposes a strong limitation on orienting to multiple objects.

Koch and Tsuchiya (2007) also argue that attention is required for priming, visual search, or thought but these things may not give rise to consciousness. The issue of whether attention is needed for priming illustrates how attention is not unified. Priming can occur even when no attention is allocated to the meaning of the prime. For example, a bias to treat the word “palm” as a tree does not eliminate the priming of finger at least for a brief time (Marcel, 1983). This shows that attention in one sense is not needed for priming. However, if attention is allocated to a letter the ability of the word of which the letter is a part to improve processing of related words (semantic priming) is reduced or eliminated. Moreover, the influence of a prime appears to depend on the person allocating attention at the proper time and place (Naccache et al., 2002; Dehaene, 2004), even if unaware that a word was presented. As the exact mechanisms of priming are better understood we may learn more about how the form of attention involved relates to its subjective experience.

Consider the process of developing the next sentence for this paper. No one would be surprised if a knock on the door to which I oriented interrupted my work and led to forgetting my place. One could argue that increased attention (in this case to the door) diminished awareness of the words of my sentence. Is this an instance of increased attention leading to decreased awareness? No one would really accept that. Rather they would say that I was simply attending to the wrong thing. However, similar confusions do infect the literature.

An example of confusion between attention networks arises in the opposite effects of attention and awareness on the duration of afterimages (van Boxtel et al., 2010; Murd and Bachmann, 2011). These experiments involve a full factorial design in which attention to the target is manipulated by a dual task while visibility is manipulated by the presence of a suppressor stimulus in the opposite eye. This is a very clever experimental design, but the interpretation of a

dissociation between attention and visibility (consciousness) may not be correct. There is much evidence that dual tasks involve a common bottleneck (Sigman and Dehaene, 2008; Tombu et al., 2011) and that frontal areas common to the executive attention network are involved (Petersen and Posner, 2012). Thus dual tasks would reduce the availability of the executive attention system, but its role on convert orienting to the Gabor inducer is simply not defined. While viewing attention as one unified thing leads one to conclude that attention is reduced the network view says only the executive attention is reduced while orienting is simply not controlled. Suppose orienting was similar regardless of the difficulty of the dual task. The afterimage should be the same. Why is there a small increase of the duration of the afterimage during the difficult dual task condition. I really do not know the answer to this, but it could have to do with fatigue of the executive system producing a small slowing of response time to the reported image (see Baumeister et al., 2007).

This may not be the correct explanation of the experiment but it illustrates how different attention networks are involved in this experiment. Reporting the length of the visual aftereffect depends on the ability of the executive system, including the anterior cingulate, anterior insula and other frontal and basal ganglia structures to produce a report of the contents of consciousness. However, determining the direction or location of a target event involves the orienting system, including the inferior and superior parietal lobe, and frontal eye fields. Not only are these networks anatomically separate, but they are poorly correlated in performance. The finding that they are negatively related during afterimages is certainly interesting and important, but it does not raise any fundamental problem for the relevance of attention networks to understanding conscious reports.

Perhaps even more striking evidence is a study (Olivers and Nieuwenhuis, 2005), in which observers report the second of two rapidly presented stimuli more often when they are distracted by another task than when they are fully concentrated on the display. This shows that a reduction of attention can be accompanied by an increase in awareness of the target. This striking demonstration may reflect different attentional networks. The attentional blink arises as the person concentrates on target 1 and as a consequence target 1 and target 2 are not perceived as separate events. The dramatic dissociation between awareness of a target and the availability of attention provides evidence that the two phenomena are not exactly the same. This dissociation may arise because there is a specific inhibition to processing a second target when it is similar to a first target which is still being attended. If concentration on the first target is reduced by a second task the inhibition may be released. These inhibitions are common in studies of attention, for example, in visual search orienting to a location slows reorienting to that same location (inhibition of return). If a second target is inhibited when an identical or related first target is focally attended, the dual task would reduce focal attention on the first target and lead to the paradoxical improved performance on the second target. Divided attention would provide a way of reducing overall focal attention thus leading to the observed improvement in performance.

VOLITION

Focal attention to the target of a visual search appears to involve an executive attention network that includes the anterior cingulate,

anterior insula, lateral prefrontal areas, and the underlying basal ganglia (Posner and Rothbart, 2007). Humans have a conviction of conscious control that allows us to regulate our thoughts, feelings, and behaviors in accord with our goals and people believe that voluntary conscious choice guides at least a part of the action we take. These beliefs have been studied under various names in different fields of psychology. In cognition, cognitive control is the usual name for the voluntary exercise of intentions, while in developmental psychology many of the same issues are studied under the name self-regulation and in the common term willpower (Posner et al., 2007b; Baumeister and Tierney, 2011).

Imaging studies suggest that whenever we bring to mind information, whether extracted from sensory input or from memory, we activate the executive attention network (Posner and Petersen, 1990; Posner, 2012). This may be because focal attention is voluntarily switched to the target information. Thus moving attention to a target in order to bring it fully to mind is one type of voluntary response. As such it has been hypothesized that it would require the executive attention network irrespective of the source of information (Posner and Petersen, 1990; Petersen and Posner, 2012).

We started out this paper with the traditional distinction between awareness and control as components of consciousness. However, one form of awareness, focal awareness, appears to involve the same underlying mechanism as involved in control. In this sense even though some forms of consciousness (e.g., ambient awareness) may have diverse sources within sensory specific cortex, there is also a degree of unity of the underlying mechanism involved in some aspects of consciousness (e.g., focal awareness and voluntary control). The distinction between focal and ambient factors in consciousness has been made before (Iwasaki, 1993) and it may help to clarify the sense of awareness that can be present even when detailed accounts of the scene are not possible as in change blindness (Rensink et al., 1997).

ISSUES AWAITING SOLUTION

The study of attention has made great strides in the last several years. It has been possible to combine imaging, genetics, and even cellular studies in humans, monkeys, and rodents to examine aspects of networks involved in the various functions of attention (Posner and Rothbart, 2007; Posner, 2012).

One way to proceed involves continuing the development of models of attention. We can then determine the constraints upon various definitions of consciousness they might provide. We need also to keep in mind that in the end these constraints may not be sufficient to entirely answer the many issues related to consciousness. It is important to realize that mapping of attention and consciousness is not one to one, but rather a mapping that involves several attentional functions or networks in addition to the several meanings of consciousness.

In many situations there is a strong correlation between orienting to and detecting a target. For example, a target at an attended location is more likely and faster to be reported. However, the separate RT subtractions of the Attention Network Test often yield low or no correlation between the orienting, alerting, and executive networks (Fan et al., 2002, 2009). In addition the networks have been shown to be separate anatomically in functional MRI studies (Fan et al., 2005), they involve different white matter tracts (Niogi

and McCandliss, 2009), separate neurotransmitters (Marrocco and Davidson, 1998), different oscillator frequencies (Fan et al., 2007), and depend on different genetic polymorphisms (Green et al., 2008). These separations between attentional networks may make the report of differences between attention and awareness in brain oscillations (Wyart and Tallon-Baudry, 2008) less surprising since different forms of attention also give rise to different oscillations (Fan et al., 2007).

Some additional avenues for exploring the relationship between attention and consciousness may involve how altered states such as those induced by brain injury, hypnotism, drugs, or meditation

that change attention vary the quality of our conscious experience. The study of each of these states has been enhanced by the use of neuroimaging both of gray matter areas and of the connectivity between activated brain areas. Real time analysis of this connectivity will probably be crucial to the full specification of the networks of attention and of consciousness (Posner et al., 2006; Raichle, 2009).

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Arousal modulates auditory attention and awareness: insights from sleep, sedation, and disorders of consciousness

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The interplay between attention and consciousness is frequently tested in altered states of consciousness, including transitions between stages of sleep and sedation, and in pathological disorders of consciousness (DoC; the vegetative and minimally conscious states; VS and MCS). One of the most widely used tasks to assess cognitive processing in this context is the auditory oddball paradigm, where an infrequent change in a sequence of sounds elicits, in awake subjects, a characteristic EEG event-related potential called the mismatch negativity, followed by the classic P300 wave. The latter is further separable into the slightly earlier, anterior P3a and the later, posterior P3b, thought to be linked to task-irrelevant “bottom-up” and task-oriented “top-down” attention, respectively. We discuss here the putative dissociations between attention and awareness in DoC, sedation and sleep, bearing in mind the recently emerging evidence from healthy volunteers and patients. These findings highlight the neurophysiological and cognitive parallels (and differences) across these three distinct variations in levels of consciousness, and inform the theoretical framework for interpreting the role of attention therein.

Keywords: attention and awareness, arousal, mismatch negativity, P300, disorders of consciousness, sleep, sedation

INTRODUCTION

In the study of auditory attention and awareness using electrophysiology, there is a rich body of scientific literature on the mismatch negativity (MMN) and the P300 components observed in the event-related potential (ERP). They are widely regarded as markers of key stages in the information processing hierarchy leading up to conscious perception. The first neural signature – the MMN – is a frontocentral negative deflection in the ERP (see **Figure 1A**), peaking at around 120–220 ms after the presentation of an “oddball” deviant auditory stimulus embedded within a stream of standard auditory stimuli (Näätänen, 1992). The MMN is often depicted as a difference wave computed by subtracting out the response to the standard stimuli from the deviant stimuli (Sams et al., 1985). In its traditional definition, it is seen as a correlate of the triggering of automatic pre-attentional “reorienting” to the deviant (Näätänen et al., 1978; Näätänen and Michie, 1979; Näätänen, 1990; Alain et al., 1994), though it is known to be modulated by attention (Alain and Woods, 1997; Woldorff et al., 1998; Näätänen et al., 2007) and might be influenced by recurrent feedback activation from frontal areas (Garrido et al., 2007, 2009).

Since the original reports of the MMN (Näätänen et al., 1978) there has been a significant amount of experimental work probing modulations of the MMN in a variety of settings (see Näätänen et al., 2007 for a review). The general conceptual picture that has emerged suggests that the MMN in fact reflects changes in a continually updated context-sensitive auditory memory trace (Winkler

et al., 1996; Sussman and Winkler, 2001). One of the main reasons for the sustained empirical interest in the MMN is that it provides researchers access to pre-conscious processing of temporal structure in auditory information beyond the basic sensory stage, but before it benefits from the spotlight of attention or enters conscious perception. Crucially, because of this property, researchers have found the MMN to be valuable in a clinical setting, to probe the abnormalities in auditory processing resulting from neurological dysfunction, and also to track the process of recovery therefrom (Wijnen et al., 2007). Alongside, evidence from sleep and sedation has shown that under certain conditions, the MMN can also be elicited in these states of behavioral unconsciousness (Atienza et al., 2002; Koelsch et al., 2006).

The P300 ERP component is the most widely studied EEG evoked potential signature in cognitive electrophysiology. The evidence in this regard commonly identifies it as positive deflection peak approximately 250–400 ms post-target, serving as a marker of conscious perception of salient events or stimuli (Sutton et al., 1965, 1967). Depending on the experimental context, it is also seen to be associated with target stimulus consolidation and working memory updating (see Donchin, 1981; Donchin and Coles, 1988; but also see Verleger, 1988). The P300 can often be considered to include two distinct subcomponents, the P3a and the P3b (see **Figure 1B**). The frontally centered P3a (usually peaking at 250–300 ms) is known to be elicited in a “bottom-up” manner, by novel, unpredictable stimuli, even if they are irrelevant to the task being performed (Courchesne et al., 1975; Squires et al., 1975). Though

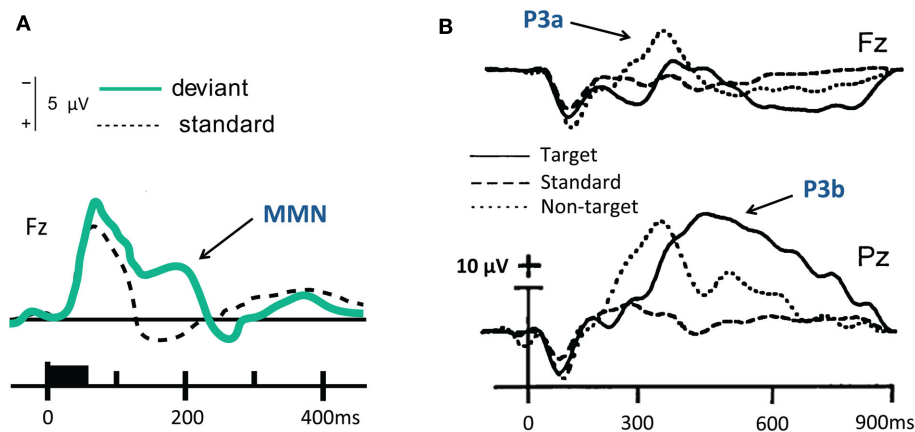


FIGURE 1 | Mismatch negativity (MMN) and P300 in healthy awake adults. (A) MMN evoked by 1032 Hz deviant tones (20% probability), when compared to 1000 Hz standard tones. Adapted from Sams et al. (1985). **(B)**

P3a and P3b evoked by 500 Hz non-target and 2000 Hz target tones (each with 10% probability), presented amongst 1940 Hz standard tones. Adapted from Comerchero and Polich (1999).

in many ways the P3a is related to the MMN, it is considered to index a distinct attention-driven process of stimulus evaluation. In this sense, it can be seen as a correlate of the process that accompanies the reorienting of involuntary attention, having been triggered by processes indexed by the MMN (Schröger, 1996; Escera et al., 2001; Ranganath and Rainer, 2003).

In contrast to the P3a, the more posterior, later P3b (peaking at around 300–350 ms) is thought to index the “top-down” deployment of selective attention to stimuli deemed as task-relevant, and their subsequent entry to conscious awareness and working memory (Kok, 2001; Polich and Criado, 2006). Like the MMN, these ERPs have been found to convey valuable information in a clinical setting, leading to applications that have informed a variety of applied questions regarding the nature of perceptual processing in impaired brains (Polich and Herbst, 2000; Polich, 2004; Duncan et al., 2009).

In this review, we highlight findings in the literature that discuss the role of the MMN, P3a and P3b in furthering our understanding of the interplay of attention and consciousness at varying levels of arousal and wakefulness. Importantly, we discuss results from studies involving patients in disorders of consciousness (DoC), a collective term commonly applied to the vegetative and minimally conscious states (VS and MCS, respectively). These studies have tried to connect these ERP components observed in patients to their diagnosis and prognosis. Historically, rates of misdiagnosis amongst patients in the vegetative state, conventionally based on purely behavioral metrics, have been disturbingly high (Schnakers et al., 2009). Given that the MMN and P300 ERPs can be evoked with auditory stimulation reasonably easily, and with relatively short passive experiments, they were the first to be applied in DoC research, with the aim of improving diagnosis and prognosis. In conjunction, we discuss MMN and P300 findings relating to attention and consciousness in the context of sleep and sedation, addressing the long-standing questions regarding the level of processing attainable with volunteers considered to be in non-pathological unconscious states.

THE MMN AND P3a IN DISORDERS OF CONSCIOUSNESS

Over the last decade, there have been many cohort studies of the prevalence of the MMN and P300 ERPs in patients diagnosed as being in VS and MCS states. Similar in design to studies involving comatose patients (see Daltrozzo et al., 2007 for a meta-analysis), the experimental paradigms in this context have typically used auditory deviant/oddball stimuli, ranging from simple tones to complex stimuli like the patient’s own name to evoke the MMN (Figure 2A) and/or P3a (Figure 2B) in DoC (Rappaport et al., 1991; Marosi et al., 1993; Witzke and Schönle, 1996; Lew et al., 1999, 2003; Jones et al., 2000; Kotchoubey et al., 2001, 2005; Kotchoubey, 2005a; Perrin et al., 2006; Wijnen et al., 2007; Qin et al., 2008; Fischer et al., 2010; Cavinato et al., 2011). Indeed, some of these studies report evidence of relatively late, parietally (in electrode space) focused P300 responses in some patients, suggestive of some level of awareness of the deviant stimuli. Furthermore, some of these studies have also demonstrated a convincing link between the detection of these ERPs and a positive prognosis for the patient (Lew et al., 2003; Kotchoubey et al., 2005; Wijnen et al., 2007).

This pattern raises interesting questions about the inter-relationship between the neural processes generating these ERPs and how they feed into conscious awareness. More specifically, the temporally predictive link between the MMN/P3a and eventual recovery of consciousness highlights some key aspects of the relationship between attention and awareness in coma and DoC. Firstly, and mostly obviously, the deeper processing of deviants that elicits the MMN/P3a is distinct from, and may not necessarily result in conscious awareness of the stimuli. In normal volunteers, a functionally equivalent experimental outcome is usually constructed by setting up another distracting, attentionally demanding task while the subject listens to streams of auditory stimuli with deviants. In such cases, though clear MMNs/P3a ERPs might be elicited, the subject usually does not have a rich conscious awareness of the deviants (Müller et al., 2002; Müller-Gass et al., 2007). Hence, the relative automaticity with which these ERPs can be evoked in volunteers implies that the presence of MMN/P3a in

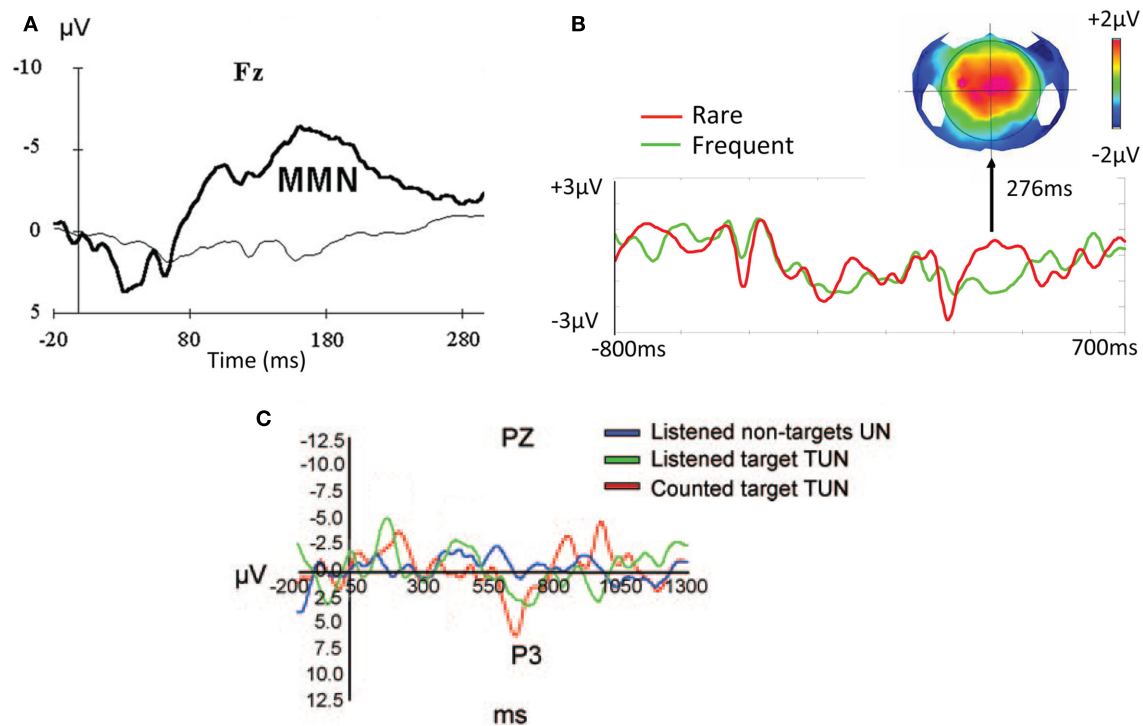


FIGURE 2 | Mismatch negativity (MMN) and P300 in disorders of consciousness. (A) MMN elicited in a VS patient by 247 Hz deviant tones (10% probability) relative to 440 Hz standard tones. Adapted from Kotchoubey et al. (2005). (B) P3a elicited in MCS patient by rare sinusoidal

tones (20% probability). Adapted from Bekinschtein et al. (2009). (C) P3b generated by MCS patient when counting task-relevant, unfamiliar target names presented amongst other unfamiliar names. Adapted from Schnakers et al. (2008).

many DoC patients does not inform the question of whether they were aware of the stimuli. Indeed, it is unlikely that most patients were conscious of them, given the severity of their neurological and clinical dysfunction as recorded by behavioral evaluations.

The second, more difficult question raised by these findings in the DoC literature relate to the underlying mechanisms of the positive link between MMN/P3a responses and later chances of recovery. Indeed, Wijnen et al. (2007) regularly tracked longitudinal changes in the MMN elicited by VS patients for an average of 3.5 months, and found that its amplitude correlated with progressively improving behavioral indices of recovery. Furthermore, the MMN amplitude reached near-normal levels around the time patients started to show inconsistent command-following, and preceded the observation of behavioral markers indicating a reliable recovery of consciousness. This evidence suggests that, though attention and consciousness are distinct phenomena, the cognitive processes and neural mechanisms of which they are comprised might share much in common. Certainly, networks that subserve attentional processing seem to be able to assist in the rehabilitation of those involved in generating the re-entrant feedback considered to be vital for conscious awareness (Boly et al., 2011a). Although the validity of these results have been debated (Boly et al., 2011b; King et al., 2011), a deeper understanding of these processes would help disambiguate the relationship between attention and awareness, and how they interact at different levels of consciousness.

THE P3b IN DISORDERS OF CONSCIOUSNESS

Building upon the oddball P300 studies highlighted in the previous section, some recent studies have attempted to explicitly dissociate levels of attentional processing in DoC (Schnakers et al., 2008; Bekinschtein et al., 2009; Faugeras et al., 2011). To do so, they have relied on the consensus that the P3b is seen as a marker of task-relevant, conscious processing of auditory information (Polich, 2007). Bekinschtein et al. (2009) and Faugeras et al. (2011) employed a paradigm consisting of series of tone sequences containing a two-level structure of occasional irregularities: short-term (“local”) violations within a five-sound sequence, and long-term (“global”) violations of the expectancies of such sequences. Importantly, in control subjects, local violations only evoked early frontal MMN/P3a. In contrast, global violations, which were counterbalanced to be completely independent of psychophysical stimulus properties, were indexed by a later, parietal P3b, but *only* when the subject was aware of the long-term structural regularities in the stimuli and was attending to them. Amongst DoC patients, qualitatively similar patterns were observed in some VS (Faugeras et al., 2011) and MCS patients (Bekinschtein et al., 2009). Furthermore, in both studies, the minority of patients who appeared to show an awareness of the global pattern violation also showed positive signs of recovery. These findings suggest that such awareness is strong indication of preserved networks that support the regaining of behaviorally evidenced consciousness. Recently, Faugeras et al. (2012) reported results from a large cohort of DoC patients tested

with this paradigm. Their findings corroborate the link between the existence of a global effect and behaviorally measurable consciousness (or subsequent recovery thereof), and with evidence of stimulus expectancy and learning effects.

Schnakers et al. (2008) went further and employed an “active” ERP paradigm with DoC patients, where their responses to context-dependent task instructions were measured. Specifically, they compared the P3b elicited across a pair of conditions: one in which patients were asked to passively listen to their own name or a pre-specified target name embedded in a sequence of unfamiliar names, and another in which they were asked to count the occurrence of their own name or pre-specified target names. They found that 9 out of 14 MCS patients generated larger P3b amplitudes when asked to count the target names (their own or unfamiliar) as compared to just listening to them (see **Figure 2C**). They took this finding to imply that, to some extent, the patients were able to exercise task-selective attentional control to follow the task instructions.

These studies demonstrate that some patients appear to be able to demonstrate the ability to deploy selective attention in a task-contingent manner. This is because, in healthy controls, they explicitly disambiguate P300 responses that could only be attributed to endogenous attentional control and awareness of task-related contingencies, from those that could be generated by differential stimulus probabilities (Polich and Kok, 1995). However, despite this, the question still remains as to whether the same or even something similar can be inferred about patients. More specifically, as highlighted by Overgaard (2009) in the distinction between “reports” and “signals,” there is still the unresolved question about the extent to which finding evidence of an endogenous attentional control signal like the P3b in a patient can be used to infer the presence of reportable conscious content. Previous research with healthy participants has found striking examples of dissociations between attention and consciousness, showing that these two processes, though often coeval, can indeed be separated under appropriate conditions (Koch and Tsuchiya, 2007; Koivisto et al., 2009). Such subtle dissociations are challenging to measure in patient populations with the passive paradigms discussed here. Addressing such issues with DoC patients might require complementary evidence from active tasks, and perhaps measurements of their metacognitive understanding of stimulus perception. Distinct from, but as important as these theoretical issues, is the clinically relevant question of why, in the significant minority of patients able to deploy endogenous attention, there was a disconnection between their covert cognitive abilities and overt behavioral signs of awareness. As before with the MMN, future research will need to explore in greater depth, how and why such attentional control predicts recovery of consciousness.

THE MMN AND P300 IN SLEEP

The research into ERPs evoked during various stages of sleep in healthy adults sheds light on how altered states of consciousness affect the attention and awareness of external stimuli (Atienza et al., 2001; Campbell and Colrain, 2002). The consensus often expressed is that there is no evidence for the MMN or the P300 in stage 2 sleep (Loewy et al., 1996, 2000; Cote, 2002; Colrain and Campbell, 2007). K-complexes appear to be the main

evoked potentials observed (Bastuji et al., 1995), in addition to delayed evoked potentials that are functionally dissimilar to the MMN/P300 (Nielsen-Bohlman et al., 1991; Van Sweden et al., 1994; Nordby et al., 1996). Evoking an MMN in this sleep stage has required the use of hyper-salient stimuli, involving very rare, extremely deviant stimuli. Similarly evocative stimuli, like the subject’s own name, are required to trigger a P300 in stage 2 sleep (Perrin et al., 1999). However, it is worth noting that such responses appear to be non-selective, as they have been observed even for other names and repetitive tones (Bastuji et al., 1995; Perrin et al., 1999, 2000). Furthermore, it has been argued that emotionally charged names might be processed quite differently to neutral words (see Bastuji et al., 2002 for a discussion). Indeed, N400 ERPs can be elicited using semantically incongruent neutral words during stage 2 sleep (Brualla et al., 1998; Perrin et al., 2002), and sentences (Ibáñez et al., 2006), though these too suggest diminished discriminative abilities.

Alongside these findings, studies into the transitions between sleep stages have found that the amplitude of the P300 reduces in sync with arousal levels of participants, and their ability to generate any behavioral responses (Sallinen and Lyytinen, 1997). This fits well with our understanding of the P300 as a reliable marker of in-depth, conscious processing of external stimuli. Generally speaking, findings of reductions in amplitudes of late ERPs are keeping in with the notion that falling asleep is marked by a global decrease in long-range thalamo-cortical connectivity occurring in the early stages of the process (Magnin et al., 2010; Goupil and Bekinschtein, 2011; Sämann et al., 2011). There is some recent fMRI evidence suggesting that cortico-cortical connectivity during sleep might remain consistent across sleep stages (Koike et al., 2011), and even increase during light sleep (Spoormaker et al., 2010). However, the implications of these findings for our understanding of the changes in ERPs during sleep remain to be explored.

Event-related potentials elicited during REM sleep present quite a different picture to sleep stage two and deep sleep. Researchers have found significant MMNs (see **Figure 3A**) to rare, deviant stimuli in REM sleep (Sabri and Campbell, 2005; Sculthorpe et al., 2009). These findings are taken to imply that though fine-tuned attentional focusing and gating might not be available in REM sleep, covert, pre-attentional monitoring of temporal auditory information is nevertheless functional. However, the greatly reduced acuity of such a monitoring system is reflected in the variability of MMN-related results reported in literature (see Kotchoubey, 2005b for review). Atienza et al. (2002) expressed the general consensus that MMNs are observable in REM sleep, but only under more constrained experimental settings, i.e., very rare deviations in pitch occurring in tone sequences with inter-stimulus intervals less than 1.5 s.

Similarly, P300s to salient stimuli have also been observed in REM sleep (Cote and Campbell, 1999; Cote et al., 2001). Cote et al. (2001) used rare pitch and intensity deviant tones to elicit the equivalent of a P3a in REM sleep (see **Figure 3B**). Interestingly, they found that when wake subjects were not attending to the tone stimuli, only the hyper-salient (very loud and very rare) deviants elicited a frontal P3a. Similarly, the P3a observed during REM sleep was also elicited only by such strong deviants, and had a similar latency (though it was reduced in amplitude, and did not have

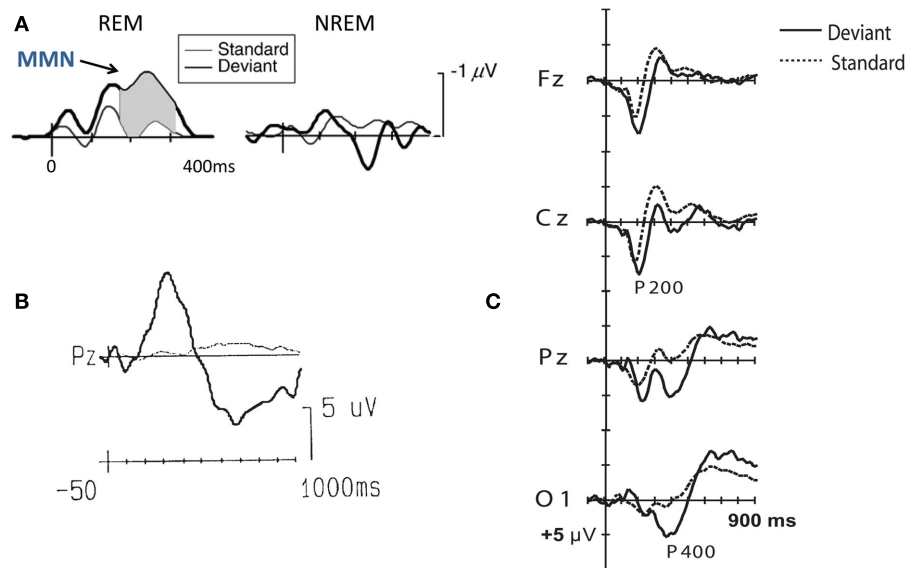


FIGURE 3 | Mismatch negativity (MMN) and P300 in sleep. (A) MMN observed during REM and Non-REM sleep by deviants (6.7% probability) embedded in alternating tone sequences. Adapted from Sculthorpe et al. (2009). **(B)** P300 observed during REM sleep by intensity deviants (5%

probability). Adapted from Cote and Campbell (1999). **(C)** Occipital P400 observed during tonic REM sleep only in participants instructed to respond to 2000 Hz deviant tones (10% probability) presented amongst 1000 Hz standard tones. Adapted from Takahara et al. (2006).

the characteristic frontal topography of the waking P3a). Based on this parallel between inattentive wakefulness and REM sleep, the authors suggest that though their subjects might have been able to “consciously” detect the deviants in REM, they were unable to attend to, or perceive them to an extent deep enough to form rich memories or be woken up. In this sense, REM sleep could be an example of an altered state of consciousness displaying a rare disjunction between attention and (semi-)conscious awareness.

In a more recent study, Takahara et al. (2006) modulated endogenous attentional bias in a study employing auditory tone streams with rare frequency deviants played to participants during REM sleep, over two overnight recording conditions. During the “passive” condition, participants were asked to passively listen to the tones, while in the other “active” condition, they were asked to attend to the auditory streams and respond with a finger movement whenever they detected a deviant. The authors found a significantly larger, occipitally focused P400 ERP in the latter condition (see Figure 3C). They interpreted this ERP as a delayed, spatially shifted P3b manifested during REM sleep, which indexed endogenous task-selective attention focused on the deviants. It is worth noting that such P400s were only observed during tonic REM sleep. A similar tonic “REM-P3” has been documented by Sallinen et al. (1996) in response to deviants in a standard oddball study. This finding, if successfully replicated, would be in contrast to findings from previous studies, and suggests that subjects might retain some amount of attentional control even during REM sleep.

THE MMN AND P300 IN ANESTHESIA

The effect of sedatives on brain dynamics is known to be complex and differentiated (Heinke and Koelsch, 2005). Brain regions are affected in different ways by different anesthetics used in clinical

medicine, and also by their dosage levels. But in general, they are thought to affect the brain in a manner that is functionally similar to sleep: by disrupting long-range interactions across key distributed networks that subserve conscious perception (Stamatakis et al., 2010).

Though the literature on ERPs in anesthesia is relatively sparse, many studies of the effect of anesthetics on the MMN have documented a decrease in amplitude. Increasing levels of the anesthetic propofol were associated with decreasing MMN amplitudes elicited by an auditory oddball paradigm (Heinke et al., 2004). At unconsciousness, the MMN was completely abolished. In fact, it has been reported that the MMN is abolished even before the subjective loss of consciousness (see Figure 4A; Simpson et al., 2002). Early measurements of changes in the P300 have also shown a similar pattern. Several studies have documented dramatic drop-offs in P3a amplitudes as subjects were progressively sedated, with complete abolishment at unconsciousness (Plourde and Boylan, 1991; Sneyd et al., 1994; Reinsel et al., 1995).

In the context of this review, studies that have investigated the onset of and recovery from sedation provide interesting insights into the complex influence of anesthetics on the interaction between attention and consciousness. Plourde and Picton (1991) tested patients who were anesthetized for surgery, at different stages: during induction of anesthesia, while in surgical anesthesia, during emergence from sedation, and during recovery from anesthesia. All through, participants were asked to press a button whenever they heard the rare, unpredictable frequency deviant presented within an oddball task. The authors reported finding a significant P300 whenever participants correctly detected a deviant during the first induction and final recovery stages. They point out that during the emergence stage, participants were able to open

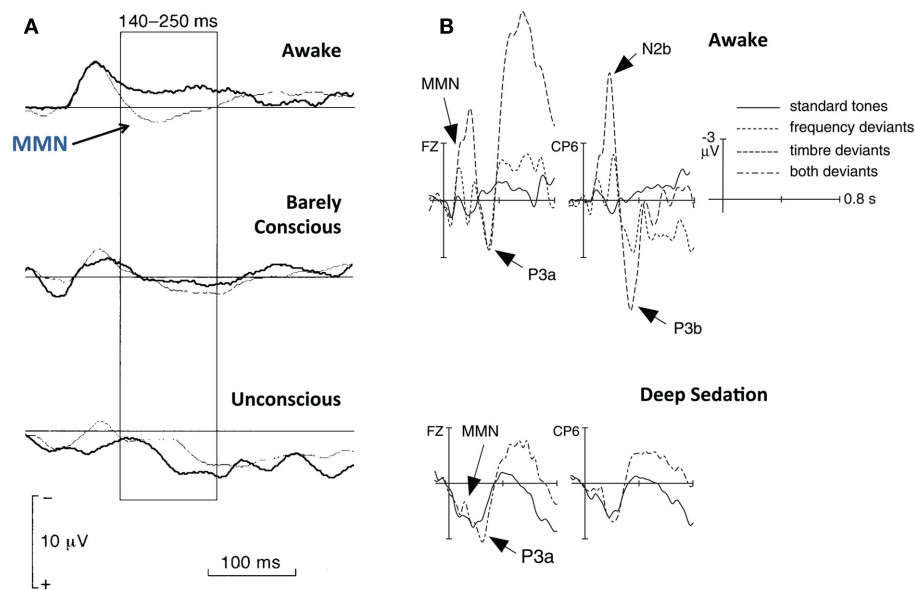


FIGURE 4 | Mismatch negativity (MMN) and P300 in anesthesia. (A) MMN elicited at different levels of consciousness by 25 ms tones (15% probability) presented amongst 75 ms tones. Adapted from Simpson et al.

(2002). **(B)** P3a observed for task-relevant timbre deviants (6.67% probability), alongside an absence of P3b during deep sedation. Adapted from Koelsch et al. (2006).

their eyes on command, but did not generate P300s, and in fact, were unable to correctly detect deviants most of the time. This finding has parallels with a more recent study by Koelsch et al. (2006), where participants were first trained to press a button only in response to deviants of timbre, but not frequency in an oddball paradigm, and then induced into a level of “deep sedation” using propofol. In this state of anesthesia – shallower than surgical anesthesia – participants were behaviorally arousable by loud/repeated utterances of their own name, or by mild prodding. The study found that both MMN and P3a ERPs were elicited during deep sedation, though they were attenuated (see **Figure 4B**). However, the P3b was absent during this period. As participants recovered from sedation, the MMN increased back to normal levels immediately, but neither the P3a nor the P3b were visible. The authors interpret this dissociation to imply that though pre-attentive auditory sensory mechanisms returned back to normal as soon as participants were able to respond behaviorally, more late-stage attentional and awareness-related processes indexed by the P300 took much longer to recover. As argued by van Hooff et al. (1997), these results support the notion that the effect of anesthesia on cognitive ERPs, including the MMN and the P300 has many similarities to that of stage 2–3 sleep.

GENERAL DISCUSSION

In this review, we have attempted to bring together a broad range of findings in the scientific literature that sheds light on the interplay between attention and consciousness by studying the impaired brain in action. These impairments, namely, clinical DoC, natural sleep, and sedation, can be considered as three distinct variations in the levels of consciousness in which cognition can exist. In particular, we suggest that by causally inducing changes between these levels, as in the case of sleep and sedation, we can improve

our understanding of the profound neurological dysfunction seen in DoC and their impact on attention and consciousness.

Of course, this is not to say that we can draw direct parallels between data or findings from states in sleep or sedation, and states in DoC. For one thing, even within such disorders, loss of consciousness arises due to a range of very different etiologies, including hypoxia, stroke and traumatic brain injury. Patients progress through different paths of recovery, which tend to depend not only on this etiology but also on their age and rehabilitative support they might receive. Hence, when assessing a patient at a particular point in time post-ictus (i.e., after the occurrence of the incident that induced the DoC), it is difficult to make accurate judgments about the nature of their cognitive processes based simply on behavior. As mentioned earlier, a high rate of misdiagnosis has been prevalent, leading to troubling ethical issues for clinical medicine (Schnakers et al., 2009). Though electrophysiology, beginning with measurements of ERPs, has begun to elucidate the nature of cognitive dysfunction in DoC and even produce compelling evidence of awareness in some patients (Cruse et al., 2011a,b; Goldfine et al., 2011), it is still difficult to draw conclusions for diagnosis or prognosis at a single patient level, because of the large number of factors contributing to the variability observed in patient data.

Consequently, any parallels that are highlighted between sleep, sedation, and DoC in this article are qualified with respect to the level of explanation at which they are addressed. Translating such general patterns to inform the diagnosis of patients with their unique histories will depend on ongoing research to delineate both the nature and extent of the individual variability in the findings. Nevertheless, as neuroimaging, and in particular EEG findings from ever larger cohorts of patients accumulate, some broad patterns have emerged more consistently. By linking these patterns

to findings from research into sleep and anesthesia, we can draw some generalizations about the interplay between attention and consciousness:

1. A considerable amount of pre-attentive and early, bottom-up attentive processing can be accomplished in the brain in the absence of rich, memorable conscious experience. This well-established fact, in the current context, is backed up by a wealth of ERP literature from sleep and sedation, and implies that observing similar ERPs in DoC patients does not provide strong evidence either way about the level of their consciousness.
2. Nevertheless, evidence of extant pre-attentive processing in seemingly unconscious patients is predictive of delayed overt behavioral recovery. In addition, the complete lack of any early pre-attentive processing of stimuli is often prognosticative of poor chances of recovery.
3. A significant minority of behaviorally unresponsive patients appear to be able to deploy selective attention to task-relevant stimuli, and generate ERPs suggesting that they might retain some form of awareness. This is complemented by evidence from sleep and sedation: apparently unconscious subjects in stage 2 (and deeper) sleep and in surgical sedation do not show similar ERP signs of awareness (with the exception of REM sleep phases).
4. During sleep and sedation, an interesting dissociation occurs between attention and consciousness. During deep (but not complete) sedation, some pre-attentive processing and bottom-up attentional orienting is spared. In contrast, task-selective endogenous processing seems to be abolished not only during sedation, but also during the recovery phase, where the subjects consciously respond to stimuli but produce no P300s. This is in contrast to REM sleep, where such processing seems to be diminished but functional.
5. Many patients in DoC show ERP signs of being in intermediate stages of cognition involving partial and temporally fluctuating dissociations between pre-attentive, post-attentive processes and conscious experience. Though they might be physically arousable, and be able to attend to certain stimuli, they might not have detailed spatial, temporal or self consciousness. Though this is currently speculative, behaviorally and in terms of their ERPs, DoC patients could be thought of as being in cognitive states similar to REM sleep or intermediate sedation. However, this comparison is currently very limited in its detail, and should be qualified in terms of the level of abstraction at which it is valid.

CONCLUSION

In this article, we have aimed to bring together the relevant ERP literature on altered states of consciousness, including DoC, sleep and sedation, which speak to questions about the interplay between auditory attention and consciousness. The findings presented here have highlighted examples of unique disconnections between these often tightly intertwined processes, providing valuable insights into the underlying nature of the behavioral states these disengagements can produce. In particular, we have focused on question of how parallels between findings from studies into sleep and sedation can inform our understanding about cognitive processing and the nature of conscious experience in DoC, while emphasizing the divergences that warrant further study.

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Against the view that consciousness and attention are fully dissociable

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In this paper, I will try to show that the idea that there can be consciousness without some form of attention, and high-level top-down attention without consciousness, originates from a failure to notice the varieties of forms that top-down attention and consciousness can assume. I will present evidence that: there are various forms of attention and consciousness; not all forms of attention produce the same kind of consciousness; not all forms of consciousness are produced by the same kind of attention; there can be low-level attention (or preliminary attention), whether of an endogenous or exogenous kind, without consciousness; attention cannot be considered the same thing as consciousness.

Keywords: attention, consciousness, visual perception

INTRODUCTION

In the controversial and unresolved debate about the relationship between attention and consciousness, Koch and Tsuchiya's (2006) article certainly had the merit of posing the problem of the relationship between attention and consciousness in a very clear, schematic, and provocative way. They maintained that top-down attention and consciousness are distinct phenomena that need not occur together, and presented evidence that all the following four cases are possible:

- (1) top-down attention with consciousness
- (2) top-down attention without consciousness
- (3) consciousness without top-down attention
- (4) no top-down attention – no consciousness

Albeit focused on a specific kind of attention, that is, top-down attention, this fourfold classification offers an ideal comprehensive framework that can be generalized in order to study the possible relationships between all forms of consciousness and attention.

I will try to show here that, even if attention cannot be considered the same thing as consciousness, some form of attention is always necessary for consciousness, and that high-level top-down attention always implies some form of consciousness (or alternatively, that there can be low-level attention or preliminary attention, whether of an exogenous or endogenous kind, without consciousness). More in general, I will also present evidence that: there are various forms of attention and consciousness; not all forms of attention produce the same kind of consciousness; not all forms of consciousness are produced by the same kind of attention.

POSITIVE EVIDENCE OF THE CLOSE CORRELATION BETWEEN ATTENTION AND CONSCIOUSNESS

The idea that attention is strictly linked to consciousness is not new (James, 1890; Posner, 1994; O'Regan and Noë, 2001). Indeed, the idea is quite intuitive, if we consider what is thought to be one of the main characteristics of attention: its selective power. When

we attend to a certain object or part of an object, we are able to isolate it from the other objects or parts, so that our conscious mind is completely and exclusively possessed and "filled" by it (La Berge, 1995). Even though this does not prove that attention is necessary or sufficient for consciousness, it shows that there is a direct connection between attention and consciousness: how we pay attention to the world is highly correlated with how the world appears to us. Moreover, well-known psychological phenomena demonstrate that attention modulates perception, directly influencing the way we consciously experience the world. Let's consider some evidence from psychological studies. These examples of a tight correlation between attention and consciousness should be taken into account for a possible falsification by all those who maintain that attention and consciousness are fully dissociable.

PSYCHOLOGICAL STUDIES OF VISUAL PERCEPTION

Carrasco's (2011) work provides empirical evidence that attention alters phenomenal appearance: it boosts the apparent stimulus contrast. For example, Liu et al.'s (2009) study shows that voluntary (endogenous, sustained) covert spatial attention alters the appearance of objects. In this study, which provides a phenomenological correlate of the effect of voluntary attention on perception, voluntary attention increases the perceived contrast of suprathreshold stimuli: attending to a peripheral location makes a cued 29%-contrast stimulus and an uncued 36%-contrast stimulus both subjectively equivalent to a 32%-contrast stimulus.

Likewise, Carrasco et al. (2004) show that when the transient covert attention (which is the stimulus-driven, exogenous, involuntary capture of attention by an abrupt, salient peripheral cue) of observers is drawn to a suprathreshold stimulus via a peripheral cue, they report this stimulus as being higher in contrast than it really is, thus indicating a change in appearance with attention (however, it should be noted that this work was not free of controversies: see Schneider, 2006; Prinzmetal et al., 2008; Schneider and Komlos, 2008. For the answer, see Carrasco et al., 2008; Carrasco, 2011).

PSYCHOLOGICAL STUDIES OF THE PERCEPTION OF TIME

Important evidence that attention modulates perception also comes from the domain of the studies of time perception. The phenomenon of prior-entry, for example, shows that when a person attends to a stimulus, he or she perceives it as having occurred earlier in time than if he or she was not attending to it (Shore et al., 2001). Experiments on duration judgments in which subjects are asked to prospectively judge the duration of the time period they have to perform a certain task, reveal that judged time decreases linearly with the increased processing demands of non-durational information, and that experienced duration increases to the extent that subjects can allocate more attentional resources to the flow of time itself (Hicks et al., 1976, 1977; Brown, 1985; Coull et al., 2004). In short, a higher amount of attention allocated to the passage of time itself produces a lengthening of the experienced duration. A similar attentional effect results when attention is directed in advance to one of two possible stimulus sources: Mattes and Ulrich (1998) show that subjects judge a stimulus as being longer when it appears at the precued stimulus source than when it appears at the uncued one; that is, directed attention prolongs the perceived duration of a stimulus.

INATTENTIONAL BLINDNESS (IB) AND CHANGE-BLINDNESS

The idea that attention is necessary for consciousness has received strong support from the work of Mack and Rock (1998) and Rensink et al. (1997). In Mack and Rock's (1998) experiments, the subject's attention was engaged in a task (such as identifying the longer arm of a cross briefly presented on the screen and centered at about 2° from fixation). After some trials, an unexpected, unsearched critical stimulus (for example, a black circle) was presented at fixation, and subjects were asked whether they had seen anything that had not been on the screen in the earlier trials. Between 60 and 80% of the subjects failed to detect the critical stimulus. A comparison between reports of the critical stimulus in the inattention, critical trials (where subjects were told to pay attention to the cross, but were not told that a critical stimulus would appear) and those in full attention control trials (where subjects were told to ignore the cross, and to report only what else they saw on the screen when the cross was present), confirmed that focal attention is clearly implicated in conscious perception. More in general, Mack and Rock's experiments show that subjects tend to be blind to a critical stimulus that appears either at, or close to, fixation when they are not searching for it, when they are occupied with a task that engages their attention, and when it is located outside the boundaries of the area on which attention is directed. These findings do not imply that there is no implicit, unconscious perception, but only that there is no explicit, conscious perception prior to the engagement of focal attention. Stimuli to which subjects are inattentionally blind, can be implicitly, unconsciously perceived. In order to bring them into consciousness, they must be attentionally processed.

Inattentional blindness (IB) results, however, could be subject to alternative interpretations involving processes other than attention, such as expectation and memory (Lavie, 2006a). Firstly, the critical stimulus is expected in control trials, and subjects are likely to look for it intentionally: therefore, the comparison of control and critical trials may confound effects of attention with effects

of expectations. Secondly, while in control trials awareness reports are made immediately following display presentation, in critical trials they are made after a task response and a surprise awareness question in critical trials: therefore, reduced rates of awareness in critical vs. control trials may reflect higher rates of forgetting during the longer delay from display presentation until the awareness question in the critical trials¹.

The alternative explanation based on expectation was ruled out by Cartwright-Finch and Lavie's (2007) study, which, manipulating perceptual load within Mack and Rock's (1998) IB paradigm, compared the rates of IB not so much between the critical and control trials, as between critical trials of different levels of load (that is, the critical stimulus was equally task-irrelevant and equally unexpected across the varying levels of perceptual load). Cartwright-Finch and Lavie found that the level of perceptual load in the task determined the rates of IB: whereas subjects were often aware of the irrelevant stimuli in situations of low load, they failed to notice the irrelevant stimulus in situations of high load. This result shows that the level of attention available for the processing of the task-irrelevant stimulus determines whether the stimulus can be consciously perceived.

The alternative explanation based on memory is ruled out by Rensink et al.'s (1997) study, which, unlike the IB paradigm, does not rely on a retrospective question about an unexpected stimulus: indeed, subjects are instructed in advance that their task is to detect whether a change occurred between two successive images and report about it immediately after seeing the images. Rensink et al. (1997) developed the "change detection flicker task" paradigm [which is a variant of the change-blindness (CB) paradigm: see for example Simons and Levin, 1997, 1998]: an original image *A* repeatedly alternates with a modified image *A'*, with brief blank fields placed between successive images; differences between original and modified images are highly visible; subjects freely view the flickering display and hit a key when they perceive the change. In order to prevent guessing, subjects are asked to correctly report the type of change and describe the changing part of the scene. Because the stimuli are available for long stretches of time and no eye movements are required, the flicker paradigm provides the best opportunity possible for an observer to build a representation conducive to perceiving changes in a scene. The CB found with the brief-display techniques adopted by previous experimental paradigms might have been caused by insufficient time to build an adequate representation of the scene; saccade-contingent CB might have been caused by disruptions due to eye movements.

¹IB results can also be subject to alternative interpretations involving different forms of consciousness. As we will see, it is possible to distinguish between a "primary" form of consciousness and a "higher-order, reflective" form of consciousness (Bartolomeo, 2008). It can be argued that in IB the subjects are aware of the critical stimulus (that is, they have a primary consciousness of the critical stimulus), but are not able to verbalize it (that is, they lack a reflective consciousness necessary to verbally describe the critical stimulus). However, it should be noted that Mack and Rock, 1998, pp. 197–204) performed some experiments explicitly aimed at verifying the hypothesis that the subject "has fleetingly perceived the critical stimulus, but fails to encode it." The experiments showed that the subjects were not even faintly aware of the critical stimulus, and that many subjects did not even see a critical stimulus visible for a total period of 700 ms (Mack and Rock, 1998, pp. 202–204), which contradicts the hypothesis that the subjects were "aware" of the critical stimulus, but were unable to verbalize it.

Both of these factors are eliminated in the flicker paradigm, so that if they are indeed the cause of the difficulties, perception of change should now become easy. But if attention is the key factor, a different outcome would be expected. And it is precisely this different outcome that Rensink et al.'s study reveals. Their experiments show that identification of changes becomes extremely difficult, even when changes are large and made repeatedly: under flicker conditions subjects take a surprisingly long time to perceive large changes in images of real-world scenes. This difficulty is due neither to a disruption of the information received nor to a disruption of its storage: it does however depend greatly on attention. The role of attention is further confirmed by the findings that: cueing the changing object removes any difficulty in detecting change (Rensink et al., 1997); objects that capture attention, either by virtue of containing a singleton feature, or by virtue of their significant socio-biological meaning, do not suffer from CB (Ro et al., 2001); the rate of change detection critically depends on the level of load in the search task, that is, subjects fail to detect the change far more often in the condition of high vs. low load in the search task (Lavie, 2006a,b).

Rensink et al.'s (1997) experiments also answer most of the criticisms raised by Mole (2008). According to Mole, what Mack and Rock's (1998) work shows is only that there are some circumstances in which attention is necessary for consciousness: that is, cases in which the stimulus is presented unexpectedly, for a fifth of a second, concurrently with something else that one is attending to, in an unfamiliar experimental paradigm, and followed by a pattern mask. As Rensink et al.'s (1997) experiments show, attention *is also* necessary with familiar, and available for long stretches of time stimuli, when the subject is aware of the kind of stimulus, and even when the subject is aware of the types of change possible and is given practice trials before the experiment.

Mole's (2008) criticisms, however, seem to imply a more general kind of criticism based on "some relatively uncontroversial features of the epistemology of perception." According to these considerations from the epistemology of perception, Mack and Rock's (1998) and Rensink et al.'s (1997) experiments would not appear to show that attention is always necessary for consciousness, but only that attention is necessary when one's experience is to provide one with knowledge of the sort probed by the experimenter's questions in a CB or IB experiment. In other words, CB and IB experiments suffer from the defect of not giving the possibility of independently ascertaining whether attention is always necessary for consciousness: as they are designed, these experiments would only reveal that attention is necessary for consciously detecting changes or unexpected stimuli but not for other cases. According to this view, a subject who has not attended to the changing item in the CB pictures or to the unexpected stimuli in the IB experiment, could theoretically have some kind of conscious experience, but the experience does not have the "structured content" needed to provide the subject with knowledge of the fact that the thing is changing or unexpectedly appearing.

I think that Mole's (2008) epistemological considerations are legitimate and that they deserve to be properly addressed. In order to do so, I will analyze some experiments that either have been explicitly conceived and designed to prove that there can be consciousness in the absence of attention or have been interpreted

as evidence that attention is not necessary for consciousness. The analysis will show that even such experiments substantially fail to prove the thesis that attention is not necessary for consciousness, and consequently that an answer can also be provided to Mole's epistemological considerations (at least until contrary evidence is offered).

EXPERIMENTS AIMED AT DEMONSTRATING CONSCIOUSNESS IN THE ABSENCE OF ATTENTION

The idea that attention is necessary for consciousness is not universally accepted (Umiltà, 1994; Baars, 1997; Hardcastle, 1997; Lamme, 2003; Koch and Tsuchiya, 2006). A very strong and paradigmatic version of the view that attention and consciousness are distinct phenomena is that held by Koch and Tsuchiya (2006). They maintain that "top-down attention and consciousness are distinct phenomena that need not occur together and that can be manipulated using distinct paradigms" (Koch and Tsuchiya, 2006, p. 16).

Given the strong position held by Koch and Tsuchiya (2006), I will start my analysis of the evidence that there can be consciousness in the absence of attention by considering the examples and arguments they put forward in favor of their hypothesis. To do so, I will proceed by separately considering some of the perceptual phenomena and behaviors they have presented as evidence of the dissociation between attention and consciousness. Additionally, I will also consider some complementary examples and arguments proposed by other researchers in support of the view that attention is not necessary for consciousness.

As my analysis will show, Koch and Tsuchiya's (2006) view that consciousness can be dissociated from top-down attention is only partly true, and needs further specification. There are cases of consciousness in the absence of a certain form of top-down attention, but in the presence of some other form of top-down attention. There are cases of consciousness in the absence of top-down attention but in the presence of some other form of attention, such as bottom-up attention. But there are never cases of consciousness in complete absence of some form of attention.

In my view, Koch and Tsuchiya's (2006) position that consciousness can be dissociated from top-down attention mainly originates from a failure to notice the varieties of forms that specifically top-down attention and more in general attention and consciousness can assume. As many authors have highlighted (Bartolomeo, 2008; Posner, 2008; Srinivasan, 2008; Koivisto et al., 2009; De Brigard and Prinz, 2010; Kouider et al., 2010), in order to correctly understand the relationship between attention and consciousness, it is essential to duly take into account the varieties and complexity of forms of attention and consciousness: overlooking this factor may lead to the wrong view that there can be consciousness without attention.

Indeed, top-down attention can assume at least two different forms: focused attention and diffused or distributed attention (Treisman, 2006; Demeyere and Humphreys, 2007; Srinivasan et al., 2009; Alvarez, 2011); it can, up to a certain extent, be split between different perceptual and processing modalities (Pashler, 1998); it can be both widely distributed for relatively long time periods in a certain location (preparatory attention) and narrowly distributed in another location for shorter periods (selective attention; La Berge, 1995); it varies according to the perceptual

Table 1 | A categorization of top-down and bottom-up attention.

Bottom-up attention (= exogenous attention)
Top-down attention (= endogenous attention)
Focused
Low-level (or preliminary)
High-level
Diffused
Low-level (or preliminary)
High-level

load (Lavie, 1995); the total amount of allocated attention can vary from a minimum, “preliminary” level (Velmans, 1991) up to a maximum limit defined by the available attentional resources, according to motivation and arousal (Kahneman, 1973); and so on. Moreover, forms of attention exist (such as bottom-up) that differ from top-down attention and which also produce consciousness.

In **Table 1**, I propose a possible finer categorization of top-down attention based on the amount of allocated attention (low-level/high-level) and the spatial extent of attention (focused/diffused). It is important to note that the distinction between focused and diffused attention does not imply two separate, opposite dimensions but rather, as Srinivasan (2008) suggests, two ends of a continuum in which the focus varies. The use of focused vs. diffused attention depends on the specific task and motivation (such as tracking a single object vs. multiple objects). Likewise, the distinction between high- and low-level attention represents two extremes of a continuum in which the amount of allocated attentional resources varies. Moreover, as showed by Kahneman (1973), the total amount of attentional resources that is allocated, is not constant for every task, but can vary according to various factors, such as the difficulty and novelty of the task, the arousal level, the expectations, etc. Usually, high-level top-down attention is used with new, interesting, or complex tasks. On the contrary, low-level top-down attention may occur with uninteresting, repetitive, or daily tasks, the secondary task in a dual-task paradigm when both tasks draw upon the same pool of resources, and when the stimulus duration does not allow for top-down attention to be fully deployed.

Similarly, a general awareness of our environment (ambient awareness) can be distinguished from a more detailed focal awareness of a scene (focal awareness; Iwasaki, 1993); a form of primary consciousness, including an awareness of the world and mental images, but not a concept of self, can be distinguished from a form of higher-order consciousness, including self-awareness, a sense of time, and language (Edelman, 1989); forms of spatial awareness can be distinguished from more reflective forms of consciousness based on intellectual acknowledgment (Bartolomeo, 2008); consciousness of sensory qualities differs from volition, which in turn differs from the simple conscious state, which neurology associates with the concept of arousal and the diurnal cycle of sleep and wake (Posner, 2008); an evolutionary primitive form of consciousness, relatively independent of voluntary attention (anoetic consciousness), can be distinguished from a more recent and complex form of self-awareness that requires the use voluntary attention (autonoetic consciousness; Vandekerckhove and Panksepp, 2009);

Table 2 | A classification of consciousness.

(a) Anoetic consciousness (pre-reflective affective and sensorial perceptual consciousness)
(b) Noetic consciousness (semantic memory, but not yet access to a full awareness of one's own ongoing subjective experience)
(c) Autonoetic consciousness (explicit self-awareness)

conscious phenomena can be differently classified according to the time scales according to which events are integrated (for example, Wittmann, 2011, identifies three levels: functional moment, experienced moment, and mental presence).

In **Table 2**, I propose a possible classification of consciousness based on Tulving (1985) and Vandekerckhove and Panksepp (2009).

ATTENTIONAL BLINK

Koch and Tsuchiya (2006) quote Olivers and Nieuwenhuis' (2005) study on the attentional blink. The attentional blink (Shapiro et al., 1994) occurs when subjects view rapid serial visual presentations of a series of stimuli presented in the same location, usually at rates of approximately 100 ms per item. Subjects have to detect two target stimuli, T1 and T2; T1 appears first and is followed by T2, which may appear immediately after T1 or at some other point in the sequence after T1, with distractors presented between T1 and T2 (that is, the temporal lag between T1 and T2 can vary). The blink effect refers to a decrement in detection of T2: the basic finding is that the decrement is often greatest when T2 occurs not immediately after T1 (position $n + 1$), but rather somewhere around positions $n + 2$ through $n + 5$ (that is, when there are one or more distractors between T1 and T2). The performance improves with a higher lag and reaches asymptote around $n + 6$ or $n + 7$. A possible explanation of the attentional blink is that processing of T1 takes up limited attentional resources: as a result, either access to these resources is denied for T2 or the representation of T2 is so vulnerable that it easily suffers from the interference of temporally surrounding distractors (for a review of the alternative theoretical accounts of the AB, see Shapiro et al., 1997; Di Lollo et al., 2005).

Olivers and Nieuwenhuis' (2005) study, which was motivated by the observation that participants in previous experiments reported rather counterintuitively improved T2 performance when being somewhat unfocused on the task, shows that the attentional blink is significantly ameliorated when observers are concurrently engaged in distracting mental activity, such as free-associating on a task-irrelevant theme or listening to music. The experiment suggests that under conditions of rapid visual presentation, target detection may benefit from a diffusion of attention.

Koch and Tsuchiya (2006) have interpreted Olivers and Nieuwenhuis' (2005) findings as indicating that top-down attention and consciousness can oppose each other. However, as Srinivasan (2008) argues, there is an alternative interpretation based on the concept of differential attentional strategy, which is more economical than Koch and Tsuchiya's because it does not require two different processes (one for attention and another for consciousness) to explain the same phenomenon, but only one process (attention). The alternative interpretation is that under certain

conditions, such as when subjects know that they need to consider a large number of items in order to report the second target stimulus in an experiment on attentional blink, diffused attention may turn out to be a better strategy than focused attention. This also corresponds to one of the three explanations that Olivers and Nieuwenhuis put forward to account for the phenomenon they found: it may have actually been the additional task itself that induced a more distributed state of attention. As attention widened to incorporate the extra task, it may have also widened temporally and thus included T2 in the series of stimuli.

However, this alternative interpretation does not account for the overall improvement in T1 performance in the music condition. In fact, diffused attention alone cannot explain how T1 detection performance can also improve as a result of an additional task. A more reliable interpretation seems to rely not only on diffused attention, but also on a temporary increase of the allocated attentional resources due to the difficulty of the task. This temporary increase seems to be implied by the two other possible explanations offered Olivers and Nieuwenhuis (2005). According to the first, the effects may be related to arousal: decreased or increased arousal – as may have occurred in the free-association and music conditions – may have made the attentional system more susceptible to other input, including T2. According to the second, thinking about one's holiday or listening to music may have induced a positive affective state, which has shown to improve performance on several cognitive tasks.

ANIMAL AND GENDER DETECTION IN DUAL-TASK

Koch and Tsuchiya (2006) also quote Li et al.'s (2002) work, which shows that subjects can rapidly detect animals or vehicles in briefly presented novel natural scenes while simultaneously performing another attentionally demanding task, and Reddy et al.'s (2004) work, which, comparing how subjects perform on a face-gender discrimination task carried out in the single task condition with the same task carried out in the dual-task condition with a known attentional demanding task (five-letter T/L discrimination), shows that the face-gender discrimination task can be performed equally well under the two conditions.

According to Koch and Tsuchiya, 2006, p.19), this kind of evidence shows that “although it cannot be said with certainty that observers do not deploy some top-down attention to the peripheral target in dual-task experiments that require training and concentration (i.e., high arousal), it seems that subjects can perform certain discriminations in the near absence of top-down attention².”

² Indeed, it is the very possibility that subjects can deploy some form of attention to the peripheral stimulus in dual-task experiments, that leads van Boxtel et al., 2010a, p. 6) to admit that “the major obstacle for solving the question of whether there is consciousness without attention is that there is no objective psychophysical way to unambiguously determine a state of ‘complete absence of attention.’ It is not known whether the conditions measured in the dual-task paradigms are cases of ‘very low attention’ or ‘no attention’” See also the observations made by Kouider et al., 2010, p. 304): not only “it seems to be extremely difficult, if not impossible, to assess whether subjects consciously perceive objects in the periphery without relying on some form of access,” but also “the possibility of consciousness without attention is usually based on a restrictive definition that does not take into account the possibility of residual attention at lower (i.e. sensory, non-conceptual) levels of processing.”

The view that this kind of evidence shows the independence of consciousness from attention, has been challenged on various grounds, even though not all the argumentations seem equally convincing.

As observed by Taylor and Fragopanagos (2007), in these experiments the subjects underwent up to 10 h of prior training on the stimuli, which makes it highly plausible that the subjects learnt to develop an automatic route to respond to the peripheral stimuli to which they were exposed. However, it should be noted that in their Experiment 4, Reddy et al. (2004) explicitly controlled whether there was a confounding effect of training in the face-gender discrimination task (they tested subjects who had been trained on a completely different dual-task experiment, that is, natural scene categorization: animal vs. non-animal or vehicle vs. non-vehicle), without finding any significant difference in performance compared with the previous experiments.

Taylor and Fragopanagos (2007) also put forward the hypothesis that the subjects were able to use multiple foci of attention to detect the presence of both the peripheral target as well as the main central one (McMains and Somers, 2004). While not completely improbable, the hypothesis seems however questionable because it does not explain why the subjects did not improve their performance in the peripheral task by taking advantage of the free extra-resources made available when asked to ignore the central task (when the subjects performed the face-gender discrimination task alone, their performance was not significantly different from performance on this task in the dual-task condition).

I think that to correctly interpret experiments such as Reddy et al. (2004) one should consider the possibilities of temporary increasing the amount of allocated attentional resources, and varying the spatial extension of the focus of attention. Just as for the case of the attentional blink, it is likely that the highly demanding task implied by dual-task paradigm induces subjects to adopt diffused attention as a better strategy than focused attention, and to increase the total amount of allocated attentional resources (compared to the single task). Moreover, it is known that meaningful stimuli such as faces capture exogenous attention. Therefore, Reddy et al.'s (2004) experiments can be interpreted as a combination of exogenous attention and increased, diffused top-down attention.

GIST

Koch and Tsuchiya (2006) observe that we are aware of the gist of a scene or of our surrounding environment even when we are not paying attention to it: “In a mere 30 ms presentation time, the gist of a scene can be apprehended. This is insufficient time for top-down attention to play much of a role. Furthermore, because gist is a property associated with the entire image, any process that locally enhances features, such as focal attention, will be of limited use” (p. 18).

Here, Koch and Tsuchiya (2006) seem to conflate top-down attention with focal attention. As we have seen, top-down attention can have two forms: focused or diffused. Even if focal attention is absent or nearly absent, one cannot exclude that some form of diffused attention may be involved, which allows us to capture the gist of a scene. This is also De Brigard and Prinz's (2010) view, who observe that there is no reason to think that attention is

absent, but rather that it is more plausible to think that attention is only diminished. Indeed, the view that attention is necessary for consciousness predicts such findings very well: when attention is nearly absent, we are aware of far less than when it is fully deployed. This is why the gist is perceived and no more.

Alternatively, it is also possible to conceive the phenomenon of gist reported by Koch and Tsuchiya (2006) as evidence of the existence of a specific form of consciousness: which Bartolomeo (2008) calls “primary consciousness.” Primary consciousness refers to the basic condition of being aware of something: as such, it must be distinguished from a higher-order, reflective form of consciousness, which can involve linguistic abilities and allows subjects to perceive and describe their own actions and thoughts. Not always what enters primary consciousness also enters the higher-order form of reflective consciousness: overlooking this fact may sometimes lead to the wrong observation that the absence of a verbal report means the absence of consciousness tout court. Bartolomeo (2008, p. 17) illustrates the difference between the two forms of consciousness by quoting an example given by Merleau-Ponty “of someone who enters a room and feels an impression of disorder, only to later discover that this impression came from a crooked picture on the wall. Before discovering that, this person’s consciousness was ‘living things that it could not spell out.’ This would by no means imply that the first impression on entering the room was unconscious. Rather, the crooked picture generated a form of consciousness whose source was not immediately amenable to verbal description.”

The existence of this form of primary consciousness is supported by findings such as Landman et al.’s (2003), who show that people’s memory of a visual image has a large capacity representation (more than four items) and remains intact for at least 1200–1500 ms after the stimulus has disappeared.

POP-OUT AND THE COCKTAIL PARTY EFFECT

Treisman and Gelade (1980) showed that when subjects search for a target defined by a conjunction of properties (say a red T) amongst a number of non-target items or distractors (say, red Xs and green Ts), search time increases linearly with the number of distractors. On the contrary, when subjects search for a target defined by a unique feature (say a red letter among green letters), search time is independent of the number of distractors. In this case, the unique feature is said to “pop-out.” The pop-out effect is sometimes interpreted as evidence of the fact that the unique feature “automatically” captures attention, in the sense that subjects can become aware of the target prior to and independently of the focusing their attention to it.

In my view, this interpretation is wrong because in visual search experiments subjects are actively looking for the target (Mack and Rock, 1998). As Most et al., 2005, p. 219) observe: “Although pop-out search has sometimes been interpreted as evidence that a target has automatically captured attention (. . .), in a strict sense this kind of evidence is insufficient to infer automatic attention capture. Because the observer is actively looking for the target, his or her attention is presumably broadly and purposefully distributed throughout the display.” A first empirical confirmation of the role of top-down attention in pop-out was obtained by Hsieh et al. (2011), who found that top-down attention is necessary for the

subliminal pop-out effect to occur (Experiment 2: unseen feature singletons do not recruit attention when subjects are distracted by a rapid sequential visual presentation task while viewing the subliminal pop-out display). Therefore, it seems wrong to consider the pop-out effect as evidence of consciousness in the absence of top-down attention.

A related but slightly different phenomenon – the cocktail party effect – shows more in general that some kind of attention – whether top-down or bottom-up – is always necessary for consciousness. Using a dichotic listening task, where subjects who were presented with two simultaneous messages to both ears via headphones were asked to attend to the message presented to one ear and to ignore the other message presented to the other ear, Moray (1959) found that subjects still recognized their name when it was presented in the unattended ear (the cocktail party effect). Cases such as this, where the subject’s name or some other meaningful stimuli can exogenously capture a subject’s attention even though the subject does not expect them or have any intention toward them, do not involve top-down attention (subjects are asked to focus on one message and ignore the other message) but rather a form of peripheral, exogenous attention. Indeed, it does not seem so implausible to think that: (a) evolution has endowed us with some mechanism that allows us to quickly orient to salient features of our environment; (b) this mechanism is (at least partly) based on the working of some form of peripheral, exogenous attention, which, being constantly applied and distributed, albeit at low levels of intensity, can be captured when salient stimuli occur.

Umiltà (1994) interprets the cocktail party effect and similar effects as evidence that attention does not coincide with consciousness and that they must be considered as independent systems. In these cases, he argues, the object is perceived consciously in a direct manner, without the intervention of attention.

Umiltà’s (1994) argument contrasts with what Mack and Rock (1998) have found. They show that by decreasing the probability that attention is paid to an object, the probability of perceiving its presence is reduced. This also applies to cases of captured or exogenous attention: when the difficulty of capture is increased by reducing the attentional zone or increasing the inhibition of attention, the probability that one’s own name is reliably perceived decreases (even if it continues to be seen significantly more often than other stimuli). Moreover, as McCormick (1997) has shown, exogenous cues presented below a subjective threshold of awareness capture attention without awareness.

These facts (as well as other instances of consciousness produced by the sole exogenous attention: Chica et al., 2011) indicate that some kind of attention is always involved in conscious perception. Even objects such as one’s own name cannot be perceived without the intervention of some form of attention: they must capture attention to become conscious. There cannot be conscious perception without attention.

ICONIC MEMORY

Lamme (2003) also proposes that there can be consciousness without attention. In his view, the attentive selection process operates at a later stage than consciousness: attention does not determine whether stimuli reach a conscious state, but determines whether a conscious report about stimuli is possible. In other words, we are

conscious of many inputs, but without attention this conscious experience cannot be reported: when we view a visual scene, we experience a richness of content that goes beyond what we can report. His model – which presupposes the existence of a short-lived, vulnerable, and not easily reportable form of visual experience, which contrasts with a more stable, reportable form of awareness – parallels: (a) Block's (1996) proposal of the existence of two distinct kinds of awareness: phenomenal and access awareness; and (b) the distinction made in the domain of sensory memory between "iconic memory" and "working memory."

In support of his view, he quotes Becker et al.'s (2000) and Landman et al.'s (2003) change detection experiments. It is known from CB experiments that the ability of subjects to detect a change in a visually presented array of items is greatly reduced if a blank interstimulus interval (ISI) is inserted between the original array (stimulus 1) and a subsequent array displaying the same items as stimulus 1 except for one item that has changed (stimulus 2). It is also known that change detection improves if the item to be changed is cued during the display of stimulus 1. The new and surprising phenomenon found by Becker et al. (2000) and Landman et al. (2003) is that change detection also improves when the location of the change is cued during the blank ISI. This may lead one to believe that all of the items of stimulus 1 are conscious and remain in consciousness even after the stimulus is removed, until it is overwritten by stimulus 2.

According to Lamme (2003), attention is a selection process that determines not so much whether stimuli reach consciousness, as whether stimuli can go from phenomenal awareness to access awareness. This model is based on the considerations that:

- (i) there are different levels of processing that stimuli can reach. More specifically, there are sensory inputs that: (1) reach a conscious state via the process of attentive selection; (2) do not reach a conscious state when not attended; (3) do not reach consciousness, not even when attended;
- (ii) these different levels of processing can be more parsimoniously explained by a model that is based on an early distinction between conscious and unconscious stimuli than by a model that is based on an early distinction between attended and unattended stimuli. Indeed, while the early distinction between attended and unattended stimuli would lead to postulating at least three different processes (one for stimuli that are conscious because attended, one for stimuli that are unconscious because unattended and one for stimuli that are purely unconscious), the early distinction between conscious and unconscious stimuli would lead to postulating only two processes (one for stimuli that are conscious and one for stimuli that are unconscious).

Lamme's (2003) model seems to overlook the fact that both attention and consciousness can assume a variety of forms. For example, when he observes that there are "non-attentional selection mechanisms" that can produce unconscious processing of stimuli, Lamme does not seem to consider the fact that some sort of "preliminary attention" (Velmans, 1991) can also exist, and that preliminary-attended stimuli, despite being processed, might not be consciously experienced. By overlooking this fact

he mistakes unconscious processing for preliminary-attended processing. Moreover, as shown by Bahrami et al. (2008), attention can also act on stimuli that have not reached awareness: stimulus competition for the allocation of attentional capacity occurs regardless of whether or not the observer is conscious of the stimulus representations.

Therefore, it certainly seems to be more plausible and economical to propose a model based on the notion that attention is necessary for consciousness than a model based on the idea that attention is not necessary for consciousness: while the latter implies two processes (one for stimuli that are conscious and one for stimuli that are unconscious), the former needs only one process (stimuli are attended: various levels and types of attention are possible).

This latter view is supported by work. Koivisto and Revonsuo found that "visual awareness negativity" (VAN, which they consider to be the most reliably and consistently observed ERP correlate for subjective visual awareness of a stimulus, vs. a stimulus that does not enter awareness) and visual awareness are dependent on spatial attention (see also Koivisto et al., 2009). According to Koivisto and Revonsuo's, 2010, p. 932), this suggests that iconic processing is not entirely independent of attention: "the visual icon has spatial boundaries limited by the scope and boundaries of spatial attention. Outside the boundaries of spatial attention, there is no visual phenomenology – the spatial boundaries of the visual icon are the spatial boundaries of momentary visual phenomenal experiences."

The finding that change detection improves when the location of the change is cued during the blank ISI (Becker et al., 2000), in my opinion does not show that there can be consciousness without attention; rather, it only confirms that: (a) there is an early component of attention – namely, the exogenous one (Nakayama and Mackeben, 1989) – that can capture a specific item in iconic memory if sufficient time is afforded (change detection and identification tend to worsen at longer ISIs between the offset of stimulus 1 and the onset of the cue); (b) once attention has captured the item, the item is (or can be) transferred to a short-term-memory buffer, where it may be compared with a later-occurring item, thus leading to change detection (change detection and identification tend to improve at longer ISIs between the offset of the cue and the onset of stimulus 2).

Lamme's (2003) idea that when we view a visual scene we experience a richness of content that goes beyond what we can report was questioned because the CB experiments show that viewers are over-confident about their capacities and suffer from an "illusion of seeing": when viewing a scene, viewers who claim to perceive the entire visual scene, actually fail to notice important changes of the elements of the scene. As argued by O'Regan and Noë (2001), the "illusion of seeing" might arise because viewers know that they can, at will, orient attention to any location and obtain information from it (for a similar view, see also Dehaene et al., 2006; for an alternative explanation of the illusion of seeing, see Kouider et al., 2010).

Despite this criticism, however, I think that Lamme's (2003) idea of the "richness of content" is not fully incompatible with an alternative and equally plausible interpretation of Becker et al.'s (2000) and Landman et al.'s (2003) findings, based on the view

that there cannot be consciousness without attention. According to this alternative interpretation, the viewer's initial application of attention to a presented array of items triggers a "primary" (non-verbalized), rich form of consciousness (Bartolomeo, 2008) of the visual scene. Subsequently, the content of the primary consciousness can be verbalized thanks to the deployment, via the cue, of an additional amount of attention.

EXPERIMENTS AIMED AT DEMONSTRATING ATTENTION IN THE ABSENCE OF CONSCIOUSNESS

The fact that attention is necessary for consciousness does not imply that attention generates or can modulate only conscious phenomena: it can also generate and modulate unconscious ones (which in turn can influence or bias both which and how stimuli will be subsequently consciously perceived: for a review, see Merikle et al., 2001). For example, Naccache et al. (2002) demonstrate that it is possible to elicit unconscious priming in a number-comparison task, but only if the subject's temporal attention is allocated to the time window during which the prime-target pair is presented: unconscious priming vanishes when temporal attention is focused away from this time window. Likewise Montaser-Kousari and Rajimehr (2005) found that attention subliminally modulates and enhances adaptation to illusory lines in the crowding condition even if the crowded item cannot be selected attentively for further processing and is not consciously perceived. Sumner et al. (2006) showed that attention modulates neural sensorimotor processes that are entirely separate from those supporting conscious perception. Bahrami et al. (2008) manipulated perceptual load for a task presented at fixation and assessed orientation specific adaptation to invisible, peripheral tilted gratings that were irrelevant to the task [peripheral gratings were rendered invisible by inter-ocular, continuous flash suppression (CFS)]. They showed that in tasks of low perceptual load any spare capacity from relevant stimulus processing spills over to the processing of irrelevant stimuli (producing orientation specific adaptation) regardless of whether or not subjects are conscious of the representations.

The fact that attention can also generate unconscious phenomena is not *per se* evidence of the fact that there can be top-down attention without consciousness. As we will see, the view that there can be top-down attention without consciousness will prove to be incorrect: actually, there can be top-down attention without consciousness only when the former is low-level (that is, it does not reach a certain threshold level). However implausible, this view can originate from either confusing the perception of absence with the absence of perception or overlooking the existence of the various forms of attention and consciousness.

Let's first examine some of the examples that were put forward to support the view that there can be top-down attention without consciousness, and then consider whether there is any kind of attention that can be dissociated from consciousness.

CONFUSING THE PERCEPTION OF ABSENCE WITH THE ABSENCE OF PERCEPTION

Koch and Tsuchiya (2006) maintain that top-down attention and consciousness are dissociated not only because there can be consciousness in the absence of top-down attention, but also because

there can be top-down attention in the absence of consciousness. They state that "Subjects can attend to a location for many seconds and yet fail to see one or more attributes of an object at that location" (Koch and Tsuchiya, 2006, p. 17). Likewise, Mack and Rock, 1998, p. 245) state that "It is not an uncommon experience to be looking for something or keenly awaiting its appearance in the absence of perceiving it (...). Both the looking for and the awaiting are part of what we mean by attention in our ordinary language, but in cases such as these the looking for is not associated with any perception."

Generally speaking, I think that when one states that there can be attention without consciousness or without perception, one should carefully specify what the expressions "without consciousness" or "without perception" imply. Indeed, there are cases in which attention can also generate and modulate unconscious phenomena and perceptual illusions. However, when such cases occur they do not imply that there is no consciousness or perception at all. Rather, they imply that a person can be aware of something without being aware of something else, or even that a person can be aware of not being aware of something. The fact that in some cases one can focus one's attention to something without perceiving it does not imply that one does not perceive anything at all: rather it means that one perceives something else, or that one perceives the absence of the thing one is focusing on. As Mole (2008) correctly observes, cases in which one is on the lookout for something that does not appear, are not cases of attention without perception; rather, these are cases where one is perceiving that nothing has yet occurred. Overlooking this means mistaking the perception of absence for the absence of perception.

Therefore, in my opinion, experiments such as Montaser-Kousari and Rajimehr's (2005) provide evidence not so much of top-down attention in the absence of consciousness, as of "top-down attention in the absence of consciousness of something, but in presence of consciousness of something else," or of "top-down attention with consciousness of the absence of something." Top-down attention (at least, in its high-level form) always implies some form of consciousness, even if only consciousness of the absence of the thing one is focusing on or is looking for. Let's consider some phenomena that are usually thought to support the view that there can be top-down attention in the absence of consciousness.

Motion-induced blindness

Motion-induced blindness (MIB) is a visual illusion in which a perceptually salient stationary visual stimulus repeatedly disappears (and subsequently reappears) when superimposed on a field of moving distracters. Target disappearance in MIB is influenced by attention. Schölvínck and Rees (2009) showed (Experiment 1) that directing spatial attention to an MIB target directly increases its probability of disappearance (compared to an unattended MIB target). Conversely (Experiment 2), increasing the attentional load in a central task unrelated to MIB (for example, performing a conjunction-detection task on the stream of stimuli presented at fixation), decreased the number of disappearances and reappearances of the MIB target.

According to Schölvínck and Rees (2009), these findings appear counterintuitive because, typically, the effect of spatial attention

is to strengthen the representation of a stimulus, whereas they found that spatial attention directed to an MIB target increased the probability of it disappearing. van Boxtel et al. (2010a) interpret these findings – as well as similar ones – as evidence that the effects of attention and consciousness can potentially be opposed to each other: “the more subjects try to see some stimulus by paying attention to, the less visible it becomes!” (van Boxtel et al., 2010a, p. 7).

In my view, the fact that paying more attention to the MIB target increases the probability of its disappearance from consciousness, simply confirms how vision works: the more you look at something, the more you see. The relevant aspect here is that that “something” is a visual illusion – MIB – and not what one usually sees daily (a familiar sight, a common object, etc.): that is, the content of visual perception is the illusion itself. Contrary to van Boxtel et al.’s (2010a) interpretation, I think that Schölvinc and Rees’s (2009) findings show that the more you look at a MIB target, the more visible the illusion becomes! In other words, they can be considered as a case of top-down attention with consciousness of the absence of something³.

OVERLOOKING THE EXISTENCE OF THE VARIOUS FORMS OF ATTENTION AND CONSCIOUSNESS: BLINDSIGHT

A very interesting experiment with a blindsight subject, G.Y., which seems to support the view that there can be top-down attention in the absence of any form consciousness (at least, in the blind area of the subject), was reported by Kentridge et al. (1999). Blindsight subjects are perceptually blind in a certain area of their visual field: they deny having any awareness whatsoever of any visual stimuli presented in that area, or they acknowledge only limited awareness of some phenomena within the blind area, such as movement, but not visual percept. Despite this fact, they are able to discriminate and localize visual stimuli presented in the blind area at levels significantly above chance. In their experiment, Kentridge et al. (1999) adopted a cue–target paradigm. A target, which could appear in one of two possible locations, was presented to the subject; the target was preceded by a cue which might or might not indicate the correct location of the target; the subject was instructed to report – upon hearing an auditory tone that followed the presentation of the visual cue signaling the probable target location – whether or not a visual target had accompanied the presentation of the auditory tone, guessing if necessary, and then to make a second response indicating whether he had had any experience whatsoever. Before the start of each experiment the subject was given instructions indicating the two possible target locations, and in which location the target was more likely to appear. Two main different cueing methods were used in the various experiments in order to investigate whether attention and awareness are inextricably linked or whether there can be endogenous, voluntary attention in the absence of awareness: in the central cueing experiment and in the direct peripheral cueing experiments, the

target was more likely to appear at the location indicated by the cue than at the other location; in the indirect peripheral cueing experiments, the target was more likely to appear at the location opposite to the one indicated by the cue than at the location indicated by the cue. It is known that indirect cues require voluntary, endogenous attention as opposed to automatic, exogenous attention: in fact, the former imply the application of an arbitrary rule (as opposed to an automatic one) relating the cue and the target location, and the suppression of automatic, exogenous orienting of attention to the cue location. Moreover, it is generally maintained that endogenous, voluntary orienting requires conscious awareness (Posner, 1994). Consequently, Kentridge et al. (1999) predicted that if G.Y. could use the indirect peripheral cue to re-orient his attention, and yet remain unaware of the cue, they would demonstrate that there could be endogenous attention in the absence of consciousness. Indeed, their experiments showed that when an indirect peripheral cue was used, G.Y. could direct voluntary, endogenous attention within his blind field, despite being unaware of the cue he used (upon being questioned after each test on whether he had had any experience whatsoever, he answered that he had had no awareness of any cues). Therefore, Kentridge et al. (1999) concluded that “the spatial selection of information by an attentional mechanism and its entry into conscious experience cannot be one and the same process.”

I think that Kentridge et al.’s (1999) findings cannot be straightforwardly interpreted as evidence of top-down attention without consciousness, but rather that they deserve further and more careful examination. In this respect, some alternative interpretations have been proposed.

According to a first alternative interpretation, the fact that G.Y. verbally reported that he had had no awareness of cues does not automatically imply that he had had no conscious experience of anything. As Bartolomeo et al., 2007, p. 157) state: “although an appropriate verbalization can be considered as a reliable indicator of conscious processing (...), the converse is not necessarily true.” Indeed, it is possible to distinguish, as the phenomenological tradition has proposed, between “spoken” and “acted” forms of perception, that is, between a high-order, reflective form of consciousness, and a primary, direct form of consciousness (Bartolomeo et al., 2007; Bartolomeo, 2008). Evidence of a dissociation between these two forms of consciousness comes from neuropsychological studies of brain-damaged patients (for example, an amnesic patient with anosognosia who is able to intellectually acknowledge the presence of his deficits, as well as his incapacity to directly appreciate them: for a review, see Bartolomeo and Dalla Barba, 2002; Bartolomeo et al., 2007), and from psychological observations (consider for example the case in which people observing an array of letters for a very short time are aware of having seen letters but can only name some of them). Therefore, from this viewpoint, it is plausible to interpret Kentridge et al.’s (1999) finding as a case of endogenous attention without reflective (autonoetic) consciousness, but with direct, primary (anoetic) consciousness.

According to a second alternative interpretation – which incidentally Kentridge et al.’s, 1999, p. 1810) themselves seem to suggest when they acknowledge that: “it is clear that, while the direction of attention toward a stimulus may be necessary if it

³ Another example of how it is possible for us to be aware that we are not aware of something, is provided by the phenomenon of the physiological blindspot, that is, the fact that a part of the field of vision cannot be perceived because of the lack of light-detecting photoreceptor cells on the optic disc of the retina where the optic nerve passes through it (see Mole, 2008).

is to reach awareness (...), attention is not sufficient for awareness," – the fact that G.Y. could re-orient his attention does not automatically mean that he could fully take advantage of all the processes and neural mechanisms entailed and elicited by endogenous attention. According to this view, attention is not so much a unitary process or entity, as a complex control system, or a set of coordinated processes; therefore it is possible to explain G.Y.'s behavior as the result of a partial working of such a complex control system. This is exactly the kind of explanation of Kentridge et al.'s (1999) experiments that has been given by Taylor (2008). According to Taylor, the result of Kentridge et al.'s (1999) experiments can be understood in terms of a corollary discharge and attention feedback amplification of the target stimulus. This would allow a response to be made through an automatic route from the partially activated sensory buffer, so as to be more successful than chance, without any need for the visual buffer to be so strongly activated as to lead to awareness.

Finally, De Brigard and Prinz (2010) explain Kentridge et al.'s (1999) findings by resorting to the distinction between spatial attention, that is, attention to a region of space, and attentional modulation of perceptual representations. In their view, in the case of spatial cueing, a two-stage process occurs: firstly, attention is shifted to the region of space indicated by the visual cue, and secondly, if anything is visible in that space, that thing gets visually represented and modulated by attention. Only the latter stage would involve consciousness, not the former. Consequently, a shift of attention to a region of unoccupied space would not result in any conscious visual percept. In Kentridge et al.'s (1999) study, only the first stage could occur, causing G.Y. to attend to a region of space, but the second stage could not occur because of G.Y.'s lesion in his primary visual cortex. De Brigard and Prinz (2010) also provide three possible reasons why the spatial cue could facilitate G.Y.'s performance: (1) attending to a region of space may lower signal-detection thresholds for stimuli presented subsequently in that region; (2) the spatial attention may cause receptive fields in the region to expand, with the subsequent increase of neural resources for the ensuing presented target; (3) spatial attention may prime the blindsighter for behavior responses in the attended region.

It should be noted, however, that De Brigard and Prinz's (2010) explanation could be questioned on the grounds that it seems to be more suitable for a case involving the automatic, exogenous orienting of attention (by a direct peripheral cue), than for a case involving the voluntary, endogenous orienting of attention (by an indirect peripheral cue).

CAN ANY KIND OF ATTENTION BE DISSOCIATED FROM CONSCIOUSNESS? ONLY LOW-LEVEL ATTENTION (PRELIMINARY ATTENTION), BUT NOT HIGH-LEVEL TOP-DOWN ATTENTION

According to Velmans (1991, p. 665), focal-attentive processing provides the necessary condition for conscious awareness, and there cannot be consciousness without attention: consciousness results from focal-attentive processing as a form of output. However, he affirms that, "in principle, it might be possible to obtain evidence of focal-attentive processing in the absence of awareness of what is being processed": that is, attention and consciousness are not the same thing, and in principle can be dissociated, because there can be attentional processing without consciousness,

even though he recognizes that: "in practice, however, a complete dissociation of consciousness from focal-attentive processing is difficult to achieve."

Velmans (1991) aim is to confute the conventional assumption by psychologists that "preconscious" processing is identical to "pre-attentive" processing and "conscious" processing is identical to "focal-attentive" processing. This assumption implies that "preconscious/pre-attentive" processing is fast, automatic, involuntary, and restricted to simple, familiar stimuli, whereas "conscious/focal-attentive" processing is slow, flexible, voluntary, and subject to intentional control. Velmans' confutation is based on evidence that preconscious processing is not inflexible and limited to simple, well-learned stimuli: he provides many examples of preconscious analysis of novel and complex phrases and sentences, implicit learning, preconscious selection and choice, unconscious control of complex, novel motor adjustments, and unconscious planning. Consequently, it would be misleading for him to think of the preconscious–unconscious processing of stimuli as non-attended or pre-attentive: preconsciously processed stimuli, being subject to sophisticated, elaborated analysis, receive attentional resources, although they may not enter consciousness. Moreover, there is evidence (Kahneman and Chajczyk, 1983) that "involuntary, preconscious" analysis of stimuli is not necessarily effortless, and that it draws on, and competes for, limited processing resources, which confirms the involvement of attentional resources in preconscious processing (see also Lavie, 1995). Therefore, rather than speaking of non-attended or pre-attentive processing (vs. focal-attentive processing), it would be better to speak of preliminary attention (vs. focal attention; Velmans, 1991, p. 655).

I think that most of the studies which Velmans cites, aimed at showing a possible dissociation between focal attention and consciousness, do not show that there can be focal-attentive processing without consciousness, but rather that preliminary attention and consciousness can be dissociated. In fact, whether they refer to dichotic listening tasks and shadowing tasks (Treisman, 1964a,b; Lackner and Garrett, 1973; MacKay, 1973), visual masking experiments (Marcel, 1980, 1983), Stroop effect, implicit learning (Hartman et al., 1987; Nissen and Bullemer, 1987), or control of action, they all only show that stimuli can be preconsciously processed if they are given at least a minimal level of attention.

Indeed, as observed by some authors (Neuman, 1984; Holender, 1986; Logan, 1995), in these cases, as well as in others such as the flanker compatibility effect or negative priming effect (Tipper, 1985), subjects do pay a certain, even if marginal, level of attention to the to-be-ignored, unwanted stimuli, even though they are instructed not to pay attention to them, or are prevented from paying attention to them. This marginal level of attention can be brought about and maintained in various ways: one of the most common is by widely distributing the focus of attention. For example, McCormick (1997, p. 178), commenting on his finding that an exogenous cue presented below a subjective threshold of awareness captures attention automatically and without awareness, explicitly observes that "this finding and the issue of the automaticity of exogenous orienting is limited to specific experimental conditions (...). In my experiments, the observers' attention was likely distributed widely over the visual field in anticipation of the pending

cue and target events, thus it could be involuntarily attracted to the cue.”

For example, the fact that amnesic patients and normal subjects, when exposed to successive exemplars of recurring patterns of which they were unaware, can implicitly learn those patterns without spontaneously noting any repeated sequence (Hartman et al., 1987; Nissen and Bullemer, 1987), does not imply that they have used their focal attention to learn those patterns: in fact, they have been instructed to pay attention to the single items composing each pattern, and not to the recurring pattern. Therefore, it is inappropriate to affirm that there is focal-attentive processing of a pattern in the absence of awareness of that pattern, because what subjects attentively process is not so much the pattern as the single items of the pattern. Most probably instead, they were able to learn the patterns because they spent a marginal amount of their attentional resources on them: such a marginal amount that they could not consciously realize what they were doing, even though it was sufficient to make them learn the patterns.

An author who does not fail to notice that only preliminary or low-level (but not high-level focal) attention can be dissociated from consciousness is Damasio (1999). In his definition, consciousness is the “umbrella term for the mental phenomena that permit the strange confection of you as observer or knower of the things observed, of you as owner of thoughts formed in your perspective, of you as potential agent on the scene” (Damasio, 1999, p. 127). Throughout his work, consciousness is seen as the main reason for the feeling we have of ourselves as the subject of our own actions, that is, for the fact that we sense that what we are doing is done by us, and not by someone else.

In his opinion, some diseases, such as akinetic mutism, epileptic automatism and advanced stages of Alzheimer’s diseases, demonstrate that there can be fleeting, low-level attention without consciousness. Evidence of the dissociation between low-level attention and consciousness is given by patients who, while exhibiting some elementary signs of attention such as the ability to form sensory images of objects and execute accurate movements relative to those images, do not develop any sense of self, of an individual organism wishing, considering, wanting, of a person with a past and a future. Moreover, they do not show any sign of emotion either. Finally, Damasio (1999, p. 91) points out that only a kind of attention that is high-level, extended in time and focused on appropriate objects is indicative of consciousness. Despite not specifying exactly what the difference is between low-level and high-level attention, these findings seem to support nonetheless the hypothesis that high-level focal attention cannot be dissociated from consciousness.

Summarizing the data provided by Velmans (1991) and Damasio’s (1999) works, we can say that consciousness can be dissociated only from low-level attention (or, as Velmans calls it, preliminary attention), whether of an endogenous or exogenous kind: high-level top-down attention cannot be dissociated from consciousness. The determination of the threshold level at which attention can be dissociated from consciousness is obviously a matter of empirical investigation. However, in principle, it cannot be excluded that attention, when applied at near-threshold, or when not fully deployed because the stimulus duration does not allow for it, gives rise to unpredictable, paradoxical

phenomena (as it frequently happens in the psychological field: see for example the phenomena of temporal displacement and continuous displacement described in Vicario, 2005)⁴.

Afterimage

Experiments in afterimage studies are sometimes used as evidence that attention and consciousness can be fully dissociated because they produce opposite effects. For example, van Boxtel et al.’s, (2010b, p. 8886) report some experiments on the formation of afterimage perception as evidence that “selective attention and stimulus consciousness have separable effects on perception (...) and, in the context of afterimages, may even have opposite effects.” In van Boxtel et al. (2010b), attention and awareness were independently manipulated during the afterimage induction phase, while the effects of these manipulations were measured in the afterimage perception phase. Attention to the afterimage inducer was manipulated by employing an attention-distracting task at fixation (i.e., the central task). This task could be easy or hard, ensuring identical visual input while manipulating the levels of attention available to the afterimage inducer. The conscious visibility of the inducer stimulus was manipulated independently of attention by means of CFS, a form of inter-ocular suppression (i.e., presenting a very salient object in one eye that completely suppresses the afterimage inducer in the other eye). With the suppression present, the Gabor patch inducing the afterimage was not perceived. This 2×2 design allowed for a full-factorial comparison (i.e., high attention/visible, low attention/visible, high attention/invisible, and low attention/invisible). According to van Boxtel et al. (2010b), these data show that paying more attention to the inducer invariably shortens afterimage duration, while increasing the visibility (i.e., consciousness) of the inducer increases afterimage duration vs. invisibility.

The interpretation of van Boxtel et al.’s (2010b) experiments as evidence that attention and consciousness can be fully dissociated is questionable for a couple of reasons at least.

Firstly, CFS is a technique that, *physically* perturbing the transmission of the information along the way from the stimulus to the brain, alters the normal processing of visual stimuli. As such, it cannot be excluded either that top-down attention is not given sufficient time to be fully deployed and to finalize its course, or that, even if top-down attention is fully deployed, only part of the stimulus is processed. I am not denying that the stimulus is not processed: empirical evidence clearly shows that the invisible stimulus is somehow processed in human primary visual cortex (Bahrami et al., 2007; Watanabe et al., 2011). What I claim is that the process initiated by top-down attention is partly interrupted or modified, and that this does not allow for the stimulus to be consciously perceived. Therefore, with respect to the stimulus, the situation can be assimilated to a situation in which there is only marginal, low-level attention, although one has tried to deploy high-level top-down attention. As such, the data in the invisible condition (when the inducer is suppressed by CFS) cannot be used to support the view that paying more attention to the inducer decreases the duration of its afterimage.

⁴ For a commentary of Vicario’s book, see Marchetti (2006).

Secondly, it could be claimed that the afterimage is the product not so much of attending as of consciously perceiving what is attended. In this view, van Boxtel et al.'s (2010b) findings would not show that "attention produces weaker afterimages"; rather they would show that "attention *via* consciousness produces weaker afterimages." Indeed, it is conceivable that selectively attending to a stimulus produces conscious perception of the stimulus, which, in turn, can produce some other (conscious or unconscious) effect (for example, a decision to search for another stimulus, or to continue to observe the previous stimulus). In the afterimage case, this would entail that attending to a Gabor patch first produces a conscious perception of the Gabor patch, which in turn produces some effect (namely, an afterimage having certain properties, such as being weaker and shorter than an afterimage produced by an unattended Gabor patch). Here, the afterimage would be a direct consequence not so much of selectively attending, as of consciously perceiving the Gabor patch. Without such conscious perceptions, afterimages might not possess any of the specific properties (namely, the characteristics of being weak and short) they acquire thanks to conscious processing. Consequently, also van Boxtel et al.'s statement that selective attention produces weaker afterimages should be reformulated: selective attention (possibly) produces weaker afterimages *indirectly and via* conscious perception of the attended stimulus.

This interpretation does in fact conflict with what the experiments seem to show, i.e., that increasing the visibility (i.e., consciousness) of the inducer increases afterimage duration vs. invisibility. However, it should be noted that the experiments say nothing about the level of visibility in the visible trials when different levels of attention are paid. That is, they do not measure whether stimuli are equally or differently visible in the two different attentional conditions (low vs. high attention). It might turn out, for example, that when the inducer stimulus is highly attended, it is more visible than when the stimulus is not/slightly attended. After all, strength of afterimages has been shown (Baijal and Srinivasan, 2009) to be modulated by the spatial spread of attention and the specific attentional strategy (for example, distributed vs. focal attention) that is adopted to perform the task and yields different types of awareness (for example, background consciousness vs. object consciousness). As Baijal and Srinivasan's (2009) experiments show, afterimage duration is significantly longer when the identification and counting task is performed with small compared to large letters, local compared to global stimuli, small compared to local stimuli, and global compared to large stimuli. Therefore, until it is determined how the level of visibility in the visible trials changes with the various levels of attention, it cannot be completely ruled out that increasing the visibility (via the increase of the amount of applied attention) produces weaker afterimages.

ATTENTION AND CONSCIOUSNESS ARE NOT THE SAME THING

The fact that attention is necessary for consciousness and that high-level top-down attention always implies some form of consciousness does not imply that attention is the same thing as consciousness.

Firstly, not always does attention generate conscious phenomena. As we have seen, attention can also generate and modulate unconscious ones (Naccache et al., 2002; Montaser-Kousari and Rajimehr, 2005; Sumner et al., 2006; Bahrami et al., 2008).

Secondly, as some authors have suggested, consciousness also needs some other components. For example, according to Srinivasan (2008), components such as expectations and capacity of anticipation are necessary for consciousness: indeed, what IB and CB experiments seem to show is that when the observers fail to detect changes this may be due to their expectations of a stable world and inability to anticipate the stimulus (in the sense that, for example, observers do not expect people to suddenly change into someone else). My model of consciousness includes additional components such as sense-organs, somatosensory organs, working memory, and a schema of self (Marchetti, 2010). It should be noted, however, that it is always possible to incorporate such components directly into the attentional system: Knudsen's (2007) proposes that attention reflects the combined contributions of four distinct processes: working memory, competitive selection, top-down sensitivity control, and automatic filtering for salient stimuli.

Thirdly, attention and consciousness can also be distinguished from a functional point of view. Consciousness can be described as *resulting* from the activity performed by attention (see also Velmans, 1991), and more precisely from the application of attention to the other organs or to attention itself, and the consequent modulation of the state of the organ of attention (Marchetti, 2010). This difference is partly captured by Baars' (1997, p. 364) description of attention as something more active than consciousness, and of consciousness as the result of this activity: "It is as if attention resembles selecting a desired television program, and consciousness is what appears on screen." The functional distinction between attention and consciousness has also been highlighted, but in different terms, by van Boxtel et al. (2010a), who conceive of selective, focal attention as an analyzer and consciousness as a synthesizer.

Therefore, my answer to the question of whether there can be human consciousness at all, as we know it, without sense-organs, somatosensory organs, working memory, and all the connections linking one component to the others and to attention, is obviously no: attention alone is not sufficient and the other components are also necessary.

CONCLUSION

In this paper, we have seen that the idea that there can be consciousness without some form of attention, and high-level top-down attention without consciousness, originates from a failure to notice the varieties of forms that top-down attention and consciousness can assume. Overlooking the fact that both attention and consciousness can assume a variety of forms may lead one to: mistake the effects of a form of attention for the effects of another form of attention; ignore that subjects can adopt different attentional strategies depending on the specific task they are required to perform; fail to notice that different attentional strategies may yield different types of awareness.

Once the varieties of forms of attention and consciousness are taken into consideration, the necessity of attention for

consciousness can hardly be denied. As we have seen, there can be low-level attention or preliminary attention without consciousness, but there cannot be high-level top-down attention without consciousness. High-level top-down attention always implies some form of consciousness. On the contrary, low-level or preliminary attention can either imply consciousness (such as when the cocktail party effect occurs) or absence of consciousness. Even if

attention cannot be considered the same thing as consciousness, some form of attention is always necessary for consciousness.

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Attentional routes to conscious perception

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The relationships between spatial attention and conscious perception are currently the object of intense debate. Recent evidence of double dissociations between attention and consciousness cast doubt on the time-honored concept of attention as a gateway to consciousness. Here we review evidence from behavioral, neurophysiologic, neuropsychological, and neuroimaging experiments, showing that distinct sorts of spatial attention can have different effects on visual conscious perception. While endogenous, or top-down attention, has weak influence on subsequent conscious perception of near-threshold stimuli, exogenous, or bottom-up forms of spatial attention appear instead to be a necessary, although not sufficient, step in the development of reportable visual experiences. Fronto-parietal networks important for spatial attention, with peculiar inter-hemispheric differences, constitute plausible neural substrates for the interactions between exogenous spatial attention and conscious perception.

Keywords: attention, conscious perception, endogenous, exogenous, fronto-parietal networks, neglect

BACKGROUND

Both “attention” and “consciousness” refer to complex concepts in search of consensus for definition. “Consciousness” can indicate a state of vigilance or wakefulness, which ranges between comatose states to being awake. It can also refer to the conscious processing of a given piece of information, such as being conscious of a person that just entered the room. In this review we will focus on the later meaning. Contrary to what introspection suggests, only a small fraction of all the information reaching our senses can be the object of verbal report or voluntary action. Although verbal reportability is one of the main measures of conscious perception, there are many situations in which we can be conscious of some information that we cannot report, essentially because it vanishes from consciousness very quickly. In this paper, we will review studies that have used verbal reports of perceptual objects as a measure of consciousness. On the other hand, attentional processes refer to a heterogeneous set of functions, subserved by partially distinct neurocognitive systems. We will refer to attention as a mechanism for the selection of information, in its different varieties of orienting, alerting, and executive control (Posner and Cohen, 1984). We will particularly focus on the relationship between distinct forms of spatial attention and conscious perception.

Historically, attention and consciousness have been intrinsically linked. Introspection suggests that when we attend to an object or part of a scene we become conscious of it. Removing attention away from the object makes it fade from consciousness. Although there seems to be a consensus on the fact that some level of general alertness is needed in order to consciously perceive (Robertson et al., 1998; Dehaene and Changeux, 2011; Kusunir et al., 2011), the relationship between spatial attention and conscious perception has proven intriguing and difficult to explore empirically. James (1890) originally provided an influential definition of

the interplay between attention and conscious perception: “(attention) is the taking possession of the mind, in clear and vivid form, of one out of several simultaneously possible objects or trains of thought.” This view led many to posit that spatial attention and conscious perception are inextricably related (Posner, 1994; O’Regan and Noë, 2001; Chun and Marois, 2002; Bartolomeo, 2008). Although most of the models do not propose that the mechanism of attention is the mechanism of consciousness itself (Posner, 1994), they implicate that consciousness emerges from the processing of attentional systems that filter out information from our crowded environment. Attentional selection is therefore considered a necessary, although maybe not sufficient, condition for consciousness. Others directly equate attentional capture and consciousness. Simons (2000) for example, distinguished between implicit and explicit attentional capture. Implicit attentional capture refers to stimuli that can speed up performance or affect eye movements without being consciously detected (Theeuwes, 1994; Theeuwes et al., 1998). Explicit attentional capture refers to stimuli that affect performance and are consciously detected. According to Simons (2000), implicit effects on behavior might not embody all aspects of attentional capture, while explicit attentional capture is equated to consciousness, i.e., it is assumed that if participants consciously reported the stimuli is because they captured spatial attention.

Some lines of evidence support the existence of a tight relationship between spatial attention and consciousness. The most classical example of interaction between the two processes is observed in the inattentive blindness paradigm, where salient changes in the features of visual stimuli are missed when unattended (Mack and Rock, 1998), even when stimuli are presented at the fovea. Moreover, such phenomenon is enhanced when the deployment of attention is challenged by increased levels of

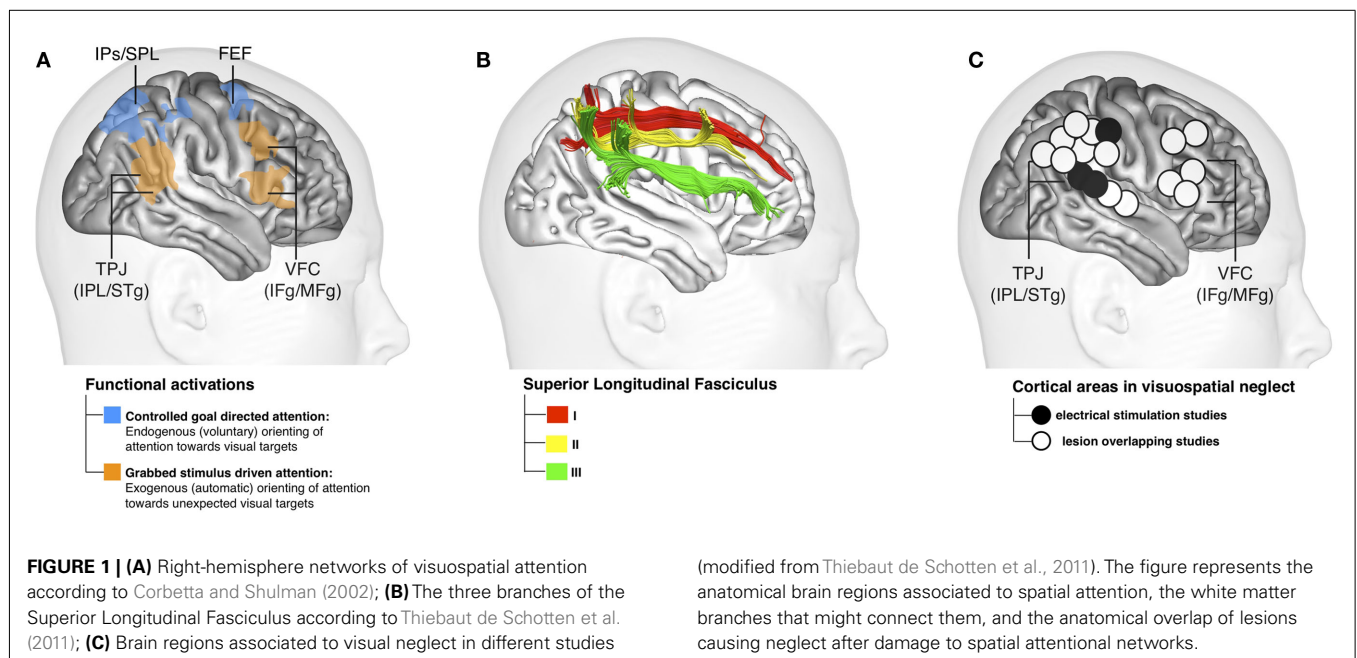
perceptual load (Lavie, 2006). It has been postulated that inattentional blindness is not produced by a lack of attention but by a lack of expectation (Braun, 2001; Mack, 2001), although expectation can be considered as a form of top-down attention (Asplund et al., 2010). One of the most striking examples of the influence of attention in consciousness has been demonstrated by the selective looking task (Neisser and Becklen, 1975). In one of the versions of this paradigm, participants were attentionally engaged in counting the passes made by two basketball teams. After some time, a man wearing a gorilla costume walked across the display. Surprisingly, 35% of the participants did not see the gorilla, which was instead detected 100% of the times when attention was not engaged in counting the passes (Simons and Chabris, 1999). These and other experiments have provided definitive evidence that important changes in our visual world can be missed when unattended.

Strong evidence supporting the existence of a link between spatial attention and conscious perception also comes from right brain-damaged patients affected by left spatial neglect. These patients suffer from damage to the right parietal lobe, or to its connections with the ipsilateral prefrontal cortex (PFC; Thiebaut de Schotten et al., 2005; Bartolomeo et al., 2007). Patients with left brain damage may also show signs of contralesional, right-sided neglect, albeit more rarely, and usually in a less severe form (Bartolomeo et al., 2001a; Beis et al., 2004). Although patients' visual capabilities can be intact, severe problems in attentional orienting are observed. Patients frequently miss contralesionally presented stimuli, especially when there is competing information in the ipsilesional visual field. In other words, neglect patients' acquired inability to orient attention toward the contralesional left hemifield makes them unaware of stimuli presented within the neglected space (Bartolomeo, 2007). This suggests a strong link between the brain circuits underlying spatial orienting and the putative neural correlates of conscious perception (Figure 1).

DISSOCIATIONS BETWEEN SPATIAL ATTENTION AND CONSCIOUS PERCEPTION

Challenging the classical view of attention as a gateway to consciousness, some studies have reported dissociations between some forms of spatial attention and conscious perception. Some of these dissociations have been described in the blindsight patient GY (Kentridge et al., 1999, 2004; Schurger et al., 2006). Blindsight can be observed after lesions in the primary visual cortex of one or both hemispheres (Weiskrantz, 1986). Although patients report to be blind in the contralesional visual field, and therefore not conscious of visual stimulation, they can perform above chance in some tasks such as guessing the orientation of movement (Weiskrantz, 1986). They can also navigate avoiding obstacles in a room, while denying to see them (de Gelder et al., 2008). The study of these patients is especially interesting in research on consciousness, because their accuracy in detecting or discriminating information in the blind hemifield can sometimes be comparable to stimuli reported as being consciously perceived. To study the relationship between spatial attention and conscious perception, Kentridge and colleagues (Kentridge et al., 1999; see also Kentridge et al., 2004) presented the blindsight patient GY with targets in the blind hemifield preceded by endogenous cues in the fovea or exogenous peripheral cues in the blind hemifield. Both cues speeded up responses to targets, even though the patient denied seeing targets as well as peripheral cues. This result demonstrates that after damage to the primary visual cortex, attention can be deployed, and speed up responses, in the absence of consciousness for cues or targets. Thus, GY can pay attention to visual information unavailable to verbal report.

Analogous dissociations between spatial attention and consciousness have been reported in normal observers. In a Posner-type paradigm, where attention was oriented by using spatially predictive central cues (arrows), non-consciously perceived primes (which were masked by subsequent targets) presented at



attentionally cued locations, sped up responses when they were color-congruent rather than incongruent with the target (Kennerly et al., 2008). Importantly, in this case attention did not allow participants to consciously report the primes, showing once more that spatial attention can be deployed in the absence of conscious perception of the attended information.

Koch and Tsuchiya (2007) have also recently reviewed some situations in which endogenous or top-down attention can be dissociated from conscious perception. For example, there are some situations in which participants attend without being conscious of the attended information. In visual crowding, for example, the orientation of a grating can be made unconscious, but it still produces an aftereffect that is supposed to require focal attention (He et al., 1996). It has also been demonstrated that priming for invisible (masked) words is only observed if participants are attending to the moment in time where the prime–target pair will occur. However, in this case, attended words do not reach consciousness (Naccache et al., 2002). Feature-based attention can also spread to invisible stimuli (Melcher et al., 2005; Kanai et al., 2006), once again demonstrating that some forms of attention deploy without subsequent conscious perception of the attended information.

There seem to be other situations in which consciousness happens in the near absence of attention. For example, the gist of a visual scene is immune to inattention blindness (Mack and Rock, 1998), and can be discriminated in 30 ms, too short a time to develop top-down attention. This observation was already made by Posner (1994), who remarked that attention seemed to be needed for focal awareness, but not for awareness of the background (Iwasaki, 1993). With attention focused to the center of the display in a dual task, participants can determine if the scene contains an animal or a vehicle, but cannot perform a simpler task, such as distinguishing a colored disk (Li et al., 2002). Following the feature binding model (Treisman and Gelade, 1980), spatial attention is considered to be important for feature integration but not for single feature extraction. It is possible that when stimuli are complex, feature integration is not necessary, because the processing of multiple single features can be enough to discriminate the object.

It is crucial to note that all these previous studies reviewed by Koch and Tsuchiya (2007) investigated the relationship between endogenous (or top-down) forms of spatial attention and conscious perception. By using magneto-encephalography, it has also been recently reported that endogenous spatial attention, oriented using central arrow cues, can be electrophysiologically dissociated from conscious perception in visual areas of the occipital cortex (Wyart and Tallon-Baudry, 2008). Whether they were attended or not, consciously perceived stimuli modulated mid-frequency gamma-band activity over the contralateral visual cortex, whereas spatial attention modulated high-frequency gamma-band activity, independent of whether targets were consciously perceived or not. This constitutes a neural dissociation of attention and conscious perception, at least in visual areas of the cortex (although see Chica et al., submitted; described below). Finally, opposite effects of endogenous attention and consciousness have been observed on afterimages (van Boxtel et al., 2010). While manipulating attention via a demanding central task, stimulus visibility

was simultaneously manipulated using a perceptual suppression procedure. van Boxtel and colleagues demonstrated that attention and consciousness produced opposite effects on afterimages: while attention decreased their duration, consciousness enhanced it. Altogether, the results from these studies suggest that top-down amplification or endogenous attention is neither necessary nor sufficient for consciousness.

EXOGENOUS SPATIAL ATTENTION INTERACTIONS WITH CONSCIOUS PERCEPTION

It is now well established that the orienting system of the human brain is not unitary. Spatial attention can be oriented either endogenously (i.e., top-down, guided by task demands, or by goals of the task at hand) or exogenously (i.e., bottom-up, driven by the saliency of stimulation, such as in attentional capture). These attentional systems are implemented in partially different brain regions (Corbetta and Shulman, 2002; Chica et al., 2011a), and produce differential effects on information processing (Klein, 2004; Chica et al., 2006). Important components of these networks include the dorsolateral PFC and the posterior parietal cortex (PPC). Physiological studies indicate that these two structures show interdependence of neural activity (Buschman and Miller, 2007). In the monkey, analogous PPC and PFC areas show coordinated activity when the animal selects a visual stimulus as a saccade target. Importantly, PFC and PPC show distinctive dynamics of interaction when attention is selected by the stimulus (bottom-up or exogenous orienting) or when it is directed by more top-down (or endogenous) goals. Bottom-up signals appear first in the parietal cortex and are characterized by an increase of fronto-parietal coherence in the gamma-band, whereas top-down signals emerge first in the frontal cortex and tend to synchronize in the beta band (Buschman and Miller, 2007). Within the right parietal cortex, regions such as the intraparietal sulcus (IPS) seem related to both endogenous and exogenous spatial attention, while the temporo-parietal junction (TPJ) is exclusively implicated in exogenous spatial attention (Chica et al., 2011a; see also Friedrich et al., 1998). Therefore, the finding that endogenous attention and conscious perception dissociate does not necessarily imply the same conclusion for exogenous attention.

Previous research on patients with right brain damage and left visual neglect (characterized by unawareness for left-sided objects) has consistently demonstrated that consciousness deficits in neglect are systematically associated to impairments of exogenous spatial orienting; endogenous orienting, on the other hand, can be relatively spared, if slowed, in these patients (Bartolomeo and Chokron, 2002). Deficits in exogenous orienting in neglect patients typically take the form of an immediate rightward orienting of attention as soon as the visual scene unfolds (Gainotti et al., 1991; D'Erme et al., 1992), followed by the so called “disengagement deficit” (Posner et al., 1984; Friedrich et al., 1998; Losier and Klein, 2001). When presented with a right-sided, ipsilesional peripheral cue followed by a left-sided, contralesional target, neglect patients respond extremely slow, and may miss the target altogether. This result is usually interpreted as an impairment of the disengagement of attention from ipsilesional stimuli. The deficit is enhanced by the presence of bilateral placeholder markers in the display (Gainotti et al., 1991; D'Erme et al., 1992;

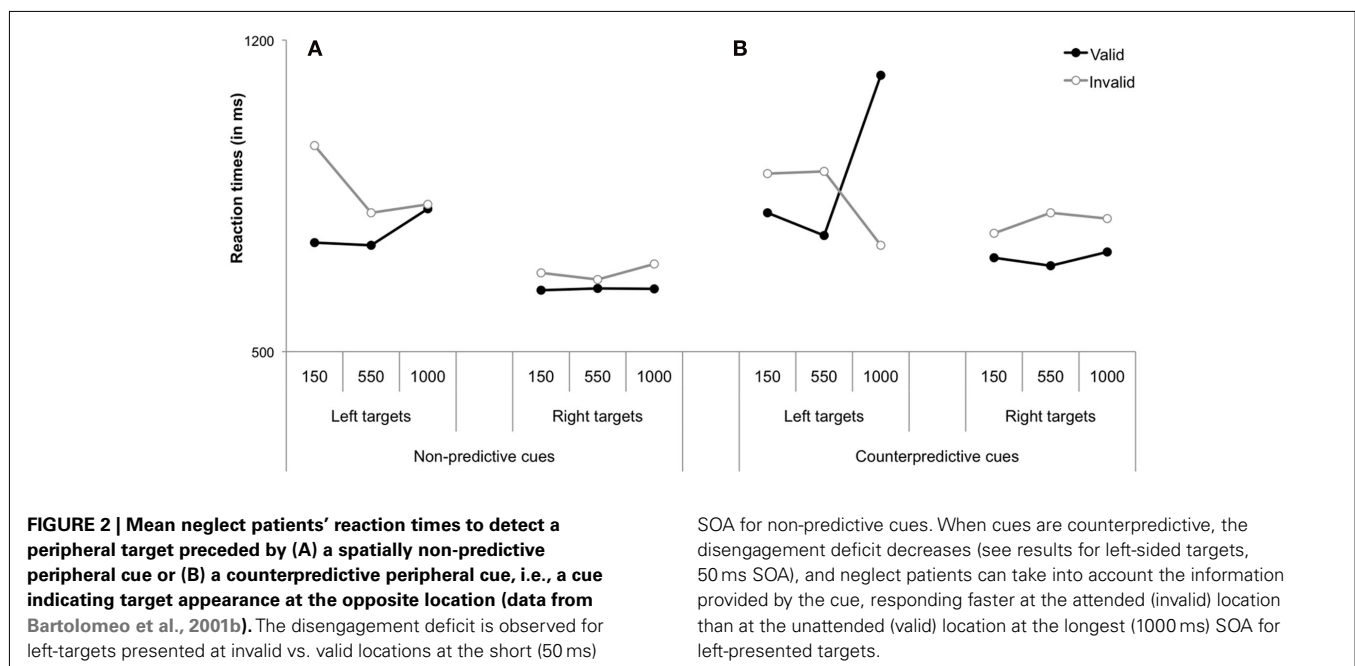
Rastelli et al., 2008), which presumably increase attentional capture from ipsilesional, right-sided objects (Bartolomeo et al., 2004). Interestingly, when peripheral cues are made spatially predictive of the future location of the target, the disengagement deficit ameliorates (Bartolomeo and Chokron, 2002). For example, if the ipsilesional cue (presented on the right hemifield) predicts with high probability target appearance on the contralesional (left) hemifield (which is known as counterpredictive cues), participants' responses are faster and less targets are missed than if the peripheral cue is not spatially predictive (Bartolomeo et al., 2001b; **Figure 2**). This indicates that brain lesions associated to neglect and causing severe deficits in consciously detecting contralesionally presented information (Thiebaut de Schotten et al., 2005; Bartolomeo et al., 2007), mostly affect exogenous rather than endogenous spatial attention.

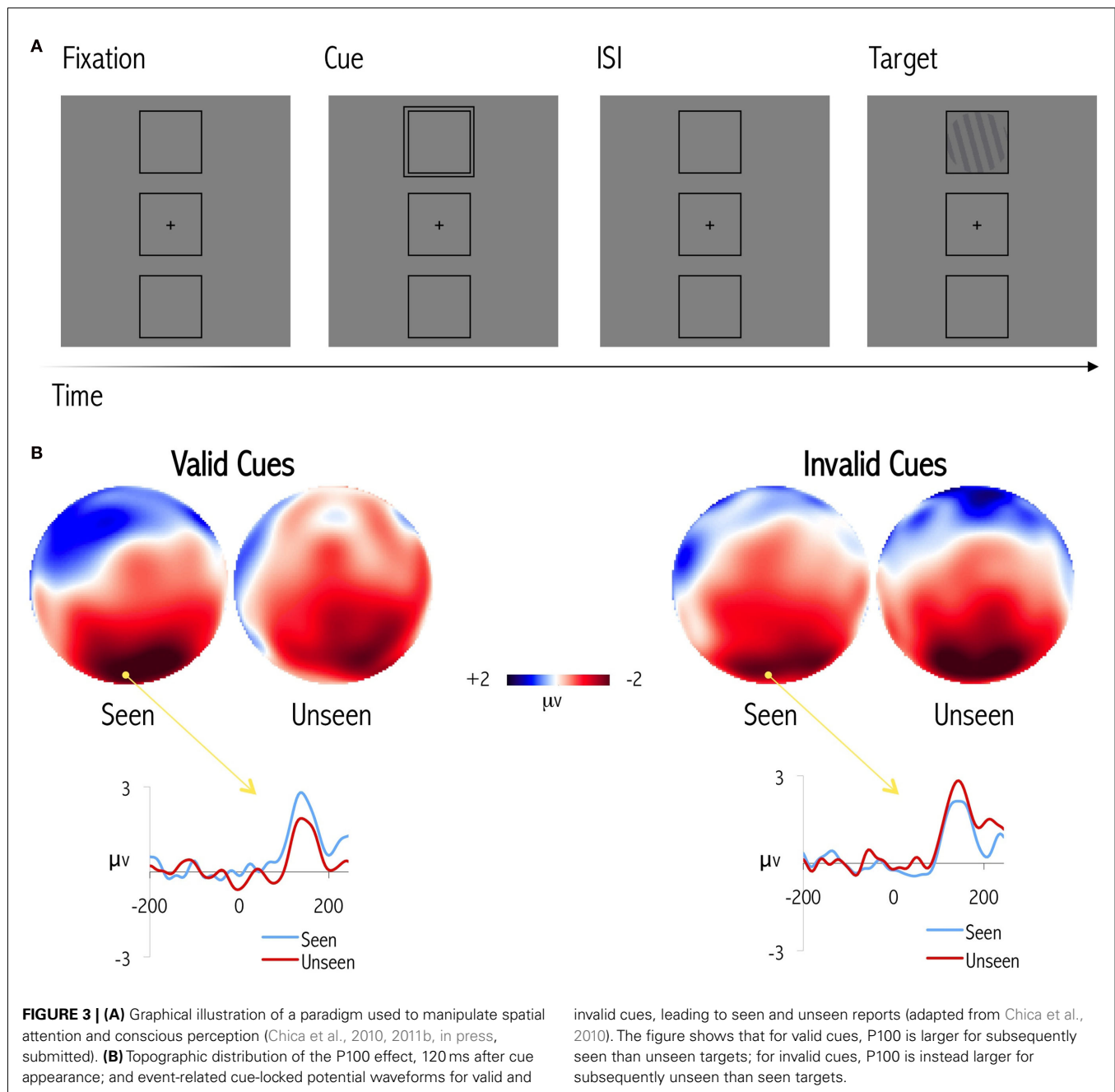
This clinical observation made us hypothesize that although endogenous spatial attention can be dissociated from conscious perception (Kentridge et al., 1999; Lamme, 2003; Koch and Tsuchiya, 2007; Wyart and Tallon-Baudry, 2008), exogenous attention might instead be an important antecedent of our conscious experience. To test for this hypothesis, we presented normal participants with near-threshold stimuli, preceded either by central symbolic cues or by peripheral cues (Chica et al., 2011b). In order to avoid the involuntary orienting produced by some central cues, such as arrows (Ristic et al., 2002), we used purely symbolic cues (letters or colors) indicating the more likely location of target appearance. Target contrast was manipulated so that participants could only perceive a proportion of the targets. If attentional orienting increased target conscious perception, more targets should be reported at the attended than at the unattended location. Consistent with previous findings (Kentridge et al., 1999; Lamme, 2003; Koch and Tsuchiya, 2007; Wyart and Tallon-Baudry, 2008) when spatial attention was endogenously oriented using central symbolic cues, weak, or null modulations of conscious reports were

observed (Chica et al., 2011b)¹. However, exogenous orienting triggered by peripheral cues produced strong and consistent modulations of conscious reports, and was able to increase conscious detection rates at the attended vs. the unattended location (Chica et al., 2011b).

Using electroencephalographic (EEG) recordings, we have also demonstrated that the attentional capture produced by the peripheral cue correlates with subsequent conscious reports of near-threshold targets (Chica et al., 2010, in press). We used non-predictive peripheral cues, which capture spatial attention exogenously, and observed that a cue-related event-related potential (ERP), the P100 component, was strictly linked to subsequent conscious reports (Chica et al., 2010). Importantly, the cue-related P100 was larger for subsequently seen targets than for unseen targets when attentional cues were valid; in contrast, P100 was larger for subsequently unseen than for seen targets when attentional cues were invalid (**Figure 3**). The P100 component elicited by the cue might well index the capture of attention that the cue produced. Thus, if valid cues captured attention to the location of the impending target, then more targets would be consciously

¹Other studies have reported significant modulations on the proportion of consciously reported targets when spatial attention was endogenously oriented using central cues (Wyart and Tallon-Baudry, 2008; Hsu et al., 2011). However, in these studies, Signal Detection Theory (Green and Swets, 1966) parameters such as perceptual sensitivity (d') and response criterion (β) could not be separately calculated for attended and unattended targets (see Chica et al., 2011b, where these analyses were performed). The fact that more false alarms (conscious reports of target presence when no target was actually presented) were committed when central cues were spatially predictive (12% in Hsu et al., 2011, Experiment 1) than when they were not (6% in Hsu et al., 2011, Experiment 1), together with the finding of significant differences in the general d' between spatially predictive and non-predictive cues, and close to significance differences in response criterion [$t(13) = 1.64, p = 0.11$], strongly suggests that participants may have adopted a stricter response criterion to report targets at the unattended vs. the attended location, especially when central cues were spatially predictive of target appearance (Hsu et al., 2011).





perceived at that location. However, if an invalid cue captured attention to a wrong location, fewer targets would be consciously perceived. Correlations between the attentional capture produced by the cue and subsequent conscious reports were observed even when cue-related responses were considered on a trial-by-trial basis. Using a paradigm in which endogenous and exogenous orienting are manipulated during the same trial, it has also been demonstrated, within the same experimental design, that while exogenous attentional capture interacts with the conscious perception of near-threshold targets, endogenous orienting can be dissociated from conscious reports (Chica et al., in press). This clearly demonstrates that exogenous attention is an important modulator

of conscious perception (see also Koivisto et al., 2009), and that the state of the attentional system before the target is presented modulates our conscious experience (see also Super et al., 2003; Linkenkaer-Hansen et al., 2004; Dehaene and Changeux, 2005).

Although some of the studies reviewed in the previous section have demonstrated that endogenous spatial attention can be dissociated from conscious perception, this has not always been the case. The seminal studies suggesting an interdependence between spatial attention and consciousness, such as inattention blindness (Mack and Rock, 1998) or the selective looking task (Neisser and Becklen, 1975), manipulated endogenous spatial attention and measured conscious reports. Research on visual search has

also demonstrated that at least under certain conditions, salient distractors might not capture attention if they do not share any relevant feature with the target (Folk et al., 1992). For example, when searching for a red letter, only red distractors will capture attention, while other colored distractors will not. This is known as “contingent attentional capture,” a phenomenon that demonstrates how top-down or endogenous expectancies interact with the exogenous attentional capture produced by the stimuli themselves. It is possible that while endogenous attention does not determine our conscious experience when there is no competing stimulation (Wyart and Tallon-Baudry, 2008; Chica et al., 2011b, in press), it does play a role when information has to be selected from crowded environments (such as in the inattention blindness paradigm or selective looking task; see Koivisto and Revonsuo, 2010; Dehaene and Changeux, 2011), or when endogenous expectancies interact with exogenous attentional capture (such as in “contingent attentional capture” paradigms). This proposal is coherent with models postulating that conscious and non-conscious perception depend on perceptual load; information can be selected out by attention under high levels of perceptual load, while more information can be consciously processed under low levels of perceptual load (Lavie, 2006; Macdonald and Lavie, 2008). Endogenous attention might thus modulate consciousness only when its functioning is required by high levels of perceptual load in crowded environments.

EXOGENOUS SPATIAL ATTENTION IS NOT SUFFICIENT FOR CONSCIOUS PERCEPTION

In the previous section we have reviewed evidence indicating that exogenous spatial attention is an important antecedent of our conscious experience. However, there are also many observations demonstrating that exogenous attentional capture does not always lead to conscious perception. As stated above, exogenous peripheral cues presented in the blind hemifield of the blind-sight patient GY, sped up responses to the target, in the absence of conscious perception of the cues or targets (Kentridge et al., 1999, 2008). Similarly, in healthy participants, subliminal peripheral cues have been observed to speed up responses to targets presented at the same spatial location, demonstrating attentional deployment in the absence of consciousness of the visually presented cue (McCormick, 1997; Lambert et al., 1999). Further evidence have demonstrated attentional capture or pre-attentive orienting to unresolvable *Gabor* patches embedded among simple luminance patches, while participants could not consciously distinguish between the two (Rajimehr, 2004). This is in line with evidence of attentional capture without consciousness of the feature that captured spatial attention.

Other studies have shown that exogenous spatial attention modulates the processing of masked stimuli that are not consciously perceived (Lachter et al., 2004; Marzouki et al., 2007). In some cases, exogenous peripheral cues are sufficient to generate priming when the primes and targets occupy different spatial locations. This result indicates that exogenous peripheral cues produce effects at early stages of visual processing (Finkbeiner and Forster, 2008), boosting the signals from primary visual areas. However, the presence of the mask disrupts further processing, avoiding conscious perception of the targets.

Woodman and Luck (2003) used an “object substitution masking” paradigm to explore the role of attention in conscious perception. In this paradigm, an object presented in a crowded environment is masked by the presentation of small objects surrounding it; when the mask offsets sometime after the display onset, the masked object is not consciously perceived. In Woodman and Luck’s study, the N2pc ERP component (a N200 observed at parietal sites, reflecting attentional capture) was used to index the orienting of attention to the target. Their results showed that the N2pc was elicited both when the target was consciously perceived and when it was not, leading the authors to conclude that attention and conscious perception are two independent processes, and that orienting of attention did not intrinsically produce conscious reports. However, as noted by the authors, the N2pc ended earlier when targets were not consciously perceived. If N2pc is a correlate of exogenous orienting of attention, these results can be interpreted as supporting the idea that exogenous attention is an important modulator of conscious perception. The fact the N2pc ended earlier when the stimulus was not consciously reported might indicate that even if the target produced an exogenous attentional capture, the corresponding fronto-parietal activation was unable to maintain the exogenous capture of attention long enough to trigger the necessary reverberation of information required for conscious processing (see below).

There is also accumulating evidence demonstrating that distractors can capture exogenous attention in visual search tasks and affect performance and eye movements, while participants are completely unconscious of the presence of these distractors and their influence on their behavior (Theeuwes, 1994; Theeuwes et al., 1998). In oculomotor capture paradigms, attentional capture is reflected by inappropriate eye movements to irrelevant distractors. Importantly, participants are not conscious of the eye movements elicited by distractors during search. All these results clearly indicate that attentional capture does not always lead to the conscious perception of the attended information.

NECESSARY CONDITIONS FOR CONSCIOUS PERCEPTION

The studies reviewed in the two previous sections indicate that at least some forms of attention, such as exogenous spatial attention, might be necessary, although by no means sufficient, for conscious perception. Some models have proposed other processes as necessary for consciousness, such as recurrent processing of information within functionally interconnected brain regions (Dehaene and Naccache, 2001; Dehaene et al., 2006; Lamme, 2006; Fahrenfort et al., 2007). During information processing, two neural processes have been distinguished: a feedforward sweep (earlier activation of cells in successive areas of the visual hierarchy) followed by recurrent processing (recurrent interactions between neurons within an area and other neurons that activated earlier at lower levels). According to a recent model (Lamme, 2003), conscious perception needs recurrent processing. This is an interesting approach because it does not point to any isolated brain region as the neural correlate of conscious perception; instead, the reverberation of information within functionally connected brain regions is deemed important. Transcranial magnetic stimulation (TMS) studies have stressed the importance of recurrent processing. For example, TMS-mediated V1 disruption prevents consciousness at

a time point far from the feedforward sweep of information (Walsh and Cowey, 1998). Moreover, TMS in visual area V5 (MT) produces motion sensation, unless V1 is stimulated at a later moment in time (Pascual-Leone and Walsh, 2001), which also indicates the importance of early visual areas in later stages of processing that are crucial for recurrent processing.

So far, for the quest for the neural correlate of consciousness have led to controversial results (see Rees et al., 2002a; Dehaene and Changeux, 2011; for reviews). When contrasting consciously seen vs. unseen stimuli, some authors have proposed that consciousness is related to activity in the thalamus and brain stem (Paus, 2000), in visual areas along the ventral cortical visual stream (Bar and Biederman, 1999; Grill-Spector et al., 2000; Moutoussis and Zeki, 2002; Pins and ffytche, 2003; Ress and Heeger, 2003; Zeki, 2003; Tse et al., 2005), or in parietal and prefrontal regions (Crick and Koch, 1995; Beck et al., 2001; Dehaene and Naccache, 2001; Rees et al., 2002a; Dehaene et al., 2003; Dehaene and Changeux, 2005; Marois and Ivanoff, 2005; Chica et al., submitted).

When using masking procedures, activity in V1 is related to conscious reports, and drawing attention away from the stimulus does not produce activity in fronto-parietal areas, but in visual areas (Tse et al., 2005). Additionally, lesions in cortical visual areas destroy conscious perception (as in cortical blindness, homonymous hemianopia, or cerebral achromatopsia), which also indicate that conscious perception needs the activity of early visual regions. Based on these sort of data, some models propose that visual consciousness resides in each particular area in charge of processing the relevant feature (Zeki, 2003). According to these proposals, consciousness of a color resides in V4, a region of the visual cortex putatively involved in color processing. However, early visual activation is not always sufficient for consciousness. For example, activity in early visual areas can be observed even when participants deny seeing the stimuli (Dehaene et al., 2001; Vuilleumier et al., 2001; Moutoussis and Zeki, 2002; Marois et al., 2004; Sergent et al., 2005). Primary visual cortex can also be selectively activated in response to perceptually indiscriminable orientation information, indicating that V1 is not sufficient for generating conscious reports (Rajimehr, 2004). The existence of high-order processing of orientation in the absence of consciousness has also been reported, demonstrating interactions between V1 and V4, and V1 and V5 (Rajimehr, 2004). Moreover, when invisibility is caused by masking (Dehaene et al., 2001) or dichoptic stimulation (Moutoussis and Zeki, 2002), activity in early visual areas is weak, which can invite the conclusion that consciousness needs a stronger activation of these regions. However, when invisibility is caused by neglect or inattention, activity in early visual areas can be strong (Vuilleumier et al., 2001; Marois et al., 2004; Sergent et al., 2005). In the case of spatial neglect, visual areas are often intact, but patients can act as if they were completely blind for the information presented in the contralesional hemi-space.

Other studies have related the emergence of conscious states to the activity in parieto-frontal structures (Crick and Koch, 1995; Beck et al., 2001; Dehaene and Naccache, 2001; Rees et al., 2002a; Dehaene et al., 2003; Dehaene and Changeux, 2005; Marois and Ivanoff, 2005; Chica et al., submitted). These sets of data have been used to substantiate “high-order” theories of consciousness (see Lau and Rosenthal, 2011; for a recent review), which

postulate that consciousness depends on neural activity in prefrontal and parietal regions, although consciousness might not add a significant utility or immediate impact on behavioral and task performance. Other models (Dehaene and Naccache, 2001; Dehaene et al., 2006) also propose the importance of prefrontal and parietal areas for consciousness, and underline the strong links of conscious processing to the flexible control of behavior, cognitive control, and the ability to perform various tasks. Dehaene and his colleagues have proposed a model in which both bottom-up stimulus strength and top-down attentional amplification are jointly needed for conscious perception; however, these features might not always be sufficient for a stimulus to cross the threshold for conscious perception. They propose the existence of two types of non-conscious processes: subliminal and pre-conscious. According to the authors, subliminal processing (i.e., information that does not reach consciousness but can affect our behavior) is the consequence of bottom-up activation of lower sensory areas that is insufficient to trigger a large-scale reverberating process to create the conditions for conscious perception. In contrast, pre-conscious processing refers to neural processes that can potentially access consciousness (i.e., they carry enough activation), but those are temporally inaccessible due to the lack of top-down attentional amplification.

Both Lamme’s (2003) model and Dehaene and colleagues’ model (Dehaene and Naccache, 2001; Dehaene et al., 2006) can be helpful to understand the controversial set of data found when consciously seen and unseen reports have been compared using different paradigms. Masked stimuli produce feedforward activation in V1, the inferior temporal cortex, frontal eye fields, and the motor cortex. However, neurophysiological manifestations of recurrent interaction are suppressed by backward masking (Lamme and Roelfsema, 2000; Lamme et al., 2002), which prevents the stimulus to reach consciousness. When masked stimuli are unattended, only occipito-temporal activation is recorded (Tse et al., 2005). When they are attended, however, activity is observed in both early visual areas and fronto-parietal regions (Dehaene et al., 2001; Haynes et al., 2005). Nevertheless, attention is not sufficient for a masked stimulus to reach consciousness, because the mask prevents recurrent processing from fronto-parietal regions to visual areas (see below). Similarly, blindsight patients can process (and respond to) unreported visual information, but due to their lesions of the visual cortex, recurrent processing from fronto-parietal regions to visual areas is altered, thus preventing consciousness to occur.

Near-threshold stimuli also differ in the activity they evoke in early visual areas and fronto-parietal regions (Pins and ffytche, 2003; Ress and Heeger, 2003; Palva et al., 2005). Their perception depends on several factors, such as recurrent processing, alertness (Kusnir et al., 2011), the amount of spontaneous activity before stimulus presentation (Super et al., 2003; Linkenkaer-Hansen et al., 2004; Dehaene and Changeux, 2005), and exogenous attentional capture to their spatial location (Chica et al., 2010, 2011b, in press, submitted). Using supra-threshold targets, previous work has consistently demonstrated that exogenous (as well as endogenous) attention increases contrast appearance (see, e.g., Pestilli and Carrasco, 2005; Carrasco, 2006). It could then be argued that exogenous attention increases conscious reports of near-threshold

targets by a similar perceptual mechanism as that increasing target contrast at the exogenously attended location. This would imply that, contrary to our proposal, exogenous attention might not be necessary for conscious perception; it might only enhance such conscious perceiving. This interpretation is consistent with models proposing an important role of early visual and/or occipito-temporal areas in conscious perception (Super et al., 2001; Lamme et al., 2002; Pins and ffytche, 2003; Zeki, 2003; Tse et al., 2005; Lamme, 2006). However, when near-threshold stimuli are made invisible under conditions of inattention, late differences involving fronto-parietal activation are often reported for seen vs. unseen stimuli (Vogel et al., 1998; Beck et al., 2001; Rees et al., 2002b; Gross et al., 2004; Marois et al., 2004; Pessoa and Ungerleider, 2004; Haynes et al., 2005; Sergent et al., 2005), which is consistent with models proposing that conscious perception emerges from the recurrent activity of fronto-parietal regions, and its long-distance reverberation with occipital areas (Dehaene and Naccache, 2001; Dehaene et al., 2006).

Recent functional magnetic imaging (fMRI) data from our group (Chica et al., submitted) also support an important role of functionally connected fronto-parietal networks in conscious perception and in the interactions between spatial attention and consciousness. fMRI signals were recorded while participants responded to near-threshold stimuli preceded by peripheral cues. Functional connectivity analyses during the orienting period (i.e., during the processing of the attentional cue, before the target was presented) demonstrated that activity in a slightly right-lateralized fronto-parietal network (including the bilateral superior and inferior parietal lobes, the left frontal eye field, the right insula, and right inferior frontal gyrus) was tightly correlated to spatial attention and conscious reports. Strong coupling within this network correlated with conscious reports when targets were presented at the attended location; however, it correlated with “unseen” reports when targets were presented at unattended locations. Coupling within this network is associated to the efficiency of attentional orienting, which is directly linked to the facilitatory effects of spatial orienting on visual consciousness. Fronto-parietal interactions can therefore be primed by attentional processes, thus increasing the likelihood of conscious reports. Evidence of interactions between spatial attention and consciousness was observed in fronto-parietal regions, but not in lower level visual areas. This result is consistent with previous reports of neural dissociations between spatial attention and consciousness in the visual cortex (Wyart and Tallon-Baudry, 2008).

Based on the fact that some stimuli do not reach consciousness even when they are attended (Cumming and Parker, 1997; Zeki and Marini, 1998; Leopold and Logothetis, 1999; Enns and Di Lollo, 2000; He and MacLeod, 2001; Intriligator and Cavanagh, 2001; Super et al., 2001), Lamme (2003) proposed that attention might not determine whether stimuli reach consciousness, but whether they can be reported. Attention would determine whether the representation of stimuli is stable enough in working memory to allow reportability. For example, in a change blindness paradigm cueing the item that might change can prevent blindness. But blindness is also prevented if the relevant item is cued long after the first stimulus (T1) has disappeared and before the onset of the second stimulus (T2; Becker et al., 2000; Landman et al., 2003). After T1 has disappeared, its representation is accessible,

and cuing can select information from working memory. However, when T2 is presented, the representation vanishes, and cuing does not help anymore. This suggests that there is a short-lived, vulnerable, and not easily reportable representation of visual experience, and a more stable and reportable representation form of consciousness. In the case of change blindness, there is a general consensus on the fact that focal spatial attention is needed in order to perceive the change. In the absence of such attentional processes, the contents of visual memory are overwritten by subsequent stimuli and cannot be used to make comparisons (Rensink et al., 1997). Koivisto and Revonsuo (2010) have formulated a related proposal based on ERP studies. Early differences on occipital ERPs (around 200–300 ms after stimulus onset) are proposed to be linked to short-lived, non-reportable representations of visual experiences, while later differences in parieto-frontal sites (around 400 ms after stimulus onset) might be more related to conscious and reportable representations. According to their proposal, spatial attention is a necessary prerequisite for both kinds of representations, at least when there is competition between stimuli (Koivisto et al., 2009).

These proposals are reminiscent of the distinction made by Block (1996) between phenomenal and access consciousness, and of a related, time-honored distinction between a form of immediate experience, not amenable to verbal description, and a reflective form of consciousness that can be verbally reported (Merleau-Ponty, 1942; Bartolomeo and Dalla Barba, 2002). According to the above mentioned evidence, attention seems necessary to go from phenomenal to access consciousness. Based on our recent observations (Chica et al., 2010, 2011b, in press, submitted) we propose that exogenously attended information is always phenomenally represented, which is not the case for endogenously attended information in the absence of exogenous attentional capture. This can explain why endogenous spatial attention can be electrophysiologically dissociated from consciousness (Wyart and Tallon-Baudry, 2008; Chica et al., in press) while exogenous spatial attention is not (Chica et al., 2010, in press, submitted). However, in order to access consciousness and reportability, information has to be endogenously attended in order to enter the reverberating flow of information within fronto-parietal regions (van Gaal and Fahrenfort, 2008). This might be the reason why making peripheral exogenous cues spatially predictive increases the behavioral modulation produced on conscious perception as compared to non-predictive cues, and modulates not only the proportion of consciously reported stimuli and decision criteria, but also the perceptual sensitivity to detect near-threshold stimuli (Chica et al., 2011b). From a physiological point of view, it is plausible that both feedforward processing (perhaps modulated by exogenous attention), and recurrent processing (perhaps enhanced by endogenous attention) in large-scale brain networks are important mechanisms to allow a stable pattern of activity of visual working memory that determines our reportable conscious experience.

CONCLUDING REMARKS

Spatial attention and conscious perception have been historically linked, though some recent studies have shown dissociations between the two processes. In the present paper we reviewed evidence indicating that although endogenous or top-down spatial attention can sometimes be dissociated from conscious reports

(mainly when there is no competing information), exogenous, or bottom-up spatial attention seems to be an important antecedent of our conscious experience. Nevertheless, exogenous attentional capture *per se* is not a sufficient condition for conscious access. Other processes such as alerting, recurrent processing and patterns of spontaneous brain activity before the stimulus occurs are proposed as being necessary for a stimulus to be consciously perceived and reported.

Even though during the last decades consciousness studies have provided important insights about conscious and unconscious processing in the human brain, many questions remain unresolved (Lau, 2008). One of the most important issues to be solved experimentally is the search for an objective measure of phenomenal consciousness. Nowadays, consciousness is measured with verbal reports or voluntary action. Although many believe that we are conscious of much information we cannot report, there is a current controversy about the existence of forms of consciousness that would not be amenable to verbal report. It has been argued that consciousness cannot be separated from the brain mechanisms supporting it, such as attention, working memory, or decision taking (Cohen and Dennett, 2011). In classical examples such as the Sperling's partial report experiment (Sperling, 1960), participants are presented with a display of 9–12 letters. Typically, only some of the items are available to verbal report. However, when cued to report a subset of letters, participants can entirely report whatever subset is cued, which might indicate that at some point they were conscious of the whole subset. Although this result is a crucial argument to claim that we are conscious of more we can report, Cohen and Dennett offer an alternative explanation (not far from Sperling's original one): once the cue is presented, participants are able to access an unconscious representation before it decays. From this point of view, there would be no form of experience not amenable to conscious report. This proposition strongly links consciousness with high-level cognitive functions such as attention, claiming that only attended items will be consciously represented. Other proposals also posit that the dissociation between phenomenal and access consciousness

is equivocal, suggesting that phenomenal consciousness might be caused by perceptual illusions and non-conscious processing (Kouider et al., 2010). These authors propose that perceptual representations vary from complete unawareness of stimuli that can eventually be processed and affect behavior while remaining inaccessible to conscious reports, to complete awareness of information that can be verbally reported. There exist other situations of partial consciousness, which correspond to intermediate cases, with conscious access only at same levels. In this latter case, access can be filled in with perceptual illusions (Kouider et al., 2010). According to this hypothesis, perceptual representations are gradually represented, although conscious access can be an all-or-none process, as proposed by other models (Baars, 1989; Sergent and Dehaene, 2004).

These theoretical and empirical issues become especially relevant in the study of consciousness in non-human animals and in human beings who are incapable of communicating. Some effort is being devoted in this sense, for example in the study of vegetative and minimally conscious states. Simple cognitive tasks are being used to determine the level of consciousness of non-communicative patients. Neurophysiological measures extracted from EEG (Bekinschtein et al., 2009) or fMRI (Cruse and Owen, 2010) are being used to determine the state of consciousness of these patients and even to try to predict whether patients will recover from coma (Faugeras et al., 2011). A better definition and measurement of phenomenal and access consciousness will certainly enable us to better explore the relationships between different forms of spatial and non-spatial attention and consciousness, as well as their underlying brain mechanisms in both the healthy and damaged brain.

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Consciousness and the prefrontal parietal network: insights from attention, working memory, and chunking

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Consciousness has of late become a “hot topic” in neuroscience. Empirical work has centered on identifying potential neural correlates of consciousness (NCCs), with a converging view that the prefrontal parietal network (PPN) is closely associated with this process. Theoretical work has primarily sought to explain how informational properties of this cortical network could account for phenomenal properties of consciousness. However, both empirical and theoretical research has given less focus to the psychological features that may account for the NCCs. The PPN has also been heavily linked with cognitive processes, such as attention. We describe how this literature is under-appreciated in consciousness science, in part due to the increasingly entrenched assumption of a strong dissociation between attention and consciousness. We argue instead that there is more common ground between attention and consciousness than is usually emphasized: although objects can under certain circumstances be attended to in the absence of conscious access, attention as a content selection and boosting mechanism is an important and necessary aspect of consciousness. Like attention, working memory and executive control involve the inter-linking of multiple mental objects and have also been closely associated with the PPN. We propose that this set of cognitive functions, in concert with attention, make up the core psychological components of consciousness. One related process, chunking, exploits logical or mnemonic redundancies in a dataset so that it can be recoded and a given task optimized. Chunking has been shown to activate PPN particularly robustly, even compared with other cognitively demanding tasks, such as working memory or mental arithmetic. It is therefore possible that chunking, as a tool to detect useful patterns within an integrated set of intensely processed (attended) information, has a central role to play in consciousness. Following on from this, we suggest that a key evolutionary purpose of consciousness may be to provide innovative solutions to complex or novel problems.

Keywords: consciousness, prefrontal cortex, parietal cortex, attention, working memory, chunking, theory

INTRODUCTION

Questions concerning the nature of consciousness have profound and widespread personal, ethical and clinical implications, and a comprehensive understanding of consciousness is one of the most important and pressing issues in biology (Seth, 2010). Although consciousness is difficult to define (Zeman, 2005), we take the base concept to be the presence of phenomenal content for an agent, and we emphasize a distinction between conscious *level* (i.e., a position on a scale from total unconsciousness as in coma to vivid and alert wakefulness) and conscious *content* (i.e., the components of any given conscious scene – the qualia; Seth et al., 2008). We assume that a non-zero conscious level is needed for any conscious contents to exist.

In recent years, the scientific study of human consciousness has been transformed from a niche field into an increasingly popular, active, and sophisticated topic of research. At the level of brain mechanisms, consciousness science now synthesizes results from a broad range of techniques, including electrophysiology, functional magnetic resonance imaging (fMRI),

magneto/electroencephalography (M/EEG), intracranial recordings, neuropsychology, and computational models (Tononi and Koch, 2008). In the next section, we will describe how a coherent pattern has emerged from these studies, in which two tiers of brain regions seem critical for consciousness: first, modality specific regions, such as those in extra-striate cortex, underlie the specific (phenomenal) contents of consciousness; second, the prefrontal parietal network (PPN) in concert with the thalamus is heavily implicated in consciousness more generally, regardless of content. The PPN can therefore be viewed as a “core correlate” of consciousness.

Although some theories of consciousness have been predicated on the link between consciousness and the PPN, others are more neutral on this issue. In the section “Theories of Consciousness,” we will outline the main theories of consciousness and discuss the extent these theories are consistent with the empirical data linking consciousness with the PPN. We will also describe the psychological components of these theories, while noting that detail is currently lacking on this front. Instead, theoretical emphasis is

given to widespread cortical network activity as a necessary component of consciousness, which is commonly discussed in terms of integrated information.

One approach to add psychological detail to models of consciousness would be to examine what other functions the PPN has been associated with. Fortunately, the PPN is one of the most studied of brain networks, and – beyond the context of consciousness science *per se* – has been closely linked with attention, among other functions (Duncan, 2006; Bor and Owen, 2007). In the section “The Overlap Between Attention and Consciousness,” we critically assess the increasingly popular view of the independence of conscious and attentional processes (van Boxtel et al., 2010b). In contrast, we will argue that all conscious events require attention in some form, and that attention has a critical role to play in selecting conscious contents.

The PPN is closely associated with a far broader set of cognitive functions than merely attention (Duncan, 2006; Bor and Owen, 2007). For instance, working memory, executive control, and chunking have been particularly robustly associated with the PPN (Bor et al., 2003, 2004; Abe et al., 2007; Bor and Owen, 2007; Erickson et al., 2007; Koechlin and Summerfield, 2007). In the section “What is the Functional Role of the Prefrontal Parietal Network?” we outline how this range of cognitive processes may furnish models of consciousness with further psychological detail. We view consciousness as serving to provide innovative solutions to otherwise intransigent problems: we suggest that consciousness involves attending to information relevant to a biological goal, especially when automatic unconscious routines are unable to carry out that goal. Typically, this will occur for novel or complex tasks, where multiple features need to be managed simultaneously or in series, via working memory. We argue that chunking may play a special role in consciousness, by detecting and encoding regularities between items in working memory, thus aiding understanding, so that a given goal is more likely to be reached and automation accelerated.

EVIDENCE LINKING THE PREFRONTAL PARIETAL NETWORK WITH CONSCIOUS CONTENT

Although studies have reported PPN activity during subliminal processing (Diaz and McCarthy, 2007; Luo et al., 2009), the overwhelming evidence, both from lesion and perturbation studies and functional imaging studies, suggests that PPN is very closely associated with consciousness.

LESION AND PERTURBATION STUDIES OF CONSCIOUS CONTENT

Both focal lesion patient studies and transcranial magnetic stimulation (TMS) experiments in normal volunteers strongly implicate the PPN in supporting conscious contents. For instance, in one study patients with unilateral prefrontal cortex (PFC) lesions and healthy controls were briefly shown a number at one of four locations, followed after a variable delay by a mask (Del Cul et al., 2009). Subjects stated whether or not they had seen the number, and then guessed what the number was. Although objective performance for seen trials was matched between patients and controls, PFC patients were significantly less likely to consciously detect trials answered correctly, compared to controls.

Though conscious contents were not abolished in these cases, more severe consciousness impairments following unilateral PFC damage may be limited by extensive plasticity in these regions, such that the undamaged hemisphere can rapidly take over function (Voytek et al., 2010). Knight and Grabowecky (1995) have described a rare bilateral PFC lesion patient who was awake, but was otherwise almost entirely unresponsive to stimuli. With respect to conscious level rather than content, bilateral diffuse damage to prefrontal and parietal white matter is associated with vegetative state or coma (Tshibanda et al., 2009), while restoration of functional connectivity between the thalamus and PFC, as well as the anterior cingulate, is associated with recovery from vegetative state (Laureys et al., 2000).

Parietal lesions also lead to impaired conscious processing. For instance, Simons and colleagues compared bilateral posterior parietal lesion patients and controls on a long-term memory task, involving the recollection of the context in which stimuli are first encountered. Although recollection performance was matched between groups, the parietal lesion group exhibited impaired subjective experience of the memories they were retrieving (Simons et al., 2010).

Complementing the patient data, studies in normal volunteers using TMS have strongly implicated the PPN in consciousness. For instance, Turatto and colleagues presented volunteers with two grids of four faces for 200 ms, separated by a 300 ms blank screen. On half the trials, the two sets of faces were non-identical. When a repetitive train of eight TMS pulses at 10 Hz was administered to right dorsolateral prefrontal cortex (DLPFC) at the onset of the first grid, the participants' ability to detect the change was impaired (Turatto et al., 2004). A further study by Beck et al. (2006) using a very similar paradigm, demonstrated that change detection is also impaired following TMS to the right posterior parietal cortex. A more recent study used a novel TMS technique, known as continuous theta burst stimulation (cTBS), which involves a rapid train of TMS pulses, for approximately 40 s, so that activity in the stimulated region is suppressed for a sustained period of time, approximately 30 min in length (Huang et al., 2005). Rou-nis et al. (2010) gave participants a masked low contrast visual detect task both before and after TMS administration bilaterally to the DLPFC. Although objective performance was titrated to 75% accuracy on both occasions, impaired visibility ratings were found during the block following TMS. Another cTBS study by Kanai et al. (2010) reported that TMS applied to posterior parietal cortex increased the perceptual duration prior to a switch in a motion-induced bistable visual stimulus. Although bilateral results were found here, Zaretskaya et al. (2010), using a similar paradigm, found results somewhat limited to the right intraparietal sulcus, although considerable individual differences were reported.

This tendency in the literature to show preferential right PPN involvement (Turatto et al., 2004; Beck et al., 2006; Zaretskaya et al., 2010) echoes findings from the attentional neurological condition, hemispatial neglect, which in the vast majority of cases follows right PPN damage (Husain and Kennard, 1996; Husain and Rorden, 2003). In addition, the parietal region in these TMS studies is very close to that associated in functional imaging studies with attentional switching processes (Corbetta et al., 1995; Yantis et al., 2002). Indeed, both Kanai and Zaretskaya posit that the

mechanism for delays in perceptual switches as a result of TMS to posterior parietal cortex is due to a reduction in attentional resources. In line with this, a similar reduction in perceptual switch rate to binocular rivalry stimuli can be induced just by diverting attention away from the bistable stimuli (Paffen et al., 2006; Alais et al., 2010). Furthermore, by indirectly inferring attention state from EEG signatures, Zhang et al. (2011) demonstrated that diverting attention away from a binocular rivalry stimulus abolishes rivalry, suggesting that not only does attention modulate binocular rivalry rates, but that it is a necessary component of the phenomenon.

The lesion and perturbation studies described above strongly implicate all key individual components of the PPN in conscious processing. However, such methods have a more limited role in examining the relationship between consciousness and the PPN as a whole. Functional neuroimaging studies, discussed next, are well placed to address this question.

FUNCTIONAL IMAGING STUDIES

In one of the first studies to examine visual consciousness using fMRI, only PPN and extra-striate activity were observed when switches in visual consciousness in a binocular rivalry paradigm were compared with a perceptually matched condition without rivalry (Lumer et al., 1998). A follow-up binocular rivalry study without behavioral responses demonstrated that motor output cannot be responsible for this pattern of activity: extra-striate activity reflecting changes in perception most closely correlated with PPN activity, whereas V1 activity failed convincingly to correlate with any other region (Lumer and Rees, 1999). The PPN has also been associated with consciousness in fMRI studies of other bistable paradigms, such as ambiguous figures (Kleinschmidt et al., 1998), the spinning wheel illusion (Sterzer et al., 2002), and flicker (Carmel et al., 2006).

It is unclear, however, whether such PPN activity reflects the cause of changes in conscious contents or alternatively the downstream effects of these changes. Knapen et al. (2011) have recently provided evidence that PPN activity, at least in the right hemisphere, is a response to perceptual change in binocular rivalry: normal participants were presented with a range of binocular rivalry stimuli, which induced variable transition periods between the two competing percepts. Longer transitions were associated with prolonged right PPN activity. Simulated external transitions, which carefully matched internal transition lengths, were associated with similar patterns of PPN activity, suggesting that the PPN was mainly associated with a response to perceptual change. Consistent with this view, fMRI responses correlating with the percept have been found in early sensory areas in many bistable paradigms (Lee et al., 2005), and in binocular rivalry even as early as the lateral geniculate nucleus (LGN) in the thalamus (Haynes et al., 2005). Sil-lito et al. (2006), however, stress the importance of cortical outputs to LGN, suggesting either that LGN perceptual-tracking activity has a cortical source, possibly in V1 or MT, or that even if LGN activity is the cause of binocular rivalry, that there are clear cortical pathways which could modulate various features of the binocular rivalry percept by differential attentional focus. Summarizing these observations, although the causal factors underlying bistable perceptual transitions remain unclear, there is little doubt that PPN activity reflects the resulting subjective conscious contents.

Another relevant class of fMRI studies utilize psychophysical masking paradigms in order to compare visible with invisible stimuli. For instance, Dehaene et al. (2001) showed that when visibility of word stimuli was modulated by masking, those stimuli which were consciously perceived additionally activated modality specific regions in fusiform gyrus, as well as inferior frontal and parietal regions. However, a general problem with masking paradigms is that they may confound conscious contents with objective performance. Addressing this concern, Lau and Passingham (2006) implemented a metacontrast masking paradigm, which ensured that objective performance was equated while subjective visibility could be manipulated. In this more controlled design, only the DLPFC portion of PPN was reported to covary with visibility.

Electroencephalography studies have also implicated the PPN in consciousness. Melloni and colleagues compared oscillatory EEG activity evoked by visible and invisible words in a delayed matching to sample task. Consistent with theories emphasizing the importance of functional connectivity in consciousness (see the next section), they found that both visible and invisible words caused increases in local gamma-band oscillations, but only visible words induced increased long-range gamma-band synchronization, consistent with PPN involvement. In addition, during the maintenance period, enhanced theta oscillations were observed over frontal regions (Melloni et al., 2007). More direct evidence is provided by a recent study by Hipp et al. (2011) in which EEG synchrony was assessed between source-localized cortical regions; the authors identified two distinct cortical networks predictive of perception: a beta-band fronto-parieto-occipital network and a gamma-band centro-temporal network.

Conventional M/EEG studies carry inevitable ambiguities regarding spatial resolution and localization, and suffer poor signal-to-noise ratios. Recent studies using intracranial EEG measurements are therefore particularly valuable. In one landmark study, intracranially implanted presurgical patients were presented with invisible (masked) or visible (unmasked) words. Sustained consciousness-related activity for the unmasked words was found most robustly in PFC (Gaillard et al., 2009).

While all studies described so far have examined visual consciousness, similar results have been reported in other modalities. For instance, Sadaghiani et al. (2009) used an auditory detection paradigm at threshold to show that conscious detection reflected prefrontal and inferior parietal activity, though other regions were also found, including the insula, thalamus, and striatum. In another intriguing study, Hasson et al. (2007) used a passive cross-modal paradigm involving the McGurk effect, in which the auditory perception of a given syllable is determined by the fusion of two different auditory and visual syllables. Using repetition priming, participants were played an audiovisual target that was preceded either by a stimulus that matched the target's visual features alone, its auditory features alone, or neither, but which instead matched the subjective percept of the fusion of the target's competing auditory and visual syllables. While auditory cortex regions tracked the objective features of the stimulus, PPN activity was associated with the conscious percept, as reflected in a reduction in activity limited to the fused prime trials.

The studies described so far have examined the neural correlates of changes in consciousness. Other experiments have shown that sustaining a percept also implicates the PPN. For instance,

Eriksson and colleagues presented participants in the fMRI scanner with fragmentary figures, which unlike bistable viewing paradigms, involve only a single perceptual transition, followed by a period of sustained perception. The PPN was found to be associated both with transient and sustained aspects of visual perception on this task (Eriksson et al., 2004).

In addition to functional imaging studies, two recent structural imaging studies have associated the PPN with consciousness. First, Kanai et al. (2010) demonstrated that individual differences in posterior parietal cortex cortical thickness, gray matter density, and white matter integrity correlate with volunteers' alternation rates when viewing bistable figures. Second, Fleming and colleagues used structural imaging to examine individual differences in metacognitive ability. Metacognitive ability is a particularly stringent test of consciousness, since it explicitly focuses on conscious report, thus avoiding the association in some other studies between neural signatures and responses which may be correct either by chance or due to unconscious knowledge (Lau and Rosenthal, 2011). Fleming and colleagues presented volunteers with two sets of six Gabor patches, with one set of six including a single Gabor patch with a marginally higher contrast. Participants made a judgment as to which set included the deviant patch and then made a confidence report on their previous decision. Using a staircase function, objective performance was fixed at 71%, but volunteers' ability to match confidence levels with performance (metacognitive ability) differed markedly. Individual differences in volunteers' metacognitive ability correlated both with prefrontal gray matter volume and white matter integrity (Fleming et al., 2010).

The association between PPN and conscious content could be further tested by reducing conscious level, thus also diminishing the capacity for conscious processing, and observing whether PPN activity falls in parallel. Complementing the data from coma and vegetative state patients mentioned above, Davis et al. (2007) have shown that parts of the PPN appear necessary for normal levels of consciousness. In this study the general anesthetic, propofol, was administered to normal participants at various intensities, while they were presented with auditory stimuli at multiple levels of complexity. Lateral prefrontal activity reduced in line with a reduction in conscious level, and reflected an impairment in sentence comprehension and subsequent recall.

In summary, PPN lesions impair normal conscious function, as does TMS when applied to these regions. Functional and structural imaging studies have strongly implicated the PPN in perceptual transitions, the conscious detection of stimuli in a range of modalities, sustaining percepts, and in metacognitive decisions on those percepts. Finally, a reduction of conscious level when under general anesthesia is associated with a reduced lateral prefrontal activity.

THEORIES OF CONSCIOUSNESS

NEURAL THEORIES OF CONSCIOUSNESS AND THE PREFRONTAL PARIETAL NETWORK

A growing set of consciousness theories have attempted to link experimental findings in consciousness science to cognitive and neurophysiological architectures (see Seth, 2007; Kouider, 2009 for reviews): prominent examples of theories articulated at the neural level include (neuronal) global workspace theory (Baars, 1988, 2005; Dehaene and Naccache, 2001; Baars et al., 2003; Dehaene and

Changeux, 2011), reentry theory (Lamme, 2006, 2010), dynamic core, integrated information theories (Tononi and Edelman, 1998; Edelman, 2003; Balduzzi and Tononi, 2008; Tononi, 2008), and causal density theory (Seth et al., 2011).

Neuronal global workspace theory is the most explicit in terms of PPN activity (Dehaene and Naccache, 2001; Dehaene and Changeux, 2011). According to this theory, conscious content, which is determined by domain-specific local processing, gains access to consciousness via integration into a "global workspace." This integration is mediated via long-range corticocortical "workspace" neuronal projections that are particularly dense in prefrontal, parietal, and cingulate regions. A specific conscious content is suggested to be encoded by the sustained activity of a fraction of these workspace neurons, the rest being inhibited (Dehaene and Changeux, 2011). Other key elements of the theory propose that conscious contents are determined in an "all or none" fashion via "ignition" of the global workspace, where ignition is reflected in late cortical potentials distributed across PFC and other high-level associative cortices, and in high frequency (e.g., gamma-band) increases in power and synchrony. Interestingly, while this theory is explicit about neurobiological substrates, it leaves behind a substantial portion of the psychological detail that was part of the original "cognitive" global workspace theory introduced by Baars (1988). We return to Baars' work in the following section.

Lamme's "neural stance" on consciousness identifies reentrant or feedback connections as the key ingredient in generating conscious content (Lamme, 2006, 2010). Synthesizing work from a large number of studies examining neural responses to masked and unmasked stimuli, Lamme proposes that reentrant connections encapsulating the PPN and lower-level modality specific cortices are necessary for cognitively accessible, subjectively reportable conscious contents. This claim is compatible with neuronal global workspace theory; the theories further align in associating late components of cortical evoked potentials with cognitive access. The theories diverge, however, with Lamme's claim that a non-accessible form of conscious content (i.e., phenomenal consciousness without access consciousness, in the terminology of Block, 2007), is generated by reentry locally within posterior cortical regions. A major challenge attending this claim is of course how to verify the existence of such conscious contents in the absence of verbal or behavioral report; a lively debate continues around this issue (Block, 2007; Kouider et al., 2010; Lamme, 2010; Dehaene and Changeux, 2011).

Zeki (2007) has proposed a related theory, micro-consciousness, which is perhaps the most ambivalent of modern theories toward the association between the PPN and consciousness. While Zeki concedes that unified forms of consciousness or those which involve access may require the PPN, he believes, like Lamme, that there is a non-reportable, purely phenomenal form of consciousness, which can be supported by local sensory regions, for instance with visual cortex representing visual consciousness. The theory of micro-consciousness diverges from Lamme's reentrant theory, however, in that for Zeki consciousness is not dependent on feedback pathways, for instance from V4 to V1 for color vision. Instead, it is suggested that the level of consciousness for a given form of phenomenal content is dependent only

on the strength of activity within the region that processes that form of information; therefore, V4 alone is capable of generating color vision, for instance. Indeed, patients with focal lesions in V1 still report significant, though degraded, visual phenomenology, despite non-functional back-projections (Ffytche and Zeki, 2011).

Although much evidence has already been cited in the section “Evidence Linking the Prefrontal Parietal Network with Conscious Content” to demonstrate the importance of the PPN for consciousness, Fisch et al. (2009) have reported indirect evidence in support of micro-consciousness. Using intracranial electrodes on a wide range of cortical surface locations in 11 patients, a backward masking paradigm was employed, where pictures of various categories were briefly presented, followed by a mask. Localized bursts of gamma-band activity were found, primarily in visual regions, and with an early time signature approximately 150–200 ms following stimulus onset. The authors note, however, that this doesn’t rule out a critical role of the PPN for conscious recognition in a later time window (>300 ms). Indeed, such activity was observed in the same study.

The dynamic core, integrated information, and causal density theories are also compatible with a key role of the PPN in consciousness, though these theories are less anatomically specific than those discussed above. The dynamic core theory (Tononi and Edelman, 1998; Edelman, 2003) proposes that consciousness depends on a flexible and dynamically constituted functional cluster of thalamocortical neurons, generating dynamics characterized by conjoined functional integration and functional segregation. According to the theory, these dynamics are mediated by highly reentrant connections within the thalamocortical system. The anatomical boundaries of the dynamic core are considered to be highly labile, so that neuronal groups or even brain regions may form part of the neural correlates of consciousness (NCC) at one time, but not at another. Having said this, the dynamic core theory may be considered an extension of Edelman’s theory of neuronal group selection (TNGS) which proposes explicitly that consciousness emerges from interactions between posterior regions involved in perceptual categorization and frontoparietal regions implicated in the formation and maintenance of value-category memories (Edelman, 1989, 2003; Edelman et al., 2011). Taken together, these theories imply a core role for the PPN in generating conscious contents.

The information integration theory of consciousness (IITC; Balduzzi and Tononi, 2008; Tononi, 2008; Barrett and Seth, 2011) shares with the dynamic core theory an emphasis on quantitative description of conjoined segregation and integration in dynamics. The IITC operationalizes this notion in a subtly but significantly different way, as the extent to which a network generates “integrated information.” In this view, “information” refers to how much the present state of a system reveals about its past state (or states), in terms of reduction of uncertainty or entropy; this aspect reflects the diversity and informativeness of conscious scenes. “Integration” reflects the degree to which this information is generated only by considering the system as a whole, over and above that generated by its parts considered independently; this aspect is argued to reflect the phenomenal unity of conscious scenes. Quantitative measures of integrated information, denoted by Φ , have been proposed both by Tononi (Balduzzi and Tononi,

2008; Tononi, 2008) and by Barrett and Seth (2011); see Seth et al. (2011) for a summary.

Tononi emphasizes that the IITC accounts for some broad anatomical facts about consciousness, including its association with the thalamocortical system. However, besides noting that general architectural features of thalamocortical and corticocortical circuits (described further below) are compatible with generating high values of integrated information, the theory does not propose specific roles for the PPN with respect to these features (Tononi and Koch, 2008). Indeed, for Tononi, the IITC is strictly agnostic about implementation; consciousness could be attributed to *any* system generating sufficiently high-levels of integrated information. There are however weaker interpretations of the IITC which view integrated information as an “explanatory correlate” mapping features of phenomenology onto features of neural dynamics (Seth, 2009; Barrett and Seth, 2011); on this view, high integrated information may be necessary but not sufficient for consciousness, and incorporation of the PPN may therefore also become a necessary feature of the neural grounding of the theory.

A similar perspective applies to causal density theory, where “causal density” provides a third means of quantifying conjoined dynamical segregation and integration (Seth, 2005; Seth et al., 2008, 2011). Causal density leverages time-series analysis methods (specifically Granger causality, which is a statistical measure of causality based on relative predictability) to quantify the overall level of causal interactivity within a system. High values of causal density are obtained when system elements combine statistical independence (so that they provide potentially useful predictive information) with statistical dependence (so that this predictive information is in fact useful). Causal density is offered explicitly as an “explanatory correlate” (Seth, 2009) and as a necessary but not sufficient criterion for consciousness. As with Φ , causal density may be compatible with general anatomical properties of the PPN and associated brain networks.

An important challenge for future work is to compare the neural theories described above in the context of structural properties of brain networks. While all theories are broadly compatible with the high-levels of interconnectedness observed in both corticocortical and thalamocortical networks (though only trivially so for Zeki’s theory), rapidly developing research on specific topological properties of these networks may allow greater discriminatory power and shed new light on the potential importance of the PPN for consciousness. For example, suggestive new findings, based on combining multiple anatomical tracing studies, identify a tightly integrated “core circuit” in the macaque brain including the PPN, with the PFC containing a very large proportion of topologically central subregions (Modha and Singh, 2010).

COGNITIVE THEORIES OF CONSCIOUSNESS AND THE PREFRONTAL PARIETAL NETWORK

As neural theories of consciousness make progress in connecting neural to phenomenal properties, they often seem to do so at the expense of psychological or cognitive detail. However, cognitive theories of consciousness have a long history, extending back to when “consciousness” as an explanandum was not often referred to explicitly (see de Gardelle and Kouider, 2009 for a review). Thus, in early work and anticipating later workspace theories,

Broadbent (1958) associated consciousness with a “limited capacity channel” involved in serial processing; this theory entailed a very close association between consciousness and attention. Some years later, Baddeley and Hitch (1974) associated conscious contents with working memory, moving yet closer toward central tenets of global workspace theory. Later cognitive theories made explicit reference to elements of the PPN. For example, Shallice identified consciousness indirectly with a “supervisory attentional system” situated in PFC, controlling the activity of “lower level” sensorimotor modules (Norman and Shallice, 1986). This theory operationalized consciousness as a form of executive control, without much reference to phenomenal aspects.

Building on much of this early work, the predominant cognitive theory of consciousness remains Bernard Baars’ global workspace theory (Baars, 1988, 2005). The core elements of this theory are (i) competition among local (unconscious) processes for access to a “global workspace” the contents which are made globally available, (ii) “broadcast” of workspace contents to a broad repertoire of receiving modules. With these core elements, global workspace theory fluently accounts for the apparent seriality and unified nature of conscious scenes, as well as the parallel processing capacity of unconscious processes. As emphasized by Dehaene and Changeux (2011), the theory seems especially well suited to account for conscious access and is not normally interpreted as a theory of “phenomenal consciousness” of the form described by Block and Lamme [i.e., consciousness without cognitive access; (Block, 2007; Lamme, 2010)].

Efforts to ground global workspace theory in neurobiology (see Neural Theories of Consciousness and the PPN) have focused on these core elements (though “broadcast” remains poorly specified in neural terms) and have arguably come at the cost of neglecting some of the psychological detail embedded in its original cognitive instantiation. For example, Baars (1988) originally emphasized that the (conscious) contents of the global workspace could correspond, at any given time, to the contents of working memory; indeed the theory has recently been summarized as suggesting a “fleeting memory capacity that enables access between brain functions that are otherwise separate” (Baars, 2005). Cognitive, as opposed to neuronal global workspace theory also placed considerable emphasis on unconscious “contextual” systems which shape the conscious contents articulated within the workspace itself (Baars, 2005).

The “higher-order” thought (HOT) theory set forth most prominently by Rosenthal also deserves mention. On this theory, a mental state is conscious when a person is aware (or disposed toward being aware) of being in that state (Rosenthal, 2005). Theories differ according to whether awareness of the mental state is achieved by perceiving it (Lycan, 2004) or thinking about it (Rosenthal, 2005). Importantly, the theory is not circular; the higher-order thoughts/perceptions themselves are not consciously reportable unless accompanied by a corresponding third-order thought or perception. Although originally a philosophical theory, HOT theories have recently attracted attention within cognitive neuroscience. Lau has suggested that HOTs could be implemented as a process of internalized signal detection, in which perceptual signals are assessed for their reliability according to the precepts of signal detection theory. The neural mechanisms underlying this

process are suggested to lie within DLPFC (Rounis et al., 2010; Lau and Rosenthal, 2011).

THE OVERLAP BETWEEN ATTENTION AND CONSCIOUSNESS

Before the connection between consciousness and the PPN was a focus of investigation, this network of brain regions was for many years associated with other cognitive processes, most notably working memory, executive functions, and attention (Cabeza and Nyberg, 2000). This overlap strongly suggests that these other cognitive processes are closely related to consciousness. In this section, we first examine the strength of the argument for treating attention and consciousness as independent processes, before outlining the common links between these two processes, as well as with related high-level cognitive functions.

THE ARGUMENT FOR A DISSOCIATION BETWEEN ATTENTION AND CONSCIOUSNESS

Even up to the start of the twenty-first century, many researchers took the view that attention and consciousness were putatively one and the same process, or that attention provided a “gateway” to consciousness (Broadbent, 1958; Posner, 1994; Rees and Lavie, 2001). For instance, Rees and Lavie (2001) noted the marked similarity in activation patterns between attention and consciousness studies and suggested that there is “a close functional relationship between attention and awareness.” Over recent years, however, there has been a growing body of opinion that these two phenomena are highly or even entirely dissociable (Koch and Tsuchiya, 2007; van Boxtel et al., 2010a,b). For instance Koch and colleagues claim that attention and consciousness can be “manipulated independently” and that attention is neither necessary nor sufficient for consciousness (van Boxtel et al., 2010b).

The crux of this lively debate undoubtedly rests on questions of the definition and scope of attention and consciousness. In their latest review, van Boxtel et al. (2010b) limit attention to top-down voluntary attention, and define this as the main process by which an over-abundant data input is filtered into a much reduced set of salient items. They summarize attention as an “analyzer” of cognition, and consciousness as a “synthesizer.” They operationally define consciousness as stimulus visibility.

In line with their position, there is good evidence that attentional processes, as defined above, can operate without the attended stimuli reaching consciousness (Bressan and Pizzighello, 2008; Kentridge et al., 2008; Bussche et al., 2010; Tapia et al., 2010). For example, Kentridge et al. (2008) demonstrated that attention can enhance the processing of unconscious targets: incongruent or congruent colored disk primes, made invisible by metacontrast masking, were followed by a subsequent visible colored annulus. When attention was directed toward the location of the invisible primed disks, the priming effect was enhanced.

Showing the opposite effect, Bressan and Pizzighello (2008) implemented a paradigm in which an invisible distracting moving stimulus nevertheless impaired accuracy on a primary task at fixation. The authors proposed that the distracting stimulus created a state of alertness and consequently a partial attentional shift away from the central task. In contrast, when the distracting stimulus was consciously detectable, accuracy was unimpaired, presumably

because full processing allowed the designation of the distracting stimulus as irrelevant to the task, with minimal attentional resources attached to it. However, since this study is putatively governed by a bottom-up attentional process, it is not strictly relevant to the arguments of van Boxtel et al. (2010b). Nevertheless, it provides intriguing evidence that attention to unconscious stimuli can both enhance and interfere with a central conscious task.

Although such examples do indicate that attention is not sufficient for consciousness, it does not follow that attention is dissociated from consciousness. Indeed, the studies described above can be interpreted as showing that attention enhances existing conscious contents, or the probability that an item will gain access to consciousness. In Bressan and Pizzighello (2008), reduced performance on the primary task could be a consequence of reduced awareness of the target when attention is partly allocated elsewhere. Furthermore, in the study of Kentridge et al. (2008), improved target detection could reflect enhanced awareness following attentional boosting of congruent primes. In line with this position, attention has been shown to lower the threshold by which a stimulus is consciously detected, or enhance apparent contrast (Carrasco et al., 2000, 2004; see **Figure 1** for illustration).

For evidence of a true (i.e., double) dissociation, what is required is a demonstration that increased attention for a specific visual feature leads to a reduction in the probability of conscious report of that feature. An apparently strong case for such a double dissociation was recently made by Koch and colleagues (van Boxtel et al., 2010a). A peripheral after-image inducer was made either visible or invisible, by continuous flash suppression. Attention was either directed to the inducer, or distracted by a central rapid serial visual presentation (RSVP) task. While increased visibility of the inducer also led to increased after-image duration, greater attention toward the inducer instead reduced after-image duration.

Although this pattern of results suggests a double dissociation between attention and consciousness, alternative interpretations do exist. For instance, it is possible that increased attention in this paradigm, rather than simply reducing the probability or duration of current conscious contents *per se*, instead provides a useful role in suppressing an unhelpful and aberrant after-image, so that other, more salient objects have a higher chance of gaining conscious access. Further experiments exploring double dissociations between consciousness and attention are needed, preferably in topics outside of visual illusory effects since such effects necessarily reflect idiosyncrasies of the visual system and may not directly reflect key mechanisms of consciousness itself.

Although the evidence that attention is not sufficient for consciousness is reasonably well established, the case for consciousness without attention is somewhat less clear. Evidence cited by van Boxtel et al. (2010b) for consciousness without attention mainly involves pop-out effects, gist effects, and detection of natural objects, such as animals and faces. In each of these examples, however, it is important to establish whether attention has been fully removed from the stimulus that the subject is conscious of, in terms of absence of both top-down attention *and* bottom-up attention. van Boxtel et al. (2010b) do not include or discuss bottom-up attentional effects, since they claim that bottom-up attention is necessarily engaged by visible moving stimuli, thus experimentally precluding the opportunity to dissociate these two processes. However, Bressan and Pizzighello (2008) findings suggest that bottom-up attention can be engaged by invisible stimuli and so there are not necessarily empirical barriers to including bottom-up attention within a discussion of relations between attention and consciousness. Furthermore, by limiting their focus to studies manipulating only top-down effects, van Boxtel and colleagues still need to entertain the possibility that, for any evidence demonstrating consciousness without attention, bottom-up attentional

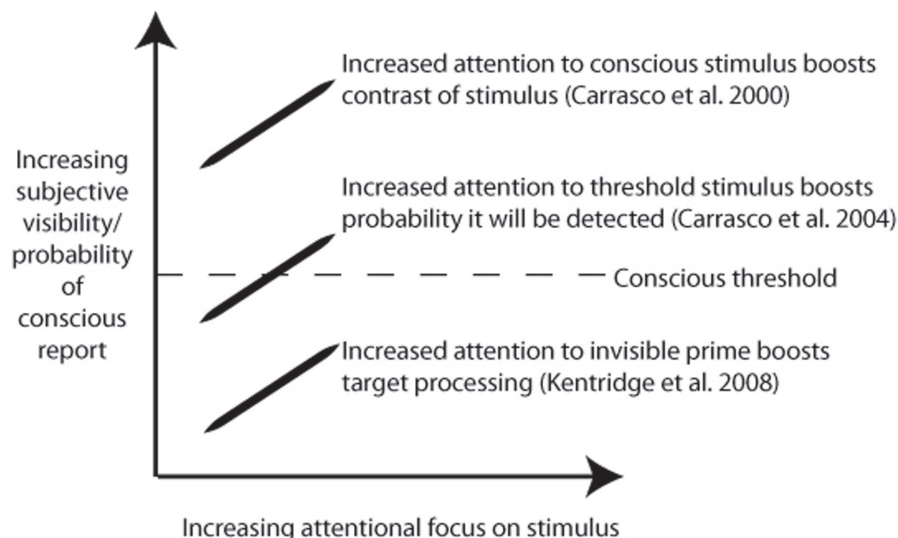


FIGURE 1 | Schematic illustration of possible relationships between attention and consciousness, with notable experimental examples. Note that although the lower example is taken by some as evidence for the

independence of attention and consciousness, it is instead possible that in this and all other cases there is a strong positive correlation between attention and consciousness.

processes may still be present and may be involved in selecting items for conscious access.

Taking each of the putative examples of consciousness without attention in turn: first, pop-out effects of primitive visual targets, for instance in a visual search task, have been assumed to occur preattentively. However, if attention is sufficiently engaged away from a simple target, such as a red element (with gray distracters) or a specific orientation (with orthogonally angled distracters), then there is a large detrimental effect on target detection (Joseph et al., 1997; Theeuwes et al., 1999). Furthermore, attention has been shown to modulate basic perceptual masking effects, such as object substitution (Tata and Giaschi, 2004) and metacontrast masking (Ramachandran and Cobb, 1995; Shelley-Tremblay and Mack, 1999; Boyer and Ro, 2007).

Second, natural scene perception, also known as “gist,” is a process where various semantic and phenomenological features of a visual scene can be extracted, even with brief viewings of 150 ms (Thorpe et al., 1996). It has been assumed that the speed of this process precludes the possibility that selective attention plays a role, since selective attention requires at least 200 ms to become established. However, one recent study has shown that if attention is appropriately removed from a natural scene, then inattentional blindness for that scene ensues (Cohen et al., 2011). Using a dual task paradigm in a set of experiments, attention was withdrawn from the natural scene by employing multi-object tracking (MOT) or a RSVP task. Using MOT, failure immediately to perceive a visual scene occurred in 88% of participants, compared with only 4% when carrying out the single task of detecting and classifying the visual scenes. Similar results occurred for the RSVP task (77% of participants were unable immediately to perceive the scene, compared with 7% for the detection and classification task alone). For both tasks, however, more participants were able to classify the scene on question probes following the trial. In follow-up experiments that modulated the difficulty of the MOT and RSVP tasks, those tasks that were more difficult and thus requiring more attentional resources further impaired conscious detection of the visual scene. This study clearly shows that a conscious sense of gist is dependent on having at least a minimal level of attentional processing available.

Third, and finally, the conscious detection of animals and faces is thought to have a privileged access due to its biological salience and can occur with very brief presentations, of the order of 20 ms. There is some evidence that detection rates are unimpaired during a dual task, where attention is directed away from the naturalistic objects (Li et al., 2002). However, these studies tend to present single stimuli in isolation. Attention might, to some degree, be automatically drawn to a single visually presented object, regardless of the inclusion of a distracting secondary task, especially if that object carries innate biological salience (such as a face), which would activate bottom-up attentional processes. Walker et al. (2008) sought to investigate the importance of this factor, by presenting animal images along with three other objects in a complex naturalistic scene. Using this approach, the dual task condition profoundly impaired detection of animal targets, even at long onset durations of approximately 500 ms. In addition, Walker and colleagues found that even animal targets presented alone were

detected less frequently under dual task than single task conditions, though to a lesser extent than when presented with the three distractors. Therefore, even the conscious detection of naturalistic objects is shown to be heavily modulated by attention, especially if complex scenes are involved.

As well as behavioral dissociations, neural dissociations between attention and consciousness have been proposed (Wyart and Tallon-Baudry, 2008; Tsubomi et al., 2011). For instance, Wyart and Tallon-Baudry (2008) used MEG while subjects either attended toward or away from a threshold stimulus, which was reported consciously 50% of the time. Independent of attention, consciously seen stimuli induced mid-gamma activity, whereas attention induced high-gamma activity independent of conscious report. However, since attention was manipulated by directing participants to a valid or invalid location, additional error monitoring processes for the attentional contrast may account for the dissociation. In addition, both the attentional and consciousness effects were largely confined to early visual regions, thus inviting further research to examine whether similar dissociations can be observed in regions more commonly and centrally associated with either attention or consciousness, such as the PPN.

A more recent study by Tsubomi et al. (2011) used fMRI to investigate similar possible dissociations. Subjects were presented with a visual backward masking flanker paradigm, in which attention to flankers enhanced target visibility and attention to the mask attenuated it. Attention to flankers compared to mask, where visibility was higher, was associated with increased occipito-temporal sulcus activity. In addition, for both attentional conditions, visibility was correlated with activity in the same sulcus. In contrast, PPN activity was observed for the two attentional conditions compared with a no-attend control, independent of target visibility. However, the extent to which this study was investigating conscious access may be limited, since almost all stimuli presented were sufficiently clear and visible for object identity to correctly occur. Indeed, if trials where subjects categorized the target as invisible were removed from the analysis, essentially the same pattern of results was found. Therefore, the observed occipito-temporal visibility effects may largely reflect the perceptual intensity of items that have already gained access to conscious.

In summary, although studies do report pop-out effects, gist processing and natural object detection occurring in the absence of attention, further research has shown that attentional resources are required in each case, in order to enable conscious report of target stimuli. Indeed, the fact that attention is required for pop-out effects of very simple visual stimuli, such as a colored element, or an oriented gabor patch (Joseph et al., 1997; Theeuwes et al., 1999) implies that for all conscious events, even those involving very primitive elements, at least some attentional resources are necessary. In addition, although a small number of studies have presented provisional evidence that neural dissociations can be found between attention and consciousness, this is in contrast to considerable evidence (see sections Evidence Linking the Prefrontal Parietal Network with Conscious Content above and What is the Functional Role of the Prefrontal Parietal Network? below) emphasizing a close neural overlap between these two processes.

SHOULD ATTENTION INCLUDE WORKING MEMORY WITHIN ITS SCOPE?

As mentioned above, the question of overlap between attention and consciousness critically depends on the corresponding definitions. If it is assumed, as argued above, that attention is necessary for consciousness, and thus may play an important role in its function, one useful approach would be to expand on the definition of attention.

One prominent model of attention is Bundesen's neural theory of visual attention (NTVA; Bundesen, 1990; Bundesen et al., 2005). In the NTVA model, two waves of processing occur. During the first wave, processing resources are distributed unselectively across the visual field. The product of this wave of processing is a saliency map, which stores the attentional weight for each object in the visual field, based on either matches with long-term memory items or biologically salient representations. The second wave of processing involves selective competition in the form of a race to populate visual short-term memory until capacity is reached (approximately four items), by the reallocation of neuronal resources for each object, according to the attentional weight assigned to it. Weighting for objects is governed by the number of neurons recruited to represent it, while weighting for a given object feature is controlled by the scaling of average neuronal activity. Both top-down and bottom-up activations are involved in assigning neuronal populations and activity.

Single neuron recording in monkeys has provided good support for the idea of a first, unselected wave of activation. For instance, Chelazzi et al. (1998) found using a visual search task, that in the first 150–200 ms following stimulus onset, monkey inferotemporal cortex neurons showed an equally raised response to any set of stimuli. Only after this stage do the neurons modulate their activity in line with the top-down goals of the task, so that neurons coding for the target continue to increase in firing rate, while those coding for non-targets rapidly reduce in activity.

One critical feature of NTVA, therefore, is that in the first wave of activity there is a positive, though weak and unbiased set of weightings for items in the visual scene, which could be thought of as an unselective attentional enhancement for the visual field. Intriguingly, this attentional feature could be a cognitive and neural implementation of “gist,” discussed in the previous section, and may explain the extraction of some phenomenological and semantic features from a brief natural scene presentation, as well as the lack of detail of the percept. In addition, similar positive, though unselective attentional weightings could in principle explain other effects, such as iconic memory persistence and partial reportability. Indirect evidence in support of this has been reported in an fMRI study by Ruff et al. (2007), who presented volunteers with both a partial report and iconic memory task. Very similar attentional networks, especially comprising the PPN, were observed for both tasks.

Suggestively, NTVA includes working memory capacity as one important parameter, such that the outputs of attentional selection, via object classification from long-term memory, are placed in a limited capacity short-term memory store.

In another prominent recent attentional model, Knudsen agrees with van Boxtel and colleagues that attention is responsible for selecting from the animal's rich sensory input a small subset of goal-relevant information for further processing, at the expense

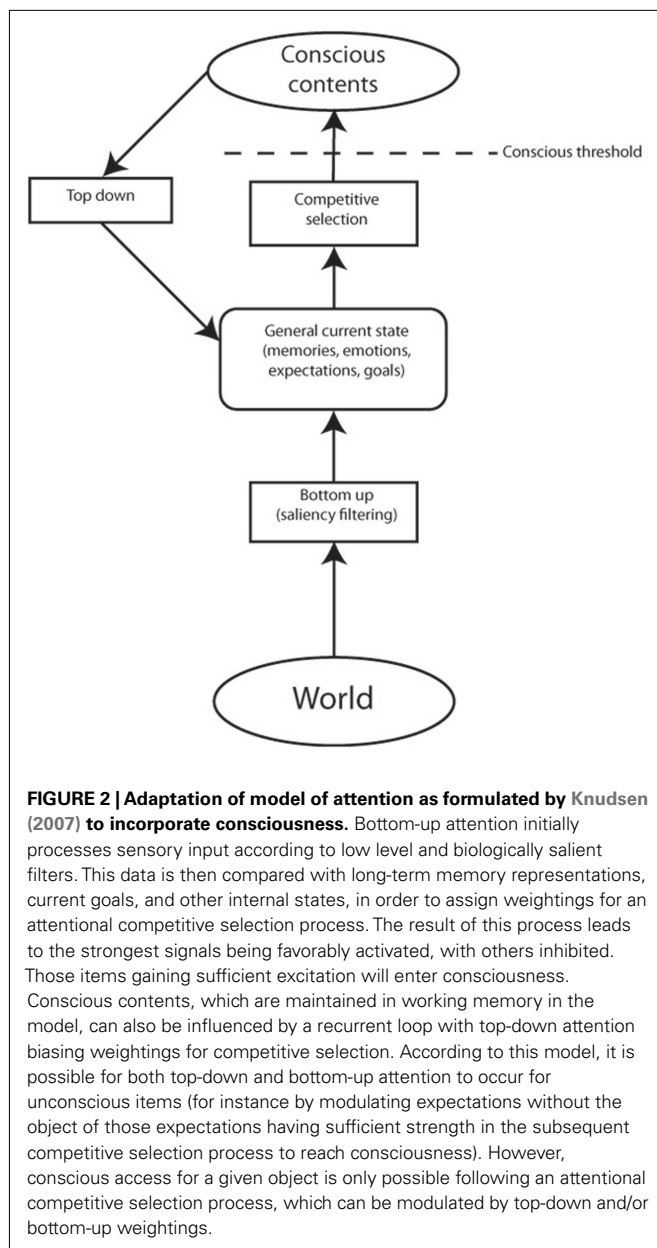
of other less useful information, which is largely unprocessed and ignored. Knudsen diverges from van Boxtel and colleagues, however, in discussing the endpoint of attentional filtering: in this case, Knudsen agrees with Bundesen and colleagues that attention is fundamentally responsible for furnishing working memory with its specific content (Knudsen, 2007). Knudsen's framework for attention involves four component processes: working memory, competitive selection, based on biased competition (Desimone and Duncan, 1995), top-down sensitivity control, and automatic bottom-up saliency filtering (Knudsen, 2007). All of these processes interact to make up what is commonly referred to as attention.

Given that working memory is by definition a conscious process, this framework suggests that attention, as a compound set of highly interconnected functions, is very closely aligned with consciousness. One interpretation of this expanded view, following arguments from a range of authors (Baars, 2005; Dehaene and Changeux, 2011) is that attention, whether top-down or bottom-up, acts as the selecting mechanism for conscious contents, while the working memory component acts as the specific store of (at least some) conscious detail (see **Figure 2**). This perspective is in accord with Dehaene and Changeux's (2011) global neuronal workspace theory, which sees attention as “serving as a ‘gateway’ that regulates which information reaches conscious processing” and that “withdrawal of attentional selection is used to modulate conscious access.” In addition, the concept of a “global workspace” of conscious access bears many similarities to working memory (Baars, 2005).

EVIDENCE FOR LINKS BETWEEN ATTENTION AND CONSCIOUSNESS

Considerable evidence exists from multiple domains supporting a tight link between attention and consciousness. For instance, a range of behavioral paradigms demonstrate that a reduction in attentional focus towards a given stimulus also leads to a reduced likelihood in consciously detecting the stimulus. Inattention blindness, coined by Mack and Rock (1998), refers to the failure to consciously detect an unexpected, but otherwise perfectly visible stimulus, when attention is engaged elsewhere. In the classic paradigm, observers have to decide which of the vertical or horizontal line of a briefly presented central cross is the longest. On crucial trials, an additional shape appears near the cross, and after the trial participants are asked whether they detected the shape. Most fail to notice it. In a more dramatic version of this experiment, approximately half of all participants fail to spot a person in a gorilla suit who unexpectedly walks across the screen in a video, when attention is devoted to a difficult task of counting basketball passes by players wearing white shirts while ignoring passes by players wearing black shirts (Simons and Chabris, 1999). The study by Cohen et al. (2011), described earlier, is another example of such a paradigm.

A related paradigm, change blindness, involves an inability to be conscious of a change in a visual scene, as long as attention is not directed to the critical changing detail (Rensink et al., 1997). For instance, if two otherwise identical images of an outdoor café scene between two people are alternated every 640 ms, separated by a blank screen, participants will fail to be conscious of a radical shift in the position of a prominent background railing for on average



10 s. Interestingly, participants more readily notice a change under these conditions if it alters the functional relationship between semantically central items in the visual scene, as compared to a visually equivalent irrelevant change (Sampanes et al., 2008). Presumably, this form of change is more likely to attract attention, which then ameliorates the change blindness effect.

Particularly relevant to exploring links between attention and consciousness are neurological cases of hemispatial neglect, which are most often considered as reflecting attentional deficits (Mesulam, 1981, 1999; Husain et al., 1997). Historically, neglect has been most closely linked with damage to right posterior parietal cortex, however more recent evidence suggests a substantial proportion of neglect patients instead have right lateral prefrontal damage (Husain and Kennard, 1996; Husain and Rorden, 2003). Neglect

is a condition signified by a marked reduction in awareness of one side of space, usually on the left (although the syndrome is equally commonly described as an impairment in being able to attend to one side of space). Unlike blindsight, which is limited to vision, neglect symptoms appear to impact all senses, including touch (Sarri et al., 2006), although perceptual tests confirm that the condition is not one of sensory impairment *per se*. Functional imaging studies in neglect patients have further demonstrated the link between consciousness and the PPN. For example, in one study, a neglect patient failed to notice a left finger touch on half the trials because of concurrent visual stimulation on the right. Activation was observed in the intact portions of the PPN only when the patient was aware of the touch (Sarri et al., 2006). Complementing the patient data, one intriguing study in normal participants simulated the symptoms of neglect: conscious detection rates for left sided targets were significantly reduced following TMS applied to right posterior parietal cortex (Muggleton et al., 2006).

These observations indicate that neglect as a syndrome is associated with the lateral prefrontal and posterior parietal regions, and by exhibiting symptoms which could easily be formulated either as attentional or as consciousness deficits, neglect reinforces the view that these two processes are closely connected.

WHAT IS THE FUNCTIONAL ROLE OF THE PREFRONTAL PARIETAL NETWORK?

Prefrontal parietal network activity is consistently reported in both attention and consciousness studies (Rees, 2007). However, as mentioned above, current views of attention describe it as a multifaceted process, closely connected to working memory, as well as executive control, which are all collectively deployed in order to carry out potentially complex goals.

Investigation into the functional role of the PPN has a long history, and has centered on working memory and executive processes (Wager and Smith, 2003). PFC lesions in particular have for many decades been associated with working memory and organizational deficits. For instance, Bor et al. (2006) used the spatial span task to demonstrate that the extent of frontal lobe damage was related to the size of working memory deficit, with those patients who had damage to the right DLPFC particularly impaired.

Prefrontal parietal network activity, however, can be found for almost any demanding or novel task (Miller and Cohen, 2001; Duncan, 2006) raising the possibility that high-level cognitive functions and consciousness may be intrinsically associated. In accord with this suggestion, studies have shown that conscious engagement is required for the use of most logical operations, assimilating information based on cause and effect, the encoding of almost all forms of stimulus sequences, counting and other non-trivial mathematic tasks, as well as for the acquisition and deployment of most social and cultural forms of knowledge (Baumeister and Masicampo, 2010). An intriguing corollary of the link between consciousness and novel or complex task processing is the robust finding that practice and automaticity reduces cognitive demand, prefrontal parietal activity, and awareness of details of a task (Jenkins et al., 1994; Landmann et al., 2007).

It should be noted, however, that rare instances of relatively sophisticated unconscious processing have also been reported,

for instance involving a speeded conscious recognition of a semantically incongruent scene (Mudrik et al., 2011) or a modulation of response to unconscious no-go signals in a go no-go paradigm (van Gaal et al., 2008). Neither of these examples, however, involve the processing of a novel series of data, which even in simple forms appears to require consciousness. Indeed, when target letters or monotonic sounds are rapidly presented in sequence, conscious detection, and effective performance of any targets aside from the initial one may be delayed or even abolished. Intriguingly, late prefrontal MEG signatures corresponding to target detection are also delayed or abolished in line with performance impairment (Marti et al., 2012).

Dijksterhuis et al. (2006) have reported an additional unconscious advantage effect, where the integration of a large set of data is performed better when unconsciously processed, for instance in a ranking task between four imaginary cars, each having 12 facts revealed about them. However, more recent attempts to replicate this finding have found either no effect, or a clear conscious advantage effect instead, raising doubt on the consistency of this finding (Newell et al., 2009; Aczel et al., 2011).

Examining how consciousness relates to other high-level cognitive processes may provide an important avenue for exploring the mechanism and details of conscious function. One approach in this context is to ask which processes most robustly activate the PPN. One recent fMRI study has suggested that PPN activity does not simply reflect task difficulty (Bor and Owen, 2007). Bor and Owen (2007) compared PPN activity for a set of high-level tasks: a standard random digit span working memory task, two structured digit span tasks where participants could improve performance using memory-based or novel mathematical chunking techniques, a long-term memory retrieval task and a mental arithmetic task. Despite the fact that the structured versions of the digit span tasks reduced task demands due to the strategic chunking of the stimuli, these conditions activated the PPN significantly more than all the other conditions, with the mathematical chunking condition activating PPN most robustly of all. In other words, detecting and utilizing regular patterns activates the PPN more robustly than working memory, long-term memory, or mental arithmetic alone – even though these tasks were equally or more difficult, according to accuracy scores. Other studies have also shown that the PPN is closely associated with similar recoding processes, including when compared with more demanding versions of the same task (Prabhakaran et al., 2000; Bor et al., 2001, 2003, 2004; Moore et al., 2006; Bor and Owen, 2007; Murray and Ranganath, 2007).

Therefore, within the general context of using consciousness to carry out complex or novel goals, there may be a special role for chunking processes, which search for, discover and exploit patterns in order to optimize task performance. The special role that chunking may play in consciousness links in closely with the critical need for conscious involvement in serial forms of data and aligns with the serial nature of phenomenal experience (Seth et al., 2005).

This perspective suggests a possible functional role for consciousness: when a given automatic, unconscious routine is either not optimal, or even detrimental (in the sense that it increases the likelihood of the animal not meeting its biological needs,

or of putting it in danger), usually due to novel or complex challenges, the relevant signals would be integrated into ongoing conscious contents in order to facilitate discovery of an innovative solution out of this impasse. Solutions, which may require sophisticated forms of learning and flexible behavior, are more likely within consciousness because only here can disparate forms of data be integrated in working memory, after attention has prioritized the processing of this data. The detection and use of “chunked” data patterns within a stimulus stream, or relating to motor output sequences, would be an especially powerful means of discovering such innovative solutions, since chunking can lower memory demands by data compression, and via regularity detection can uncover profound, mechanistic features of the environment. Chunking greatly facilitates automatization, which in turn reduces the burden on conscious contents so that other complex or novel tasks could gain conscious access and benefit from further optimization.

Although this process is likely to be metabolically expensive, requiring activity within a large cortical network, this view of consciousness is nevertheless evolutionarily valuable because metabolic costs can in other ways be reduced, by more efficiently streamlining many tasks, and by discovering novel techniques to intelligently avoid complex threats or obtain challenging rewards.

CONCLUSION

There is compelling evidence that at least some of the “core” correlates of consciousness reside in the PPN. Many current neurobiological theories of consciousness reflect this view, either explicitly or implicitly, in their models. Despite this, such theories tend not to dwell on the psychological and cognitive processes that the PPN may support; these include, prominently, attention, working memory, and chunking. Indeed, the attentional functions supported by the PPN have been argued to be dissociable from the core processes underlying consciousness.

Here, we have argued that these dissociations have been overstated. The relevant empirical evidence is open to alternative explanations, and two critical issues complicate any interpretation in favor of a double dissociation: (i) the way that attention is defined theoretically (e.g., as bottom-up, top-down, or both) and (ii) how attentional deployment can be adequately controlled for empirically. An alternative view, following (Rees and Lavie, 2001; Baars, 2005), among others, is that attention is intimately linked with consciousness, and may be best understood as involved in the selection of specific conscious contents. On this view, some form of attention is necessary for consciousness, although attention (without working memory) is not sufficient for consciousness.

Attention is best viewed as part of an integrated set of processes, including working memory, whose purpose is to achieve complex or novel goals. Activity within the PPN is associated both with consciousness and with this flexible set of processes, and is especially prominent if the task involves the chunking or recoding of information into regular patterns in order to optimize performance and reduce demands. Chunking is one of the most profound learning mechanisms available for human cognition (Ericsson et al., 1980; Gobet et al., 2001), and thus a powerful means by which

integrated information is “reshaped” in the brain. Therefore, further investigations about the role that chunking, as well as attention and working memory, plays in consciousness might prove highly useful in understanding the psychological features of consciousness and their relation to underlying neural mechanisms. More generally, consciousness science is likely to benefit from a broader consideration of the functional role of the PPN including, and

indeed exploiting, its intimate links to attention, working memory, and chunking.

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On the neural mechanisms subserving consciousness and attention

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Consciousness, as described in the experimental literature, is a multi-faceted phenomenon, that impinges on other well-studied concepts such as attention and control. Do consciousness and attention refer to different aspects of the same core phenomenon, or do they correspond to distinct functions? One possibility to address this question is to examine the neural mechanisms underlying consciousness and attention. If consciousness and attention pertain to the same concept, they should rely on shared neural mechanisms. Conversely, if their underlying mechanisms are distinct, then consciousness and attention should be considered as distinct entities. This paper therefore reviews neurophysiological facts arguing in favor or against a tight relationship between consciousness and attention. Three neural mechanisms that have been associated with both attention and consciousness are examined (neural amplification, involvement of the fronto-parietal network, and oscillatory synchrony), to conclude that the commonalities between attention and consciousness at the neural level may have been overestimated. Last but not least, experiments in which both attention and consciousness were probed at the neural level point toward a dissociation between the two concepts. It therefore appears from this review that consciousness and attention rely on distinct neural properties, although they can interact at the behavioral level. It is proposed that a “cumulative influence model,” in which attention and consciousness correspond to distinct neural mechanisms feeding a single decisional process leading to behavior, fits best with available neural and behavioral data. In this view, consciousness should not be considered as a top-level executive function but should rather be defined by its experiential properties.

Keywords: attention, consciousness, vision, imaging, MEG, electrophysiology, fMRI, review

INTRODUCTION

Attention and consciousness have traditionally been considered as closely related. In 1890, William James famously wrote “Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence” (James, 1890). About a 100 years later, it was argued (Posner, 1994) that “an understanding of consciousness must rest on an appreciation of the brain networks that subserve attention.” In this view, attention and consciousness reflect related concepts, much as temperature and heat. The idea that attention acts as a gateway for consciousness has been formalized in influential theories of consciousness (Baars, 1997; Dehaene and Naccache, 2001; Dennett, 2001): those events that enter consciousness are those that have been selected and amplified by attention.

Before examining whether this intuitive view on the intrinsic link between attention and awareness fits with experimental evidence, it is worth reminding why it is important to uncover the link between attention and consciousness. First, from a purely scientific point of view, one cannot confuse intuition with evidence. We do have the intuition that the sun revolves around the earth, but this intuition proved to be incorrect in the face of scientific

evidence. It is therefore important to submit our intuition on the intrinsic link between attention and consciousness to careful experimental scrutiny and confront theories with facts. Second, we still do not know whether consciousness has a function on its own, whether it confers an evolutionary advantage (Block, 1995; Chalmers, 1995). It is an important issue because it impinges on the definition of consciousness. Is consciousness the natural companion of all high-level cognitive functions? When consciousness disappears, as in deep sleep or in vegetative state, cognition seems to disappear as well. Besides, consciousness apparently shares limited capacities with attention and working memory. On the other hand, consciousness could be characterized by its experiential properties, rather than by its accompanying cognitive abilities (Block, 2007). Probing the nature of the links between the cognitive function “attention” and consciousness therefore taps right into the debate on the definition of consciousness: if consciousness is intrinsically related to attention, then its functional role and evolutionary advantage should pertain to executive functions. Alternatively if attention and consciousness are distinct, then consciousness should no longer be considered as an executive function, but be defined by its experiential properties. Although attention and consciousness are notoriously ill-defined concepts, some operational definitions are commonly accepted: attention is

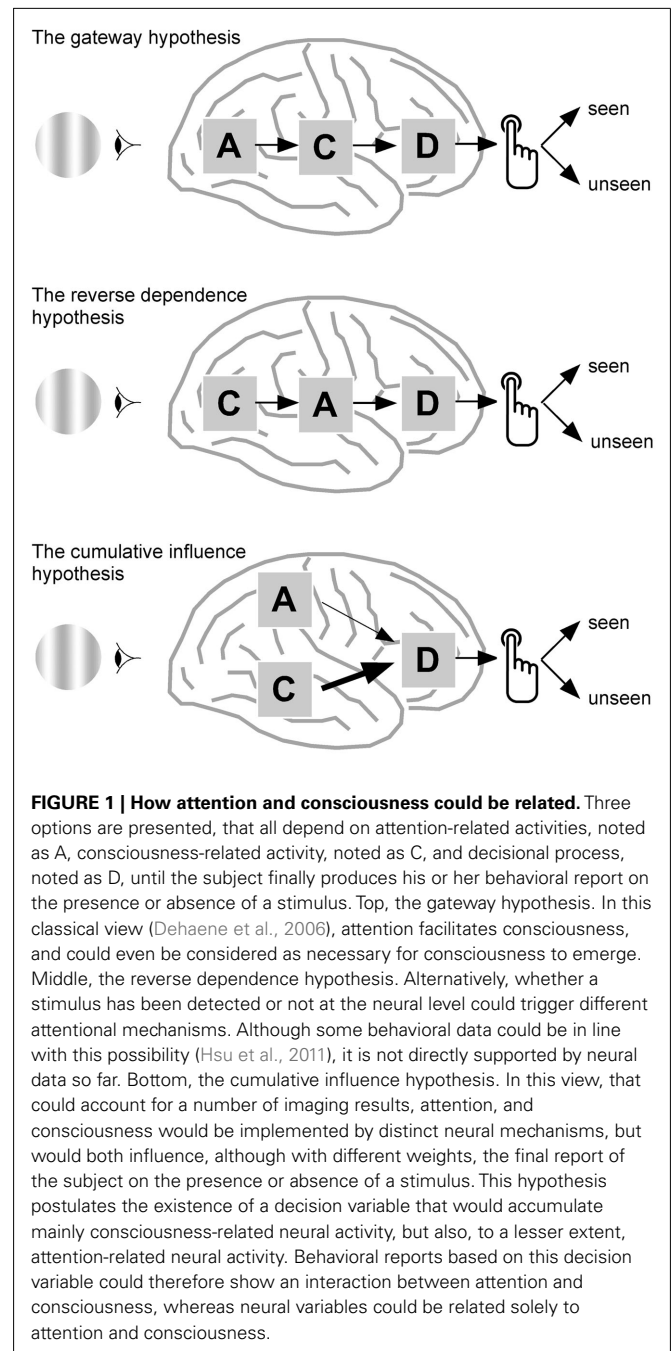
manipulated when a relevant aspect of the stimulus (i.e., location, color, direction of motion, etc.) is specified beforehand to the subject, consciousness is measured when the subject reports seeing or hearing something (note that I consider here mainly sensory consciousness, leaving aside the issues of self-consciousness and volition). I will rely on those operational definitions in the following of the paper, to analyze how neuroimaging results relying on those definitions can shed light on the links between attention and awareness, and, in turn, can help us to refine the theoretical definitions of those two concepts.

There are many different ways the links between attention and consciousness can be studied. Numerous behavioral findings, not extensively reviewed here, suggest a strong link: attention can facilitate detection (Solomon, 2004) and alter the subjective appearance of stimuli (Carrasco et al., 2004). Conversely, in the absence of attention, salient stimuli may not be reported by the subjects, as in inattention blindness (Mack and Rock, 1998), change blindness (Simons and Levin, 1997), or during the attentional blink (Shapiro et al., 1997). However a growing number of elegant behavioral manipulations in patients (Kentridge et al., 1999, 2004) and normal participants (Sumner et al., 2006; Kentridge et al., 2008; Van Boxtel et al., 2010b; Faivre and Kouider, 2011) show that attention and consciousness can sometimes be distinguished, within a disputed theoretical framework (Lamme, 2003; Van Boxtel et al., 2010a; Cohen and Dennett, 2011). I will focus here on the neural mechanisms subserving attention and consciousness. The rationale is quite simple: if attention and consciousness functionally and conceptually overlap, they should share common neural mechanisms. Conversely, if attention and consciousness turn out to rely on independent neural mechanisms, then they probably reflect distinct concepts and functions. Let us consider an analogy: looking at a contemporary painting can be a disconcerting experience. To see better, both a powerful lamp and the explanations of an art critic can be extremely useful. The means employed to see better – speech and light – fundamentally differ, and should therefore not be confused. Note that this analogy does not imply that speech and light are analogous to awareness and attention, but rather that seeing better, in other words the end-product of both attention and awareness, can be achieved by different means.

I will first present how the links between attention and consciousness can be conceived at the neural level, and then review and discuss three points of apparent convergence between the neural mechanisms involved in attention and consciousness. The first one is sensory amplification: for a stimulus to reach awareness, enough sensory activation must be present. Because attention selectively amplifies sensory inputs, it could foster consciousness. Second, attention is controlled by activity in the fronto-parietal network, that has been repeatedly found to correlate with consciousness reports. Last, oscillatory neural synchrony has been proposed to play a role in both attention and consciousness. I will then review those imaging experiments that simultaneously manipulated attention and measured consciousness.

HOW THE LINK BETWEEN ATTENTION AND CONSCIOUSNESS CAN BE CONCEIVED

Figure 1 attempts at schematically formalizing how the links between attention and awareness can be conceived. It is clearly



inspired by Lamme's influential paper (Lamme, 2003), but introduces new options and, importantly, an additional component: decision. Indeed, consciousness is experimentally studied mainly by sorting out behavioral or neural measures according to subjects' report, for instance depending on whether the subject saw a face or vase, a grating, or a blank screen. Reporting one's perceptual state implies deciding which option should be chosen. It is therefore important to incorporate the decisional step into models of consciousness. Decisional processes have been so far analyzed in the perceptual decision-making model (Smith and Ratcliff, 2004), without any explicit reference to consciousness.

In this model, a decision variable accumulates sensory evidence until a response criteria is reached. Decision depends on the initial bias, i.e., whether the response criterion is *a priori* lower for one option, and on the rate of accumulation of sensory evidence. This model explains well reaction times distributions (Smith and Ratcliff, 2004), and evidence for the existence of decision variable in areas downstream to sensory regions has been obtained both in monkeys (Gold and Shadlen, 2007) and humans (Heekeren et al., 2008).

The first option is that attention is a prerequisite for awareness: those stimuli that are voluntarily attended to, or that are salient enough to attract attention, can reach consciousness and be reported. I will call this possibility the gateway model. For the sake of completeness, one should also consider the possibility that attention depends on consciousness. In other words, the type of attentional processes mobilized in a given task could depend on whether the subject is aware of the stimulus ("reverse dependence"). Last, attention and consciousness could be initially independent, but combined at a later, decisional stage leading to the final verbal report of the subject. I will call this last option the cumulative influence model. Note that in all models, when either the neural mechanisms involved in attention and consciousness are affected, the subjective report of the subject is modified. Measuring directly the neural mechanisms related to attention and consciousness may therefore prove useful to discriminate between the three hypothesis. In an experiment in which attention is manipulated and consciousness measured, if all observed neural correlates of consciousness depend on attentional manipulation, then the gateway model is likely to be the correct one. Finding distinct correlates of attention depending on whether the subject reported the stimulus or not would favor the reverse dependence model. Last, if some neural correlates of consciousness are independent from attention and some neural correlates of attention are independent from consciousness, then the cumulative influence view is more likely.

NEURAL AMPLIFICATION IN ATTENTION AND CONSCIOUSNESS

The role of attention is to prioritize incoming sensory processing to enable optimized behavioral responses given the task at hand. The main neural mechanisms associated to the attentional modulation of sensory processing are target amplification and distractor suppression. By combining these two mechanisms, sensory regions would be able to selectively amplify target-related neural signals to facilitate the transmission of target-related information further along the information processing chain (Desimone and Duncan, 1995). A huge amount of experimental evidence for target amplification in sensory regions has been obtained in the last 30 years in monkeys and humans (Desimone and Duncan, 1995; Kastner and Ungerleider, 2000; Corbetta and Shulman, 2002; Reynolds and Chelazzi, 2004; Raz and Buhle, 2006). Target enhancement can be observed in all correlates of neural activity, from firing rates (Treue, 2003; Reynolds and Chelazzi, 2004; Bisley and Goldberg, 2010) to gamma-band oscillatory synchrony (Gruber et al., 1999; Fries et al., 2001; Tallon-Baudry et al., 2005; Siegel et al., 2008), event-related potentials (Hillyard and Anllovento, 1998; Luck et al., 2000), and BOLD signal (Corbetta et al., 1990; Kastner et al., 1998). Evidence

for distractor suppression has also been obtained, by showing that when two stimuli are presented in the receptive field of the neuron, the overall response of this neuron is similar to the response to the target presented alone (Moran and Desimone, 1985; Chelazzi et al., 1993; Reynolds et al., 1999). Active mechanisms of distractor suppression have also been described in humans (Luck et al., 1997; Vanduffel et al., 2000; Worden et al., 2000; Hopf et al., 2006; Thut et al., 2006; Andersen and Muller, 2010). Those results lend strong support to the biased competition model of attention (Desimone and Duncan, 1995) as well as to the idea of priority maps (Itti and Koch, 2001).

Many influential theories of consciousness posit that selective neural amplification plays a key role for an information to reach awareness. This assumption is explicit in the global workspace model (Baars, 1997; Dehaene et al., 1998), the multiple draft theory (Dennett, 1991), but is also present in the dynamic core hypothesis (Tononi and Edelman, 1998; Edelman, 2003). Competition between different inputs is central to all those models: the neural information that has been most amplified is the winner, the one that reaches consciousness (Crick and Koch, 2003). In this view, a neural correlate of consciousness is by definition an activity that is larger in response to consciously seen stimuli than to unseen stimuli. Experimentally, neural amplification is at the heart of most experimental results on consciousness: in most cases, activity in sensory regions appear to be larger for consciously seen stimuli (Tong et al., 1998; Polonsky et al., 2000; Rees et al., 2000; Dehaene et al., 2001; Vuilleumier et al., 2001; Ress and Heeger, 2003; Haynes et al., 2005; Tse et al., 2005; Hesselmann et al., 2011; Sergent et al., 2011). Note however that although consciousness has been associated most often with response amplification, response attenuation has also been described in humans (Melloni et al., 2011). In monkey area V4 in a binocular rivalry paradigm, single neuron activity can either increase or decrease before the animal reports perceiving the cell's preferred orientation (Leopold and Logothetis, 1996), suggesting that both response enhancement and response suppression can be informative. Despite those two results, response amplification is most often considered to play a crucial role in consciousness. It could be tempting to infer that enhanced sensory responses to seen stimuli are due to a mechanism of neural amplification akin to the one used by attention. This is all the more true that sensory activities correlating with consciousness have been observed between 100 and 200 ms using stimuli at detection threshold (Pins and Ffytche, 2003) or a modified rivalry paradigm (Roeber et al., 2008), a latency range that is typically affected by attention (Luck et al., 2000).

To what extent does the parallelism between sensory responses amplified by attention and sensory responses reaching consciousness hold true? Behaviorally, spatial attention is considered to facilitate detection by enhancing perceived contrast (Carrasco, 2011), although there is some ongoing controversies (Solomon, 2004; Schneider and Komlos, 2008). This proposal seems to be in line with the enhanced responses to attended stimuli in visual cortices, but this convergence between behavioral studies and physiological recordings may be only superficial. Indeed, increasing the physical contrast of the stimulus induces a robust latency shift of the neural sensory response, with high-contrast grating peaking 30–40 ms earlier in monkey area V1 (Gawne et al., 1996).

Surprisingly, there is no available evidence that attended stimuli, that are supposed to be neurally encoded with an enhanced contrast leading to detection, give rise to faster responses than unattended stimuli. In humans, the best-studied attentional modulation (Hillyard and Anlovento, 1998; Luck et al., 2000) is the amplitude enhancement by spatial attention of the so-called P1, a wave of activity that occurs around 100 ms in early extra-striate areas (Di Russo et al., 2002). P1 amplitude enhancement by spatial attention is not accompanied by a shortening of its latency. Magneto-encephalographic data, that have a better spatial resolution than EEG data, revealed a spatially fine-grained attentional suppression/enhancement of the P1 amplitude but nevertheless failed to reveal a shortening of latency by spatial attention (Hopf et al., 2006). The only report of a P1 latency shortening has been obtained with eye-gaze cues (Schuller and Rossion, 2001, 2004). Spatial attention could potentially induce latency shifts coupled with amplitude increases at longer latencies only, after 200 ms (Noguchi et al., 2007). A direct comparison of the effects of contrast and of spatial attention has been performed in monkey area V4 (Lee et al., 2007). Both attention and contrast enhancement affected the magnitude of single cell responses. However, attention did not change the response latency, while contrast did. It has even been recently suggested that visual attention and stimulus contrast rely on separable neural codes in monkey area V1 (Pooresmaeili et al., 2010). To conclude, the neural mechanisms used by attention are not directly equivalent to contrast enhancement: there may be different ways of coding saliency at the neural level. This conclusion does not in itself allow to distinguish between the three hypothesis described in **Figure 1**, but it leaves open the possibility that the same final behavioral output, here enhanced detection, may be achieved by distinct neural mechanisms.

INVOLVEMENT OF THE FRONTO-PARIETAL NETWORK IN ATTENTION AND CONSCIOUSNESS

Attention operates in sensory regions, but the top-down control of voluntary or goal-directed attention largely relies on parietal and frontal cortices in humans (Corbetta and Shulman, 2002; Bressler et al., 2008; Corbetta et al., 2008; Greenberg et al., 2010) and monkeys (Bisley and Goldberg, 2003; Reynolds and Chelazzi, 2004; Buschman and Miller, 2007; Ekstrom et al., 2008). In parallel, parietal and frontal correlates of awareness have been often reported (Rees et al., 2002). Activity in those regions is abnormal in altered states of consciousness, such as in vegetative patients (Laureys, 2005) or during generalized epileptic seizures accompanied by a loss of consciousness (Blumenfeld et al., 2003). Frontal regions are also the first areas to deactivate when falling asleep and the last ones to reactivate after awakening (Hobson and Pace-Schott, 2002). Imaging studies of consciousness repeatedly underlined the role of the dorsolateral prefrontal cortex (Sahraie et al., 1997; Lumer et al., 1998; Beck et al., 2001; Lau and Passingham, 2006), parietal regions (Kleinschmidt et al., 1998; Lumer et al., 1998; Beck et al., 2001, 2006; Vuilleumier et al., 2001; Carmel et al., 2006; Hesselmann et al., 2011), the inferior frontal cortex (Lumer et al., 1998; Dehaene et al., 2001; Vuilleumier et al., 2001; Sergent et al., 2005; Carmel et al., 2006; Hesselmann et al., 2011), as well as the anterior cingulate cortex (Dehaene et al., 2001; Sergent et al., 2005; Carmel et al., 2006). In monkeys, the perceived direction of an ambiguous

motion correlates with activity in the parietal region LIP (Williams et al., 2003), and correlates of detection of somatosensory stimuli at threshold are best observed in the medial premotor cortex (De Lafuente and Romo, 2005, 2006).

All the areas listed above as correlates of consciousness have also been associated with attention and control. The dorsolateral prefrontal cortex and the anterior cingulate are well known to be involved in control and performance monitoring (Macdonald et al., 2000). The dorsolateral prefrontal cortex is also an important structure for the maintenance of sensory information in memory (Constantinidis et al., 2001; Curtis and D'Esposito, 2003), and could potentially participate to the attentional selection of information (Lebedev et al., 2004; Buschman and Miller, 2007). The posterior parietal cortex/anterior intraparietal sulcus (IPS) region is a key structure of the dorsal attentional network, while the inferior frontal region belongs to the ventral attentional network (Corbetta et al., 2008). A meta-analysis of imaging studies on attention, working memory, episodic retrieval, and consciousness (Naghavi and Nyberg, 2005) reveals a large overlap in the posterior parietal cortex, that belongs to the dorsal attentional network, and in the dorsolateral prefrontal cortex, associated to decision-making. From this convergence one could be tempted to deduce the existence of a central executive based on the posterior parietal cortex and dorsolateral prefrontal cortex, that would be necessary for all high-level functions. This central executive could constitute a core component of consciousness (Dehaene et al., 2006; Del Cul et al., 2009). Alternatively, fronto-parietal activations in some studies could be due to uncontrolled fluctuations of attention and/or memory affecting subjects' reports. To what extent do fronto-parietal activations correlate with consciousness *per se*?

First, it should be noted that not all experiments searching for the neural correlates of consciousness found a significant involvement of frontal or parietal regions (Tong et al., 1998; Tse et al., 2005). Potentially, the fronto-parietal activations observed in some consciousness studies could reflect a consequence of consciousness, rather than a cause. A stimulus that is consciously perceived can be cognitively manipulated, and therefore activate fronto-parietal regions. In line with this idea, it has been recently shown that activity in the right dorsolateral prefrontal cortex, typically associated with transitions between different conscious contents, would be a consequence of perceived transitions rather than a cause (Knapen et al., 2011). However, a high-level of activity in the dorsal attentional network before stimulus onset can, depending on the experiment, either foster (Boly et al., 2007) or impair (Sadaghiani et al., 2009) the detection of stimuli at threshold. This latter finding can be understood in the framework of the cumulative influence hypothesis: attention-related activity can either positively participate, or actively inhibit, the final decision about the presence or absence of a stimulus.

Second, at least some of the fronto-parietal regions that have been associated with consciousness can be activated unconsciously. Activity in the anterior cingulate, dorsolateral prefrontal, and parietal cortices is modulated by events that are not consciously perceived (Berns et al., 1997). The IPS reacts to subliminally presented numbers (Naccache and Dehaene, 2001). The anterior cingulate cortex is activated by errors subjects were aware of as well as by those they were not aware of making (Hester

et al., 2005), and medial prefrontal – occipital coupling is present in conscious as well as unconscious errors (Cohen et al., 2009). The dorsolateral prefrontal cortex (Lau and Passingham, 2007) and areas of the medial frontal cortex involved in the control of voluntary action (Sumner et al., 2007) participate to unconscious and involuntary control, and non-consciously triggered inhibitory control is associated with frontal brain potentials (Van Gaal et al., 2008).

Third, none of the studies listed above tried to disentangle the relative contributions of attention, control, memory, and consciousness to fronto-parietal activations. For instance, since the dorsolateral prefrontal cortex participates to the maintenance of information in short-term memory, it could appear activated in many consciousness studies: to report the presence of a stimulus, information about this stimulus has to be kept in memory until the production of the behavioral response. Besides, the same paradigm has sometimes been used to probe either attention or consciousness, thereby implying that the same neural structures appear, by definition, as a correlate of both attention and consciousness. For instance, the attentional blink paradigm has been used to identify neural correlates of consciousness (Sergent et al., 2005; Kranczioch et al., 2007) or to probe the temporal limitations of attention (Husain et al., 1997; Gross et al., 2004). As a result, the parietal involvement common to all these studies could refer to either attention or consciousness.

In the light of those three lines of arguments, the fronto-parietal network contribution to consciousness should be re-evaluated: fronto-parietal activations appear neither necessary nor sufficient for consciousness, and/or could reflect other functions such as attention and memory. However it should be noted that the term “fronto-parietal” is often used to refer to a vast ensemble of loosely defined regions, supporting “high-level” functions in general. It may be necessary to be much more specific. For instance, different subregions of the right superior parietal lobule appear to play distinct roles on perceptual fluctuations in binocular rivalry (Kanai et al., 2011). Applying TMS stimulation over right parietal regions can lead to a shortening (Carmel et al., 2010) or a lengthening (Kanai et al., 2010; Zaretskaya et al., 2010) of dominance durations in binocular rivalry, depending on whether TMS stimulation is applied online or offline whether the stimulated sites are more anterior or posterior. Last, to make the story even more complex, the frontal lobes have been repeatedly associated with a hierarchical organization of cognitive control (Koechlin et al., 2003; Botvinick, 2008; Badre and D’Esposito, 2009), but those models are essentially mute on consciousness: so far, understanding the frontal lobe functions did not require to take consciousness into account.

OSCILLATORY SYNCHRONY

There is a strong consensus in the literature that consciousness is a distributed process, involving the coordination of neural activity across a number of cortical regions. Oscillatory synchrony is considered as a neural mechanism that could flexibly coordinate activity within and between neural populations, in a task-dependent manner (Singer and Gray, 1995). Schematically, two neural groups, that encode distinct aspects of the stimulus for instance in their rate code, may temporarily signal to each other

that they are working on related pieces of information by synchronizing their activity at the population level. Oscillatory synchrony was therefore quickly identified as a potential neural mechanism involved in the emergence of consciousness (Engel and Singer, 2001).

Experimentally, both gamma (~30–90 Hz) and beta (~15–30 Hz) bands oscillatory synchrony have been linked to visual consciousness. In humans, stimuli at threshold elicit gamma-band (30–100 Hz) oscillations in posterior regions only when they are consciously perceived (Schurger et al., 2008; Wyart and Tallon-Baudry, 2008, 2009; Luo et al., 2009), and independently from objective performance (Schurger et al., 2006). In masking paradigms, word visibility is associated with enhanced long-range synchronization in the gamma (Melloni et al., 2007) or beta (Gaillard et al., 2009) range. In conditions of bistable perception, perceptual transitions are preceded and accompanied by increased gamma-band oscillatory synchrony (Doesburg et al., 2005) and by a modulation of beta-range oscillatory synchrony in a network comprising the frontal eye fields, posterior parietal cortices, lateral occipital regions, and occipital pole (Hipp et al., 2011). Failure to report the second target in the attentional blink paradigm correlates with decreased fronto-parietal beta synchrony (Gross et al., 2004). In monkeys, target visibility manipulated by flash suppression is characterized by increased gamma-band oscillations in area V4 and reduced alpha (8–12 Hz) and beta suppressions in areas V1, V2, and V4, while spiking activity is almost unchanged (Wilke et al., 2006). The link between gamma and beta-band oscillatory synchrony and consciousness is of course not confined to the visual modality. For instance, nociceptive somatosensory stimuli around pain threshold elicit gamma-band oscillations in primary somatosensory cortex whose amplitude is tightly related to subjective pain ratings (Gross et al., 2007).

In parallel to this role in establishing the neural cooperativity thought to be necessary for consciousness to emerge, oscillatory synchrony could also be used to set up a selective filter and therefore be a core component of attentional processes (Womelsdorf and Fries, 2007). Neurons are highly sensitive to the temporal structure of incoming inputs. If a neuron receives inputs within a brief time window, it is much more likely to fire in response to those inputs and transmit information further downstream than if the inputs are dispersed in time. Because of its temporal structure, oscillatory synchrony imposes windows of increased or decreased excitability (Steriade et al., 1993; Buzsáki and Draguhn, 2004) that can facilitate the transfer of information between two neural populations (Fries, 2005). Let us consider two structures, A and B, that compete for transmitting information to a target area T further along the processing chain. If A and T are synchronized but not B and T, then A will win the competition over B to get its information transmitted to T. This represents an elegant way of implementing an attentional filter, that can be used by both bottom-up and top-down attention. There is clear experimental evidence that selective attention enhances gamma-band oscillatory synchrony, in monkey area V4 (Fries et al., 2001), in human scalp EEG (Tallon-Baudry et al., 1997; Gruber et al., 1999), or MEG (Bauer et al., 2006; Vidal et al., 2006) data, as well as in intracranial recordings (Tallon-Baudry et al., 2005; Engell and McCarthy, 2010). Importantly, the strength of gamma-band synchronization

in monkey area V4 predicts behavioral response times (Womelsdorf et al., 2006). There is also growing evidence that oscillatory synchrony plays an important role in the control of top-down attention. Indeed, during attentional deployment, oscillatory synchrony increases between sensory regions and frontal and parietal regions, both in humans (Doesburg et al., 2008; Siegel et al., 2008) and monkeys (Buschman and Miller, 2007; Gregoriou et al., 2009).

The fact that the same neural mechanism is involved in both attention and consciousness could suggest that the two functions are intrinsically linked. Alternatively, oscillatory synchrony could be seen as a population code, that can be used by any cognitive function – much as spikes constitute the core signaling mechanism at the single neuron level. For instance, gamma-band oscillatory synchrony is known to be involved not only in attention and consciousness, but also in feature binding, memory, and learning (Tallon-Baudry and Bertrand, 1999; Jensen et al., 2007; Fries, 2009; Tallon-Baudry, 2009). It recently appeared that when distinct cognitive processes are simultaneously active, gamma-band oscillations are elicited in distinct, narrow frequency bands (Vidal et al., 2006; Schurger et al., 2008; Wyart and Tallon-Baudry, 2008; Chaumon et al., 2009). Oscillatory synchrony is now considered as an essential population code that takes advantage of neurons fine temporal tuning, not a specific marker of a given cognitive function (Jensen et al., 2007; Fries, 2009; Tallon-Baudry, 2009).

PROBING ATTENTION AND CONSCIOUSNESS SIMULTANEOUSLY AT THE NEURAL LEVEL

As underlined above, the apparent convergence between the neural correlates of attention and awareness is mainly based on experiments that either manipulated attention or measured consciousness. However, the two concepts often overlap in those experiments – for instance, is attention or consciousness probed in the attentional blink paradigm? To address more thoroughly the issue of the link between attention and consciousness, some studies attempted at manipulating attention while measuring consciousness.

Several EEG studies convincingly demonstrated that attentional mechanisms can be triggered by attentional cues that do not reach consciousness. The N2pc is a lateralized evoked component that reflects the orienting of spatial attention. It is observed between 200 and 300 ms after stimulus onset, over the hemisphere contralateral to the attended location. Targets rendered invisible by object-substitution masking elicit an N2pc, thereby demonstrating that attention can be attracted by stimuli that cannot be accurately reported (Woodman and Luck, 2003). In line with this idea, source modeling of EEG data reveals that seen and unseen attentional cues are initially processed in the same manner along the dorsal stream (Babiloni et al., 2006). Attention can also modulate the neural processing of stimuli that do not reach consciousness, from 200 ms after stimulus onset for spatial attention (Koivisto and Revonsuo, 2007) to 400–600 ms for temporal attention (Kiefer and Brendel, 2006). Conversely, early differences between seen and unseen stimulus, before 200 ms, can be independent from the attentional status of the stimulus (Koivisto et al., 2006; Boehler et al., 2008; Koivisto and Revonsuo, 2008). Altogether, these results suggest that attention and consciousness can operate via a least partly independent mechanisms.

The possibility that spatial attention and visual awareness rely on at least partly independent mechanisms was directly tested in an experiment comparing neural responses to stimuli that were physically strictly identical, but that could be consciously perceived or not and attended or not, on a trial-by-trial basis (Wyart and Tallon-Baudry, 2008). In this experiment, subjects oriented their attention according to a central cue in a typical Posner paradigm, toward faint gratings, at threshold for awareness. The factorial analysis of the magneto-encephalographic data revealed the existence of high-frequency gamma-band oscillations that were larger for attended stimuli, either seen or unseen, and the existence of low-frequency gamma-band oscillations that were larger for seen stimuli, either attended or unattended. The attention-independent correlate of awareness was localized in the posterior lateral occipital cortex (Wyart and Tallon-Baudry, 2009). The double dissociation observed in this experiment between the neural correlates of attention and consciousness is only compatible with the cumulative influence model in **Figure 1**. Interestingly in this experiment, although a neural correlate of visual consciousness independent from attention was identified, subjective reports were affected by spatial attention: subjects were more likely to detect the stimulus when it appeared at the attended location. A parametric analysis at the single-trial level was compatible with the existence of a decisional stage integrating both the consciousness-related and attention-related activity into the final subjective report. In other words, the results of this experiment are strongly in favor of the cumulative influence model. This model would also explain why late neural correlates of stimulus visibility (Fernandez-Duque et al., 2003; Sergent et al., 2005; Del Cul et al., 2007; Lamy et al., 2009; Genetti et al., 2010), close to the subject behavioral report, can be influenced by parameters such as attention (Koivisto et al., 2009) or confidence in one's decision (Eimer and Mazza, 2005): attention and confidence evaluation could enter the final decisional process about whether the stimulus has been experienced or not, providing additional sources of neural evidence to finally report the stimulus as seen or unseen.

There is also ample evidence that the state of the nervous system before stimulus onset can deeply influence the conscious report of the subject (Linkenkaer-Hansen et al., 2004; Palva et al., 2005; Pourtois et al., 2006; Boly et al., 2007; Hanslmayr et al., 2007; Hesselmann et al., 2008b; Monto et al., 2008; Van Dijk et al., 2008; Britz et al., 2009; Busch et al., 2009; Mathewson et al., 2009; Sadaghiani et al., 2009). Spontaneous modifications of neural activity are often attributed to fluctuations in vigilance (Linkenkaer-Hansen et al., 2004; Boly et al., 2007), gain modulation, or attention (Hanslmayr et al., 2007; Van Dijk et al., 2008), although those factors are not explicitly controlled.

According to this view, a sensory area could be in a state of high neural excitability, corresponding to a state of higher vigilance or attention, and would therefore generate a larger response when the stimulus occurs. While this explanation may hold true in some cases, it is not the only way prestimulus activity in sensory areas can influence the seen or unseen fate of a stimulus (Hesselmann et al., 2008a; Wyart and Tallon-Baudry, 2009). Indeed, a high baseline level of activity influencing the subject's behavioral report is not necessarily followed by a large response to the stimulus. The influence of baseline fluctuations thus cannot be explained only by

an enhanced excitability leading to stronger responses to incoming stimuli. Rather, it seems that prestimulus activity in sensory regions could directly bias the decision process, by shifting the initial level of the decision variable toward one option. In other words, the sensory cortex of a subject could be biased toward judging that a stimulus is present (Wyart and Tallon-Baudry, 2009), or that the stimulus content is vase or a face (Hesselmann et al., 2008a), independently from the strength of the sensory response to the stimulus. These results show that decision-making matters in consciousness studies, and that the decision process does not fully map onto parieto-frontal regions: decisional determinants can be implemented in sensory regions as well, even before stimulus onset.

CONCLUSION

To summarize, attention does operate in sensory regions, but neural amplification by attention appears functionally distinct from the neural amplification related to consciousness: attention does not shorten response latencies, as more contrasted objects would (Lee et al., 2007), attention-related and consciousness-related neural activities in retinotopic areas can be dissociated (Wyart and Tallon-Baudry, 2008). There is growing evidence that events that do not reach consciousness nevertheless activate parietal and frontal regions, suggesting that they are not sufficient for consciousness to emerge. Because frontal regions are not always activated, one can even wonder whether they are necessary. An alternative possibility is that they reflect a consequence of consciousness, rather than a cause (Knapen et al., 2011). Last, oscillatory synchrony is not associated exclusively with a single process, be it feature binding, memory and learning, attention, or consciousness, but should rather be considered as a generic mechanism governing neural interactions.

The fact that there can be an independence of the sensory correlates of attention and of consciousness, together with late correlates of visibility modulated by attention and behavioral interactions between attention and consciousness, argues in favor of the cumulative influence: consciousness-related and attention-related neural activities would be integrated in a single decision variable. This decision variable would accumulate not only sensory evidence, as in the classical perceptual decision-making framework (Smith and Ratcliff, 2004; Gold and Shadlen, 2007; Heekeren et al., 2008), but more processed neural information related to either consciousness or attention. Whether and how such a variable is implemented remains to be determined experimentally. In any case, one should keep in mind a number of limitations of this model. First, the visual representation of the cumulative influence model as presented in **Figure 1**, does not capture its complexity. For instance, one could assume that a decisional process necessarily takes place in anterior regions, and at a late

time point along the processing chain. However, a decisional bias can be implemented in sensory regions and be already present before stimulus onset (Hesselmann et al., 2008a; Wyart and Tallon-Baudry, 2009). Second, the arguments developed in this paper are based on experimental results obtained in fMRI as well as MEG–EEG studies. One should keep in mind that the relationship between the BOLD signal and electrophysiological data is not well established yet (Logothetis, 2003), and that the different measures sometimes provide inconsistent results (Buracas and Boynton, 2007). Third, there are many different types of attention – space-based or feature-based attention, divided or selective attention, top-down and stimulus-driven attention, endogenous or exogenous spatial attention. There is already good evidence that different forms of attention rely on different networks (Corbetta and Shulman, 2002; Chica et al., 2011a) or different forms of neural communication (Buschman and Miller, 2007). Because the different types of attention are implemented differently, it is likely that they interact differently with awareness (Chica et al., 2011b; Hsu et al., 2011).

Even if the cumulative influence hypothesis has its limitations, it is so far the model that fits best with experimental data. Interestingly this model points toward the existence of a sensory neural activity related to consciousness, uncontaminated by other cognitive processes such as attention. Such an activity could potentially be very close to the immediate subjective experience of the subject. This is reminiscent of the idea of phenomenal awareness, that could be distinct from cognitive access (Block, 2007). Experimentally, the only possibility to study consciousness is to rely on the subject's final subjective report, that relies on a complex decisional process. It is therefore all the more interesting that neural data sorted according to this integrated subjective report should point toward the existence of an activity in upper visual areas uncontaminated by attention (Wyart and Tallon-Baudry, 2008) that could potentially be directly related with phenomenal consciousness (Hesselmann et al., 2011). It therefore seems that consciousness can be distinguished from accompanying cognitive functions at the neural level. It still remains to be determined what is the advantage, from a functional or evolutionary perspective, of having two amplification systems, one related to consciousness and the other to attention, and to what extent the nature of the decisional process is modified by consciousness-related entries. In particular, is it because of consciousness-related inputs that a capacity-limited cognitive bottleneck appears? Answering those questions would provide us with important clues about the still elusive functional role of consciousness.

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Attention and conscious perception in the hypothesis testing brain

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Conscious perception and attention are difficult to study, partly because their relation to each other is not fully understood. Rather than conceiving and studying them in isolation from each other it may be useful to locate them in an independently motivated, general framework, from which a principled account of how they relate can then emerge. Accordingly, these mental phenomena are here reviewed through the prism of the increasingly influential predictive coding framework. On this framework, conscious perception can be seen as the upshot of prediction error minimization and attention as the optimization of precision expectations during such perceptual inference. This approach maps on well to a range of standard characteristics of conscious perception and attention, and can be used to interpret a range of empirical findings on their relation to each other.

Keywords: prediction error minimization, precision expectation, free energy, inattentional blindness, change blindness, unconscious processing

INTRODUCTION

The nature of attention is still unresolved, the nature of conscious perception is still a mystery – and their relation to each other is not clearly understood. Here, the relation between attention and conscious perception is reviewed through the prism of predictive coding. This is the idea that the brain is essentially a sophisticated hypothesis tester (Helmholtz, 1860; Gregory, 1980), which continually and at multiple spatiotemporal scales seeks to minimize the error between its predictions of sensory input and the actual incoming input (see Mumford, 1992; Friston, 2010). On this framework, attention and perception are two distinct, yet related aspects of the same fundamental prediction error minimization mechanism. The upshot of the review here is that together they determine which contents are selected for conscious presentation and which are not. This unifies a number of experimental findings and philosophical issues on attention and conscious perception, and puts them in a different light. The prediction error minimization framework transpires as an attractive, if yet still speculative, approach to attention and consciousness, and their relation to each other.

Attention is difficult to study because it is multifaceted and intertwined with conscious perception. Thus, attention can be endogenous (more indirect, top-down, or motivationally driven) or exogenous (bottom-up, attention grabbing); it can be focal or global; it can be directed at objects, properties, or spatial or temporal regions, and so on (Watzl, 2011a,b). Attentional change often seems accompanied by a change in conscious perception such that what grabs attention is a new stimulus, and such that whatever is attended to also populates consciousness. It can therefore be difficult to ascertain whether an experimental manipulation intervenes cleanly on attention or whether it intervenes on consciousness too (Van Boxtel et al., 2010).

Consciousness is difficult to study, partly because of the intertwinement with attention and partly because it is multifaceted

too. Consciousness can apply to an overall state (e.g., awake vs. dreamless sleep) or a particular representation (e.g., conscious vs. unconscious processing of a face) all somehow tied together in the unity of the conscious stream (Bayne, 2010); it can pertain to the notion of a self (self-awareness) or just to being conscious (experience), and so on (Hohwy and Fox, 2012)¹. There are widely accepted tools for identifying the neural correlates of conscious experience, though there is also some controversy about how cleanly they manipulate conscious states rather than a wide range of other cognitive processes (Hohwy, 2009). In the background is the perennial, metaphysical mind–body problem (Chalmers, 1996), which casts doubt on the possibility of ever achieving a fundamentally naturalist understanding of consciousness; (we will not discuss any metaphysics in this paper, however).

Functionally, attention is sometimes said to be an “analyzer,” dissecting and selecting among the many possible and often competing percepts one has at any given time. Consciousness in contrast seems to be a “synthesizer,” bringing together and organizing our multitudinous sensory input at any given time (Van Boxtel et al., 2010). On the other hand, attention may bring unity too, via binding (Treisman and Gelade, 1980), and consciousness also has a selective role when ambiguities in the sensory input are resolved in favor of one rather than the other interpretation, as seems to happen in binocular rivalry.

Attention and consciousness, then, are both difficult to define, to operationalize in functional terms, and to manipulate experimentally. Part of the trouble here has to do with the phenomena themselves, and possibly even their metaphysical underpinnings. But a large part of the trouble seems due to their intertwined relations. It is difficult to resolve these issues by appeal to

¹ In addition to perceptual forms of consciousness there is also a live debate, set aside here, about non-perceptual forms of consciousness, such as conceptual thought (Bayne and Montague, 2011).

commonsense or empirically informed conceptual analyses of each phenomenon in isolation of the other. For this reason it may be fruitful to appeal to a very general theoretical framework for overall brain function, such as the increasingly influential prediction error minimization approach, and review whether it implies coherently related phenomena with a reasonable fit to attention and conscious perception.

Section “Aspects of Prediction Error Minimization” describes heuristically the prediction error minimization approach. Section “Prediction Error and Precision” focuses on two aspects of this approach, here labeled accuracy and precision, and maps these onto perceptual inference and attention. Section “Conscious Perception and Attention as Determined by Precise Prediction Error Minimization” outlines why this mapping might be useful for understanding conscious perception and its relation to attention. In Section “Interpreting Empirical Findings in the Light of Attention as Precision Optimization,” the statistical dimensions of precision and accuracy are used to offer interpretations of empirical studies of the relation between attention and consciousness. The final section briefly offers some broader perspectives.

ASPECTS OF PREDICTION ERROR MINIMIZATION

Two things motivate the idea of the hypothesis testing brain: casting a core task for the brain in terms of causal inference, and then appealing to the problem of induction.

The brain needs to represent the world so we can act meaningfully on it, that is, it has to figure out what in the world causes its sensory input. Representation is thereby a matter of causal inference. Causal inference however is problematic since a many–many relation holds between cause and effect: one cause can have many different effects, and one effect can have many different causes. This is the kernel of Hume’s problem of induction (Hume, 1739–1740, Book I, Part III, Section vi): cause and effect are distinct existences and there are no necessary connections between distinct existences. Only with the precarious help of experience can the contingent links between them be revealed.

For the special case of the brain’s attempt to represent the world, the problem of induction concerns how causal inference can be made “backwards” from the effects given in the sensory input to the causes in the world. This is the inverse problem, and it has a deep philosophical sting in the case of the brain. The brain *never* has independent access to both cause and effect because to have that it would already have had to solve the problem of representation. So it cannot learn from experience by just correlating occurrences of the two. It only has the effects to go by so must somehow begin the representational task *de novo*.

The prediction error minimization approach resolves this problem in time. The basic idea, described heuristically here, is simple whereas the computational details are complex (Friston, 2010). Sensory input is not just noise but has repeatable patterns. These patterns can give rise to expectations about subsequent input. The expectations can be compared to that subsequent input and the difference between them be measured. If there is a tight fit, then the pattern generating the expectation has captured a pattern in the real world reasonably well (i.e., the difference was close to expected levels of irreducible noise). If the fit is less good, that is, if there is a sizeable prediction error, then the states and parameters of

the hypothesis or model of the world generating the expectation should be revised so that subsequent expectations will, over time, get closer to the actual input.

This idea can be summed up in the simple dictum that to resolve the inverse problem all that is needed is prediction error minimization. Expected statistical patterns are furnished by generative models of the world and instead of attempting the intractable task of inverting these models to extract causes from generated effects, prediction error minimization ensures that the model recapitulates the causal structure of the world and is implicitly inverted; providing a sufficient explanation for sensory input.

This is consistent with a Bayesian scheme for belief revision in the light of new evidence, and indeed both Bayes as well as Laplace (before he founded classical frequentist statistics) developed their theories in response to the Humean-inspired inverse problem (McGrayne, 2011). The idea is to weight credence in an existing model of the world by how tightly it fits the evidence (i.e., the likelihood or how well it predicts the input) as well as how likely the model is in the first place (i.e., the prior probability or what the credence for the model was before the evidence came in).

The inverse problem is then resolved because, even though there is a many–many relation between causes in the world and sensory effects, some of the relations are weighted more than others in an optimally Bayesian way. The problem is solved *de novo*, without presupposing prior representational capability, because the system is supervised not by another agent, nor by itself, but by the very statistical regularities in the world it is trying to represent.

This key idea is then embellished in a number of different ways, all of which have bearing on attention and conscious perception.

HIERARCHY

The prediction error minimization mechanism sketched above is a general type of statistical building block that is repeated throughout levels of the cortical hierarchy such that there is recurrent message passing between levels (Mumford, 1992). The input to the system from the senses is conceived as prediction error and what cannot be predicted at one level is passed on to the next. In general, low levels of the hierarchy predict basic sensory attributes and causal regularities at very fast, millisecond, time scales, and more complex regularities, at increasingly slower time scales, are dealt with at higher levels (Friston, 2008; Kiebel et al., 2008, 2010; Harrison et al., 2011). Prediction error is concurrently minimized across all levels of the hierarchy, and this unearths the states and parameters that represent the causal structure and depth of the world.

CONTEXTUAL PROBABILITIES

Predictions at any level are subject to contextual modulation. This can be via lateral connectivity, that is, by predictions or hypotheses at the same hierarchical level, or it can be through higher level control parameters shaping low level predictions by taking slower time scale regularities into consideration. For example, the low level dynamics of birdsong is controlled by parameters from higher up pertaining to slower regularities about the size and strength of the bird doing the singing (Kiebel et al., 2010). Similarly, it may be that the role of gist perception is to provide contextual clues for fast classification of objects in a scene (Kveraga et al., 2007). The entire cortical hierarchy thus recapitulates the causal structure of

the world, and the bigger the hierarchy the deeper the represented causal structure.

EMPIRICAL BAYES

For any appeal to Bayes, the question arises where do the priors come from (Kersten et al., 2004)? One scheme for answering this, and evading charges of excessive subjectivity, is empirical Bayes where priors are extracted from hierarchical statistical learning (see, e.g., Casella, 1992). In the predictive coding scheme this does not mean going beyond Bayes to frequentism. (Empirical) Priors are sourced from higher levels in the hierarchy, assuming they are learned in an optimally Bayesian fashion (Friston, 2005). The notion of hierarchical inference is crucial here, and enables the brain to optimize its prior beliefs on a moment to moment basis. Many of these priors would be formed through long-term exposure to sensory contingencies through a creature's existence but it is also likely that some priors are more hard-wired and instantiated over an evolutionary time-scale; different priors should therefore be malleable to different extents by the creature's sensation.

FREE ENERGY

In its most general formulation, prediction error minimization is a special case of free energy minimization, where free energy (the sum of squared prediction error) is a bound on information theoretical surprise (Friston and Stephan, 2007). The free energy formulation is important because it enables expansion of the ideas discussed above to a number of different areas (Friston, 2010). Here, it is mainly the relation to prediction error minimization that will be of concern. Minimizing free energy minimizes prediction error and implicitly surprise. The idea here is that the organism cannot directly minimize surprise. This is because there is an infinite number of ways in which the organism could seek to minimize surprise and it would be impossibly expensive to try them out. Instead, the organism can test predictions against the input from the world and adjust its predictions until errors are suppressed. Even if the organism does not know what will surprise it, it can minimize the divergence between its expectations and the actual inputs encountered. A frequent objection to the framework is that prediction error and free energy more generally can be minimized by committing suicide since nothing surprises a dead organism. The response is that the moment an organism dies it experiences a massive increase in free energy, as it decomposes and is unable to predict anything (there is more to say on this issue, see Friston et al., in press; there is also a substantial issue surrounding how these types of ideas can be reconciled with evolutionary ideas of survival and reproduction, for discussion see, Badcock, 2012).

ACTIVE INFERENCE

A system without agency cannot minimize surprise but only optimize its models of the world by revising those models to create a tight free energy bound on surprise. To minimize the surprise it needs to predict how the system's own intervention in the world (e.g., movement) could change the actual input such as to minimize free energy. Agency, in this framework, is a matter of selectively sampling the world to ensure prediction error minimization across all levels of the cortical prediction hierarchy

(Friston et al., 2009, 2011). To take a toy example: an agent sees a new object such as a bicycle, the bound on this new sensory surprise is minimized, and the ensuing favored model of the world lets the agent predict how the prediction error landscape will change given his or her intervention (e.g., when walking around the bike). This prediction gives rise to a prediction error that is not minimized until the agent finds him or herself walking around the bike, hence the label "active inference." If the initial model was wrong, then active inference fails to be this kind of self-fulfilling prophecy (e.g., it was a cardboard poster of a bike). Depending on the depth of the represented causal hierarchy this can give rise to very structured behavior (e.g., not eating all your food now even though you are hungry and instead keeping some for winter, based on the prediction this will better minimize free energy).

There is an intuitive seesaw dynamic here between minimizing the bound and actively sampling the world. It would be difficult to predict efficiently what kind of sampling would minimize surprise if the starting point was a very poor, inaccurate, bound on surprise. Similarly, insofar as selective sampling never perfectly minimizes surprise, new aspects of the world are revealed, which should lead to revisiting the bound on surprise. It thus pays for the system to maintain both perceptual and active inference.

TOP-DOWN AND BOTTOM-UP

This framework comes with a re-conceptualization of the functional roles of the bottom-up driving signal from the senses, and the top-down or backward modulatory signal from higher levels. The bottom-up signal is not sensory information *per se* but instead just prediction error. The backward signal embodies the causal model of the world and the bottom-up prediction error is then essentially the supervisory feedback on the model (Friston, 2005). It is in this way the sensory input ensures the system is supervised, not by someone else nor by itself, but by the statistical regularities of the world.

The upshot is an elegant framework, which is primarily motivated by principled, philosophical and computational concerns about representation and causal inference. It is embellished in a number of ways that capture many aspects of sensory processing such as context-dependence, the role of prior expectations, the way perceptual states comprise sensory attributes at different spatiotemporal resolutions, and even agency. We shall appeal to all these elements as predictive coding is applied to attention and conscious perception.

PREDICTION ERROR AND PRECISION

As discussed above, there are two related ways that prediction error can be minimized: either by changing the internal, generative model's states, and parameters in the light of prediction error, or keeping the model constant and selectively sampling the world and thereby changing the input. Both ways enable the model to have what we shall here call *accuracy*: the more prediction error is minimized, the more the causal structure of the world is represented².

²There is a simplification here: surprise has both accuracy and complexity components, such that minimizing surprise or free energy increases accuracy while minimizing complexity. This ensures the explanations for sensory input are parsimonious and will generalize to new situations; c.f., Occam's razor.

So far, this story leaves out a crucial aspect of perceptual inference concerning *variability* of the prediction error. Prediction error minimization of the two types just mentioned assumes noise to be constant, and the variability of all prediction errors therefore the same. This assumption does not actually hold as noise or uncertainty is state dependent. Prediction error that is unreliable due to varying levels of noise in the states of the world is not a learning signal that will facilitate confident veridical revision of generative models or make it likely that selective sampling of the world is efficient. Prediction error minimization must therefore take variability in prediction error messaging into consideration – it needs to assess the precision of the prediction error.

Predictions are tested in sensory sampling: given the generative model a certain input is predicted where this input can be conceived as a distribution of sensory samples. If the actual distribution is different from the expected distribution, then a prediction error is generated. One way to assess a difference in distributions is to assess central tendency such as the mean. However, as is standard in statistical hypothesis testing, even if the means seem different (or not) the variability may preclude a confident conclusion that the two distributions are different (or not). Hence, any judgment of difference must be weighed by the magnitude of the variability – this is a requirement for trusting prediction error minimization.

The inverse of variability is the precision (inverse dispersion or variance) of the distribution. In terms of the framework used here, when the system “decides” whether to revise internal models in the light of prediction errors and to sample the world accordingly, those errors are weighted by their precisions. For example, a very imprecise (i.e., noisy, variable) prediction error should not lead to revision, since it is more likely to be a random upshot of noise for a given sensory attribute.

However, the rule cannot be simply that the more the precision the stronger the weight of the prediction error. Our expectations of precision are context dependent. For example, precisions in different sensory modalities differ (for an example, see Bays and Wolpert, 2007), and differ within the same modality in different contexts and for different sensory attributes. Sometimes it may be that one relatively broad, imprecise distribution should be weighed more than another narrower, precise distribution. Similarly, an unusually precise prediction error may be highly inaccurate as a result of under-sampling, for example, and should not lead to revision. In general, the precision weighting should depend on prior learning of regularities in the actual levels of noise in the states of the world and the system itself (e.g., learning leading to internal representations of the regularity that sensory precision tends to decline at dusk).

There is then a (second order) perceptual inference problem because the magnitude of precision cannot be measured absolutely. It must be assessed in the light of *precision expectations*. The consequence is that generative models must somehow embody expectations for the precision of prediction error, in a context dependent fashion. Crucially, the precision afforded a prediction has to be represented; in other words, one has to represent the known unknowns.

If precision expectations are optimized then prediction error is weighted accurately and replicates the precisions in the world. In

terms of perceptual inference, the learning signal from the world will have more weight from units expecting precision, whereas top-down expectations will have more influence on perception when processing concerns units expecting a lot of imprecision; one's pre-conceptions play a bigger role in making sense of the world when the signal is deemed imprecise (Hesselmann et al., 2010). This precision processing is thought to occur in synaptic error processing such that units that expect precision will have more weight (synaptic gain) than units expecting imprecision (Friston, 2009).

Given a noisy world and non-linear interactions in sensory input, first order statistics (prediction errors) and second order statistics (the precision of prediction errors) are then necessary and jointly sufficient for resolving the inverse problem. In what follows, the optimization of representations is considered in terms of both *precision* and *accuracy*, precision refers to the inverse amplitude of random fluctuations around, or uncertainty about, predictions; while accuracy (with a slight abuse of terminology) will refer to the inverse amplitude of prediction errors *per se*. Minimizing free energy or surprise implies the minimization of precise prediction errors; in other words, the minimization of the sum of squared prediction error and an optimal estimate of precision.

Using the terminology of accuracy and precision is useful because it suggests how the phenomena can come apart in a way that will help in the interpretation of the relation between consciousness and attention. It is a trivial point that precision and accuracy can come apart: a measurement can be accurate but imprecise, as in feeling the child's fever with a hand on the forehead or it can be very precise but inaccurate, as when using an ill calibrated thermometer. This yields two broad dimensions for perceptual inference in terms of predictive coding: accuracy (via expectation of sensory input) and precision (via expectation of variability of sensory input). These can also come apart. Some of the states and parameters of an internal model can be inaccurate and yet precise (being confident that the sound comes from in front of you when it really comes from behind, Jack and Thurlow, 1973). Or they can be accurate and yet, imprecise (correctly detecting a faint sound but being uncertain about what to conclude given a noisy background).

With this in mind, assume now that *conscious perception* is determined by the prediction or hypothesis with the highest overall posterior probability – which is overall best at minimizing prediction error (this assumption is given support in the next section). That is, conscious perception is determined by the strongest “attractor” in the free energy landscape; where, generally speaking, greater precision leads to higher conditional confidence about the estimate and a deeper, more pronounced minimum in the free energy landscape.

On this assumption, precision expectations play a key role for conscious perception. We next note the proposal, which will occupy us in much of the following, that optimization of precision expectations maps on to attention (Friston, 2009). It is this mapping that will give substance to our understanding of the relation between attention and consciousness. It is a promising approach because precision processing, in virtue of its relation to accuracy, has the kind of complex relation to prediction error minimization that seems appropriate for capturing both the commonsense notion that conscious perception and attention are intertwined

and also the notion that they are separate mechanisms (Koch and Tsuchiya, 2007; Van Boxtel et al., 2010).

We can usefully think of this in terms of a system such that, depending on context (including experimental paradigms in the lab), sensory estimates may be relatively accurate and precise, inaccurate and imprecise, accurate and imprecise, or inaccurate and precise. With various simplifications and assumptions, this framework can then be sketched as in **Figure 1**.

By and large, conscious perception will be found for states that are both accurate and precise but may also be found for states that are relatively accurate and yet imprecise, and *vice versa*. Two or more competing internal models or hypotheses about the world can have different constellations of precision and accuracy: a relatively inaccurate but precise model might determine conscious perception over a competing accurate but imprecise model, and *vice versa*. Similarly, a state can evolve in different ways: it can for example begin by being very inaccurate and imprecise, and thus not determining conscious perception but attention can raise its conditional confidence and ensure it does get to determine conscious content.

On this framework, it should then also be possible to speak to some of the empirical findings of dissociations between attention and consciousness. A case of attention without consciousness would be where precision expectations are high for a state but prediction error for it is not well minimized (expecting a precise signal, or, expecting inference to be relatively bottom-up driven). A case of consciousness without attention would be where

prediction error is well minimized but where precision is relatively low (expecting signals to be variable, or, expecting inference to be relatively top-down driven). It is difficult to say precisely what such states would be like. For example, a conscious, inattentive state might have a noisy, fuzzy profile, such as gist perception may have (Bar, 2007). It is also possible that increased reliance on top-down, prior beliefs could in fact paradoxically sharpen the representational profile (Ross and Burr, 2008)³. In general, in both types of cases, the outcome would be highly sensitive to the context of the overall free energy landscape, that is, to competing hypotheses and their precision expectations.

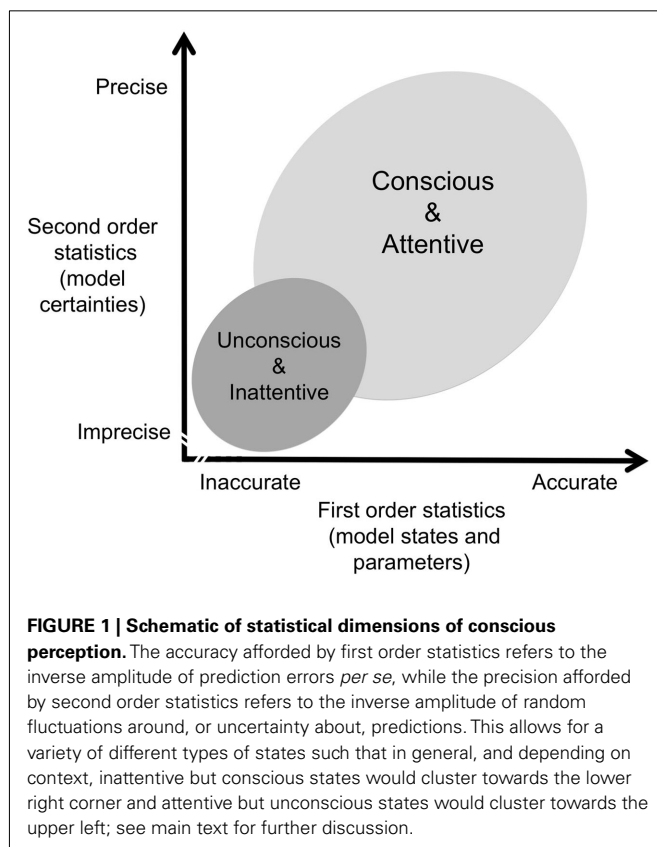
Section “Interpreting Empirical Findings in the Light of Attention as Precision Optimization” will begin the task of interpreting some studies in the field according to these accuracy and precision dimensions. The next section, however, will provide some *prima facie* motivation for this overall framework.

CONSCIOUS PERCEPTION AND ATTENTION AS DETERMINED BY PRECISE PREDICTION ERROR MINIMIZATION

In this section, conscious perception and attention are dealt with through the prism of predictive coding. Though the evidence in favor of this approach is growing (see the excellent discussion in Summerfield and Egner, 2009) much of this is still speculative⁴. The core idea is that conscious perception correlates with activity, spanning multiple levels of the cortical hierarchy, which best suppresses precise prediction error: what gets selected for conscious perception is the hypothesis or model that, given the widest context, is currently most closely guided by the current (precise) prediction errors⁵.

Conscious perception can then thought to be at the service of representing the world, and the currently best internal, generative model is the one that most probably represents the causal structure of the world. Predictions by other models may also be able to suppress prediction error, but less well, so they are not selected. Conversely, often some other, possible models could be even better at suppressing prediction error but if the system has not learnt them yet, or cannot learn them, it must make do with the best model it has.

It follows that the predictions of the currently best model can actually be rather inaccurate. However, if it has no better competitor then it will win and get selected for consciousness. Conscious



³There is also a very good question here about how this kind of confidence assessment fits with the psychological confidence of the organism, which appears a defining feature of consciousness, and which is often assessed in confidence ratings. (Thanks to a reviewer for raising this issue).

⁴A further disclaimer: the speculation that conscious perception is a product of accuracy and precision in predictive coding is a limited speculation about an information processing mechanism. It is not a speculation about *why* experience is conscious rather than not conscious – predictive coding can after all be implemented in unconscious machines. The mystery of consciousness will remain untouched.

⁵This claim depends on optimal Bayesian inference actually being able to recapitulate the causal structure of the world. Here we bracket for philosophical debate the fact that this assumption breaks down for perfect skeptical scenarios, such as Cartesian deceiving demons or evil scientists manipulating brains in vats, where minimizing free energy does not reveal the true nature of the world. We also bracket deeper versions of the problem of induction, such as the new riddle of induction (Goodman, 1955), though we note that when two hypotheses are equally good at predicting new input the free energy principle prefers the one with the smallest complexity cost.

perception can then be far from veridical, in spite of its representational nature. This makes room for an account of illusory and hallucinatory perceptual content, which is an important desideratum on accounts of conscious perception. These would be cases where, for different reasons, poor models are best at precisely explaining away incoming data only because their competitors are even poorer.

The job of the predictive coding system is to attenuate sensory input by treating it as information theoretical surprise and predicting it as perfectly as possible. As the surprise is attenuated, models should stop being revised and predictive activity progressively cease throughout the hierarchy. This seems consistent with repetition suppression (Grill-Spector et al., 2006) where neural activity ceases in response to expected input in a manner consistent with prediction error minimization (Summerfield et al., 2008; Todorovic et al., 2011). At the limit it should have consequences for conscious perception too. When all the surprise is dealt with, prediction and model revision should cease. If it is also impossible to do further selective sampling then conscious perception of the object in question should cease. This follows from the idea that what we are aware of is the “fantasy” generated by the way current predictions attenuate prediction error; if there is no prediction error to explain away, then there is nothing to be aware of. Presumably there is almost always some input to some consumer systems in the brain (including during dreaming) but conceivably something close to this happens when stabilized retinal images fade from consciousness (Ditchburn and Ginsborg, 1952). Because such stimuli move with eye and head movement predictive exploration of them is quickly exhausted.

Conscious perception is often rich in sensory attributes, which are neatly bound together even though they are processed in a distributed manner throughout the brain. The predictive coding account offers a novel approach to this “binding” aspect of conscious perception. Distributed sensory attributes are bound together by the causal inference embodied in the parameters of the generative model. The model assumes, for example, that there is a red ball out there so will predict that the redness and the bouncing object co-occur spatiotemporally. The binding problem (Treisman, 1996) is then dealt with by default: the system does not have to operate in a bottom-up fashion and first process individual attributes and then bind them. Instead, it assumes bound attributes and then predicts them down through the cortical hierarchy. If they are actually bound in the states of the world, then this will minimize prediction error, and they will be experienced as such.

It is a nice question here what it means for the model with the highest posterior probability to be “selected for consciousness.” We can only speculate about an answer but it appears that on the predictive coding framework there does not have to be a specific selection mechanism (no “threshold” module, cf. Dennett, 1991). When a specific model is the one determining the consciously perceived content it is just because it best minimizes prediction error across most levels of the cortical hierarchy – it best represents the world given all the evidence and the widest possible context. This is the model that should be used to selectively sample the world to minimize surprise in active inference. Competing but less probable models cannot simultaneously determine the target of active inference: the models would be at cross-purposes such that the

system would predict more surprise than if it relies on one model alone (for more on the relation between attention and action, see Wu, 2011).

Though there remain aspects of consciousness that seem difficult to explain, such as the conscious content of imagery and dreaming, this overall approach to conscious perception does then promise to account for a number of key aspects of consciousness. The case being built here is mainly theoretical. There is not yet much empirical evidence for this link to conscious perception, though a recent dynamical causal modeling study from research in disorders of consciousness (vegetative states and minimally conscious states) suggests that what is required for an individual to be in an overall conscious state is for them to have intact connectivity consistent with predictive coding (Boly et al., 2011).

As we saw earlier, in the normal course of events, the system is helped in this prediction error minimization task by precision processing, which (following Feldman and Friston, 2010) was claimed to map on to attention such that attention is precision optimization in hierarchical perceptual inference. A prediction error signal will have a certain absolute dispersion but whether the system treats this as precise or not depends on its precision expectations, which may differ depending on context and beliefs about prior precision. Precise prediction errors are reliable signals and therefore, as described earlier, enable a more efficient revision of the model in question (i.e., a tighter bound and better active inference). If that model then, partly resulting from precision optimization, achieves the highest posterior probability, it will determine the content of conscious perception. This begins to capture the functional role often ascribed to attention of being a gating or gain mechanism that somehow optimizes sensory processing (Hillyard and Mangun, 1987; Martinez-Trujillo and Treue, 2004). As shall be argued now, it can reasonably account for a wider range of characteristics of attention.

EXOGENOUS ATTENTION

Stimuli with large spatial contrast and/or temporal contrast (abrupt onset) tend to “grab” attention bottom-up, or exogenously. These are situations where there is a relatively high level of sensory input, that is, a stronger signal. Given an expectation that stronger signals have better signal to noise ratio (better precision), than weaker signals (Feldman and Friston, 2010, p. 9; Appendix), error units exposed to such signals should thus expect high precision and be given larger gain. As a result, more precise prediction error can be suppressed by the model predicting this new input, which is then more likely to be the overall winner populating conscious experience. Notice that this account does not mention expectations about *what* the signal stems from, only about the signal’s reliability. Also notice that this account does not guarantee that what has the highest signal to noise ratio will end up populating consciousness, it may well be that other models have higher overall confidence or posterior probability.

ENDOGENOUS ATTENTION

Endogenous attention is driven more indirectly by probabilistic context. Beginning with endogenous cueing, a central cue pointing left is itself represented with high precision prediction error (it grabs attention) and in the parameters of the generative model

this cue representation is related to the representation of a stimulus to the left, via a learned causal link. This reduces uncertainty about what to predict there (increases prior probability for a left target) and it induces an expectation of high precision for that region. When the stimulus arrives, the resulting gain on the error units together with the higher prior help drive a higher conditional confidence for it, making it likely it is quickly selected for conscious perception.

The idea behind endogenous attention is then that it works as an increase in baseline activity of neuronal units encoding beliefs about precision. There is evidence that such increase in activity prior to stimulus onset is specific to precision expectations. The narrow distributions associated with precise processing tell us that in detection tasks the precision-weighted system should tend to respond when and only when the target appears. And indeed such baseline increases do bias performance in favor of hits and correct rejections (Hesselmann et al., 2010). In contrast, if increased baseline activity had instead been a matter of mere accumulation of evidence for a specific stimulus (if it had been about accuracy and not precision), then the baseline increase should instead have biased toward hits and false alarms.

A recent paper directly supports the role of endogenous attention as precision weighting (Kok et al., 2011). As we have seen, without attention, the better a stimulus is predicted the more attenuated its associated signal should be. Attention should reverse this attenuation because it strengthens the prediction error. However, attention depends on the predictability of the stimulus: there should be no strong expectation that an unpredicted stimulus is going to be precise. So there should be less attention-induced enhancement of the prediction error for unpredicted stimuli than for better predicted stimuli. Using fMRI, Kok et al. very elegantly provides evidence for this interaction in early visual cortex (V1).

In more traditional cases of endogenous attention (e.g., the individual deciding herself to attend left) the cue can be conceived as a desired state, for example, that something valuable will be spotted to the left. This would then generate an expectation of precision for that region such that stimuli located there are more likely to be detected. Endogenous attention of this sort has a volitional aspect: the individual decides to attend and acts on this decision. Such agency can range from sensorimotor interaction and experimentation to a simple decision to fixate on something. This agential aspect suggests that part of attention should belong with active inference (selective sampling to minimize surprise). The idea here would be that the sampling is itself subject to precision weighting. This makes sense since the system will not know if its sampling satisfies expectations unless it can assess the variability in the sampling. Without such an assessment, the system will not know whether to keep sampling on the basis of a given model or whether the bound on the model itself needs to be re-assessed. In support of this, there is emerging evidence that precision expectations are also involved in motor behavior (Brown et al., 2011).

BIASED COMPETITION

An elegant approach to attention begins with the observation that neurons respond optimally to one object or property in their receptive field so that if more than one object is present,

activity decreases unless competition between them is resolved. The thought is that attention can do this job, by biasing one interpretation over another (Desimone and Duncan, 1995). Attention is thus required to resolve ambiguities of causal inference incurred by the spatial architecture of the system. Accordingly, electrophysiological studies show decreased activity when two different objects are present in a neuron's receptive field, and return to normal levels of activity when attention is directed toward one of them (Desimone, 1998).

The predictive coding framework augmented with precision expectations should be able to encompass biased competition. This is because, as mentioned, precision can modulate perceptual inference when there are two or more competing, and perhaps equally accurate, models. Indeed, computational simulation shows precision-weighted predictive coding can play such a biasing role in a competitive version of the Posner paradigm where attention is directed to a cued peripheral stimulus rather than a competing non-cued stimulus. A central cue thus provides a context for the model containing the cued stimulus as a hidden cause. This drives a high precision expectation for that location, which ensures relatively large gain, and quicker response times, when those error units are stimulated. This computational model nicely replicates psychophysics and electrophysiological findings (Feldman and Friston, 2010, pp. 14–15).

Attentional competition is then not a matter somehow of intrinsically limited processing resources or of explicit competition. It is a matter of optimal Bayesian inference where only one model of the causal regularities in the world can best explain away the incoming signal, given prior learning, and expectations of state-dependent levels of noise.

Binding of sensory attributes by a cognitive system was mooted above as a natural element of predictive coding. Attention is also thought to play a role for binding (Treisman and Gelade, 1980; Treisman, 1998) perhaps via gamma activity (Treisman, 1999) such that synchronized neurons are given greater gain. Again, this can be cast in terms of precision expectations: sensory attributes bound to the same object are mutually predictive and so if the precision-weighted gain for one is increased it should increase for the other too. Though this is speculative, the predictive coding framework could here elucidate the functional role of increased gamma activity and help us understand how playing this role connects to attention and conscious perception.

Perhaps we should pause briefly and ask why we should adopt this framework for attention in particular – what does it add to our understanding of attention to cast it in terms of precision expectations? A worry could be that it is more or less a trivial reformulation of notions of gain, gating, and bias, which has long been used to explicate attention in a more or less aprioristic manner. The immediate answer is that this account of attention goes beyond mere reformulations of known theories, not just because its basic element is precision, but also because it turns on learning precision regularities in the world so different contexts will elicit different precision expectations. This is crucial because optimization of precision is context dependent and thus requires appeal to just the kind of predictive framework used here.

There is also a more philosophical motivation for adopting this approach. Normally, an account of attention would begin with

some kind of operational, conceptual analysis of the phenomenon: attention has to do with salience, with some kind of selection of sensory channels, resource limitations, and so on. Then the evidence is consulted and theories formulated about neural mechanisms that could underpin salience and selection etc. This is a standard and fruitful approach in science. But sometimes taking a much broader approach gives a better understanding of the nature of the phenomenon of interest and its relation to other phenomena (*cf.* explanation by unification, Kitcher, 1989). In our case, a very general conception of the fundamental computational task for the brain defines two functional roles that must be played: estimation of states and parameters, and estimation of precisions. Without beginning from a conceptual analysis of attention, we then discover that the element of precision processing maps on well to the functional role we associate with attention. This discovery tells us something new about the nature of attention: the reason why salience and selection of sensory channels matter, and the reason why there appears to be resource limitations on attention, is that the system as such must assess precisions of sensory estimates and weight them against each other.

Viewing attention from the independent vantage point of the requirements of predictive coding also allows us to revise the concept of attention somewhat, which can often be fruitful. For example, there is no special reason why attention should always have to do with conscious perception, given the ways precision and accuracy can come apart; that is, there may well be precision processing—attention—outside consciousness. The approach suggests a new way for us to understand how attention and perception can rely on separate but related mechanisms. This is the kind of issue to which we now turn.

INTERPRETING EMPIRICAL FINDINGS IN THE LIGHT OF ATTENTION AS PRECISION OPTIMIZATION

The framework for conscious perception sketched in Section “Prediction Error and Precision” (see **Figure 1**) implied that studies of the relation between consciousness and attention can be located according to the dimensions of accuracy and precision. We now explore if this implication can reasonably be said to hold for a set of key findings concerning: inattentional blindness, change blindness, the effects of short term and sustained covert attention on conscious perception, and attention to unconscious stimuli.

The tools for interpreting the relevant studies must be guided by the properties of predictive coding framework we have set out above, so here we briefly recapitulate: (1) even though accuracy and precision are both necessary for conscious perception, it does not follow that the single *most* precise or the *most* accurate estimate in a competing field of estimates will populate consciousness: that is determined by the overall free energy landscape. For example, it is possible for the highest overall posterior probability to be determined by an estimate having high accuracy and relatively low precision even if there is another model available that has relatively low accuracy yet high precision, and so on. (2) Attention in the shape of precision expectation modulates prediction error minimization subject to precisions predicted by the context, including cues and competing stimuli; it can do this for prediction errors of different accuracies. (3) Precision weighting only makes sense if weights sum to one so that as one goes up the others must go

down. Similarly, as the probability of one model goes up the probability of other models should go down – the other models are explained away if one model is able to account for and suppress the sensory input. This gives rise to model competition. (4) Conscious experience of unchanging, very stable stimuli will tend to be suppressed over time, as prediction error is explained away and no new error arises. (5) Agency is active inference: a model of the agent’s interaction with the world is used to selectively sample the world such as to minimize surprise. This also holds for volitional aspects of attention, such as the agency involved in endogenous attention to a spatial location.

The aim now is to use these properties of predictive coding to provide a coherent interpretation of the set of very different findings on attention and consciousness.

TYPES OF INATTENTIONAL BLINDNESS

The context for a stimulus can be a cue or an instruction or other sensory information, or perhaps a decision to attend. Various elements of this context can give a specific generative model two advantages: it can increase priors for its states and parameters (for this part of the view, see also Rao, 2005) and it can bias selection of that model via precision weighting. When the target stimulus comes, attention has thus already given the model for that stimulus a probabilistic advantage. If in contrast the context is invalid (non-predictive) and a different target stimulus occurs, the starting point for the model predicting it can be much lower both in terms of prior probability and in terms of precision expectation. If this lower starting point is sufficiently low, and if the invalidly contextualized stimulus is not itself strongly attention grabbing (is not abrupt in some feature space such as having sharp contrast or temporal onset), then “the invalid target may never actually be perceived” (Feldman and Friston, 2010, pp. 9–10).

This is then what could describe forms of inattentional blindness where an otherwise visible stimulus is made invisible by attending to something at a different location: an attentional task helps bias one generative model over models for unexpected background or peripheral stimuli. A very demanding attentional task would have very strong bias from precision weighting, and correspondingly the weight given to other models must be weakened. This could drive overall posterior probability below selection for consciousness, such that not even the gist of, for example, briefly presented natural scenes is perceived.

It is natural to conclude in such experiments that attention is a necessary condition for conscious perception since unattended stimuli are not seen, and as soon as they are seen performance on the central task decreases (Cohen et al., 2011). This is right in the sense that any weighting of precision to the peripheral or background stimulus must go with decreased weight to the central task. However, the more fundamental truth here is that in a noisy world precision weighting is necessary for conscious perception so that at the limit, where noise expectations are uniform, there could be conscious perception even though attention plays very little actual role.

When inattentional blindness is less complete, the gist of briefly presented natural scenes can be perceived (see, Van Boxtel et al., 2010). This is consistent with relatively low precision expectation since gist is by definition imprecise. So in this case some, but

relatively little prediction error is allowed through for the natural scene, leaving only little prediction error to explain away. It seems likely that this could give rise to gist rather than full perception. However, the distinction between gist and full perception is not well understood and there are more specific views on gist perception, also within the broad predictive coding framework (Bar, 2003).

In some cases of inattention blindness, large and otherwise very salient stimuli can go unnoticed. Famously, when counting basketball passes a gorilla can be unseen, and when chasing someone a nearby fistfight can be unseen (Simons and Chabris, 1999; Chabris et al., 2011). This is somewhat difficult to explain because endogenous attention as described so far should raise the baseline for precision expectation for a specific location such that any stimulus there, whether it is a basketball pass or a gorilla, should be more likely to be perceived. A smaller proportion of participants experience this effect, so it does in fact seem harder to induce blindness in this kind of paradigm than paradigms using central-peripheral or foreground-background tasks. For those who do have inattention blindness under these conditions, the explanation could be high precision expectations for the basketball passes specifically, given the context of the passes that have occurred before the gorilla enters. This combines with the way this precision error has driven up the conditional confidence of the basketball model, explaining away the gorilla model, even if the latter is fed some prediction error. This more speculative account predicts that inattention blindness should diminish if the gorilla, for example, occurs at the beginning of the counting task.

This is then a way to begin conceptualizing feature- and object-based based attention instead of purely spatial attention. Van Boxtel et al. (2010) suggest that in gorilla type cases the context provided by the overall scene delivers a strong gist that overrides changes that fit poorly with it: “subjects do perceive the gist of the image correctly, interfering with detection of a less meaningful change in the scene as if it was filled in by the gist.” The predictive coding approach can offer an explanation of this kind of interference in probabilistic terms.

A further aspect can be added to this account of inattention blindness. Attending, especially endogenous attending, is an activity. As such, performing an attention demanding task is a matter of active inference where a model of the world is used to selectively sample sensory input to minimize surprise. This means that high precision input are expected and sampled on the basis of one, initial (e.g., “basketball”) model, leaving unexpected input such as the occurrence of a gorilla with low weighting. Since the active inference required to comply with an attentional task must favor one model in a sustained way, blindness to unexpected stimuli follows.

The benefit of sustained attention viewed as active inference is then that surprise can be minimized with great precision, given an initial model's states and parameters. On the other hand, the cost of sustained attention is that the prediction error landscape may change during the task; increasing the free energy and making things evade consciousness.

It can thus be disadvantageous for a system to be stuck in active inference and neglecting to revisit the bound on surprise by updating the model (e.g., if the gorilla is real and angry). Perhaps the reason attention can be hard to maintain is that to avoid

such disadvantage the system continually seeks, perhaps via spontaneous fluctuations, to alternate between perceptual and active inference. Minor lapses of attention (e.g., missing a pass) could thus lead to some model revision and conscious perception; if the model revision has relatively low precision it may just give rise to gist perception (e.g., “some black creature was there”).

It is interesting here to speculate further that the functional role of exogenous attention can be to not only facilitate processing of salient stimuli but in particular to make the system snap out of active inference, which is often associated with endogenous attention, and back into revision of its generative model. Exogenous and endogenous attention seem to have opposing functional roles in precision optimization.

There remains the rather important and difficult question whether or not the unseen stimulus is in fact consciously perceived but not accessible for introspective report, or whether it is not consciously perceived at all; this question relates to the influential distinction between access consciousness and phenomenal consciousness (Block, 1995, 2008). To some, this question borders on the incomprehensible or at least untestable (Cohen and Dennett, 2011), and there is agreement it cannot be answered directly (e.g., by asking participants to report). Instead some indirect, abductive answer must be sought. We cannot answer this question here but we can speculate that the common intuition that there is both access *and* phenomenal consciousness is fueled by the moments of predictive coding such that (i) access consciousness goes with active inference (i.e., minimizing surprise though agency, which requires making model parameters and states available to control systems), and (ii) phenomenal consciousness goes with perceptual inference (i.e., minimizing the bound on surprise by more passively updating model parameters and states).

If this is right, then a prediction is that in passive viewing, where attention and active inference is kept as minimal as possible, there should be more possibility of having incompatible conscious percepts at the same time, since without active inference there is less imperative to favor just one initial model. There is some evidence for this in binocular rivalry where the absence of attention seems to favor fusion (Zhang et al., 2011).

Overall, some inroads on inattention blindness can be made by an appeal to precision expectations giving the attended stimulus a probabilistic advantage. A more full, and speculative, explanation conceives attention in agential terms and appeals to the way active inference can lead to very precise but eventually overall inaccurate perceptual states.

CHANGE BLINDNESS

These are cases where abrupt and scene-incongruent changes like sudden mudsplashes attract attention and make invisible other abrupt but scene-congruent changes like a rock turning into a log or an aircraft engine going missing (Rensink et al., 1997). Only with attention directed at (or on repeated exposures grabbed by) the scene-congruent change will it be detected. This makes sense if the distractor (e.g., mudsplashes) has higher signal strength than the masked stimuli because, as we saw, there is a higher precision expectation for stronger signals. This weights prediction error for a mudsplash model rather than for a natural scenery model with logs or aircrafts. Even if both models are updated in the light of their

respective prediction errors from the mudsplashes and the rock changing to the log, the mudsplash model will have higher conditional confidence because it can explain away precisely a larger part of the bottom-up error signal.

More subtly, change blindness through attention grabbing seems to require that the abrupt stimuli activate a competing model of the causes in the world. This means that the prediction error can be relevant to the states and parameters of one of these models. Thus, the mudsplashes mostly appear to be superimposed on the original image, which activates a model with parameters for causal interaction between mudsplashes and something like a static photo. In other words, the best explanation for the visual input is the transient occlusion or change to a photo, where, crucially, we have strong prior beliefs that photographs do not change over short periods of time. This contrasts with the situation prior to the mudsplashes occurring where the model would be tuned more to the causal relations inherent in the scene itself (that is, the entire scene is not treated as a unitary object that can be mudsplashed). With two models, one can begin to be probabilistically explained away by the other: as the posterior probability of the model that treats the scene as a unitary object increases, the probability of the model that treats it as composite scene will go down. Once change blindness is abolished, such that both mudsplashes and scene changes are seen, a third (“Photoshop”) model will have evolved on which individual components can change but not necessarily in a scene-congruent manner. All this predicts that there should be less change blindness for mudsplashes on dynamic stimuli such as movies because the causal model for such stimuli has higher accuracy; it also predicts less blindness if the mudsplashes are meaningful in the original scene such that competition between models is not engendered.

For some scene changes it is harder to induce change blindness. Mudsplashes can blind us when a rock in the way of a kayak changes into a log, but blinds us less when the rock changes into another kayak (Sampanes et al., 2008). This type of situation is often dealt with in terms of gist changes but it is also consistent with the interpretation given above. The difference between a log and another kayak in the way of the kayak is in the change in parameters of the model explaining away the prediction error. The change from an unmoving object (rock) to another unmoving object (log) incurs much less model revision than the change to a moving, intentional object (other kayak): the scope for causal interaction between two kayaks is much bigger than for one kayak and a log. The prediction error is thus much bigger for the latter, and updating the model to reflect this will increase its probability more, and make blindness less likely.

A different type of change blindness occurs when there is no distractor but the change is very slow and incremental (e.g., Simons et al., 2000), such as a painting where one part changes color over a relatively long period of time. Without attention directed at the changing property, the change is not noted. In this case it seems likely that each incremental change is within the expected variability for the model of the entire scene. When attention is directed at the slowly changing component of the scene, the precision expectation and thus the weighting goes up, and it is more likely that the incremental change will generate a prediction error. This is then an example of change blindness due to imprecise prediction error minimization. If this is right, a prediction is that change of

precision expectation through learning, or individual differences in such expectations, should affect this kind of change blindness.

SHORT TERM COVERT ATTENTION ENHANCES CONSCIOUS PERCEPTION

If a peripheral cue attracts covert attention to a grating away from fixation, then conscious experience of its contrast is enhanced (Carrasco et al., 2004). Similar effects are found for spatial frequency and gap size (Gobell and Carrasco, 2005). In terms of precision, the peripheral cue induces a high precision expectation for the cued region, which increases the weighting for prediction error from the low contrast grating placed there. Specifically, the expectation will be for a stimulus with an improved signal to noise ratio, that is, a stronger signal. This then seems to be a kind of self-fulfilling prophecy: an expectation for a strong bottom-up signal causing a stronger error signal. The result is that the world is being represented as having a stronger, more precise signal than it really has, and this is then reflected in conscious perception.

From this perspective, the attentional effect is parasitic on a causal regularity in the world. Normally, when attention is attracted to a region there will indeed be a high signal to noise event in that region. This is part of the prediction error minimization role for attention described above. If this regularity did not hold, then exogenous attention would be costly in free energy. In this way the effect from Carrasco’s lab is a kind of attentional visual illusion. A further study provides evidence for just this notion of an invariant relation between cue strength and expectation for subsequent signal strength: the effect is weakened as the cue contrast decreases (Fuller et al., 2009). The cue sets up an expectation for high signal strength (i.e., high precision) in the region and so it makes sense that the cue strength and the expectation are tied together. It is thus an illusion because a causal regularity about precision is applied to a case where it does not in fact hold. If it is correct that this effect relies on learned causal regularities, then it can be predicted that the effect should be reversible through learning, such that strong cues come to be associated with expectations for imprecise target stimuli and vice versa⁶.

At the limit, this paradigm provides an example of attention directed at subthreshold stimuli, and thereby enabling their selection into conscious perception (e.g., 3.5% contrast subthreshold grating is perceived as a 6% contrast threshold grating (Carrasco et al., 2004). This shows nicely the modulation by precision weighting of the overall free energy landscape: prediction error, which initially is so imprecise that it is indistinguishable from expected noise can be up-weighted through precision expectations such that the internal model is eventually revised to represent it. Paradoxically, however, here what we have deemed an attentional illusion of stimulus precision facilitates veridical perception of stimulus occurrence.

⁶It is a tricky question whether or not this attentional effect is then explained without appealing to “mental paint” (Block, 2010), and whether it is therefore a challenge to representationalism about conscious perception. Precision optimization is an integral part of perceptual inference, which is all about representing the causal structure of the world. As such the explanation is representational. But it concerns precision, which is an often neglected aspect of representation: the representationalism assumed here allows that a relatively accurate representation can fail to optimize precision. What attention itself affords is improved precision, not accuracy (see Prinzmetal et al., 1997).

It is an interesting question if the self-fulfilling prophecy suggested to be in play here is always present under attention, such that attention perpetually enhances phenomenology. In predictive coding terms, the answer is probably “no.” The paradigm is unusual in the sense that it is a case of *covert* attention, which stifles normal active inference in the form of fixation shifts. If central fixation is abolished and the low contrast grating is fixated, the bound on free energy is again minimized, and this time the error between the model and the actual input from the grating is likely to override the expectation for a strong signal.

This attentional illusion works for exogenous cueing but also for endogenous cueing (Liu et al., 2009), where covert endogenous attention is first directed at a peripheral letter cue, is sustained there, and then enhances the contrast of the subsequent target grating at that location. There does not seem to be any studies of the effect of endogenous attention that is entirely volitional and not accompanied by high contrast cues in the target region (even Ling and Carrasco, 2006 has high contrast static indicators at the target locations).

From the point of view of predictive coding, the prediction is then that there will be less enhancing effect of such pure endogenous attention since the high precision expectation (increased baseline) in this case is not induced via a learned causal regularity linking strong signal cues to strong signal targets.

A more general prediction follows from the idea that attention is driven by the (hyper-) prior that cues with high signal strength have high signal to noise ratio. It may be possible to revert this prior through learning such that attention eventually is attracted by low strength cues and stronger cues are ignored. In support of this prediction, there is evidence that some hyperpriors can be altered, such as the light from above prior (Morgenstern et al., 2011).

This attentional effect is then explained by precision optimization leading to an illusory perceptual inference. It is a case of misrepresented high precision combined with relatively low accuracy.

SUSTAINED COVERT ATTENTION DIMINISHES CONSCIOUS PERCEPTION AND ENHANCES FILLING-IN

In Troxler fading (Troxler, 1804) peripheral targets fade out of conscious perception during sustained central fixation. If attention but not fixation is endogenously directed at one type of sensory attribute, such as the color of some of the peripheral stimuli, then those stimuli fade faster than the unattended stimuli (Lou, 1999).

It is interesting that here attention seems to diminish conscious perception whereas in the cases discussed in the previous section it enhances it. A key factor here is the duration of trials: fading occurs after several seconds and enhancement is seen in trials lasting only 1–2 s. This temporal signature is consistent with predictive coding insofar as when the prediction error from a stimulus is comprehensively suppressed and no further exploration is happening (since active inference is subdued due to central fixation during covert attention) probability should begin to drop. This follows from the idea that what drives conscious perception is the actual process of suppressing prediction error. It translates to the notion that the system expects that the world cannot be unchanging for very long periods of time (Hohwy et al., 2008).

In Troxler fading there is an element of filling-in as the fading peripheral stimuli are substituted by the usually gray background. This filling-in aspect is seen more dramatically if the background is dynamic (De Weerd et al., 2006): as sustained attention diminishes perception of the peripheral target stimuli, it also amplifies conscious perception by illusory filling-in. A similar effect is seen in motion induced blindness (MIB). Here peripheral targets fade when there is also a stimulus of coherently moving dots, and the fading of the peripheral dots happens faster when they are covertly attended (Geng et al., 2007; Schölvink and Rees, 2009).

The question is then why attention conceived as precision weighting should facilitate the fading of target stimuli together with enhancing filling-in in these cases. In Troxler fading with filling-in of dynamic background as well as in MIB there is an element of model competition. In MIB, there is competition between a model representing the coherently moving dots as a solid rotating disk, which if real would occlude the stationary target dots, and a model representing isolated moving dots, which would not occlude the target dots. The first model wins due to the coherence of the motion. An alternative explanation is that there is competition between a model on which there is an error (a “perceptual scotoma”) in the visual system, and a model where there is not; in the former case, it would make sense for the system to fill-in (New and Scholl, 2008). In the Troxler case with a dynamic background, there is competition between models representing the world as having vs. not having gaps at the periphery, with the latter tending to win. Sustained attention increases the precision weighting for *all* prediction error from the attended region, that is, for both the target stimuli and the context in which they are shown (i.e., the dynamic background or, as in MIB, the coherently moving foreground). This context is processed not only at that region but also globally in the stimulus array and this would boost the confidence that it fills the locations of the target stimuli. This means that as the prediction error for the peripheral target stimuli is explained away, the probabilistic balance might tip in favor of the model that represents the array as having an unbroken background, or a solid moving foreground (or a perceptual scotoma).

It is thus possible to accommodate these quite complex effects of covert attention within the notion of attention as precision expectation. On the one hand, exogenous cues can engender high precision expectations that can facilitate target perception, and, on the other hand these expectations can facilitate filling-in of the target location. At the same time, covert attention stifles active inference and engenders a degree of inaccuracy.

EXOGENOUS ATTENTION TO INVISIBLE STIMULI

During continuous flash suppression, perceptually suppressed images of nudes can attract attention in the sense that they function as exogenous cues in a version of the Posner paradigm (Jiang et al., 2006). This shows that a key attentional mechanism works in the absence of conscious perception. When there are competing models, conscious perception is determined by the model with the highest posterior probability. It is conceivable that though the nude image is a state in a losing model it may still induce precision-related gain for a particular region. In general, in the processing of emotional stimuli, there is clear empirical evidence to suggest

that fast salient processing (that could mediate optimization of precision expectations) can be separated from slower perceptual classification (Vuilleumier et al., 2003). Evidence for this separation rests on the differences in visual pathways, in terms of processing speeds and spatial frequencies that may enable the salience of stimuli to be processed before their content. Even though a high precision expectation could thus be present for the region of the suppressed stimulus, it is possible for the overall prediction error landscape to not favor the generative model for that stimulus over the model for the abruptly flashing Mondrian pattern in the other eye. The result is that the nude image is not selected for conscious perception but that there nevertheless is an expectation of high precision for its region of the visual field, explaining the effect.

CONCLUDING REMARKS

The relation between conscious perception and attention is poorly understood. It has proven difficult to connect the two bodies of empirical findings, based as they are on separate conceptual analyses of each of these core phenomena, and fit them into one unified picture of our mental lives. In this kind of situation, it can be useful to instead begin with a unified theoretical perspective, apply it to the phenomena at hand and then explore if it is possible to reasonably interpret the bodies of evidence in the light of the theory.

This is the strategy pursued here. The idea that the brain is a precision-weighted hypothesis tester provides an attractive vision of the relationship. Because the states of the world have varying levels of noise or uncertainty, perceptual inference must be modulated by expectations about the precisions of the sensory signal (i.e., of the prediction error). Optimization of precision expectations, it turns out (Feldman and Friston, 2010), fits remarkably well the functional role often associated with attention. And the perceptual inference which, thus modulated by attention, achieves the highest posterior probability fits nicely with being what determines the contents of conscious perception.

In this perspective, attention and conscious perception are distinct but naturally connected in a way that allows for what appears to be reasonable and fruitful interpretations of some key empirical studies of them and their relationship. Crudely, perception and attention stand to each other as accuracy and precision, statistically speaking, stand to each other. We have seen that this gives rise to reasonably coherent interpretations of specific types of experimental paradigms. Further mathematical modeling and empirical evidence is needed to fully bring out this conjecture, and a number of the interpretations were shown to lead to testable predictions.

To end, I briefly suggest this unifying approach also sits reasonably well with some very general approaches to attention and perception.

From a commonsense perspective, endogenous and exogenous attention have different functional roles. Endogenous attention can only be directed at contents that are already conscious (how can I direct attention to something I am not conscious of?) and when states of affairs grab exogenous attention they thereby become conscious (if I fail to become aware of something then

how could my attention have been grabbed?). This is an oversimplification, as can be seen from the studies reviewed above. The mapping of conscious perception and attention onto the elements of predictive coding can explain the commonsense understanding of their relationship but also why it breaks down. Normally endogenous attention is directed at things we already perceive so that no change is missed, i.e., more precision is expected and the gain is turned up. But precision gain itself is neutral on the actual state of affairs, it just makes the system more sensitive to prediction error, so if we direct attention at a location that seems empty but that has a subthreshold stimulus we are still more likely to spot it in the end. Conversely, even if precision expectations are driven up by an increase in signal strength somewhere, and attention in this sense is grabbed, it does not follow that this signal must drive conscious perception. A competing model may as a matter of fact have higher probability.

It is sometimes said that a good way to conceive of conscious perception and attention is in terms of the former as a *synthesizer* that allows us to make sense of our otherwise chaotic sensory input, and the latter as an *analyzer* that allows us to descend from the overall synthesized picture and focus on a few more salient things (Van Boxtel et al., 2010). The predictive coding account allows this sentiment: prediction error minimization is indeed a way of solving the inverse problem of figuring out what in the world caused the sensory input, and attention does allow us to weight the least uncertain parts of this signal. The key insight from this perspective is however that though these are distinct neural processes they are both needed to allow the brain to solve its inverse problem. But when there are competing models, they can work against each other, and conscious perception can shift between models as precisions and bounds are optimized and the world selectively sampled.

Perhaps the most famous thing said about attention is from James:

Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatter-brained state which in French is called *distracted*, and *Zerstreuung* in German (James, 1890, Vol. I, pp. 403–404).

The current proposal is that “attention is simply the process of optimizing precision during hierarchical inference” (Friston, 2009, p. 7). This does not mean the predictive coding account of attention stands in direct opposition to the Jamesian description. It is a more accurate, reductive and unifying account of the mechanism underlying parts of the phenomenon James is trying to capture: James’ description captures many of the aspects of endogenous attention and model competition that are discussed in terms of precision in this paper.

The sentiment that attention is intimately connected with perception in a hypothesis testing framework was captured very early on by Helmholtz. He argued, for example, that binocular rivalry is an attentional effect but he explicated attention in terms of

activity, novelty, and surprise, which is highly reminiscent of the contemporary predictive coding framework:

The natural unforced state of our attention is to wander around to ever new things, so that when the interest of an object is exhausted, when we cannot perceive anything new, then attention against our will goes to something else. [...] If we want attention to stick to an object we have to keep finding something new in it, especially if other strong sensations seek to decouple it (Helmholtz, 1860, p. 770; translated by JH).

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Attention as a process of selection, perception as a process of representation, and phenomenal experience as the resulting process of perception being modulated by a dedicated consciousness mechanism

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Equivalence of attention and consciousness is disputed and necessity of attentional effects for conscious experience has become questioned. However, the conceptual landscape and interpretations of empirical evidence as related to this issue have remained controversial. Here I present some conceptual distinctions and research strategies potentially useful for moving forward when tackling this issue. Specifically, it is argued that we should carefully differentiate between pre-conscious processes and the processes resulting in phenomenal experience, move the emphasis from studying the effects of attention on the modality-specific and feature-specific perception to studying attentional effects on panmodal universal attributes of whatever conscious experience may be the case, and acknowledge that there is a specialized mechanism for leading to conscious experience of the pre-consciously represented contents autonomous from the mechanisms of perception, attention, memory, and cognitive control.

Keywords: attention, consciousness, phenomenal experience, mechanism of consciousness

INTRODUCTION

In terms of subjective intentionality, unity and integration consciousness is panmodal or supramodal, but in terms of qualitative informational contents consciousness can be modally and intramodally varied, selective and specific (Metzinger, 1995; Searle, 1997; Koch, 2004; Tononi, 2010). Consciousness has its contents in the form of feelings and sensations, perceptions, memories, and imagery dynamically representing external and/or internal environment in subject's experience. The representational contents can be processed by brain unconsciously or pre-consciously and only part of the processed perceptual- or memory-contents reach the status of being phenomenally/explicitly experienced (Dixon, 1981; Greenwald et al., 1996; Kinoshita and Lupker, 2003; Goodale and Milner, 2004; Dehaene et al., 2006; Dijksterhuis and Nordgren, 2006; van Gaal and Lamme, 2011). But what is the mechanism of consciousness? In the current debate the main question is: whether consciousness necessarily depends on the mechanism(s) of attention or can consciousness-level representation be possible without attention being applied. Increasingly more specialists, departing from theoretical arguments and empirical data accept that attention and consciousness are separate and different, however possibly interacting (e.g., Baars, 1997b; Hardcastle, 1997; Lamme, 2003; Bachmann, 2006; Koch and Tsuchiya, 2007; van Gaal and Fahrenfort, 2008; Wilimzig et al., 2008; Tsuchiya and Koch, 2009; Brascamp et al., 2010; van Boxtel et al., 2010a,b). Why this twist away from the earlier dominating views that consciousness needs attention? In what follows I will list the arguments in favor of attention and consciousness being dissociable, discuss why the controversy over the present issue persists,

and suggest some steps for moving forward in a less confusing way.

WHY IT CAN BE SAID THAT ATTENTION IS NOT THE BASIS FOR CONSCIOUSNESS

There are many reasons for seeing why attention is not necessary for consciousness. First, maximum concentration of attention does not guarantee consciousness of a stimulus that is the focus of attention. In metacontrast masking, binocular rivalry, visual crowding, motion-induced blindness (MIB), and some other experimental phenomena of consciousness (Kim and Blake, 2005; Bachmann et al., 2011) loss of conscious experience of a target-stimulus is inevitable despite of the maximum attempts to attend to it. Binocular rivalry is perhaps the most used and discussed paradigm here.

Some recent work claiming that attention is necessary for binocular rivalry presents questionable evidence and conclusions—e.g., Zhang et al. (2011). Frequency-tagged brain responses were induced for rivalrous stimuli with the effect that for the unattended stimulus this response was weak. However, the frequency-tagged brain response did not disappear under inattention conditions but was simply weakened. The correlation between frequency-tagged brain response and attentional condition is not a proof of a causal relation; this is especially if it is not sure that frequency-tagged EEG signature is a valid NCC. Data and discussion presented by Roeber et al. (2011) points to the controversy over electrophysiological signatures as fully reliable NCC and also reinstates that rivalry continues while attention is diverted from the competing stimuli.

Second, selective attention mechanisms are effective in improving processing of unconscious information. In many cases the nature and relative extent of the effect is comparable to those when attention improves processing of the consciously experienced stimuli. For example, attention can improve unconscious processing by augmenting priming effects or ERP components associated with pre-conscious processing (Jaśkowski et al., 2002; Naccache et al., 2002; Bahrami et al., 2007; Custers and Aarts, 2011). Conversely, unconsciously processed stimuli influence conscious attention and attention and awareness effects may be independent (Lambert and Shin, 2010; Schmidt and Schmidt, 2010; Hsieh et al., 2011; Hsu et al., 2011; Most and Wang, 2011; Tapia et al., 2011). The main difference is that in one case selective attention works on unconscious information and in the other case on consciously experienced information.

Third, attention can select between stimuli that are already, and to an equal extent, consciously perceived. Equally phenomenally salient perceptual objects precede attentional selection. Fourth, research shows that conscious awareness has specialized brain mechanisms of its own that are not the very mechanisms of selective attention (Purpura and Schiff, 1997; Jones, 2001; Koch, 2004; Ribary, 2005; Tsubomi et al., 2011). Experimental work has also shown that electrophysiological signatures of the effects of attention and awareness, especially when studied by the contrastive methods, can be different or independent (Kiefer and Brendel, 2006; Wyart and Tallon-Baudry, 2008; Aru and Bachmann, 2009a,b; Busch et al., 2009; Britz and Pitts, 2011).

The fifth argument derives from the experiments showing that in some specific conditions attention has an adverse effect on conscious experiences (Lou, 2001; Tsuchiya and Koch, 2009; Rahnev et al., 2011). Voluntary covert attention to color afterimage, afterimage of spatially modulated contrast, or spatially localized motion aftereffect tends to speed up their decay from awareness (Lou, 2001; Suzuki and Grabowecki, 2003; Wede and Francis, 2007; Bachmann and Murd, 2010; van Boxtel et al., 2010a; Murd and Bachmann, 2011). Sixth, some aspects of a scene such as the gist or animated objects can be explicitly noticed without attention and without compromising the competing focused attention task (van Boxtel et al., 2010b; see, however, Cohen et al., 2011). Seventh, consciousness-level sentience can in principle emerge spontaneously and without a preset selective attention. The typical cases are waking from sleep where one does not pay attention to the need to wake up now (while in sleep, we do not decide to begin attending to the environment) or involuntary hallucinating or tinnitus-like experiences.

On the other hand, nobody denies strong and very common examples where attention facilitates conscious experiences and often is the *sine qua non-condition* for conscious perception. These examples come from the phenomena of spatial and object attention, divided attention, prior entry, change blindness, inattention blindness, working-memory analysis, understanding a demanding intellectual problem, etc. (Mack and Rock, 1998; Posner, 2004; Lavie, 2006; Srinivasan, 2007; Carrasco, 2011). Thus why the controversy over attention versus consciousness continues?

WHY THE CONTROVERSY OVER THE ATTENTION VERSUS CONSCIOUSNESS ISSUE STUBBORNLY PERSISTS

In my opinion there are four main reasons for this.

1. Researchers seem to implicitly assume that the solution to the problem of relation between attention and consciousness mechanisms should be *exclusive* – either the attention = consciousness, mechanism, view should win, or attention $\neq$ consciousness view take the upper hand. Actually, there is a possibility that attention mechanisms are part of the mechanisms influencing consciousness. Depending on the mode of its participating action on the consciousness mechanism, attention can have both facilitative and adverse effects on the phenomena of consciousness.
2. Either implicitly or explicitly, specialists tend to *limit their repertoire of brain mechanisms* underlying cognition and affect too much restrictively. There are acknowledged mechanisms of sensation/perception (for building up representations), affect, memory storage, attention (as the selection device between objects or space-time locations or both), cognitive control and efferent control, and execution. The job of giving rise to consciousness is assumed to be accomplished by some of the listed mechanisms or combination of their activities. However, things become more tractable and also more consistent with neurobiological realities when we add a special mechanism to the list – a specialized mechanism for upgrading or modulating the data provided by the representational mechanism up to the level sufficient for direct phenomenal experience of its contents. Why so? First of all, the mechanisms for the listed specialized functions can work pre- or unconsciously (Dixon, 1981; Greenwald et al., 1996; Kinoshita and Lupker, 2003; Goodale and Milner, 2004; Dehaene et al., 2006; Dijksterhuis and Nordgren, 2006; Fiacconi and Milliken, 2011; van Gaal and Lamme, 2011; Zmigrod and Hommel, 2011). Quite specific perceptual and conceptual content can be discriminated by the brains in vegetative state and under anesthetic sedation (Kotchoubey, 2005; Laureys and Tononi, 2010). Thus it is a logical option to consider a mechanism dedicated to producing the changes in the processed contents so that they become explicitly experienced, a mechanism in addition to the listed ones. While often this function has been given to the attention mechanisms, the facts that attention is either independent of, insufficient for, or works against target information awareness (Hardcastle, 1997; Lou, 2001; Lamme, 2003; Koch and Tsuchiya, 2007; van Gaal and Fahrenfort, 2008; Wilimzig et al., 2008; Tsuchiya and Koch, 2009; Bachmann and Murd, 2010; Brascamp et al., 2010; van Boxtel et al., 2010a,b; Carlson et al., 2011; Hsu et al., 2011; Kaunitz et al., 2011; Lathrop et al., 2011; Morgan, 2011; Murd and Bachmann, 2011; Shin et al., 2011; Watanabe et al., 2011) suggest the need for a specialized consciousness mechanism. (This standpoint is even more strengthened by sound arguments about the non-existence of attention – Anderson, 2011). If specific perceptual encoding and attention cannot explain conscious experience as a dependent variable in the experiments, something else should. Furthermore, mechanisms of attention are heavily modality-specific (although work according to similar general principles), but conscious experience

is integrated and unitary intermodally. The general anesthetics act on consciousness in a modality-invariant way, thus hinting at a common mechanism (Hudetz and Pearce, 2010). Importantly, the suggestion to add a specialized consciousness mechanism to the typical list is not founded on a mere speculation because neurobiological facts prove the existence of such mechanisms. Having no specialized function of specific processing of perceptual contents and being also not a dedicated selective attention mechanism, this mechanism is responsible for regulating the level of cortical processing by modulating the activity of specific content-representing mechanisms (Magoun, 1958; Mass and Smirnov, 1970; Llinás and Ribary, 2001; John, 2005; Ribary, 2005). Sufficient facilitative and oscillatory modulation is the precondition for consciousness. Earlier, I have suggested perceptual retouch as a panmodal or intermodally steered, universal mechanism that itself does not carry informational contents, that is autonomous from the mechanism of attention (although can be influenced by it) but is necessary for upgrading the pre-consciously processed representational contents to the consciousness-level (Bachmann, 1984, 1994, 1999, 2000). Thus, and importantly, there is a conceptual need for the conscious-status-“awarding” (CSA) mechanism, whether retouch or something else. Now, instead of asking whether consciousness mechanism is the attention mechanism and vice versa we just ask how the attention mechanism can influence the retouch- (i.e., CSA-) mechanism. Also, whether the effect is always facilitative or can it be sometimes also restrictive, independent, or even adverse. Why the perception mechanism cannot be used for this purpose is simple – perceptual representations – whether dynamic process kind of representations or more structural ones – can be and when related to the possibly available memory information, mostly are, pre- or unconscious. Why the attention mechanism cannot be the consciousness mechanism is also simple – there are too much experimental data showing irrelevance or adverse relation of attention with regard to consciousness.

3. When discussing the attention versus consciousness issue, the prevailing style has been to remain either overly abstract (i.e., consciousness as such, but not asking consciousness *how*) when speaking about consciousness or too much restricted to the specific perceptual/attentional phenomena as examples of consciousness. At the same time, *no universal, intermodal attributes of conscious experience* have been the main substance of discussion.
4. In tackling the issue of attention versus consciousness an often present implicit confusion tends to make the debates unfruitful. Surprisingly often the *processes* of attention are not clearly distinguished from the *results* of these processes as they take one or another form of experience. It is easily possible that when attention aids consciousness then selection among the candidate objects or locations is carried out by the attention mechanism (either bottom-up evoked or top-down controlled), but the results of this selection as experienced at the phenomenal level (e.g., enhanced clarity in consciousness of the attended object) are determined by some mechanism other than attention. Attention interacts with that other mechanism (e.g., the CSA), which results in a qualitatively different phenomenal

experience. Taking into account all four above considerations, let me suggest an approach for how to choose the super-modal attributes of phenomenal perception in order to evaluate them in terms of the effects of attention. Let us see what the effects of attention look like when we analyze them with regard to these attributes as surfacing in published research and common scientific knowledge. Thereafter, I will suggest also some other potentially useful steps for moving forward.

SOME SUGGESTIONS

The principal modality-invariant attributes of phenomenal experience in the context of the present article are as follows:

- *presence* of phenomenal experience (either there is or there is not)
- subjective *clarity* of phenomenal experience (e.g., vividness, PAS level, etc.)
- selective *emphasis* in phenomenal experience (e.g., focus)
- *duration* of phenomenal experience (e.g., short-lived or longer)
- post-perturbation *delay* of phenomenal experience (e.g., stimulus perception latency)
- *veridicality* of content of phenomenal experience (e.g., illusory, distorted, etc.).

All six listed attributes are emphasized or augmented when CSA is activated (Mass and Smirnov, 1970; Bachmann, 1994; Baars, 1997a; Ribary, 2005). What about attention? In the following table the typical or expected effects of attention on the principal phenomenal attributes are systematized. Some of the table entries indicate the effects consistent with published experimental facts, some refer to the effects yet to be tested. (It can be easily concluded that the effects are very much dependent on what empirical phenomena we are considering).

Now, based on the table, let us compare some examples of the attentional effects. By 1a we specify phenomena where attention facilitates detection or description of the presence of target objects such as in the change blindness displays (Jensen et al., 2011), covert spatial pre-cueing (Carrasco, 2011), bottom-up pop-out in filtering tasks (Itti et al., 2005), partial report selection from iconic memory (Ruff et al., 2007; Sligte et al., 2010), etc. By 1b we specify effects of attention counteracting awareness, such as in the MIB (Schölvinck and Rees, 2009). By 1c we specify animal object detection (van Boxtel et al., 2010b), understanding that one is awake and present in the habitat after spontaneous awakening, involuntary perception of the alternatives in rivalry displays

Effects of attention on phenomenal attributes of consciousness.

Attribute	a: Attention facilitates	b: Attention counteracts	c: Attention-independent
Presence (1)	Yes	Yes	Yes
Clarity (2)	Yes	?	No
Selective emphasis (3)	Yes	No	No
Duration (4)	Yes	Yes	?
Post-stimulus delay (5)	Yes	No	?
Veridicality (6)	Yes	Yes	?

(Kim and Blake, 2005), attentional blink to the second target (Dux and Marois, 2009), delusional compulsory experiences, etc. By 2a such effects can be listed as covert spatial attention (Störmer et al., 2009; Carrasco, 2011), vividness of subjective experiences dependent on arousal states, etc. The entry 3a refers to the selective attention effects in visual search, scene analysis, bottom-up and top-down spatial attention, dichotic listening, selection from iconic memory, etc. (Itti et al., 2005; Sligte et al., 2010; Bachmann et al., 2011). The entry 4a refers to increase of apparent duration by attention (Seifried and Ulrich, 2011) while 4b refers for example to the adverse effect of attention on the duration of after-images (van Boxtel et al., 2010a; Murd and Bachmann, 2011). For 5a there are phenomena such as prior entry under attention (Hilkenmeier et al., 2011), release from masking by a pre-cue in perceptual latency priming (Scharlau and Neumann, 2003), perceptual facilitation in flash-lag displays (Nijhawan and Khurana, 2010), selective spatial attention by pre-cueing (Carrasco, 2011), etc. With 6a we refer to the cases where attending increases correct discrimination and content perception (Itti et al., 2005; Carrasco, 2011) while 6b refers to the adverse effects of attention on veridicality of perception. The selection of examples for the latter is surprisingly rich: illusory percepts due to expectancy, stereotypical distortions because of learning effects, bias effects from frequency of use or experimenter effects, etc.

In the table the most interesting cases are where attention can have mutually opposite effects (e.g., 1a–1b, 4a–4b, 6a–6b). This may be interpreted as evidence against attention being the mechanism of consciousness, which is the view supported in this paper. However, this interpretation can be consistent with two different views on the issue of relations between attention and consciousness. For one view, assuming that attention is the very mechanism of consciousness the above contradictory facts are detrimental. However, if we take a broader view and assume that attention is only one of the many mechanisms having an impact on the work of the consciousness mechanism then there is an easy way to understand why attention can have opposite effects on conscious experience. In this it-depends-type of view attention simply has one or another effect on consciousness depending on how it is applied onto perceptual data processing.

Here is an analogy: blowing air on the flame can either ignite and facilitate fire or exterminate it, depending on the intensity and time of action on the flame. If attention is the ambient “wind” and consciousness is the “flame,” a sufficiently strong and durable attending can speed up the decay of conscious experience (e.g., with afterimage experience). Yet, when air is standstill and no wind is present, the flame still burns. Attention as a mechanism that itself is not a consciousness mechanism can lead also to both the increase of veridicality of perception or increase of non-veridicalities. This depends on whether the bottom-up perceptual data or top-down, memory based, and expectancy-controlled information is fostered relatively more by attention. But what is clear though is that attention is neither sufficient nor necessary for consciousness in general. It alone cannot explain the various phenomena. It also need not guarantee consciousness of content when steadily applied on a sensory experience having that content. However, it may be necessary for some aspects of consciousness to show up (e.g., extreme clarity or priority in entry) or take one or another value (e.g., duration of experience).

If none of the different traditional mechanisms is separately sufficient for consciousness then a nagging question emerges: what is different in the activities of the constituent mechanisms of the unspecialized set of traditional mechanisms when consciousness with its content emerges? I do not have a good answer to this. As we saw above, attention cannot be the decisive mechanism. Perceptual and memory representation can be and often largely are pre-conscious. Cognitive control does not have content. Intuitively, it seems more natural that there is a mechanism specialized for “awarding” consciousness quality for the representational contents mediated by the specific, specialized memory systems and perceptual content systems. In this case with CSA at hand it is easier to understand why attention in one case facilitates consciousness of contents and in some other case does not or even dampens it. Attention as the principal mechanism of selection out of alternative informational options can either facilitate the working or use of the CSA or inhibit (or abstain from use of) it.

The likely possibilities of relationship between attention mechanisms and the CSA mechanism are as follows: (1) attention mechanism acting upon CSA, which in turn leads to either facilitation of consciousness-level microgenesis of the explicit experience or to inhibition of the consciousness of target; (2) attention mechanism and CSA acting independently and in parallel first, only then followed by mutual interaction (e.g., conscious experience capturing attentional resources, or attentionally amplified pre-conscious representation capturing CSA resources). Which one of the above relationships is valid or whether both can be implemented requires special research in future.

At present there are several candidate mechanisms for acting as the special mechanistic intermediate between *pre-conscious* information-representing activity and *conscious-level* information-representing means. In the family of thalamocortical interaction theories assuming a special role for the so-called non-specific-thalamic units for upgrading the pre-conscious cortical contents there are several varieties (e.g., Magoun, 1958; Bachmann, 1984, 1999, 2007; Bogen, 1995; Newman, 1995; Baars, 1997a; Purpura and Schiff, 1997; Llinás and Ribary, 2001; John, 2005; Ribary, 2005; Ward, 2011). Despite the “family resemblances,” these researchers think that the pre-conscious cortical contents quite reliably represented after specific relay units transfer information from receptors to cortical modules become conscious contents as soon as they are modulated by thalamocortical general-purpose activity (the CSA mechanism). In some of the models post-synaptic EPSPs of the content-carrying cortical neurons are the targets for non-specific-thalamic modulation (e.g., Bachmann, 1994). In other models oscillating activity of the specific representational neurons and non-specific modulation-system neurons becomes synchronized for consciousness with its specific content to emerge (Llinás and Ribary, 2001; John, 2005). In a recent conceptualization termed “binding binding” Bachmann (2007) envisaged two processes of binding by oscillatory synchrony – first-order binding of features into perceptual objects by synchronizing feature-specific neurons pre-consciously and second-order binding of the bound pre-conscious objects into general consciousness-level representation. The second-order binding is executed via the oscillations of the non-specific CSA system. In this version, a representation is essentially a dynamic representation. Attentional

network can be though either to aid pre-conscious binding, binding for consciousness, or exhausting (or desynchronizing) the oscillatory resources in case of adverse effects on consciousness.

In the reentrant theory it is assumed that for the specific contents represented by primary sensory cortices to become consciously represented, they need to be accessed by the reentrant signals from the higher-order cortical nodes sent back to the already activated earlier units (Lamme, 2003; van Gaal and Lamme, 2011). Bottom-up plus top-down cycles of mutual activation are sufficient for consciousness of its contents. In this theory the mechanism is not neuroanatomically distinct (albeit interacting with differently placed other modules) as is the case with thalamic theories. It is functionally defined, implemented by the neural units that are neuroanatomically the same. Although Lamme and van Gaal explain attentional effects both independent and associated with consciousness, there are some questionable aspects to this theory. First of all, it would be computationally and adaptively suspect to leave both the functions of representation and modulation to the units of the same neural system. One and the same structural system should have difficulty in transforming from content-representing system to a control system and vice versa, unless some mystique would be brought in.

Let me end with a few concluding remarks. In order to better understand the nature of attention and consciousness and their relation (i) some conceptual distinctions either absent or only implicitly involved in theorizing so far are necessary. This applies to the distinction between: processes and dynamic results of the

processes; content-specific attributes of conscious experiences and universal, content-invariant attributes of conscious experiences; possibly opposite effects of the same mechanism (e.g., attention) on consciousness depending on the characteristics of influence that the same mechanism has. Also, (ii) it may be advisable to abandon both the attention-as-consciousness, view, and the view that consciousness emerges by default from the work of traditional mechanisms of perception, memory, and attention. Instead, let us find a deserved place for the special mechanism of consciousness in addition to the perceptual, attentional, memory, cognitive control, and other standard mechanisms long acknowledged. Methodologically, (iii) in addition to the mostly correlational studies (NCC) more mechanistic and causal-effects related research is needed. Let us accept that there is a special (thalamocortical interactive?) mechanism and a corresponding theoretical mechanistic concept for the dedicated CSA brain process(es) responsible for upgrading pre-conscious results of the perception up to the consciousness-level results. This concept is functionally apart from the concepts of perception and attention. Therefore, we may have better chances to solve the attention versus consciousness puzzle. Indeed, both perception and attention can be independent of the explicit conscious experience.

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Attention, awareness, and the perception of auditory scenes

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Auditory perception and cognition entails both low-level and high-level processes, which are likely to interact with each other to create our rich conscious experience of soundscapes. Recent research that we review has revealed numerous influences of high-level factors, such as attention, intention, and prior experience, on conscious auditory perception. And recently, studies have shown that auditory scene analysis tasks can exhibit multistability in a manner very similar to ambiguous visual stimuli, presenting a unique opportunity to study neural correlates of auditory awareness and the extent to which mechanisms of perception are shared across sensory modalities. Research has also led to a growing number of techniques through which auditory perception can be manipulated and even completely suppressed. Such findings have important consequences for our understanding of the mechanisms of perception and also should allow scientists to precisely distinguish the influences of different higher-level influences.

Keywords: auditory scene analysis, multistability, change deafness, informational masking, priming, attentional blink

INTRODUCTION

Understanding conscious experience of the external world has been a pursuit of theorists since the early days of experimental psychology. For example, Wundt and Titchener were among those who used introspection of their own perceptions to try and arrive at the fundamental units of experience (Boring, 1953; Danzinger, 1980). However, since then perception science and other areas of experimental psychology and neuroscience have been dominated by more objective psychophysical methods of understanding perception that have as a consequence, or by design, pushed the inquiry of subjective experience to the background. This objective measurement of perception has provided exquisite information about our perceptual skills to detect, discriminate, and categorize particular stimuli, and the underlying neuro-computational mechanisms of these abilities.

Recently, however, theorists have made an important contribution to reviving the scientific study of consciousness, perhaps most notably by defining accessible empirical problems such as how to explain the generation of perceptual *awareness* or *consciousness* (Crick and Koch, 1995, 2003), which we operationally define as the explicit reporting of a particular stimulus or how it is perceptually organized. This has led to investigations into the necessary and sufficient conditions for people to be aware of stimuli, especially in visual perception. For example, researchers have investigated the role of particular brain areas (Leopold and Logothetis, 1999; Tong et al., 2006; Donner et al., 2008) and particular neural processes such as feedback from higher to lower areas (Pascual-Leone and Walsh, 2001; Hochstein and Ahissar, 2002; Lamme, 2004; Wibral et al., 2009) that are associated with visual awareness. In many cases, these investigations have made use of multistable visual stimuli that can be perceived in more

than one way (e.g., the well-known Necker cube, Long and Topino, 2004), enabling the investigation of changes in perception without any confounding stimulus changes. The development of techniques to manipulate whether people are aware of particular stimuli (Kim and Blake, 2005) has additionally led to evaluating awareness (e.g., of a prior stimulus) as an independent variable (i.e., rather than studying awareness as the outcome variable) that can affect perception of subsequent stimuli (e.g., Kanai et al., 2006; for a review Koch and Tsuchiya, 2007). Much less work of these types has been done on auditory awareness, but several promising lines of research have begun, which we discuss in detail below.

In this review of the literature, we focus on three main types of research on auditory perception. First, we review research that demonstrates effects of attention and other high-level factors on auditory perceptual organization, with an emphasis on the difficulty in manipulating attention separately from other factors. Next, we discuss the fact that perception of sound objects exhibits the hallmarks of multistability and therefore shows promise for future studies of auditory perception and its underlying neural mechanisms. In this section, we also review research on the neural correlates of subjective auditory perception, which provides clues as to the areas of the brain that determine perception of sound objects. Finally, we discuss a number of recent demonstrations in which auditory events can be made imperceptible, which like their visual counterparts can enable researchers to identify the mechanisms of auditory awareness. Some of the studies that have been done permit interesting comparisons between perception of sound and conscious perception of stimuli in other sensory modalities. When possible, we will point out the similarities and differences across modalities, and point out the need for future research to delineate the extent to which similar phenomena

and similar mechanisms are present across the senses during perception.

AUDITORY SCENE ANALYSIS AS A FRAMEWORK TO STUDY AWARENESS

Auditory scene analysis (ASA) is a field of study that has been traditionally concerned with how the auditory system perceptually organizes incoming sounds from different sources in the environment into sound objects or streams, such as discrete sounds (e.g., phone ringing, gunshot) or sequences of sounds (e.g., melody, voice of a friend in crowded restaurant), respectively (Bregman, 1990). For example, in a crowded restaurant in which many people are talking at the same time, an individual must *segregate* the background speech from his or her dining partner's speech and *group* the various sound components of the partner's speech appropriately into a meaningful stream of words. ASA has mainly been studied with the goal of understanding how listeners segregate and group sounds; however, research in this field has also developed paradigms that are highly suitable for studying more general perceptual mechanisms and how low-level stimulus factors and higher-level factors such as attention, intention, and previous knowledge influence perception. In ASA studies, participants are often asked to report on their subjective experience of hearing two or more segregated patterns; and as mentioned earlier, when sounds are kept constant the operation of perceptual mechanisms can be studied directly without confounding effects of stimulus manipulations. However, indirect performance-based measures of segregation can also be informative because they tend to show the same effects as subjective measures (e.g., Roberts et al., 2002; Stainsby et al., 2004; Micheyl and Oxenham, 2010). Another important aspect of many ASA studies is that they often use rather simple arrangements of sounds that are easy to generate and manipulate. They also do not involve many of the complications associated with using real-world sounds (e.g., speech and music), such as the activation of long-term memory or expertise-related processes. Thus,

such high-level processes can be controlled and studied with relative ease.

Bregman (1990) proposed two main classes of ASA mechanisms: (1) *primary* mechanisms that process incoming mixtures of sounds in an automatic fashion using simple transformations, and (2) *schema-based* mechanisms that are more likely to be attention-, intention-, and knowledge-dependent. An example of the operation of primary ASA is the well-known effect of frequency separation (Δf) during segregation of sequential tone patterns (Miller and Heise, 1950; Bregman and Campbell, 1971; Van Noorden, 1975). In the laboratory, auditory stream segregation has been studied extensively as an example of sequential segregation by playing two alternating pure tones of different frequencies (A and B) in a repeating pattern (e.g., ABA-ABA-... , where “-” corresponds to a silence), as shown in **Figure 1**. At first, the tones are heard as a single stream with a galloping rhythm, but after several repetitions of the sequence, the tones are often heard as splitting into two streams or “streaming” (i.e., A-A-A-A-... and B-B-B-B-...). The larger the Δf between the A and B tones and the more rapidly they are presented, the more likely participants report hearing two streams as opposed to one stream. The characteristic time course of pure-tone streaming, called *buildup*, is likely to have its basis in the adaptation of frequency-tuned neurons in early brainstem and/or primary cortical stages of processing (Micheyl et al., 2005; Pressnitzer et al., 2008; for reviews, Micheyl et al., 2007a; Snyder and Alain, 2007). But more recent research has shown that a number of stimulus cues besides pure-tone frequency can result in perception of streaming, even cues that are known to be computed in the central auditory system (for reviews, Moore and Gockel, 2002; Snyder and Alain, 2007). This evidence that streaming occurs at central sites raises the possibility that auditory perception results from a combination of activity at multiple levels of the auditory system, including those that can be influenced by schema-based mechanisms.

In addition to segregation of sequential patterns, another important aspect of scene analysis is the segregation of sounds

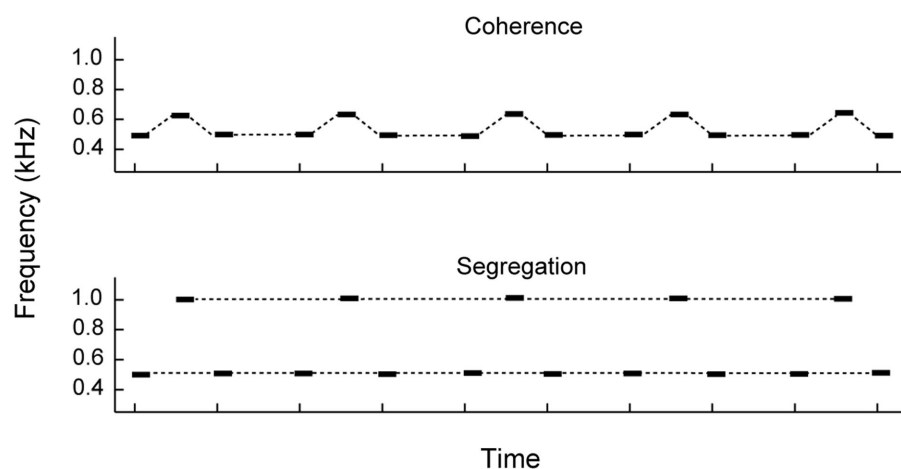


FIGURE 1 | In auditory stream segregation experiments, low and high tones are alternated repeatedly. When the frequency difference between the tones is small (top), this typically leads to perception of one coherent stream. For large frequency differences (bottom), one is more likely to be heard as two segregated streams.

that occur concurrently, such as when two individuals speak at exactly the same time. In social gatherings, human listeners must perceptually integrate the simultaneous components originating from one person's voice (i.e., fundamental frequency or f_0 , and harmonics that are integer-multiples of f_0) and segregate these from concurrent sounds of other talkers. Psychophysical research has identified several cues that influence how concurrent sounds will be grouped together (for reviews, Carlyon, 2004; Alain, 2007; Ciocca, 2008). For instance, sounds that are harmonically related, begin at the same time and originate from the same location are more likely to emanate from the same physical object than those that are not. In the laboratory, experimenters can induce the perception of concurrent sound objects by mistuning one spectral component (i.e., a harmonic) from an otherwise periodic harmonic complex tone (see **Figure 2**). Low harmonics mistuned by about 4–6% of their original value stand out from the complex so that listeners report hearing two sounds: a complex tone and another sound with a pure-tone quality (Moore et al., 1986). While several studies have investigated the role that attention plays in auditory stream segregation, which we review below, far less research has been done on the impact of high-level factors on concurrent sound segregation.

EFFECTS OF HIGH-LEVEL FACTORS ON AUDITORY SCENE ANALYSIS

Attention

Attention during auditory stream segregation. Psychophysical studies have shown that buildup of stream segregation is modulated by attention, suggesting the involvement of high-level factors in perception of streaming. In these studies, participants were presented with an ABA- pattern to one ear. The role attention plays in auditory stream segregation was examined by assessing the

buildup of streaming while participants were engaged in a separate auditory, visual, or non-sensory task in which participants counted backward (Carlyon et al., 2001, 2003; Thompson et al., 2011). By having participants engaging a primary task, attention was diverted away from the ABA- pattern. When attending to the ABA-pattern, participants showed a typical pattern of buildup. However, when attending the other task for the first part of the ABA- pattern, participants failed to show any sign of buildup when they switched their attention. Thus, buildup either did not occur while attention was diverted to the primary task or it was reset following the brief switch in attention (Cusack et al., 2004), a distinction that has been quite difficult to resolve using psychophysical measurements. These effects occurred regardless of the task used to capture attention (Carlyon et al., 2003), suggesting that buildup involves mechanisms within central auditory areas, multimodal pathways, and/or in peripheral areas that can be influenced in a top-down fashion by attention. To explain these results, Cusack et al. (2004) proposed a hierarchical model of stream segregation. According to this model, preattentive mechanisms segregate streams based on acoustic features (e.g., Δf) and attention-dependent buildup mechanisms further break down outputs (streams) of this earlier process that are attended to. For example, when talking to a friend at a concert, low-level processes automatically segregate the friend's voice from the music. However, since attention is allocated to the friend's voice and not the concert, buildup processes do not further decompose the music into its constituent parts (e.g., guitar, drums, bass, etc.; also, see Alain and Arnott, 2000).

Consistent with this model, Snyder et al. (2006) provided event-related potential (ERP) evidence for at least two mechanisms contributing to stream segregation: an early preattentive segregation mechanism and an attention-dependent buildup mechanism. In particular, auditory cortical responses (P2 and N1c) to an ABA-pattern increased in amplitude with increasing Δf and correlated with behavioral measures of streaming; this enhancement occurred even when attention was directed away from the ABA-pattern. Additionally, a temporally broad enhancement following the onset of an ABA- pattern progressively increased in positivity throughout the course of the pattern. The time course of this progressive increase indicated a strong link with the buildup of streaming. Importantly, this enhancement was diminished when participant's attention was directed away from the ABA- pattern. These findings support the existence of an attention-dependent buildup mechanism in addition to a preattentive segregation mechanism. Also, since buildup-related processes were measured during passive listening these findings are more consistent with an effect of sustained attention as opposed to the possibility that buildup is simply reset following brief switches in attention (cf. Cusack et al., 2004).

However, Sussman et al. (2007) showed that buildup does not always require attention. They showed that deviant stimuli embedded within a high-tone stream of an ABA- pattern resulted in a mismatch negativity response during perception of two streams (Sussman et al., 1999, 2007). Furthermore, deviants were more likely to evoke a mismatch negativity when they occurred at the end of ABA- patterns compared to when they occurred early on, consistent with the time course of buildup. Importantly, these findings were similar whether or not the ABA- patterns were attended,

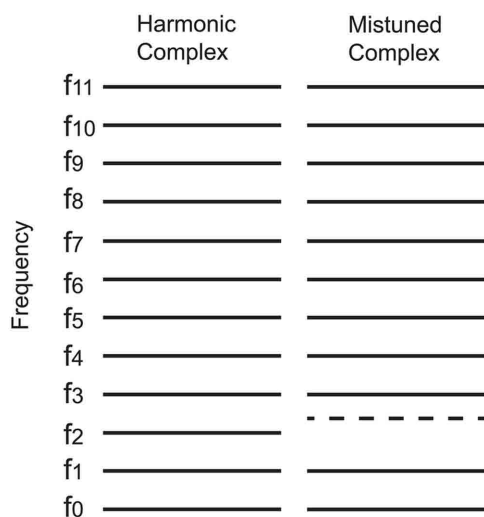


FIGURE 2 | In mistuned harmonic experiments, a complex harmonic sound composed of frequency components that are all multiples of the fundamental frequency (f_0) is heard as a single sound with a buzzy quality (left). When one of the components is mistuned, it stands out as a separate pure-tone object in addition to the remaining complex sound (right).

suggesting that attention may not be required for buildup to occur, in contrast to the findings discussed above. Because this study used relatively large Δf_s , it is possible that attention only modulates buildup in the absence of robust segregation cues (i.e., large Δf_s ; Sussman et al., 2007). Indeed, Snyder et al. (2006) included several conditions with Δf_s smaller than that used by Sussman et al. (2007). Additionally, close inspection of Cusack et al. (2004) shows that preattentive buildup processes were more prevalent for larger than smaller Δf conditions.

Several additional physiological studies have examined the effects of selective attention on streaming. These studies have supported a *gain* model in which attention to a target stream enhances neural processing of sounds within that stream while suppressing unattended streams. An early ERP study showed that selective attention to a stream facilitated early sensory processing of that stream and inhibited processing of unattended streams (Alain and Woods, 1994). More recent studies have focused on the effects of selective attention on continuous neural activity to sound streams. For example, in addition to enhanced transient responses generated in associative auditory areas (Bidet-Caulet et al., 2007), selective attention enhanced steady-state responses generated in primary auditory cortex to attended streams (Bidet-Caulet et al., 2007; Elhilali et al., 2009b; Xiang et al., 2010). Furthermore, these responses were entrained to the rhythm of the target stream and constrained by known entrainment capabilities within auditory cortex (i.e., better entrained for low vs. high frequencies; Xiang et al., 2010). High-density ERP and neuromagnetic studies have recently examined neural responses to continuous speech streams played amongst distracting speech (Kerlin et al., 2010; Ding and Simon, 2012). Both studies demonstrated that low-frequency (4–8 Hz) speech envelope information was represented in the auditory cortex of listeners. These representations were measured as either a continuous low-frequency response phase-locked to the speech (Kerlin et al., 2010) or a phase-locked N1-like neuromagnetic response that was primarily driven by low-frequency features of the speech (Ding and Simon, 2012). Consistent with a gain model, selectively attending to a speech stream enhanced the continuous low-frequency response to the attended speech and (possibly) suppressed responses to unattended speech (Kerlin et al., 2010). In a separate study, attention enhanced an N1-like response to attended speech and suppressed responses to unattended speech (Ding and Simon, 2012). In this latter case, the relatively short latency of these effects suggests that attention modulated bottom-up segregation and/or selection processes. Furthermore, this finding generalizes similar effects of selective attention on the auditory N1 ERP response from simple tones (Hillyard et al., 1973) to more naturalistic speech stimuli. Taken together, these findings are consistent with a gain model in which attention to a sound stream improves its neural representation while suppressing representations of irrelevant streams.

An issue with this type of gain model is that it is not uncommon for separate streams of speech to share similar acoustic features and, accordingly, activate overlapping neuronal receptive fields. In this case, attention-related enhancement or suppression would act on both attended and unattended streams. Therefore, in addition to gain, attention may also serve to narrow neuronal receptive fields of neurons within the auditory cortex (Ahveninen et al., 2011).

This would, in effect, increase feature selectivity and decrease the likelihood that separate streams of speech activate overlapping neurons. To test this model, participants were presented with target sequences of repeating tones embedded within notch-filtered white noise that did not overlap with the frequency of the target. Auditory cortical responses (N1) to unattended sounds were reduced in amplitude reflecting lateral inhibition from the masker. In contrast, these attenuated effects disappeared for attended target stimuli. Here, selective attention may have narrowed the width of the receptive fields processing the target stream and, consequently, increased the representational distance between task-relevant and task-irrelevant stimuli. Furthermore, these neuronal changes correlated with behavioral measures of target detection suggesting that attention-related receptive field narrowing aided segregation, in addition to any helpful effects of gain.

A third way in which selective attention influences neural processes of streaming is enhancing temporal coherence between neuronal populations. In particular, attention to a target stream enhanced synchronization between distinct neuronal populations (both within and across hemispheres) responsible for processing stimuli within that stream and this correlated with behavioral measures of streaming (Elhilali et al., 2009b; Xiang et al., 2010). Enhanced synchronization may have facilitated the perceptual boundary between acoustic features belonging to attended and unattended streams as detected by a temporal coherence mechanism (Shamma et al., 2011). Consistent with the role of temporal coherence in streaming, when presented with a modified ABA- pattern in which low- (A) and high- (B) pitched tones were played simultaneously rather than sequentially participants reported hearing one stream even for very large Δf_s (Elhilali et al., 2009a). Taken together, these physiological studies revealed at least three ways in which attention modulated streaming: (1) enhanced processing of the stimuli within the task-relevant stream and suppressed processing of those within the task-irrelevant stream (Alain and Woods, 1994; Bidet-Caulet et al., 2007; Elhilali et al., 2009b; Kerlin et al., 2010; Xiang et al., 2010; Ding and Simon, 2012), (2) enhanced feature selectivity for task-relevant stimuli (Ahveninen et al., 2011), and (3) enhanced temporal coherence between distinct neuron populations processing task-relevant stimuli (Elhilali et al., 2009b; Xiang et al., 2010).

Jones et al. (1981) theorized that rhythmic attention plays a role in the stream segregation process. Rhythmic attention is assumed to be a time-dependent process that dynamically fluctuates in a periodic fashion between a high and low state (Large and Jones, 1999). According to this theory, rhythmic attention aids listeners in picking up relations between adjacent and non-adjacent events when they are nested in a common rhythm. Therefore, when stimuli have a regular periodic pattern, rhythmic attention can detect sounds that do and do not belong to that stream. Indeed, when two streams of tones differed in rhythm they were more likely to be segregated even for tones relatively close in frequency (Jones et al., 1981). These findings are consistent with physiological studies that showed steady-state brain responses to be entrained to the rhythm of the segregated target stream (Elhilali et al., 2009b; Xiang et al., 2010). However, follow-up studies to Jones et al. (1981) have yielded conflicting results. For example, Rogers and Bregman (1993) showed that the likelihood of a context

sequence of B-only tones to increase segregation in a short ABA-pattern was similar for context sequences that matched or mismatched the ABA- rhythm. Therefore, manipulating rhythm only minimally enhanced the effect of Δf during perception of streaming. However, it is not clear whether the buildup observed during these single-tone contexts was mediated by similar mechanisms as those that are active while listening to an ABA- context pattern (Thompson et al., 2011). Therefore, it is possible that rhythmic attention modulates these two types of buildup in a different manner. Studies by Alain and Woods (1993, 1994) also provided little evidence that rhythm has a role in streaming. They showed that the likelihood of segregating a target stream of tones from distracters was similar for sequences that had regular or irregular rhythms. However, because the rhythms of target and distracter streams were never manipulated independently, rhythm could not be used as a reliable cue for segregation. Therefore, in light of these issues, it still seems possible that rhythmic attention may modulate stream segregation, especially in cases where Δf is not sufficient for segregation to occur.

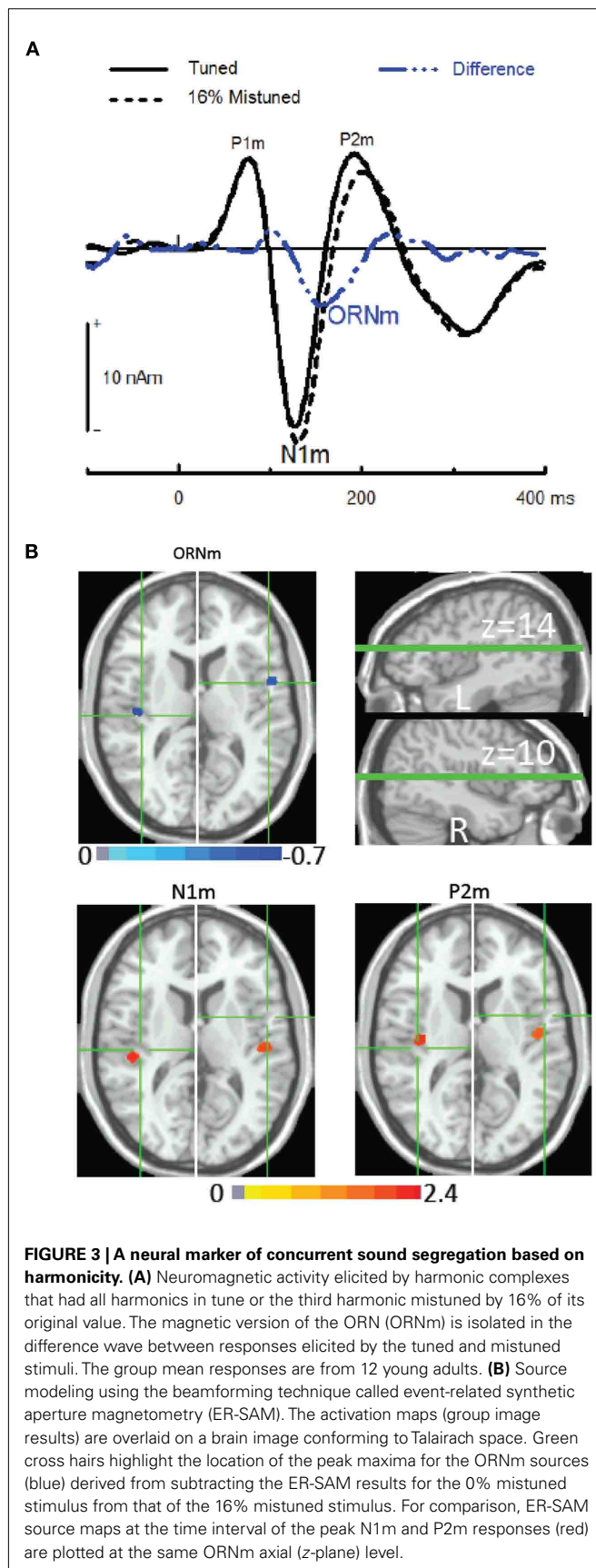
Indeed, the role of rhythmic attention in streaming has been the focus of several recent studies, which have proven more consistent with the ideas of Jones et al. (1981). For example, when Δf s were small, listeners were more likely to segregate an irregular target stream from a distracter stream when the distracter was isochronous (Andreou et al., 2011). However, given a large enough Δf , rhythm had a marginal influence on measures of streaming. Therefore, it may be that large Δf s are a dominant cue for streaming, but that listeners consider other cues such as rhythm when Δf is small. Other studies, in which participants detected a target melody interleaved with irrelevant melodies, showed that participants used rhythmic pattern to attend to points in time during which notes of the target melody occurred (Dowling et al., 1987) and reduce the distracting effects of irrelevant melodies (Devergie et al., 2010). Finally, listeners used rhythmic differences between streams to maintain perception of segregated streams (Bendixen et al., 2010). A plausible explanation for these results is that attention to the task-relevant stream was facilitated when the target stream had a regular rhythm distinct from other streams. Additionally, increased suppression of isochronous distracter streams facilitated attention to an irregular task-relevant stream. Taken together, studies suggest that rhythmic attention may modulate streaming, perhaps in conditions in which more salient cues are unavailable, but more work is needed to assess the generality of these findings.

Attention during concurrent sound segregation. As with stream segregation, scalp-recorded ERPs have proven helpful in investigating the role of attention during concurrent sound perception because it allows one to examine the processing of auditory stimuli while they occur outside the focus of attention. Alain et al. (2001) measured auditory ERPs while participants were presented with harmonic complex tones with or without a mistuned harmonic; in one condition they indicated whether they heard one vs. two sounds, while in another condition they listened passively (i.e., read a book of their choice, with no response required). The main finding was an increased negativity that superimposed the N1 and P2 wave elicited by the sound onset. **Figure 3** shows

examples of neuromagnetic activity elicited by tuned and mistuned stimuli and the corresponding difference wave referred to as the object-related negativity (ORN), so named because its amplitude correlated with the observers' likelihood of hearing two concurrent sound objects. The ERP recording by Alain et al. (2001) during the passive listening condition was instrumental in showing that the ORN, thought to index concurrent sound segregation and perception, occurred automatically. The proposal that low-level concurrent sound segregation mechanisms are not under attentional control was confirmed in subsequent ERP studies using active listening paradigms that varied auditory (Alain and Izenberg, 2003) or visual attentional demands (Dyson et al., 2005).

In addition to providing evidence for primary sound segregation, ERPs also revealed attention-related effects during the perception of concurrent sound objects. Indeed, when listeners were required to indicate whether they heard one or two sounds, the ORN was followed by a positive wave that peaked about 400 ms after sound onset, referred to as the P400 (Alain et al., 2001). It was present only when participants were required to make a response about the stimuli and hence is thought to index perceptual decision-making. Like the ORN, the P400 amplitude correlated with perception and was larger when participants were more likely to report hearing two concurrent sound objects. Together, these ERP studies revealed that both bottom-up (attention-independent) and top-down controlled processes are involved in concurrent sound perception.

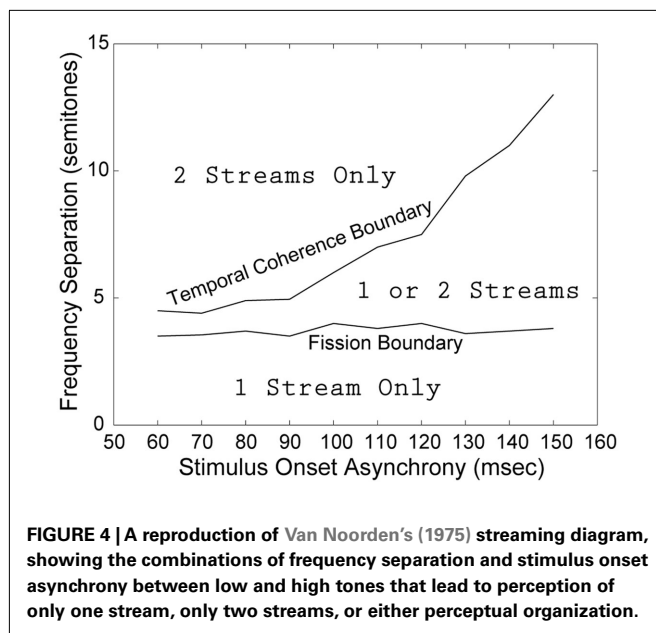
In the ERP studies reviewed above, the perception of concurrent sound objects and mistuning were partly confounded, making it difficult to determine whether the ORN indexes conscious perception or simply the amount of mistuning. If the ORN indexes perception of concurrent sound objects, then it should also be present when concurrent sounds are segregated on the basis of other cues such as spatial location. McDonald and Alain (2005) examined the role of location on concurrent sound perception. Using complex harmonic tones with or without a mistuned harmonic, these authors found that the likelihood of reporting two concurrent sound objects increased when the harmonic was presented at a different location than the remaining harmonics of the complex. Interestingly, the effect of spatial location on perception of concurrent sound objects was paralleled by an ORN. The results from this study indicated that the ORN was not limited to mistuning but rather relates to the subjective experience of hearing two different sounds simultaneously. Moreover, this study showed that listeners can segregate sounds based on harmonicity or location alone and that a conjunction of harmonicity and location cues contributes to sound segregation primarily when harmonicity is ambiguous. Results from another research group also found an ORN during concurrent sound segregation with cues other than harmonicity, further supporting the interpretation that the ORN is related to conscious perception rather than stimulus processing (Johnson et al., 2003; Hautus and Johnson, 2005). However, an even stronger test of this account would be to present multistable versions of the mistuned harmonic (i.e., with an intermediate amount of mistuning) to see if the ORN is enhanced when listeners hear two objects compared to when they hear one object for the exact same stimulus.



Though the mistuned harmonic paradigm has proven helpful in identifying neural correlates of concurrent sound perception, the conclusions from these studies often rely on subjective assessment. Moreover, it is unclear whether the mechanisms involved in parsing a mistuned harmonic in an otherwise harmonic complex share similarities with those involved during the segregation and identification of over-learned stimuli such as speech sounds. In addition to data-driven processes, speech stimuli are likely to engage schema-driven processes during concurrent speech segregation and identification. To examine whether prior findings using the mistuned harmonic paradigms were generalizable to more ecologically valid stimuli, Alain et al. (2005) recorded ERPs while participants performed the double vowel task. The benefit of this task is that it provides a more direct assessment of speech separation and also evokes processes involved in acoustic identification. Here, participants were presented with a mixture of two phonetically different synthetic vowels, either with the same or different f_0 , and participants were required to indicate which two vowels were presented. As previously reported in the behavioral literature (e.g., Chalikia and Bregman, 1989; Assmann and Summerfield, 1990), accuracy in identifying both vowels improved by increasing the difference in the f_0 between the two vowels. This improvement in performance was paralleled by an ORN that reflected the difference in f_0 between the two vowels. As with the mistuned stimuli, the ORN during speech segregation was present in both attend and ignore conditions, consistent with the proposal that concurrent speech segregation may involve an attention-independent process. In summary, while it is not yet possible to propose a comprehensive account of how the nervous system accomplishes concurrent sound segregation, such an account will likely include multiple neuro-computational principles and multiple levels of processing in the central auditory system.

Intention

One of the first in-depth investigations of streaming provided an elegant demonstration of the large influence that manipulating an observer's intention can have on conscious perception (Van Noorden, 1975). Participants listened to an ABA- pattern in which the A tone started out being much higher (or lower) than the B tone and increased (or decreased) in frequency after each presentation while the B tone stayed constant. This resulted in a continuously changing Δf between the A and B tones, and thus a continuously changing likelihood of hearing one or two streams. The stimulus onset asynchrony (SOA) from one tone to the next was also varied to promote auditory streaming. In addition to the changing stimulus, the participants' intention varied as a result of the following instructions: (1) try and hear a single stream, or (2) try and hear two streams. The participants' continuous "one stream" vs. "two streams" responses as a function of Δf and SOA provided a way to assess the limits of hearing a sequence of tones as integrated or segregated (see Figure 4). The Δf at which it was no longer possible to hold this percept was called the "fission boundary," and did not vary much with SOA. In contrast, when participants were asked to hold the one stream percept, the Δf at which it was no longer possible (the "temporal coherence boundary") varied substantially with SOA. Importantly, these two perceptual boundaries did not overlap with each other, resulting in a large number of



combinations of Δf and SOA in which either percept was possible. Not only did this demonstrate the large effect intention can have on conscious perception, it also was suggestive of other properties associated with conscious visual perception such as hysteresis and multistability (cf. Hock et al., 1993), foreshadowing more recent research to be discussed in detail below. Interestingly, Van Noorden used the term “attentional set” instead of “intention” to describe the manipulated variable in his study, which raises the important possibility that the effects he observed were due most directly to the scope of selective attention of the listener on either both the A and B tones or just one of the tones. Thus, while selective attention may be a mediating mechanism for the effect of intention to hear a particular perceptual organization on perception, it might not be the only way that a listener’s intention can affect conscious perception. Given that, surprisingly little research has been done since Van Noorden’s study to distinguish between effects of attention and intention, at either the behavioral or neurophysiological level, this remains a rich area to be investigated further.

Prior experience

One way to study higher-order cognitive processes during perception is to assess the impact of prior experience, which can inform the role of explicit and implicit memory during perception. For example, streaming studies have tested for effects of prior knowledge of stimuli as a possible mediating mechanism for a listener’s intention to hear segregated patterns in an auditory scene. In one early study, listeners were presented with two melodies at the same time, with the tones of melody A interleaved with the tones of melody B (i.e., $A_1, B_1, A_2, B_2, \dots$, where A_1 is the first note of melody A). This results in a melody that is more complex than the typical ABA- pattern used for streaming experiments because the A and B tones frequently change during a trial (Dowling, 1973). When both melodies were familiar tunes, it was easier to identify them when the frequency ranges of

the two melodies were greatly separated, as in standard streaming paradigms. Importantly, when the name of one of the tunes was given prior to hearing the interleaved melodies, it was easier to perceptually segregate it even when the two melodies were closer in pitch, demonstrating an effect of prior knowledge on perceptual segregation. However, knowing the name of the background melody did not help participants identify the target melody, suggesting that prior knowledge does not attenuate the distracting influence of background sounds (also, see Newman and Evers, 2007). Instead, it seems more likely that attentional focus upon expected notes in the target melody helped segregate it from the background. A later study directly tested this idea, showing that target melodies with events presented at points of high temporal expectation due to the rhythm of the A and B melodies were recognized better than melodies with events presented at points of low expectation (Dowling et al., 1987). This form of temporal attention is consistent with the dynamic attending theory of Jones and colleagues (Jones, 1976; Jones and Boltz, 1989; Large and Jones, 1999). A caveat to the work by Dowling on effects of familiarity is a more recent study showing that previously unfamiliar interleaved melodies were not easier to segregate when the target melody had just been presented by itself prior to the interleaved melodies (Bey and McAdams, 2002). Thus, the beneficial effects resulting from familiarity may only occur when the patterns are stored in long-term memory. Alternatively, it is possible that representations for familiar melodies are simply stronger than short-term traces for melodies that have been presented only once, regardless of the storage mechanism.

In some cases discussed thus far it is difficult to rule out attention as the most direct factor that enhances processing when manipulating familiarity of stimuli or the listener’s intention. However, it is also possible that familiarity, priming, and other memory-related factors might be able to directly influence perception through non-attention-related mechanisms. For example, adults of all ages benefit from semantic predictability of words in a sentence segregation task (Pichora-Fuller et al., 1995). Another study showed that complex stimuli that are embedded in noise became easier to segregate when they were presented repeatedly, as long as on each new presentation they were mixed with a different noise (McDermott et al., 2011). Because the noises are unlikely to be perceived as auditory objects prior to the first time they are successfully segregated, this result suggests that short-term memory traces are able to automatically facilitate segregation. Finally, studies of streaming context effects have shown that both prior stimuli and prior perception of those stimuli can have large effects on a subsequent perceptual decision, an example of implicit memories influencing perception (Snyder et al., 2008, 2009a,b; Snyder and Weintraub, 2011; for similar findings in continuity perception, see Riecke et al., 2009, 2011; for related research in speech perception, see McClelland et al., 2006). In particular, a prior ABA- pattern with a large Δf biases following patterns to be heard as one stream, a *contrastive* or *suppressive* effect; in contrast, prior perception of two streams biases subsequent patterns to be heard with the same percept, a *facilitative* effect. Importantly, these streaming context effects are likely to be implicit because listeners are not explicitly asked to compare prior and current patterns nor are they typically aware that the prior patterns are affecting their perception. Also

of note is that the context effects are consistent with similar effects of prior stimuli and prior percepts observed in vision, suggesting the operation of general memory mechanisms that implicitly influence perception (Pearson and Brascamp, 2008).

One account of perception, known as reverse hierarchy theory, might help explain how high-level factors such as intention and prior experience might enhance segregation (Hochstein and Ahissar, 2002). This theory assumes that a stimulus activates the sensory system in a bottom-up manner without conscious access of each low-level representation; when the information finally reaches a high-level representation, this is accessed in the form of a gist or category related to the stimulus (also, see Oliva and Torralba, 2001; Greene and Oliva, 2009). Once this high-level activation occurs, low-level representations of the stimulus can be accessed only in specific circumstances in which a top-down path is possible. The reverse hierarchy theory is consistent with visual learning studies and a number of other visual phenomena including change blindness and illusory conjunctions (Hochstein and Ahissar, 2002). Recently, the theory was also able to predict novel findings in a word segregation task (Nahum et al., 2008). Hebrew-speaking listeners were unable to use a low-level binaural difference cue that would have aided segregation when the task was to make a semantic judgment on one of two possible Hebrew words that were phonologically similar (e.g., /tamid/ and /amid/). This was likely due to the fact that the semantic task primarily involved accessing high-level representations and the acoustically similar words were processed in highly overlapping ascending auditory pathways. Interestingly, even when the task was not inherently high-level such as in word identification, binaural cues were not used unless they were available on every trial within a block, suggesting that listeners implicitly learn over the course of a block of trials to not access low-level representations unless they were consistently useful. For our purposes, these results are interesting because they support a theory that might be able to explain how high-level information about stimuli and recent experience can guide the accessing of low-level cues for conscious auditory perception.

MULTISTABILITY

The fact that subjective and objective measures of perception can be substantially modulated by attention and other high-level factors suggests that auditory perception is multistable like visual perception (Leopold and Logothetis, 1999; Long and Toppino, 2004; Pearson and Brascamp, 2008). However, it was not until relatively recently that a thorough quantitative comparison was made between auditory and visual multistable perception (Pressnitzer and Hupé, 2006). In this study, the authors assessed auditory streaming using ABA- patterns with an intermediate Δf presented with many more repetitions per trial than usual. The same observers were also tested on perceptual segregation of moving plaid patterns, which has been studied in detail at the psychophysical (e.g., Hupé and Rubin, 2003) and neurophysiological (e.g., Movshon et al., 1985) level. Perception of the moving plaid pattern was appropriate for this comparison with perception of ABA-patterns because the two stimuli share a number of psychophysical properties. First, they are both segregation tasks, resulting in either the perception of a single pattern or two distinct patterns. Second,

in both paradigms the initial perception is of a single pattern and only after a buildup period does perception of two patterns occur. The study went further by showing that after the initial switch to perceiving two patterns, observers then showed similar stochastic switching between the two percepts in both modalities. And the initial period of perceiving one stream was longer in duration than subsequent periods of either stable percept. They also showed that it was possible to intentionally control perception but it was not possible to completely eliminate switching between percepts, consistent with the findings of Van Noorden (1975) discussed earlier. The finding that even for ABA- patterns with rather large or rather small Δf values (i.e., not “ambiguous”) switching between one and two streams continued to occur, despite an overall bias for one percept, emphasizes the robustness of multistability in streaming (Denham and Winkler, 2006).

Pressnitzer and Hupé (2006) further showed that despite the similar multistable perceptual phenomena in the visual and auditory paradigms, the number of switches per unit time in one modality did not predict the switching rate in the other modality, suggesting similar but functionally distinct mechanisms for controlling perception in vision and hearing. In a subsequent study, these authors further explored the mechanisms controlling multistable perception by presenting visual and auditory patterns at the same time (Hupé et al., 2008). In the first experiment, they presented ABA- and plaid patterns together and participants reported any switches observed in each modality. In the second experiment, they presented ABA- and apparent motion patterns together that were spatially and temporally coupled with each other, in order to increase the likelihood of cross-modal interactions in perception. The results showed that a switch in one modality did increase the likelihood of switching in the other modality, that the likelihood of perceiving the same percept in the two modalities was higher than expected based on chance, and these two effects were largest for the experiment using cross-modally coupled patterns. Thus, while there is likely to be interaction between the two modalities in controlling perception, this latter finding suggested that there is not a supramodal mechanism that controls perception in both modalities; rather, perceptual mechanisms in vision and hearing may interact depending on how likely signals in the two modalities are coming from the same physical objects in the environment. This conclusion is consistent with a study showing that intentional control over perceptual interpretations is strongly enhanced when stimuli are cross-modally consistent with each other (van Ee et al., 2009).

Neurophysiological studies also support the idea that perception may be determined primarily within modality-specific brain areas. In vision, the majority of findings show robust correlates in areas that are thought to be primarily dedicated to visual processing (Leopold and Logothetis, 1999; Tong et al., 2006). In hearing, although there are only a few studies on neural correlates of multistable perception, the findings also suggest the involvement of auditory-specific processes. However, it is important to be cautious in interpreting the precise role of brain areas measured in neurophysiological studies because of the correlational nature of the data.

In a streaming study measuring neuromagnetic brain activity signals from the superior temporal plane, small modulations in

sensory-evoked response amplitude were observed depending on whether listeners were hearing two streams. These perception-related modulations occurred in similar components as those that were modulated by increased Δf , but they were smaller in amplitude (Gutschalk et al., 2005). Intracranial ERPs from several lateral superior temporal lobe locations measured during neurosurgery in epilepsy patients also showed some dependence on perception, but these were also much less robust compared to Δf -dependent modulations (Dykstra et al., 2011). In a functional magnetic resonance imaging (fMRI) study, listeners showed more activity in auditory cortex when hearing two streams as opposed to one stream (Hill et al., 2011). In another fMRI study, which examined neural correlates of switching between one- and two-stream percepts, switching-related activations were observed in non-primary auditory cortex as well as the auditory thalamus in a manner that suggested the importance of thalamo-cortical interactions in determining perception (Kondo and Kashino, 2009). In an fMRI study on streaming using inter-aural time difference as the cue to segregating A and B tones, switching-related activity in the auditory cortex was again found, in addition to activity in the inferior colliculus, which is an important brainstem area for processing binaural information (Schadwinkel and Gutschalk, 2011). Future studies should directly compare the effect of perceiving one vs. two streams and the effect of switching between perceiving one and two streams; without such a direct comparison using the same participants and similar stimuli, it is difficult to determine whether similar brain circuits are implicated in these possibly distinct processes.

Exceptions to evidence for modality-specific auditory perception mechanisms are fMRI studies showing enhanced activity while perceiving two streams compared to perceiving one stream in the intraparietal sulcus, an area that is thought to also be involved in visual perceptual organization and attention shifting (Cusack, 2005; Hill et al., 2011). Interestingly, increasing the spectral coherence of complex acoustic stimuli in such a way that increases perceptual segregation also modulated the fMRI signals in intraparietal sulcus, in addition to the superior temporal sulcus, a higher-order auditory processing area (Teki et al., 2011). However, these brain modulations were observed while participants were not making perceptual judgments so it is unclear the extent to which they reflect perceptual processing, as opposed to automatic stimulus processing. At this point it is difficult to conclusively state which of the brain areas found to correlate with perception in these studies are most likely to be important for determining perception because of the different stimuli and tasks used. But these studies have provided a number of candidate areas that should be studied in future neurophysiological studies, as well as studies that assess the consequences of disrupted processing in the candidate areas.

Although other ASA tasks (e.g., mistuned harmonic segregation) have not been studied as thoroughly for signs of multistable perception observed in streaming, it stands to reason that they would show some of the same phenomena and could be useful in determining the generality of the streaming findings. For example, a multistable speech perception phenomenon is *verbal transformation* in which repeated presentation of a word results in the perceived word changing to another word, often

with many different interpretations during a single trial (e.g., the four-phoneme stimulus TRESS being heard as the following sequence of words “stress, dress, stress, dress, Jewish, Joyce, dress, Jewess, Jewish, dress, florist, florist, Joyce, dress, stress, dress, purse”; Warren, 1968). Ditzinger and colleagues showed that rather than randomly changing between all the possible alternatives, pairs of alternatives tended to alternate with each other, suggesting that the principles underlying the phenomenon are more similar to other multistable phenomena (Ditzinger et al., 1997b; Tuller et al., 1997). Indeed, a dynamic systems model that was similar to a model of multistable visual perception was able to reproduce the time course of verbal transformations (Ditzinger et al., 1997a).

A more recent study took a different theoretical approach to verbal transformations by trying to explain them in terms of auditory streaming and grouping mechanisms (Pitt and Shoaf, 2002). Listeners were presented three-phoneme (consonant–vowel–consonant) pseudowords and reported instances of hearing transformations in addition to instances of hearing more than one stream of sounds. A large majority of the transformations reported were accompanied by hearing more than one stream of sounds, suggesting that part of the original pseudoword was segregated from the remainder, changing how the remainder sounded. Changes in perception also occurred for sine-wave speech that was repeated, with transformations occurring after more stimulus repetitions when perceived as speech rather than as tones, suggesting an influence of top-down knowledge on stabilizing perception, consistent with evidence from streaming paradigms discussed above. Behavioral evidence that overt and covert speech production constrains perception of verbal transformations (Sato et al., 2006) further implicates speech-specific (e.g., articulatory) mechanisms being important for generating verbal transformations, as does neurophysiological activity in left inferior frontal speech areas associated with transformations (Sato et al., 2004; Kondo and Kashino, 2007; Basirat et al., 2008).

In addition to speech perception paradigms, signs of multistable perception have also been observed in a variety of musical tasks (e.g., Deutsch, 1997; Toivainen and Snyder, 2003; Repp, 2007; Iversen et al., 2009). Additional research on musical multistability would be especially interesting in light of evidence suggesting distinct mechanisms for resolving ambiguous stimuli in vision vs. hearing and speech-specific mechanisms in verbal transformations. For instance, it would be important to determine whether different types of ambiguous auditory stimuli (e.g., speech vs. music) are resolved in distinct neural circuits. This would suggest that multistability is controlled not by centralized mechanisms in only a few brain areas but rather by the normal dynamics that are available throughout the cerebral cortex or other brain areas.

FROM SOUNDS TO CONSCIOUS PERCEPTS, OR NOT

While the research described above demonstrates the promise of using segregation paradigms to understand the role of high-level factors in resolving ambiguous stimuli, another important topic is to understand why some auditory stimuli fail to become accessible to awareness in the first place. Fortunately, researchers have developed a number of clever techniques, often inspired by similar research in vision, to manipulate whether an auditory event is made consciously accessible to observers. Such techniques are critical to understand the mechanisms underlying stimulus awareness,

and also evaluating the influence of being aware of a stimulus on processing subsequent stimuli, separate from the influence of other factors such as attention (Koch and Tsuchiya, 2007).

ENERGY TRADING

Traditional ASA theory (Bregman, 1990) makes a common, but perhaps erroneous, assumption of the existence of energy trading. According to the energy trading hypothesis, if one auditory component contributes to two objects simultaneously, then the total energy in that component should be split between the two objects so that the sum of the amount of energy the component contributes to each object equals the total amount of energy in the component. Research on this topic provides important insights about how low-level sound components contribute to perception of auditory objects and streams. However, the object representations in a scene do not always split the total amount of energy available in a zero-sum fashion (Shinn-Cunningham et al., 2007). In this study, a pure-tone target was used that could be perceptually grouped with either a rhythmic sequence of pure tones of the same frequency (tone sequence) or with concurrent pure tones of different frequencies (a vowel). If the target was incorporated into the vowel, the category of the vowel would change from /I/ to /ε/, and if the target was incorporated into the sequence, its rhythm would change from “galloping” to “even.” The tone sequence, vowel, and target were presented together with varying spatial configurations. The target could be presented at the same spatial location as the vowel (or tone sequence) to increase the probability of perceptual grouping, or the target could be presented at a different spatial location. The authors conducted trials in which listeners attended to the vowel while ignoring the tone sequence or vice versa.

They found that in the attend-tone block, listeners heard the target as contributing to the tone sequence in all spatial configurations, except when the target was presented at the same location as the vowel. Oddly, in the attend-vowel block, when the feature was presented at the same spatial location as the vowel, the feature did not group with the vowel – the vowel was perceived as /I/. Because the target did not contribute to either percept (the tone sequence or the vowel), it was as if the target tone disappeared from the mixture. This curious case of a feature disappearing suggests that energy trading does not always hold between objects in scenes and that there can be sounds in a scene that do not reach conscious perception even though they are otherwise audible. Shinn-Cunningham et al. (2007) further suggest that listeners require more evidence to allocate an auditory component to a sound in a perceptual figure than to reject it to the auditory ground. It should be noted that in two other studies (Shinn-Cunningham et al., 2008; Shinn-Cunningham and Schwartz, 2010), the same researchers used a simultaneous tone complex rather than a vowel as a competing sound with the tone sequence, and found results that were more consistent with energy trading (see also Leung et al., 2011). However, these two studies also used a richer harmonic target sound, which changed the perceived pitch of the tone complex when the target was integrated.

Another line of research that is problematic for the energy trading hypothesis is the well-established finding of duplex perception: an auditory component can contribute to two sounds at the same time (Rand, 1974; Fowler and Rosenblum, 1990). Duplex

perception was first demonstrated by Rand (1974). In this study, the second and third formant transitions from a syllable, e.g., “da,” were presented to one ear while the rest of the syllable (i.e., the first formant and the remaining second and third formants) was presented to the other ear. This stimulus generated two simultaneous percepts: listeners reported hearing a fully intact syllable in one ear and a non-speech chirp-like sound in the other ear. The identity (“da” vs. “ga”) of the syllable was determined by the third formant transition. Even though the critical feature for identification of the syllable was presented at a separate spatial location from the rest of the syllable, the feature was integrated with the other components to create a coherent, identifiable percept (while at the same time creating the separate percept of a chirp).

Duplex perception has been found to be surprisingly resistant to a variety of other manipulations of the third formant transition, such as SOA (e.g., Bentin and Mann, 1990; Nygaard and Eimas, 1990; Nygaard, 1993), amplitude differences (Cutting, 1976; Whalen and Liberman, 1987; Bentin and Mann, 1990), f_0 (Cutting, 1976), and periodicity differences (Repp and Bentin, 1984). The effect is so strong that it has even been found to occur when the isolated formant transition is not necessary to form a coherent percept (Nygaard and Eimas, 1990). Duplex perception phenomena are not limited to speech objects. For example, when two simultaneous piano notes are presented to one ear while a single note is presented simultaneously to the other ear, the resulting percept is of both the single tone and a fused chord (Pastore et al., 1983). Duplex perception also has been demonstrated with environmental sounds (see Fowler and Rosenblum, 1990).

In summary, it is necessary to either modify ASA theory (Bregman, 1990) or to look beyond it for an explanation of the non-veridical perceptual organization of auditory scenes. Collectively, the findings of duplex perception and the recent case of feature non-allocation contradict the energy trading hypothesis and call into question the amount of low-level detail we are aware of in our acoustic environment (cf. Nahum et al., 2008). Future research on energy trading using denser and more naturalistic auditory scenes is needed to provide a more complete picture of how ASA is accomplished to generate our conscious perception of auditory objects and streams.

CHANGE DEAFNESS

Change deafness is the surprising failure to notice striking changes to auditory scenes. A visual analog to this phenomenon has been extensively studied in the visual domain, where it is referred to as change blindness (for reviews, see Rensink, 2002; Simons and Rensink, 2005). And a related auditory phenomenon was actually demonstrated as early as the work of Cherry (1953) who showed that changes to an unattended stream of auditory input (such as a change of the speaker's identity) are often missed while shadowing a spoken message presented to an attended stream of auditory input (Vitevitch, 2003; Sinnett et al., 2006). Studies using the one-shot technique, in which presentation of a scene is followed by an interruption and then either the same or a modified scene, have been the most common way of examining change deafness. Listeners were found to often miss changes to environmental objects, such as a dog barking changing to a piano tune (e.g., Eramudugolla et al., 2005; Gregg and Samuel, 2008, 2009). It is important to note

that change deafness occurs even though scenes sizes are typically quite small: ~45% change deafness occurred in Gregg and Samuel (2008) with just four objects per scene. An understanding of the mechanisms underlying change deafness has the potential to inform several issues in auditory perception, such as the completeness of our representation of the auditory world, the limitations of the auditory perceptual system, and how auditory perception may limit auditory memory for objects (for a review, see Snyder and Gregg, 2011). Change deafness might also be useful for studying unconscious processing of changes, as well as the mechanisms that enable changes to reach awareness.

One study has shown that change deafness is reduced with directed attention to the changing object (Eramudugolla et al., 2005). In this study, a 5-s scene was presented, followed by a burst of white noise, and then another 5 s scene that was either the same or different. On Different trials, an object from Scene 1 was either deleted in Scene 2 or two objects switched spatial locations from Scene 1 to Scene 2. The experimental task was to report whether the two scenes were the “Same” or “Different,” and substantial change deafness was found when not attending to the to-be-changed object. However, when attention was directed to the to-be-changed object via a verbal cue, change detection performance was nearly perfect. One problem with this study, however, is that attention cues were always valid. As a result, participants could have listened for the cued sound in Scene 2, rather than actually comparing the two scenes. An interesting question to address in future research is what aspects of auditory objects must be attended to enhance performance.

Failures to detect changes may not necessarily reflect a failure to encode objects in scenes. Gregg and Samuel (2008) presented an auditory scene, followed by a burst of noise, and then another scene that was either the same as or different than the first scene. Participants performed a change detection task, followed by an object-encoding task, in which they indicated which of two objects they had heard in one of the two scenes. Gregg and Samuel found that object-encoding had a lower error rate than change detection (28 vs. 53%). This study also found that the acoustics of a scene were a critical determinant of change deafness: performance improved when the object that changed was more acoustically distinct from the sound it replaced. But the acoustic manipulation had no effect on object-encoding performance, even though it resulted in more spectral differences within one of the scenes. Gregg and Samuel suggested that successful change detection may not be based on object identification, as is traditionally assumed to underlie visual scene perception (e.g., Biederman, 1987; Edelman, 1998; Ullman, 2007), but is instead accomplished by comparing global acoustic representations of the scenes.

Recently, however, McAnally et al. (2010) distinguished between object-encoding on detected and not detected change trials and found that performance in identifying which object was deleted was near ceiling when changes were detected but at chance when changes were not detected. This finding suggests that changes may only be detected if objects are well encoded, contrary to the findings of Gregg and Samuel (2008). However, it should be noted that the extent of change deafness that occurred in McAnally et al. (2010) was quite modest. They obtained 15% change deafness for scene sizes of four objects, whereas Gregg and Samuel obtained

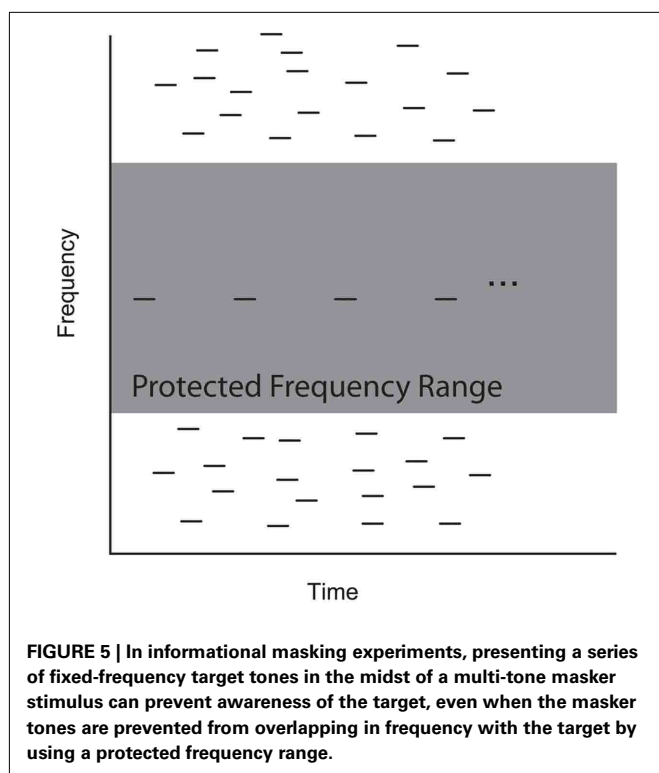
45% change deafness for scene sizes of four objects. One potential reason for the discrepancy across studies may be that the task in McAnally et al. (2010) did not elicit much change deafness. In their study, a changed scene consisted of an object that was missing, rather than an object replaced by a different object as in Gregg and Samuel. Despite the task differences, the results of McAnally et al. (2010) do question the extent to which objects are encoded during change deafness, and this is an issue that warrants further investigation.

One major issue in the change deafness research is the question of whether change deafness actually reflects verbal or semantic processing limitations, rather than a sensory-level process. Gregg and Samuel (2009) have shown that abstract identity information seems to be encoded preferentially compared to intricate physical detail. In this experiment, within-category changes (e.g., a large dog barking changing to a small dog barking) were missed more often than between-category changes (e.g., a large dog barking changing to a piano tune). It is important to note that this result occurred even though acoustic distance for within- and between-category changes was controlled. In fact, the finding that within-category changes elicited more change deafness was so robust that it occurred even when the within-category changes were acoustically advantaged compared to between-category changes. Gregg and Samuel did not address the specific nature of the high-level representation being used; it is possible that subjects may have been forming a mental list of verbal labels for all of the objects in the pre-change scene, as has been suggested (Demany et al., 2008). Alternatively, higher-order representations might be activated that reflect the semantic similarity between objects within and between categories.

In summary, change deafness is a relatively new and intriguing line of research. Future research is needed to resolve theoretical issues about why failures to detect auditory changes occur. For example, the issue still remains to what extent sensory-related, attention, memory, or comparison processes are responsible for failures to detect changes and how the interaction of these processes contributes to change deafness.

MASKING

Masking of a target stimulus by another stimulus presented around the same time has been used extensively to study low-level mechanisms of auditory processing. Typically, masking has been observed most strongly when the target and masking stimuli are similar in acoustic features such as frequency, which can be attributed to interference in early frequency-specific stages of processing (e.g., Moore, 1978). This form of masking is referred to as “energetic masking,” in contrast to “informational masking,” which is assumed to occur when sounds do not have acoustic overlap. Rather, informational masking is assumed to take place at later anatomical sites in the auditory system and to result from a variety of higher-level factors including perceptual grouping and attention (Durlach et al., 2003a; Kidd et al., 2007; Shinn-Cunningham, 2008). The notion of informational masking has generated interesting research that can inform perceptual mechanisms relevant to the current discussion. In particular, a variant of the multi-tone masker paradigm (see Figure 5) bears some similarity to streaming paradigms in its use of repeating pure tones (Neff and Green,



1987). An important difference, however, is the fact that the task typically used in informational masking experiments is to detect whether a fixed-frequency tone is present or absent in a scene along with numerous other masking tones of different frequencies. Peripheral masking can be prevented by not presenting any of the masking tones within a critical band around the target tone.

Several results in the literature have demonstrated interesting similarities between factors that cause streaming and factors that cause release from informational masking. In particular, faster presentation rate, greater target-mask dissimilarity, and cueing the location of the target all facilitate release from masking (Kidd et al., 1994, 2003, 2005; Durlach et al., 2003b; Micheyl et al., 2007b). Similarities may also exist at the neural level: in one study a long-latency response from secondary auditory cortex occurred in response to target tones in a multi-tone masker, but only when participants detected them; remarkably, when the tones were not detected all long-latency brain responses were conspicuously absent (Gutschalk et al., 2008). The response was referred to as an awareness-related negativity (ARN) and was later in latency than (but had similar scalp distribution to) the well-studied N1 response (Näätänen and Picton, 1987), which is consistent with the involvement of negative long-latency responses in streaming and concurrent sound segregation (e.g., Alain et al., 2001; Gutschalk et al., 2005; Snyder et al., 2006). Activity from primary auditory cortex was present regardless of whether the target was detected, strongly suggesting that neural activity must reach beyond primary auditory cortex in order to generate perception. The results were also consistent with the reduction in the N1 observed when sounds are ignored and during sleep (Crowley and Colrain, 2004). The N1 is thought to be an obligatory stimulus-driven response,

but if the ARN were related to the N1 (as was suggested by similar source locations), this study would be the first to demonstrate that the N1 generators require participants to be aware of a stimulus to be activated. However, some caution is warranted because the ARN was found to have a longer latency than is typical of the N1, and could therefore be more related to a later negative wave (Nd), which is linked to selective attention (Hansen and Hillyard, 1980). This raises the possibility that the ARN could simply be an index of fluctuations in attention, rather than a direct correlate of awareness.

These results are interesting to compare with findings from a single patient with bilateral superior temporal auditory cortex lesions due to stroke, who performed well on sound detection tasks as long as attention was paid to the tasks (Engelien et al., 2000). However, it is not totally clear what the exact experience of this patient was. In particular, the patient may have had normal conscious experience of detecting sounds as long as enough attention was used; alternatively, the patient may have had little conscious experience of the sounds that he was nevertheless able to reliably detect, in an analogous fashion to patients with blindsight as a result of visual cortex damage (e.g., Stoerig and Cowey, 1997). The same patient showed activation during attention to auditory tasks in a number of brain areas, measured by positron emission tomography, such as in the prefrontal and middle temporal cortices, caudate nucleus, putamen, thalamus, and the cerebellum. Thus, detection of sounds (whether accompanied by conscious experience of the sound or not) may be possible by activating non-auditory brain areas, raising the question of the extent to which superior temporal auditory cortex is necessary or sufficient for awareness to occur. For example, it is possible that the ARN found by Gutschalk et al. (2008) is the result of input from higher-level brain areas that are responsible for generating awareness. Recently, evidence in support of the importance of feedback for generating awareness was found by recording electrophysiological responses in patients in a vegetative state, who compared to controls showed a lack of functional connectivity from frontal to temporal cortex during processing of changes in pure-tone frequency (Boly et al., 2011; for evidence from the visual domain supporting the importance of top-down feedback for perceptual awareness in fully awake, non-brain-damaged individuals, see Pascual-Leone and Walsh, 2001; Wibral et al., 2009).

SUBLIMINAL SPEECH

Recently, researchers have made speech inaudible to determine the extent of auditory priming that can occur without awareness of the priming stimulus. This is one of the only examples of research that has addressed the necessity or sufficiency of auditory awareness for prior stimuli to influence later processing. In one study, priming words were made inaudible by attenuation, time-compression, and masking with time reversals of other time-compressed words immediately before and after the priming words (Kouider and Dupoux, 2005). Compressing words so they were as short as 35 or 40% of their original duration led to very little awareness of the primes as measured on independent tests in which participants had to decide whether the masked sound was a word vs. non-word or a word vs. reversed word. The test word, which was not attenuated or compressed, was played immediately after the

priming word (and simultaneously with the post-priming mask). Non-word pairs were also used that were the same or acoustically similar. Based on the speed with which participants made word vs. non-word decisions about the target, this study showed that repetition of the same word caused priming (i.e., faster responses compared to unrelated prime–target pairs) at all time compressions, including ones that made the prime inaudible (35 and 40%), although the priming effect was larger for audible primes (50 and 70%). Priming also occurred when the prime and target were the same words spoken by different-gender voices, even for the 35% compression level, suggesting that subliminal priming can occur at the abstract word level, independent of the exact acoustics of the sound. Priming effects did not occur for non-words or for semantically related (but acoustically different) words at the subliminal compression levels, suggesting that semantic processing may require conscious perception of words.

A second study used primes that were compressed by 35%, but this time the researchers made the prime audible on some trials by presenting them with a different inter-aural time difference compared to the masking sounds (Dupoux et al., 2008). Again, word priming only occurred for masked words but not masked non-words; priming occurred for both words and non-words when unmasked; and priming was larger for unmasked compared to masked sounds. Additionally, priming did not decline with longer prime–target delays for unmasked words, but the effect declined rapidly for masked sounds over the course of 1000 ms, suggesting a qualitatively different type of robust memory storage for audible sounds.

The basic masked priming effect was recently confirmed by a separate group, who additionally showed that priming occurs mainly for targets with few phonological neighbors (Davis et al., 2010). But a recent study found semantic priming using auditory prime–target word pairs (Daltrozzo et al., 2011), which was in contrast to the study by Kouider and Dupoux (2005). However, the more recent study showing semantic priming used very low-intensity primes that were not possible to categorize, instead of also using time-compression and masking, which could account for the discrepant findings.

Kouider et al. (2010) recently performed an fMRI study using their masking paradigm. They showed priming-related suppression of activity which may prevent processing of stimuli that have already been presented (Schacter et al., 2004). Decrease in activity was found in the left superior temporal auditory cortex (including Heschl's gyrus and planum temporale) for within-gender word pairs and cross-gender word pairs, and in the right insula for within-gender word pairs. For non-words, a different pattern of activity decrease was found in the frontal lobe and caudate nucleus, in addition to response enhancement in the superior temporal cortex. The function of the brain changes should be interpreted cautiously, however, because the magnitudes of activity decrease did not correlate with the magnitudes of behavioral priming. Nevertheless, the results do show that information about unconscious auditory stimuli can reach fairly high levels of processing, with the particular brain areas involved being dependent on the familiarity or meaningfulness of the stimuli.

Speech-priming results are also interesting to compare with a recent study that used fMRI to measure acoustic sentence

processing in individuals who were fully awake, lightly sedated, or deeply sedated (Davis et al., 2007). Neural activity in temporal and frontal speech-processing areas continued to differentiate sentences from matched noise stimuli in light sedation and superior temporal responses continued in deep sedation. In contrast, neural activity did not distinguish sentences with vs. without semantically ambiguous words, consistent with the lack of semantic priming observed by Kouider and Dupoux (2005) but inconsistent with the study by Daltrozzo et al. (2011).

AUDITORY ATTENTIONAL BLINK

Attentional blink (AB) refers to a phenomenon where the correct identification of a first target (T1) impairs the processing of a second target (T2) when presented within several hundred milliseconds after T1 (e.g., Broadbent and Broadbent, 1987; Raymond et al., 1992; Chun and Potter, 1995). Although the AB has been studied primarily in the visual modality, there is some evidence to suggest that AB also occurs in the auditory modality (e.g., Duncan et al., 1997; Soto-Faraco et al., 2002; Tremblay et al., 2005; Vachon and Tremblay, 2005; Shen and Mondor, 2006).

In a typical auditory AB experiment, participants are presented with a rapid sequence of auditory stimuli. Participants indicate whether they heard T1 and T2 by sequentially pressing two different buttons. The magnitude of the auditory AB decreases with increased time between successive stimuli (Shen and Mondor, 2006; Shen and Alain, 2010). This is not surprising as the increased SOA provides more time to process T1. Increasing the salience of T1 also increased the auditory AB (Horváth and Burgyan, 2011), most likely by momentarily capturing attention, thereby causing a processing deficit for T2. This effect is short lived and is present only when T2 immediately follows T1.

The auditory AB shows a monotonic linear improvement in performance as a function of the interval between the target and the probe (Shen and Mondor, 2006, 2008). This pattern differs from that observed in the visual modality, where the time course of AB has a U-shaped pattern (Raymond et al., 1992). Based on such findings, some researchers have argued that, instead of reflecting the limitation of attention, the auditory AB may simply reflect the cost of task-switching from searching for T1 to searching for T2 (Potter et al., 1998; Chun and Potter, 2001). However, Shen and Mondor (2006) have argued that the difference between a linear and a U-shaped curve occurs because the auditory system has better temporal resolution than the visual system, allowing T1 and T2 to be processed sequentially rather than simultaneously as in the visual modality.

There is increasing evidence that visual AB is sensitive to attentional allocation during the rapid serial visual presentation task. For instance, providing information about the occurrence of the second target attenuates the visual AB (e.g., Martens and Johnson, 2005; Nieuwenstein, 2006; Zhang et al., 2008; Du and Abrams, 2010). These studies indicate that attention can be directed toward the probe feature or temporal position, thereby facilitating its detection. The findings from these studies also suggest that there is some degree of flexibility in the allocation of processing resources despite the existence of processing bottlenecks (Kahneman, 1973).

There is evidence that auditory AB, like visual AB, can also be modulated by attention orienting in a rapid serial auditory

presentation task (Shen and Alain, 2011). Temporal attention was manipulated by task instruction and was blocked for an entire recording session to emphasize focused attention at the designated temporal position. Behavioral results showed a typical pattern of auditory AB. The hit rate at each position when T2 was attended was significantly higher than the false alarm rate at the same position, indicating that participants were able to temporally allocate their attention to the designated temporal position. The latency of the P3b wave elicited by T2 was shortened when attention was oriented to the designated temporal position. More importantly, the electrophysiological results suggest that the initiating of short-term consolidation for T2 was facilitated when attention was oriented to the designated temporal position.

SUMMARY AND CONCLUSION

The research reviewed here clearly shows that much progress has been made in understanding the influence that high-level factors can have on conscious auditory perception and that tasks developed to study ASA are well suited for such investigations. There is now compelling evidence that one or more attention-related factors (i.e., sustained attention to an entire auditory scene, selective attention to particular objects or streams within a scene, attention switching, attention limitations) can have dramatic influences on perceptual organization of scenes and the ability to detect important events in the environment. However, there is evidence that other high-level mental processes, such as intention and previous knowledge, also greatly impact auditory perception. In some cases, these processes are likely to affect

perception indirectly through attention-related processes and in other cases to have more direct influences, although a limitation of the studies reviewed here is that they did not compare effects of attention to other high-level influences to see if they indeed have dissociable effects on perception. In vision studies, one process that has been identified as having distinct influences from attention is the awareness of prior stimuli on perception of subsequent stimuli (Koch and Tsuchiya, 2007). Thus, future studies should attempt to manipulate awareness of prior stimuli, in addition to the other high-level factors discussed here, and directly compare their effects. Fortunately, researchers have made substantial progress in manipulating awareness of acoustic stimuli, as we reviewed here, which should make such efforts possible in the future. However, much additional research is needed to fully understand the mechanisms that mediate various types of auditory awareness, such as measured by informational masking, change deafness, priming, and AB paradigms. More work on patients with damage to auditory brain areas, in addition to neurostimulation, neurophysiology, and computational studies are also likely to reveal important findings about the mechanisms of auditory awareness.

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Attention and olfactory consciousness

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Understanding the relation between attention and consciousness is an important part of our understanding of consciousness. Attention, unlike consciousness, can be systematically manipulated in psychophysical experiments and a law-like relation between attention and consciousness is waiting to be discovered. Most attempts to discover the nature of this relation are focused on a special type of attention: spatial visual attention. In this review I want to introduce another type of attention to the discussion: attention to the olfactory modality. I will first clarify the position of attention to smells in a general taxonomy of attention. I will then review the mechanisms and neuroanatomy of attention and consciousness in the olfactory system before using the newly introduced system to provide evidence that attention is necessary for consciousness.

Keywords: olfaction, attention, consciousness, odor, orbitofrontal cortex, piriform cortex

INTRODUCTION

Knowledge about the relation between attention and consciousness is invaluable for the empirical study of consciousness because attention can be varied experimentally and its effect on conscious perception can be measured. The discussion of how attention relates to consciousness has so far been based primarily on empirical results from the study of spatial visual attention (Dehaene et al., 2006; De Brigard and Prinz, 2010; Prinz, 2010; Van Boxtel et al., 2010). The goal of this paper is to introduce attentional shifts toward the olfactory modality as a second system in which attention and consciousness interact. The advantage of opening up the discussion to facts from a second type of attention is that it reduces the likelihood of mistaking special adaptations for general principles.

The main motivation to study attention in olfaction is the computational and anatomical simplicity of the olfactory system (Haberly, 2001; Lledo et al., 2005; Isaacson, 2010; Sela and Sobel, 2010). The study of simple systems to reveal general principles has contributed significantly to our understanding of many biological processes and the olfactory system is an ideal model system for consciousness research. It may even represent the minimal neuroanatomy that is required for conscious processing (Morsella et al., 2010).

Toward the goal of introducing attentional shifts toward olfaction as a system for the study of attention, this paper has three aims. The first aim is to develop a taxonomy of olfactory attention that is integrated into a general taxonomy of attention (Chun et al., 2011). The second aim is to review what is known about the brain structures that are involved in attentional shifts toward the olfactory modality and in the conscious processing of olfactory information. These first two parts together introduce a system in which questions about the relation between attention and consciousness can be studied. The third aim is to demonstrate the utility of the newly introduced system by answering one of these questions: is attention to smells necessary for the conscious processing of smells?

A TAXONOMY OF OLFACTORY ATTENTION

The study of attention in the olfactory modality is in its infancy. A search of literature databases will reveal that there are almost a thousand times more papers on visual attention than on olfactory attention. Before discussing attention in the olfactory modality it is therefore necessary to clarify what types of olfactory attention there are and how they relate to other types of attention. I will accomplish this by placing olfactory attentional processes into a recently introduced general taxonomy of attention (Chun et al., 2011).

The taxonomy proposed by Chun et al. (2011) is based on what type of information attention operates over. The most basic distinction is between external and internal attention. Internal attention operates over internally generated information such as memories, thoughts, or task rules. External attention operates over sensory information. The types of olfactory attention discussed in this paper are types of external attention. External attention can be further subdivided into attention to space, time, objects, or features of objects. In addition, there is attention to information generated by a specific modality. I will now discuss these five types of external attention (spatial attention, temporal attention, attention to objects, attention to features, and attention to a modality) in olfaction.

SPATIAL OLFACTORY ATTENTION

The paradigmatic case of spatial attention is the allocation of visual attention to positions in visual space. Visual spatial attention can be shifted overtly by body, head, and eye movements or covertly by computational means while the fixation point is unchanged. In every-day experience overt shifts of spatial visual attention are more prominent but covert shifts are also significant (for example, Wojciulik et al., 1998). Other senses with spatially structured phenomenology, like passive touch, also have computational mechanisms for covert spatial attention (Forster and Eimer, 2004).

Overt spatial shifts of attention are possible in olfaction. In the same way in which visual attention can be shifted in space by

turning the head, olfactory attention can be shifted in space by placing the nose over different objects that are giving off odors. These overt shifts of olfactory spatial attention allow us to locate sources of odors and to track scents (Porter et al., 2006). The study of overt shifts of spatial attention to elucidate the relation between attention and consciousness is complicated by the fact that overtly shifting olfactory or visual attention changes the sensory input. Covert shifts, in which the sensory input remains the same and the only difference is how attention is distributed over the visual field, have been more informative for questions about consciousness and attention.

However, covert spatial shifts of attention are only possible in modalities in which the sensory experience has a spatial structure. Odor experiences are one example of spatially unstructured sensory experiences (Radil and Wysocki, 1998; Frasnelli et al., 2008). Some researchers have suggested that an olfactory experience has a very simple spatial structure that consists of two locations: left (nostril) and right (nostril; Porter et al., 2005, 2006). Even if this is the spatial structure of an olfactory experience, there is no evidence that attention can be shifted between the nostrils. There is therefore no evidence for covert spatial olfactory attention.

TEMPORAL OLFACTORY ATTENTION

It has been shown that in vision attention can not only be allocated over space but also over time (Coull and Nobre, 1998). This type of attention can be tested in experiments which involve a cue that informs the subject at what time after the cue a stimulus can be expected. The subject will then allocate attention toward the time window in which the stimulus is expected. Allocating attention temporally is also possible in olfaction. It is, for example, possible to pay attention to odors only on Wednesdays, but not on the other days of the week. However, olfactory experiences have a peculiar temporal structure which makes the fast attentional shifts that are characteristic of temporal visual attention impossible.

Visual stimuli are normally experienced as long, uninterrupted stretches of experience. In contrast, olfactory experience is temporally discontinuous. It consists of short, discreet, temporally unstructured, olfactory experiences every 1.6 s (Laing, 1983; Mainland and Sobel, 2006). The reason for the interruptions in olfactory experiences is that the access of odorant molecules to the sensory neurons in the nose is controlled by sniffs. Sniffing is a complex behavior and the odor-induced brain responses are coupled to the rhythm of the sniffs (Kepecs et al., 2006). Modulating the sniffing behavior dramatically changes olfactory experiences (Verhagen et al., 2007). It is easy to temporally interrupt an unpleasant olfactory experience by not inhaling and in normal sniffing this interruption occurs every 1.6 s. As a consequence, changes over time that occur in less than a second are not part of olfactory experiences.

Many studies of temporal visual attention involve rapid (several per second) serial visual presentations. The most prominent phenomenon of visual temporal attention is the attentional blink. The attentional blink is the phenomenon that salient visual stimuli are often not consciously detected when they are presented (at the same spatial location) between 200 and 500 ms after another stimulus (Raymond et al., 1992). In olfaction there is no analog to the attentional blink. The olfactory experience during a sniff is

temporally unstructured. The experience in one sniff can be influenced by the previous sniff, but these influences are generally not considered to be an olfactory version of the attentional blink but rather effects of habituation or adaptation.

In summary, attention toward smells can be temporally structured. One can allocate attention toward smells during lunchtime but not for the rest of the day. However, olfaction is a “slower” sense than vision. Photons are faster than the odor molecules diffusing through the olfactory mucus that covers the olfactory sensory neurons in the nose. As a consequence many phenomena of fast temporal attention shifts that are studied in vision have no equivalent in olfaction.

ATTENTION TO OLFACTORY OBJECTS

Several different notions of “olfactory objects” have been introduced but none of them has become widely accepted. Olfactory objects could be clouds of molecules (Lycan, 2000). Alternatively, it has been suggested that “olfactory sources (objects that produce odors, such as a lion) and olfactory events (odors that emanate from objects, such as a musky lion smell) can be thought of as olfactory objects” (Gottfried, 2010). A third notion has been introduced by Yeshurun and Sobel (2010) who propose that the odor object is the pleasantness of an odor.

The relevant question for the possibility of attention to olfactory objects is if more than a single odor object can be experienced at the same time. If every odor experience consists of a single object, there is nothing for olfactory object-based attention to operate over. The different notions of “olfactory object” lead to different answers to this question. An analogy to vision, where visual objects cannot occupy the same location in visual space at the same time, would suggest that because there is only one location in olfactory space, only one olfactory object can be experienced at any given time. Nevertheless, some researches argue that there can be several olfactory objects simultaneously and that an olfactory object can be separated from an olfactory background (Stevenson and Wilson, 2007).

Because there is no accepted notion of “olfactory object” the disagreement over the possibility of simultaneous olfactory objects and therefore the existence of potential targets for object-based olfactory attention is merely a verbal dispute. I will adopt a notion of “olfactory object” in analogy to the notion of “visual object” according to which an olfactory experience consists of a single olfactory object at any time. There can therefore be no object-based olfactory attention. At any time during an olfactory experience there is only a single olfactory object present. There are no simultaneous objects between which attention could be shifted.

ATTENTION TO FEATURES OF OLFACTORY OBJECTS

In vision research, the term “feature-based attention” is used to describe two similar types of attention (Carrasco, 2011). The first type of attention is when attention is allocated toward one feature of a visual object, for example color, shape, or orientation, at the expense of other features (Liu, 2003). A second way in which “feature-based attention” is used is to describe attention toward part of the quality space of one feature (Muller, 2006). This is the attentional strategy used in guided search; for example when an object of known color is searched for among other objects. If

an orange book is searched for on a book shelf, then attention is shifted toward the area of the color quality space surrounding orange and away from all the blue, black, and green books.

Olfactory objects only have a single feature, their smell. There are therefore no features between which olfactory attention could be shifted. Attending to the olfactory modality is attending to the single feature of the single olfactory object that is present at that time. The first type of feature-based attention, attention toward one but not the other features of an object, is therefore not possible in olfaction. However, attention can be selectively allocated to certain smell qualities just as it can be allocated toward certain color qualities. When smelling the complex odor of a glass of wine we seem to be able to attend either to the fruity qualities of the smell or to the woody qualities.

In this type of feature-based attention, attention is shifted within a perceptual quality space. The color quality space is relatively simple. Psychophysical investigation of color vision has shown that mental color qualities can be arranged in a three dimensional space (for example the Munsell color solid) in which the dimensions represent hue, saturation, and lightness (Hardin, 1988). Unfortunately, the situation is much more complex for the odor quality space. Our current understanding of odors and their perception does not allow us to order smells in a quality space similar to the color space. It is possible that the odor space has a complex structure and that multidimensional scaling techniques will eventually discover an ordered multidimensional odor space (Clark, 1993; Lycan, 2000). So far, those attempts have not come close to describing an ordered space. They have, instead, confirmed Plato's view that the most important dimension in odor quality space is pleasantness (Khan et al., 2007). From the fact that no odor quality space has been discovered yet, it can be concluded that if it exists it has a very large number of dimension and a complex structure.

Regardless of its exact structure there is empirical evidence that olfactory attention can be selectively distributed over the odor quality space. The reaction time to an odor for example has been shown to be influenced by expectation. When subjects are looking at a picture of oranges, the reaction time to orange odor is shorter than when looking at a picture of fishes (Gottfried and Dolan, 2003). These authors suggest that this and similar findings are best interpreted as subjects directing their olfactory attention toward a particular (orange-like) odor quality.

In contrast, experiments with odor mixtures have been interpreted as showing that features of an odor *cannot* be attended to. In these experiments subjects were asked to identify the components of odor mixtures. They were either instructed to report if a single component (for example benzaldehyde) is present in the mixture, or to report all the components (up to six out of six different components) that they can identify in the mixture. There was little difference in the ability to identify components of mixtures between the two conditions (Laing and Glemarec, 1992). However, these results are not relevant for a discussion of feature-based attention because the features of an odor over which attention can operate are perceptual features and not types of molecules. Instead of showing the failure of attention toward features in olfaction these results show that the perceptual features of an odor mixture are not a combination of the perceptual features of

its components, a well-established fact (Jinks and Laing, 1999). The results from mixture studies are therefore consistent with the notion that attention can be directed to a specific area of the odor quality space in analogy to feature-based visual attention.

ATTENTION TO OLFACTION

The fifth type of attention in the taxonomy proposed by Chun et al. (2011) is different from the types discussed so far. In the types of attention discussed so far attention is shifted through space, time, or a quality space within a single modality. In attention toward a modality attention is shifted between modalities. Of these inter-modal attentional shifts the shift between audition and vision has been studied in detail (Spence and Driver, 1997). Because of the potential applications in the management of chronic pain, the shifts of attention to and from nociceptive stimuli are also well understood (Eccleston, 1995).

Several psychophysical studies have shown that attention can be shifted toward olfaction in the same way it is shifted toward the other modalities. It has been shown that attention to odors decreases the response time to odors (Spence et al., 2000, 2001a,b). In one study, Spence et al. (2001b) instructed subjects to discriminate either between two different intensities of an odor or between two different light intensities emitted by a diode. The odor was presented through a tube in the subject's nose. There was a continuous flow of odorless air through the tube and when an odor had to be presented, a computerized valve opened, thereby mixing the odorless air with the odor. An auditory cue primed the subjects to attend to either the light (low-pitched tone) or the odor (high-pitched tone). The cue was valid in most – but not all – cases. Subjects had a shorter response time to the odor when the cue was valid because they were attending to olfaction rather than to vision.

In addition to these behavioral effects of attending to olfactory information physiological effects of attending to smells have been described. Olfactory event-related brain potentials show attentional modulation (Pause et al., 1997; Krauel et al., 1998; Geisler and Murphy, 2000; Masago et al., 2001) and more recently attention to odors has been shown to alter both behavioral responses to odors and patterns of brain activity in response to odors in functional magnetic resonance imaging (fMRI) experiments (Sabri et al., 2005; Zelano et al., 2005; Plailly et al., 2008). Together these data show that it is possible to attend to olfaction in much the same way in which we may attend to vision or audition.

TYPES OF ATTENTION FOUND IN OLFACTION

In this section I have developed a taxonomy of olfactory attention that is modeled on a recent general taxonomy of attention (Chun et al., 2011). I have used types of visual attention as reference points. This direct comparison shows that many types of visual attention are modality-specific adaptations to modality-specific information processing requirements. Each modality is adapted to provide us with specific information about our environment. Some systems are specialized for processing spatial information (like vision and passive touch) and in them a special mechanism for spatial attention has evolved. Temporal attention and feature-based attention are the two types of intramodal attentional shift that are found in both vision and olfaction. Temporal attention

is probably a universal type of attention. As long as attention can be allocated, it can be allocated in time. Feature-based attention is also found both in vision and in olfaction. However, this does not mean that feature-based attention is not modality-specific. It seems that for example in proprioception there are no features that can be attended to. Like the other types of intramodal attention, feature-based attention is an adaptation to specific functions of some sense organs.

It is often overlooked that modality-specific attentional mechanisms are adaptations to sense organs and not adaptations to stimulus types. Facts about the temporal and spatial structure of human olfactory experiences are contingent on how we evolved to sense odors. Insects smell with their antennae which are continuously exposed to the ever-changing odorous ambient air. If we would have evolved olfactory sensors on the tip of our nose, then our olfactory experiences would be uninterrupted by sniffing and smelling would be much more like hearing. Similarly, some single-celled organisms are entirely covered with chemoreceptors. If we would be covered in odorant receptors over our entire body surface, smelling would be much more like passive touch and we would have evolved the mechanisms for covert spatial olfactory attention. Without turning our head we could shift attention from what we are smelling on our knee to what we are smelling on our neck. The attentional mechanisms in the different modalities have co-evolved with the sensory structures themselves and are independent of the physical nature of the stimuli.

In contrast to intramodal attentional shifts, intermodal shifts of attention like the shift of attention toward the olfactory modality are not adaptations to a certain way of information gathering and processing. These shifts are attentional shifts between information that is processed in different ways in different areas of the brain. They are similar to shifts from external to internal attention and to shifts within internal attention, for example from memories to task rules. I will in the next section introduce the shift of attention from other modalities (or internal attention) toward the olfactory modality as a system for the study of the relation between attention and consciousness. Because this type of attention is found in all modalities (and in internal attention), my hope is that results from this system will generalize over a wide range of systems in which attention and consciousness interact.

NEURAL CORRELATES OF OLFACTORY ATTENTION AND CONSCIOUSNESS

The anatomical structure underlying the processing of olfactory information is simple and radically different from the one found in the other sensory modalities (Figure 1). It has been suggested that the olfactory system represents the “minimal neuroanatomy for a conscious brain” (Morsella et al., 2010). The simplicity of this system may help reveal the mechanisms underlying attentional selection and conscious processing.

Odors are sensed by olfactory sensory neurons in the nose. These neurons project to a layered structure in the forebrain called “olfactory bulb” (Shepherd et al., 2004). The main connection from the olfactory bulb to higher brain centers is to the piriform cortex (which is sometimes also called the “olfactory cortex” or the “primary olfactory cortex”; Bower, 1991). Unlike the visual cortex, auditory cortex, or somatosensory cortex, the piriform cortex is

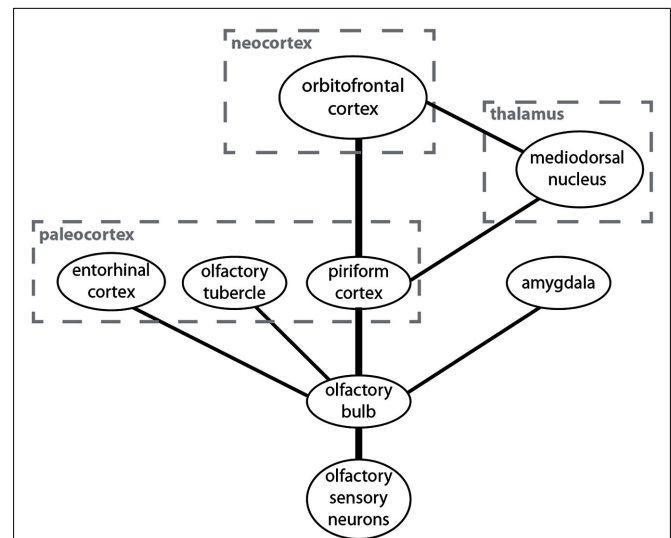


FIGURE 1 | A simplified overview over brain centers involved in the processing of olfactory information and their connectivity. The anatomically most prominent and best understood pathway is from the olfactory sensory neurons to the olfactory bulb and from there to the piriform cortex and the orbitofrontal cortex.

not a neocortical but a paleocortical structure. The paleocortex is phylogenetically older than the neocortex (hence the names) and it consists of three rather than six layers but the cellular architecture is similar. The piriform cortex is the main target for neurons from the olfactory bulb but it is not their only target. They also project to other paleocortical structures like the olfactory tubercle and the entorhinal cortex as well as to the amygdala. I will here only discuss the piriform cortex.

From the piriform cortex the main pathway is directly to the orbitofrontal cortex, which is the neocortical structure in which odor information is processed (Zald and Rauch, 2008). There is also a much less prominent indirect pathway from the piriform cortex to the orbitofrontal cortex via the mediodorsal thalamic nucleus. There are also projections to other brain regions from the piriform cortex, but they are not important for the discussion of neural correlates of attention and consciousness in olfaction.

There are two prominent anatomical differences between the olfactory system and the other sensory systems in the human brain. First, unlike other sensory information the majority of olfactory information never passes through the thalamus. Second, olfactory information is first processed in the paleocortex (specifically in the piriform cortex) and then in the neocortex (specifically in the orbitofrontal cortex). Sensory information from most other modalities is processed only in the neocortex. Two questions arise from these anatomical peculiarities of the olfactory system. (1) What is the functional olfactory analog of the thalamus which is responsible for attentional selection in the other modalities? (2) Is the piriform cortex or the orbitofrontal cortex the functional olfactory analog of the sensory cortices that are responsible for conscious information processing in the other modalities? I will now discuss the two questions and then present a model of attention and consciousness in olfaction based on the answers.

ATTENTIONAL SELECTION IN OLFACTION

The attentional selection in visual spatial attention is believed to occur in the thalamus (Crick, 1984; Mcalonan et al., 2008; Geraint, 2009). Furthermore, shifts of attention between modalities are also believed to require the thalamus (Newman, 1995; Smythies, 1997) through thalamic sensory gating (McCormick and Bal, 1994). However, the majority of olfactory information bypasses the thalamus on its way to the neocortex. This poses the question of which brain structure performs the function of the thalamus in the olfactory system. It has been suggested that attentional selection in olfaction occurs in the olfactory bulb or in the piriform cortex. A third proposal is that the minor indirect pathway that connects the nose to the neocortex via the thalamus is involved in olfactory attention. I will review the evidence for these three proposals.

Attentional selection in the olfactory bulb

The olfactory bulb is an outgrowth of the forebrain in which the axons of the olfactory sensory neurons terminate (Shepherd et al., 2004). At this first level of processing of olfactory information “molecular features” of odor molecules are encoded, a function that is reminiscent of the encoding of simple features of visual objects in the primary visual cortex (Haberly, 2001). It has also been pointed out that lateral inhibition is found both in the olfactory bulb and in the retina and that these two structures may play similar roles in vision and olfaction, respectively (Devriesa and Baylora, 1993; Nakanishi, 1995; Ghatpande, 2008). Recently it has been proposed that both of these comparisons are valuable and that “the bulb is directly comparable not only to the retina but also to primary visual cortex” (Cleland, 2010).

The motivation to suggest that the olfactory bulb in addition performs the function of the thalamus comes from electrophysiological recordings from neurons in the olfactory bulb of behaving rats. It has been shown that when rats attend to olfaction, neurons in the olfactory bulb fire in tonic mode (as opposed to bursts of spikes when olfaction is not attended to; Kay and Laurent, 1999). This shift between burst and tonic mode depending on attentional state is reminiscent of a similar shift in the thalamus that is associated with attentional processes (Sherman, 2001). There are also broad structural similarities between the thalamus and the olfactory bulb. Most notably, there are excitatory feedback neurons which can produce oscillating patterns of neuronal activity in both systems (Kay and Sherman, 2007).

Attentional selection in the piriform cortex

From the olfactory bulb, neurons project to the piriform cortex. In analogy to the visual system, it has been suggested that in the piriform cortex the “molecular features” that are processed in the olfactory bulb are combined to form “olfactory objects” (Bower, 1991). The piriform cortex is also the last processing stage for most olfactory information before the neocortex. In all other sensory systems the last processing stage before the neocortex is the thalamus and because of this analogy it has been long speculated that the piriform cortex is an “olfactory thalamus” (Lorente De No, 1938). Support for this model comes from electrophysiological recordings in rats that showed that there are state-dependent changes in odorant-evoked responses in a majority of

piriform cortex neurons, but not in neurons in the olfactory bulb (Murakami et al., 2005). The apparent discrepancy between this study and the study by Kay and Laurent (1999) may be due to the fact that in this study the states on which the neuronal changes depended were defined by neocortical electroencephalograms (in anesthetized animals), whereas in the study by Kay and Laurent (1999) they were defined behaviorally (in behaving animals).

Two fMRI studies of subjects attending to odors have uncovered attentional modulation in the piriform cortex (Zelano et al., 2005; Veldhuizen and Small, 2011). Two other studies did not show attentional modulation of piriform cortex activity (Sabri et al., 2005; Plailly et al., 2008). The four studies used different methodology, stimuli, and thresholds for statistical significance and the different results may reflect these differences. The effects of piriform cortex lesions can be studied in epilepsy patients who underwent temporal lobectomy (for references, see Gottfried, 2010). These procedures are performed unilaterally. In one study in which patients’ olfactory performance was tested before and after the procedure, left-resected patients did show no effect of the procedure on olfactory perception whereas right-resected patients showed some decline. The ability to attend to the olfactory modality has to my knowledge not been tested in subjects with piriform cortex lesions.

Attentional selection in the thalamus

The piriform cortex is for most olfactory information the last processing stage before the neocortex. However, in addition to the main direct pathway between piriform cortex and neocortex, there is also a minor indirect pathway via the mediodorsal thalamus (Carmichael et al., 1994). This indirect pathway has been demonstrated anatomically and electrophysiologically in rats (Price and Slotnick, 1983; Price, 1985), rabbits (Benjamin et al., 1978), and monkeys (Yarita et al., 1980; Takagia, 1986). At least in rats it is very sparse (Price, 1985; Price et al., 1991). The existence of this indirect pathway suggests the attractive possibility that attentional selection of all sensory information including olfactory information occurs in the thalamus.

Consistent with this idea it was shown in an elegant study that attention to the olfactory modality strengthened the connectivity between the mediodorsal thalamic nucleus and the neocortex (specifically the orbitofrontal cortex), suggesting that a thalamic relay for olfactory information is activated by attending to olfaction (Plailly et al., 2008). Traditional fMRI studies do not measure the connectivity between different brain areas but merely the response magnitude in different parts of the brain. Out of three traditional fMRI studies of attention to olfaction only one identified the thalamus as a structure that is involved in attention toward olfaction (Veldhuizen and Small, 2011). Instead, these studies found attentional modulation in the orbitofrontal cortex (Sabri et al., 2005; Veldhuizen and Small, 2011), the olfactory tubercle (Zelano et al., 2005), the cerebellum (Zelano et al., 2005; Veldhuizen and Small, 2011) as well as in several other structures (Veldhuizen and Small, 2011).

The results of studies of olfactory defects in patients with lesions in the mediodorsal thalamus (Potter and Butters, 1980; Rousseaux et al., 1996; Asai et al., 2008; Sela et al., 2009; Tham et al., 2011a,b) have been interpreted as showing that it is “likely” that patients

with mediodorsal thalamic nucleus lesions have an impairment in olfactory attention (Tham et al., 2011a). However, the findings in these patients are not consistent with the idea that in the absence of the indirect pathway from the piriform cortex to the orbitofrontal cortex via the mediodorsal thalamus the olfactory modality cannot be attended to.

A further problem for any model that assigns the mediodorsal thalamus a role in attending to olfaction is that the indirect connection between the piriform cortex and the orbitofrontal cortex via the thalamus has not been found (to my knowledge) in humans yet. Even if large scale neuroanatomy projects like the Human Connectome Project (Wig et al., 2011) will show that this connection exists in humans, it is unclear how much information can be transferred through such a sparse connection. Discussing the indirect pathway in the rat brain, Price et al. (1991) remarked that it is “not well equipped to convey detailed sensory information to the thalamus for relay to the neocortex.”

In summary, it is not plausible that the indirect thalamic pathway is responsible for shifts of attention toward the olfactory modality. The weak effects of thalamic lesions suggest a more subtle role of the thalamus in olfaction. If not in the thalamus, attentional selection has been speculated to occur in the olfactory bulb or the piriform cortex. The evidence for attentional selection in the piriform cortex is more convincing although a study of olfactory attention in patients with lesions of the piriform cortex would help strengthen the evidence considerably.

The thalamus plays a role both in intramodal attentional shifts in vision (Crick, 1984; Mcalonan et al., 2008; Geraint, 2009) and in intermodal shifts for example between vision and audition (Newman, 1995; Smythies, 1997). According to the view presented here, in olfaction the piriform cortex plays the role of the thalamus in intramodal attentional shifts between, for example, fruity and flowery odors. Furthermore, the piriform cortex is also necessary for shifts to and from olfaction. Accordingly, the role of the thalamus in attentional shifts is not universal but modality-specific. Attention can be shifted from memories to task rules, from thoughts to olfaction, from vision to audition, or from olfaction to vision. Different brain structures are involved in these different types of attentional shifts. There has to be a connection between the different structures to coordinate their activity. Maybe the few fibers that connect the piriform cortex with the thalamus (Carmichael et al., 1994) do not relay information about the olfactory stimulus to the thalamus but are involved in the coordination of attentional shifts between olfaction and the other sensory modalities.

NEURAL CORRELATES OF CONSCIOUS OLFACTORY PROCESSING

According to computational theories of consciousness being conscious is a property of certain types of information processing (Cleeremans, 2005). Structures in the brain in which information is processed consciously have been called the neural correlates of consciousness (Metzinger, 2000; Tononi and Koch, 2008). Somewhere in the brain olfactory information is processed consciously and the structure in which this computation happens is the neural correlate of olfactory consciousness. Since there are several concepts of consciousness, there can be several neural correlates of olfactory consciousness. I will discuss here the phenomenal neural

correlate of consciousness (Block, 2005; Stevenson, 2009) which is the structure in the brain in which information about the content of olfactory experience is processed consciously.

Olfactory information is processed both in the paleocortical piriform cortex and in the neocortical orbitofrontal cortex. The contribution of these two cortical sites to conscious processing of olfactory information is unclear (Shepherd, 2007). The paleocortical piriform cortex is a three-layered cortex that is only a single synapse away from the odor molecules. It is structurally simpler and phylogenetically older than the six-layered neocortical orbitofrontal cortex which is only found in mammals (Gottfried, 2007).

There are reasons to assume that the phenomenal neural correlate of olfactory consciousness is found in the neocortical orbitofrontal cortex. First, the neural correlates of visual consciousness, which have been explored in some detail, are also assumed to be found in neocortical structures and associated brain regions (Crick and Koch, 2003). Second, a recent lesion study of a single patient showed that brain injury that was largely limited to the right orbitofrontal cortex did completely abolish conscious processing of olfactory information. In contrast, the patient's ability to modulate his sniffing behavior in response to olfactory stimuli was unaffected and he showed normal skin conductance responses to odors (Li et al., 2010). This study is consistent with previous studies of patients with orbitofrontal damage or lesions (see references in Li et al., 2010).

However, the most important question for locating the neural correlate of phenomenally conscious olfactory experiences is what the content of those experiences is and where the information specifying these contents is processed. I will now first describe the phenomenal content of conscious olfactory experiences and then review what type of information is processed in the piriform cortex and in the orbitofrontal cortex. A comparison will show that the neural correlate of olfactory consciousness is likely to be found somewhere in the orbitofrontal cortex.

The content of olfactory consciousness

The content of olfactory consciousness is determined partially by the physical features of the odor molecule. There are prominent physical features that have a strong influence on the content of olfactory consciousness. For example sulfur atoms in an odor molecule result reliably in a characteristic sulfuric smell (Boelens and van Gemert, 1993). However, the content of olfactory consciousness is also strongly influenced by contextual factors. The influence of contextual factors on the content of olfactory consciousness means that, even in theory, complete knowledge of the physical features of the odor molecule is not sufficient to accurately predict the content of the conscious olfactory experience. I use “contextual factors” here as an umbrella term for remembered associations with the odor, internal states (hunger, sadness, etc.), and sensory input from other modalities. I will now discuss the influence of each of these types of context.

Associations with the odor that were established during a previous encounter can change how the odor is experienced. Tequila smells different before and after tequila-induced alcohol poisoning. In the laboratory, changes like this have been demonstrated in a series of experiments that investigated how odors can acquire

the odor quality “sweet” through association. Several experiments (reviewed in Stevenson and Boakes, 2003) have shown that when odors are repeatedly paired with sugar, they acquire the odor quality “sweet” and are subsequently described as sweet smelling when they are experienced in the absence of sugar.

The influence of internal states on the content of olfactory consciousness is seen in the satiety dependent difference in how the same odor stimulus is perceived at different times. It has been suggested that the smell of a “grilled 40-oz. dry-aged porterhouse steak” is experienced differently after one has just consumed such a steak than before (Gottfried, 2007). Similarly, Yeshurun and Sobel (2010) write that “banana odor when you are hungry is a different object from banana odor when you are satiated.”

The most dramatic example of information from other sensory modalities that modulates olfactory experiences is the perception of flavor. Flavor is a combination of olfactory, gustatory, tactile, and other sensations. The olfactory component in flavor is not experienced as a distinct experience but as part of a flavor experience.

These examples demonstrate the strong contribution of contextual factors to the content of olfactory conscious experience. This is not a novel proposal. Others have defended similar positions in much more detail. Gottfried and Wu (2009) called this effect the “perceptual pliability of odor objects,” whereas Yeshurun and Sobel (2010) called odor a “sensory emotion.” Stevenson and Boakes (2003), who focused on the effect of memories and association on odor experiences, proposed “a mnemonic theory of odor perception.”

What information is processed in the piriform cortex and in the orbitofrontal cortex

If both the physical features of the odor molecules and the context contribute to the content of conscious olfactory experience then the neural correlate of consciousness must be located in a structure that processes both information about the stimulus and information about the context. The two candidate structures for the neural correlate of consciousness are the piriform cortex and the orbitofrontal cortex and I will now discuss to what extent information about context is processed in these two structures.

Information processing in the piriform cortex (Bower, 1991; Neville and Haberly, 2004) and the orbitofrontal cortex (Gottfried and Zald, 2005; Zald and Rauch, 2008) has been comprehensively reviewed elsewhere. I will focus here on studies in which olfactory stimuli are presented in different contexts to identify brain structures in which activity is influenced both by the stimulus and by the context. fMRI studies allow to directly compare activity in the piriform cortex and the orbitofrontal cortex under these conditions. Several such studies have been performed and the results show clearly that context is processed mainly or exclusively in the orbitofrontal cortex. Remembered associations with the odor, internal states, and sensory input from other modalities have all been investigated.

Changes of perceived odor quality through remembered associations have been studied in most detail psychophysically for the acquisition of a “sweet” odor quality by odors that are paired with sugars (reviewed in Stevenson and Boakes, 2003). To my knowledge it has not been investigated in which brain regions the

representation of odors changes when they acquire the “sweet” odor quality. However, it has been shown that orbitofrontal cortex activity depends on how likely it is that a given odor–taste combination has been experienced previously. There is a superadditive response in the orbitofrontal cortex to pairs that have presumably been experienced together before (vanilla-sugar), but not to pairs that presumably have not been experienced before (vanilla-salt; Small et al., 2004). Another study has investigated the processes of pairing an odor with an electric shock (Li et al., 2008). Pairing an odor with an electric shock changes the odor representation in both the piriform and the orbitofrontal cortex. However, the changes in the piriform cortex are qualitative whereas the changes in the orbitofrontal cortex are quantitative.

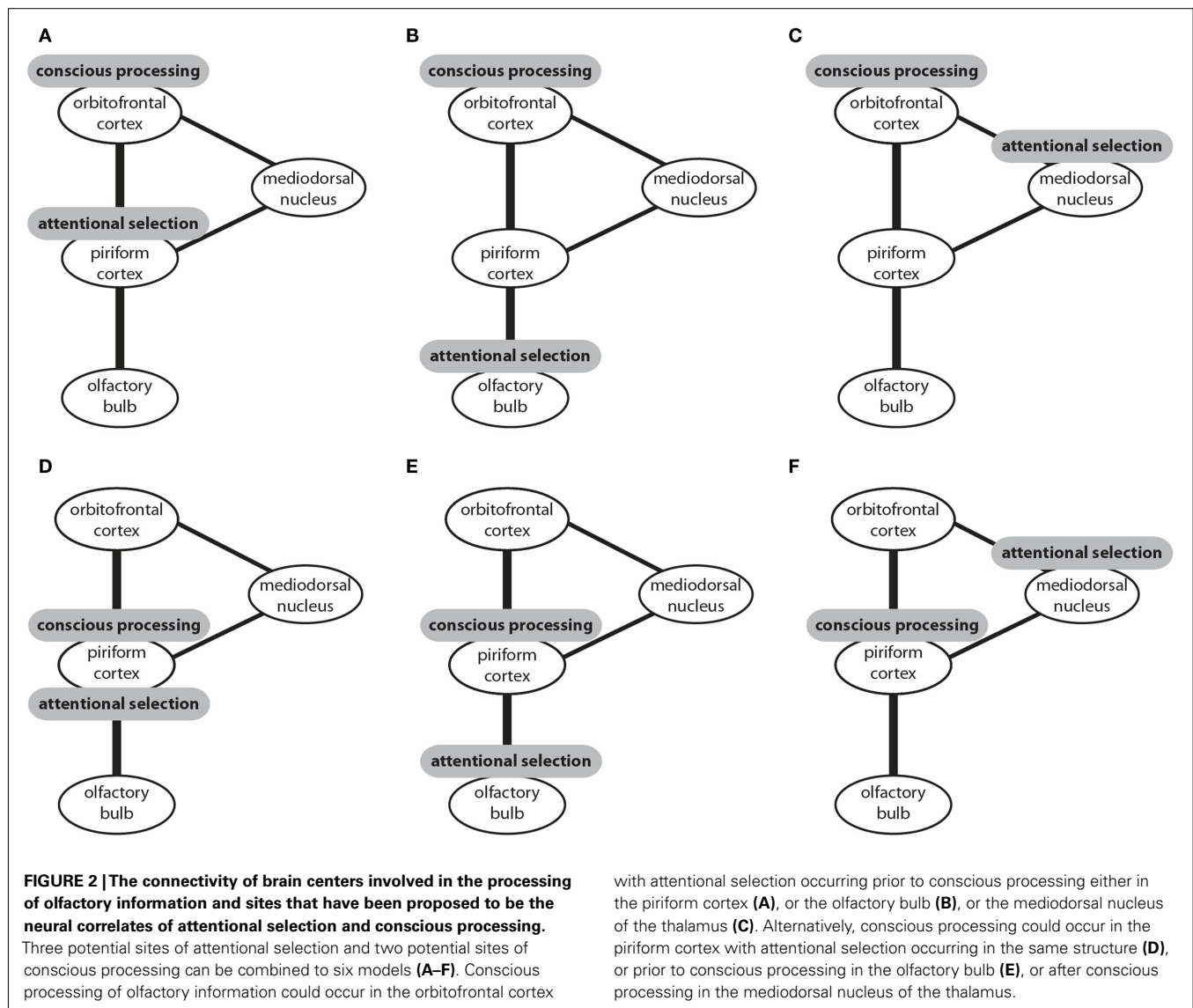
Among internal states, the influence of satiety on olfactory information processing has been studied extensively. It has been shown that odor representation in the orbitofrontal cortex (but not in the piriform cortex) is satiety dependent (O’Doherty et al., 2000). The odor of banana in these experiments has been shown to be represented differently in the orbitofrontal cortex after subjects ate banana to satiety. The representation of the odor of unrelated food did not change.

Odor representations in the orbitofrontal cortex also change when odors are paired with stimuli in other modalities. Neural activation in the orbitofrontal cortex was increased, for example, when an odor was presented in the expected visual context, for example when a rose odor was combined with the picture of a rose compared to the same odor combined with a picture of a bus (Gottfried and Dolan, 2003). This effect is not limited to pictures but extends to visually perceived verbal labels (De Araujo et al., 2005). The same odor (isovaleric acid) elicited different orbitofrontal cortex responses when labeled “cheddar cheese” than when labeled “body odor.” In this study the results for the piriform cortex were ambiguous and the authors state that there “may” be modulation of the piriform cortex response. In addition to visual stimuli, gustatory stimuli can also influence the odor representation in the orbitofrontal cortex (De Araujo et al., 2003).

Taken together these results show that much of the information about context that contributes to the content of olfactory consciousness is processed in the orbitofrontal cortex but not in the piriform cortex. Although it is clear from the results of some of the studies in humans that were discussed above as well as from electrophysiological recordings in rodents (Wilson, 2010; Doucette et al., 2011) that some types of context can influence processing in the piriform cortex, the most prominent function of the piriform cortex is to process information about physical features of odor molecules. In contrast, the most prominent function of the orbitofrontal cortex is to integrate information about physical features of the stimulus with information about the context. The information processed in the orbitofrontal cortex is the information that determines the content of conscious olfactory experiences.

NEURAL CORRELATES OF OLFATORY ATTENTION AND CONSCIOUSNESS

In this section I introduced three candidate structures for attentional selection and two candidate structures for conscious



processing in the olfactory system. These structures could be combined to six models of olfactory information processing (Figure 2). In four of these models attentional selection occurs prior to conscious processing. In one model attentional selection operates over consciously processed information (Figure 2F) and in another model both attention and conscious processing are accomplished by the piriform cortex (Figure 2D). To my knowledge, only three of these models have been suggested. It has been proposed that that attentional selection occurs in the olfactory bulb and conscious processing in the piriform cortex (Figure 2E; Kay and Sherman, 2007). Alternatively, it has been suggested that, like in other sensory modalities, attentional selection occurs in the thalamus and conscious processing in the neocortical orbitofrontal cortex (Figure 2C; Plailly et al., 2008). The data I reviewed here supports the third model which proposes that the piriform cortex performs attentional selection and the orbitofrontal cortex conscious processing of olfactory information (Murakami et al., 2005; Figure 2A).

IS ATTENTION TOWARD THE OLFACTORY MODALITY NECESSARY FOR OLFACTORY CONSCIOUSNESS?

Identifying the neural structures underlying attention and consciousness is an important step for the conceptual analysis of the relation between the two processes. Many questions can be and have been asked about the relation of attention to consciousness. Is attention the same as consciousness (Posner, 1994; Lamme, 2003)? Is attention necessary and/or sufficient for consciousness (Prinz, 2010; Van Boxtel et al., 2010)? Or is it the other way around and consciousness is necessary and/or sufficient for attention (Mole, 2008)? Is information first consciously processed and then attention acts on it or does attention act on information before it is consciously processed (Lamme, 2003)? All these are fundamental conceptual questions that remain unanswered. I will focus here on the question about the necessity of attention for consciousness.

The question if attention is necessary for consciousness has been investigated previously in some types of visual attention using a variety of paradigms. Inattention blindness (Mack and Rock,

1998), attentional blink (Raymond et al., 1992), change blindness (Simons and Rensink, 2005), and load induced blindness (Macdonald and Lavie, 2008) are striking phenomena in visual perception in which stimuli that are consciously processed when attended to are not consciously processed when not attended to. On the other hand, there are other phenomena in which stimuli are consciously processed in the absence of attention (see Van Boxtel et al., 2010 and references therein). A (possibly insurmountable) weakness of these experiments is that it is currently not possible to achieve and demonstrate *complete* absence of all attention to an area of the visual field (De Brigard and Prinz, 2010).

I will now attempt to answer the question about the necessity of attention for consciousness for the olfactory modality. I will present two types of evidence, observational and experimental, that attention is necessary for conscious processing of olfactory information and then address the main objection to this claim. Based on the evidence, I will argue that attention to smells is necessary for consciousness of smells.

OBSERVATIONAL EVIDENCE THAT ATTENTION IS NECESSARY FOR OLFACTORY CONSCIOUSNESS

Olfaction researchers often seem to presuppose that attention is necessary for olfactory consciousness. Sela and Sobel (2010) for example write that “olfactory stimuli are less prone to attract attention, and therefore humans have poor awareness to the olfactory environment.” Similarly, Plailly et al. (2008) conclude from their finding that the thalamic relay is involved in directing attention to smells that olfaction requires a thalamic relay for the conscious processing of smells, a conclusion that presupposes that directing attention to smells is necessary to consciously process them.

The assumption that attention to olfaction is necessary for consciousness of olfaction is consistent with most normal, everyday olfactory experiences. With almost every breath we inhale air containing odors at relatively high concentrations; yet olfactory experiences are very rare (compared, for example, with visual experiences). This shows that there is an additional cognitive factor necessary to turn the presence of an olfactory stimulus into conscious olfactory experience. Because attending to the olfactory modality almost always results in a conscious olfactory experience, it seems plausible that this cognitive factor is attention.

The importance of the role of attention for olfactory experiences is further illustrated by the fact that people are very often wrong in their judgments about changes in their own olfactory abilities or in the odorous environment. The natural assumption, when a person’s conscious olfactory experiences change systematically is that either the stimuli or the sensory apparatus has changed. However, in numerous well studied situations this is not the case. Instead, the change in conscious olfactory experience is entirely caused by a change in attention to the olfactory modality. Increased consciousness of smells due to increased attention to smells is seen during pregnancy, but also in people in which the cause for the change is not known.

The vast majority of pregnant women report that their olfactory sensitivity is enhanced during pregnancy. Studies have shown that this is not the case. The olfactory acuity is not changed during pregnancy (Cameron, 2007; Doty and Cameron, 2009). Instead the systematic differences in conscious olfactory experiences are caused by attentional factors. The involuntary increase in attention

to odors during pregnancy is probably an adaptive response to the fact that the fetus is especially volatile to environmental poisons and spoiled food. These attentional changes result in a radically altered olfactory conscious experience.

In the case of heightened odor awareness during pregnancy the cause for the attentional shift toward olfaction is known, but there are also vast differences in the attention to olfaction among non-pregnant individuals. Psychophysically measured olfactory abilities, in the general population, do not correlate with how annoyed subjects are by environmental odors or with how the subjects rate their own olfactory abilities. How annoyed they are by odors and how they rate their abilities however does correlate (Knaapila et al., 2008). This shows that people attribute changes in their conscious olfactory experience that are caused by attentional processes to changes in their olfactory abilities. In extreme cases, heightened attention to the olfactory modality can cause debilitating conditions that are part of a heterogeneous group of conditions called “multiple chemical sensitivity” or “idiopathic environmental intolerances” (Dalton and Hummel, 2000).

EXPERIMENTAL EVIDENCE THAT ATTENTION IS NECESSARY FOR OLFACTORY CONSCIOUSNESS

These observations about the fundamental role of attention in olfactory consciousness suggest that attention is necessary for consciousness in olfaction. Unfortunately, there is no empirical study directly addressing the question of necessity that could support this conclusion. All studies of the role of attention in olfactory consciousness present the stimulus through a plastic tube that is inserted into the subject’s nostril. It can be assumed that under this condition subjects will always attend to some degree to the olfactory modality, regardless of the experimenter’s instructions. This experimental setup is therefore not suitable to study olfactory consciousness in the absence of attention to olfaction.

Alternative experimental setups make it possible to reduce the subjects’ attention to the olfactory modality further. The most covert way to deliver an odor stimulus is to add it to the ambient air that the subject is breathing. Such experiments have revealed a stunning failure of subjects to become conscious of unattended smells (Lorig, 1992; Degel and Koester, 1999). In one study (Lorig, 1992), in which the influence of odors on the appeal of pictures was studied, only 3 out of the 93 subjects became aware of the odor manipulations whereas several other subjects reported a perceived (although non-existent) change in luminance.

Studies like this demonstrate dramatically the absence of olfactory consciousness in the absence of attention. However, what would be needed to test the necessity of attention for odor consciousness would be a study that determines the detection threshold for ambient odor in a situation in which subjects are engaged in some non-olfactory task and have no indication that odors are part of the experiment. This could then be compared to the detection threshold for ambient odor when subjects are told to attend to ambient odors. My prediction is that such an experiment would reveal a very strong influence of attention on olfactory consciousness. However, I also predict that at very high odor concentrations subjects would consciously perceive the odor even under minimal attention conditions. This would be an apparent counterexample to the claim that attention is necessary for olfactory consciousness.

THE STRONG STIMULUS OBJECTION AGAINST THE NECESSITY OF ATTENTION FOR OLFACTORY CONSCIOUSNESS

Examples of apparent olfactory consciousness in the absence of attention to olfaction can also be found in every-day experiences. Ethyl mercaptan, which is added as a warning agent to propane gas to alert us to gas leaks, for example, is often perceived by people who do not attend to smells at all. It has to be added at 57,000-times the concentration at which it is detected when it is attended to (Sela and Sobel, 2010), but a case of conscious detection in the absence of attention would refute the claim that attention is necessary regardless of the stimulus intensity. This objection is not limited to the cases of attention in the olfactory system. In the visual system the phenomenon of change blindness seems to show that attention is necessary for conscious perception. However, when the change that is introduced outside the attended area is a large red triangle in a black and white image, then the change will be processed consciously although it occurred in an unattended area.

A usual response to this objection is to distinguish between top-down attention, which is a cognitive process, and bottom-up attention, which is a feature of the stimulus. I prefer to not call anything “attention” that is not a cognitive process and therefore do reject this response. Instead, I have two responses to the strong stimulus objection. The first is that it is possible that attention to olfaction is never completely absent and that the minimum attention that could possibly be allocated to the olfactory modality is sufficient for conscious processing of ethyl mercaptan at 57,000-times the concentration at which it is consciously processed when attended to. The second response is that not everything that is attributed to the sense of smell is actually mediated by the sense of smell. There is a second sensory system that senses volatile chemicals in our nose.

Although it has not been demonstrated experimentally, it is plausible that the extent to which attention is allocated to the olfactory modality allows of degrees. “Attended to” and “not attended to” are most likely idealized extreme cases of a continuous process. If this is the case then subjects would perform best at tasks requiring conscious processing of olfactory information when instructed to attend to olfaction. The performance would drop in the resting state and further drop when they are instructed to attend to the visual modality. If they perform a complex visual task for which they are highly motivated, the olfactory performance would drop even further.

If it is true that attention to olfaction allows for degrees then the question is over which range attention to olfaction can be modulated and if it is ever completely absent. A case in which one may expect attention to olfaction to be minimal is sleep. And indeed, odor stimuli at very high concentration, unlike stimuli in other modalities, fail to awake sleeping subjects (Carskadon and Herz, 2004). This is consistent with the notion that attention is necessary for consciousness of smells. The apparent counterexamples are cases in which minimal attention is allocated to olfaction. Because of the intensity of the stimulus and the long time the stimulus is present this minimal attention is sufficient for conscious processing.

The second response to the strong stimulus objection is to point out that experience is not a good guide to judge if there are smells that are consciously processed in the absence of attention to olfaction because what is experienced as a “smell” is a multimodal

sensory experience, only partially mediated by the olfactory system. It may be surprising, for example, that smells can’t wake sleeping subjects (Carskadon and Herz, 2004). Sleepers often get woken up by the smell of smoke and “smelling salts” have brought countless fainted women in Victorian England and knocked-out boxers back to consciousness. However, neither smoke nor the ammonia gas released by smelling salts is perceived by the olfactory system. Instead, these and many other stimuli are perceived by nerve endings of the trigeminal nerve in the nasal cavity (Doty, 1995). The trigeminal nerve is a warning system that evolved to prevent us from inhaling dangerous substances. As such, it is always attended to and if the stimuli are strong enough to activate it (it is much less sensitive than the olfactory system), the information will be consciously processed. Because both the olfactory system and the trigeminal nerve detect stimuli inside the nasal cavity, the perceptions mediated by them are often collectively referred to as “smelling.” However, unlike olfactory information, trigeminal information is not processed in the paleocortex and instead, like all sensory non-olfactory information, is relayed through the thalamus to the neocortex (Huait et al., 2009). Apparent cases of “smells” being perceived without being attended to are likely to be mediated by this warning system and not by the olfactory system.

In summary, the fact that very strong olfactory stimuli are often consciously processed by subjects who are not attending to olfaction seems to show that attention is not necessary for olfactory consciousness. However, two things have to be considered. First, it is unlikely that there are many situations in which subjects do not attend to one of their five senses at all. And second, there is a dedicated warning system to alert us to dangerous volatile chemicals, the trigeminal nerve, which may be responsible for most of the cases in which volatile chemicals are sensed in the absence of attention to olfaction. The strong stimulus objection is therefore no reason to assume that attention is not necessary for consciousness of smells.

CONCLUSION

My goal in this review was to introduce attention to the olfactory modality as a simple system in which to study the relation between consciousness and attention. Toward this goal I first showed how this system fits into a general taxonomy of attention. I then discussed the neuroanatomy of the olfactory system to illustrate how this system differs from the more complicated visual system. I also demonstrated the utility of this model system by using it to weigh in on the question of the necessity of attention for consciousness.

The visual system, despite being extremely specialized and complicated, has become the *de facto* model system for perceptual cognitive neuroscience. I hope that I succeeded here in showing the potential of very simple and basic systems like olfaction for revealing basic conceptual truths about entities like “attention” and “consciousness.”

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Yoga lessons for consciousness research: a paralimbic network balancing brain resource allocation

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Consciousness has been proposed to play a key role in shaping flexible learning and as such is thought to confer an evolutionary advantage. Attention and awareness are the perhaps most important underlying processes, yet their precise relationship is presently unclear. Both of these processes must, however, serve the evolutionary imperatives of survival and procreation. They are thus intimately bound by reward and emotion to help to prioritize efficient brain resource allocation in order to predict and optimize behavior. Here we show how this process is served by a paralimbic network consisting primarily of regions located on the midline of the human brain. Using many different techniques, experiments have demonstrated that this network is effective and specific for self-awareness and contributes to the sense of unity of consciousness by acting as a common neural path for a wide variety of conscious experiences. Interestingly, hemodynamic activity in the network decreases with focusing on external stimuli, which has led to the idea of a default mode network. This network is one of many networks that wax and wane as resources are allocated to accommodate the different cyclical needs of the organism primarily related to the fundamental pleasures afforded by evolution: food, sex, and conspecifics. Here we hypothesize, however, that the paralimbic network serves a crucial role in balancing and regulating brain resource allocation, and discuss how it can be thought of as a link between current theories of so-called “default mode,” “resting state networks,” and “global workspace.” We show how major developmental disorders of self-awareness and self-control can arise from problems in the paralimbic network as demonstrated here by the example of Asperger syndrome. We conclude that attention, awareness, and emotion are integrated by a paralimbic network that helps to efficiently allocate brain resources to optimize behavior and help survival.

Keywords: consciousness, attention, reward, pleasure, cingulate cortex, orbitofrontal cortex, precuneus, paralimbic network

INTRODUCTION

Biological evolution is a complex process allowing species and organisms to try to resist the second law of thermodynamics. Over time, this has led to the evolution of increasingly sophisticated brains allowing organisms to adapt and survive longer by learning from experience and predicting future events. Yet, this increase in adaptability also leads to an increasingly difficult resource allocation problem of how to best select between competing wants and likes (Kringelbach and Berridge, 2009). Human consciousness can be thought of as one particular successful solution to this taxing problem, primarily facilitated by the processes of attention and awareness.

The scientific study of human consciousness is growing beyond its infancy and many interesting properties of its underlying neuronal substrates have been established (Changeux and Lou, 2011). Yet countless fundamental discoveries remain, however, and in particular understanding the precise relationship between attention and awareness has remained elusive (although this special issue is

beginning to address the issue). In addition to the main tenet of the present discussion, namely of a bidirectional and intimate relationship between attention and self-awareness networks, it should be noted that in particular for the attentional network, there are asymmetries between hemispheric involvement. For instance, Mesulam (1999) drew attention to the prime role of the right hemisphere in generating spatial neglect, and more recently it has been demonstrated that the functional connectivity of the insula to the paralimbic network is asymmetrical as well (Cauda et al., 2011).

One way to conceptualize the relationship between attention and awareness is to think of attention as an executive function allowing the focusing of the mind, while awareness is its closely associated counterpart at the highest level of sensory processing. Yet, this conceptualization leaves out the importance of reward and emotion in guiding the crucial decision making involved in optimizing resource allocation of brain resources, which we discuss in this review.

Some progress has been made in identifying how self-awareness can help in shaping the decision making. Interestingly, part of this progress has been made possible by studying the introspective states involved in meditation. Studies of highly experienced Yoga-nidra practitioners have shown that there are significantly different brain networks involved in the states related to relaxation meditation (Yoga-nidra) and normal resting state (i.e., at rest, without intended motor, or mental function), and that these networks vary greatly with the changing contents of consciousness during the two conditions (Lou et al., 1999). In contrast, common to both states and traits is sustained activity in a paralimbic network consisting of midline frontal regions (anterior cingulate and medial prefrontal cortices), parietal regions (primarily precuneus), and striatum (Kjaer and Lou, 2000; see **Figures 1 and 2**).

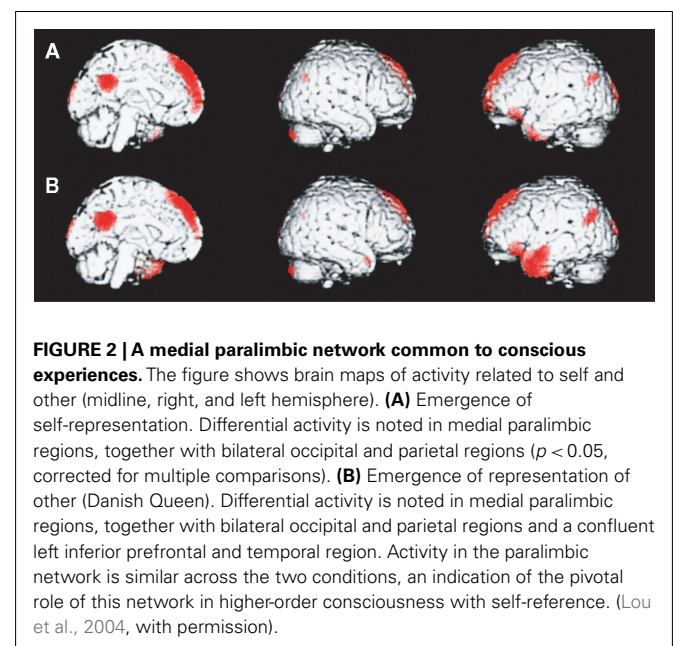
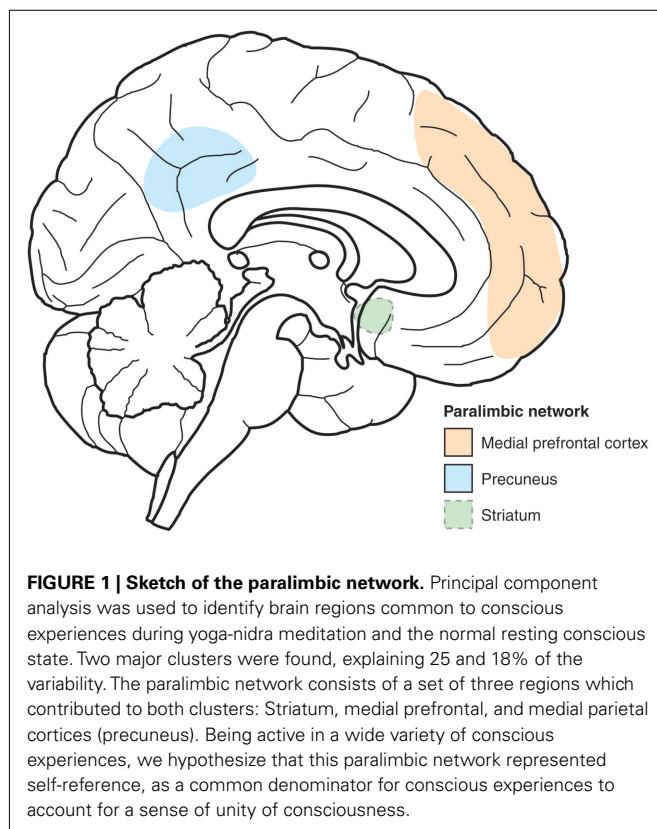
This discovery led to the hypothesis that the paralimbic network contributes to the regulation of conscious experience by acting as a common reference of self-perspective for changing conscious states and traits (Kjaer and Lou, 2000). Such a role for the paralimbic network would be consistent with ontogenetic considerations of brain development (Feinberg and Keenan, 2005). Accordingly, animals with a *paleomammalian* brain, a brain with developed limbic system, but scarcely developed neocortex, may display quite sophisticated social behaviors like maternal nurturing, separation distress calls, and play, while the adjacent neocortex is essential for perception of the self in space and time, a prerequisite for abstract thinking.

The neuroanatomical evidence also supports the hypothesis that the paralimbic network plays a special role in guiding the

allocation of brain resources by mediating between attention, awareness, and emotion. The paralimbic regions are anatomically located at the interface between the limbic and the neocortical brain, the former providing information on the bodily state and emotions, while the heteromodal neocortical association regions provide extrapersonal sensory and mnemonic information on the highest level of integration available for attention and awareness. Relying on this broad outline and on anatomical, physiological, and behavioral experiments in the monkey, Mesulam (1998) proposed that the cerebral cortex is organized into five hierarchically arranged subtypes: Limbic, paralimbic, heteromodal association, unimodal association, and primary sensory motor regions.

In the present review we synthesize the evidence from the literature to show that the paralimbic network is active and efficient in self-processing, a prime organizer of conscious experience. We show how the paralimbic network uses information from both the external world and introspection to balance the resource allocation, and how the access and balance in this system is regulated by emotion and by neurotransmitters such as dopamine. Finally, we show how disturbances in the paralimbic network may be involved in developmental disorders such as autism.

Before proceeding, however, a brief note of caution regarding the limits of neuroimaging. As such it is important to realize that neuroimaging findings resulting from a comparison of active and control conditions usually are correlative only and will not imply causality. Also they will not necessarily uncover the full network of brain regions involved. Instead, what neuroimaging may reveal are the *changes* in activity in the important nodes and hubs of the human brain which can bring about changes in the balance of resource allocation between different brain networks, the associated behavior, and the resulting experience. In addition, also electromagnetic methods may have important caveats. One example is the fact that microsaccades may elicit gamma synchrony in the frontal cortex, while the parietal lobe is



unaffected (Carl et al., 2012). The parietal lobe is a key constituent of the paralimbic network discussed in this review. Therefore the gamma synchrony described here cannot be attributed to eye-movements.

THE PARALIMBIC NETWORK IS EFFECTIVE AND SPECIFIC IN SELF-PROCESSING

The conscious sense of self serves as a common reference for making decisions about the allocation of resources ensuring survival, whether related to any of the fundamental pleasures of food, sex, or other people or even higher-order pleasures such as music or monetary reward. Establishing the functional neuroanatomy of the self is thus potentially a fruitful strategy for identifying the hubs and key nodes in the brain networks important for maintaining the balance between the competing processes of attention, awareness, and emotion.

One essential role for the self is to be a common reference point in space and time for conscious experiences (Gallagher, 2000). Together, they are all experienced in unity, coherent in space and time. Even when someone enters the room, or the phone rings, and the scene and our focus of attention shifts completely, we usually experience the changed scene as continuous with the preceding (Tononi and Edelman, 1998). To account for this coherence of widely different conscious percepts, the self offers a possibility: per definition, we cannot have free-floating sensations with no self to experience them, and we cannot have a self completely devoid of sensory experiences, memories, or feelings. In other words: non-self sensations and memories and the self are two sides of the same coin.

If each of the different, ever-changing sensations and memories are attached to the same coherent self-structure across space and time, these types of information will be bound to each other via the self. A coherent self across time requires a system to retrieve memories of personal experiences, i.e., episodic memory. Correlational evidence suggests that this system is involved not only in retrieval of past personal memories, but also in conceptualizing the future (Ingvar, 1985; Andreasen et al., 1995). Consequently, episodic memory retrieval appears as an indispensable component of the more complex forms of self-awareness and consciousness, which are described in various terms such as extended self, meta-consciousness, auto-noetic consciousness, or narrative self (Gallagher, 2000). In a particular amnesic syndrome, transient global amnesia, a rudimentary sense of self is preserved. This state is characterized by loss of episodic memory, while working memory, and semantic memory are relatively spared (Quinette et al., 2003).

The neural organization of episodic memory retrieval involves hemodynamically synchronized activity in medial paralimbic regions including the anterior cingulate and posterior cingulate cortices and adjacent neocortical structures, as well as in the thalamus (Henson et al., 1999; McDermott et al., 1999; Wiggs et al., 1999; Cabeza and Nyberg, 2000; Gardiner, 2001; Tulving, 2002). Further hemodynamic studies have confirmed that the paralimbic network is active in self-awareness (Kjaer et al., 2002b), and single pulse transcranial magnetic stimulation confirmed the specificity and causality of the network in extended self-awareness (Lou et al., 2004; see Figure 3).

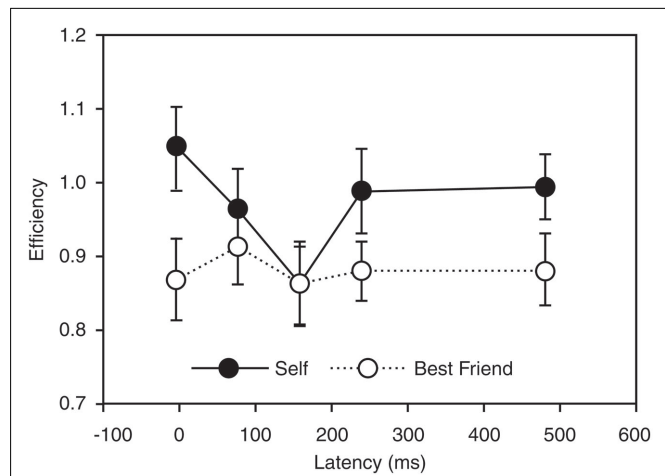


FIGURE 3 | Causality and specificity of one node of the paralimbic network in self-reference. The figure demonstrates the effects of applying transcranial magnetic stimulation (TMS) in targeting the precuneus/posterior cingulate region in a task probing self-reference. The causality of this region in self-reference is seen by the fact that retrieval of self-judgment was significantly less efficient with TMS at a latency of 160 ms than with a latency of 0 ms ($p = 0.003$), suggesting that neural activity at that time interval after stimulus presentation is particularly important for self-representation. Specificity of this region in self-reference is provided by the fact that the difference between self and other (best friend) is significant at most latencies ($p < 0.05$), except at the specific causal latency. (Lou et al., 2004, with permission).

In contrast to extended self-awareness, the minimal self is pre-reflexive, immediate, normally infallible, and involves the sense of ownership of experiences. For the minimal self, data on the neural organization are scarcer, but indicate that the same paralimbic structures are active here as well (Vogeley et al., 2004), being a “common denominator” for the self, independent of its complexity, and consisting mainly of a network of paralimbic regions. Functional magnetic resonance imaging (fMRI) have shown a consistent pattern of activity in self-processing for a paralimbic network including anterior cingulate/medial prefrontal cortices, posterior cingulate/medial parietal cortices (with precuneus), and pulvinar thalamus (Lou et al., 2004). In addition, other brain regions including striatum and cerebellum have also been implicated.

This network of paralimbic regions not only shows correlated activity with self-reference, but has also been shown to be causally related to self-reference. Transcranial magnetic pulses (TMS) can transiently disturb the neural function of key regions in the paralimbic network with decreased efficiency specifically of self-reference as a result (Lou et al., 2004).

Anatomically, the medial prefrontal/anterior cingulate and medial parietal/posterior cingulate regions are connected directly via the cingulum bundle, and indirectly, through their rich connections via the “limbic” and intralaminar thalamic nuclei, located centrally at the base of the forebrain (Lou et al., 2004).

Each structure in the paralimbic circuitry contributes fundamental properties to extended self-awareness (Northoff and Bermpohl, 2004). The evidence shows that many of the regions on

the midline of the prefrontal cortex are involved in self-reference. The medial orbitofrontal cortex at the base of the frontal lobes has been shown to be related to evaluating the valence of the convergence of intero- and exteroceptive stimuli, including the remarkable valence of human infants (Nauta, 1971; Kringelbach and Rolls, 2004; Kringelbach et al., 2008). This region has been called the “entrance door to self-awareness” based on EEG and MEG studies showing comparatively early engagement after onset of emotional stimuli (Northoff and Bermpohl, 2004). Self-referential stimuli are then monitored in the dorsal anterior cingulate cortex in the sense that stimuli are selected here among competing stimuli for access to consciousness. The supplementary motor area is closely functionally related to the anterior cingulate cortex in preparation for action, in particular when there are no external cues to tell the subject what to do. Self-referential stimuli are thought to be evaluated in the dorso-medial prefrontal cortex as judged to be pertaining to one-self or other persons (Northoff and Bermpohl, 2004). “Theory of the mind,” or attributing mental states to others, is also associated with activity in the region, which therefore may constitute a link between introspection and understanding others (Frith and Frith, 1999).

These frontal monitoring and evaluative functions of self-awareness are complemented by functions in the posterior midline establishing spatial and diachronic unity of self and of consciousness: Spatial organization in a first person framework involves posterior cingulate/medial parietal cortex (Northoff and Bermpohl, 2004) which is also active in linking new information with prior knowledge on the subject matter (Maguire et al., 1999). In auto-noetic consciousness, the region is active in retrieval of episodic memory for autobiographical self-consciousness (Cavanna and Trimble, 2006). The functional integrity of medial parietal cortex is critical for extended self-awareness. This has been shown by TMS targeting precuneus to transiently disrupt the normal function of this region (Lou et al., 2004). The central role of the intralaminar nuclei for consciousness is illustrated by the fact that even minute lesions here may cause loss of consciousness (Schiff, 2008).

THE ROLE OF THE PARALIMBIC NETWORK IN BALANCING THE DYNAMICS BETWEEN NETWORKS

Neuroimaging experiments support the proposed role of the paralimbic network as a central integrator and arbitrator of resource allocation in the human brain. In particular, in addition to evidence from indirect techniques such as fMRI and PET, more direct and faster methods such as magnetoencephalography (MEG) have recently provided very useful information regarding the dynamics of the underlying physiology.

When sampling data from the most important hubs of the paralimbic network including the anterior cingulate/medial prefrontal and posterior cingulate/medial parietal cortices as well as thalamic regions, it has been demonstrated that gamma synchrony is a common neural event in both minimal self-reference and extended self-reference, where the degree of synchrony is clearly related to the degree of self-reference (Lou et al., 2010). As noted above, this mechanism of gamma synchrony is not likely to be affected by the recent discovery that microsaccades may give rise to gamma oscillations. These gamma oscillations are induced by extra cerebral sources primarily in the frontal lobe, and have not

been found in the parietal cortices (Carl et al., 2012). In addition we used beamforming for source localization which allows a clear distinction between sources.

The degree of gamma synchrony in the paralimbic network is a potential mechanism between conscious experiences and widely different degrees of self-reference. This mechanism of gamma synchrony in the paralimbic network thus meets one of the main requirements needed to bind conscious experience in the so-called neuronal global workspace theory (Dehaene et al., 1998) based on earlier theoretical work (Baars, 1989).

Yet, theories of consciousness abound and while the global workspace theory has been highly influential, other potential candidate theories exist. An equally important concept developed over the last decade is the default mode theory (Gusnard and Raichle, 2001; Raichle et al., 2001). According to this theory, sensory information arriving from the outside world will lead to a decrease in perfusion and energy metabolism of the medial default mode network, in analogy with the re-direction of brain activity with shifting modalities of sensory stimulation (Lam et al., 1999).

At first glance these two theories would seem contradictory, with the global workspace theory referring to a single global brain network processing consciousness, while the default mode theory posits one brain network for processing the outer world, and another network for the inner world.

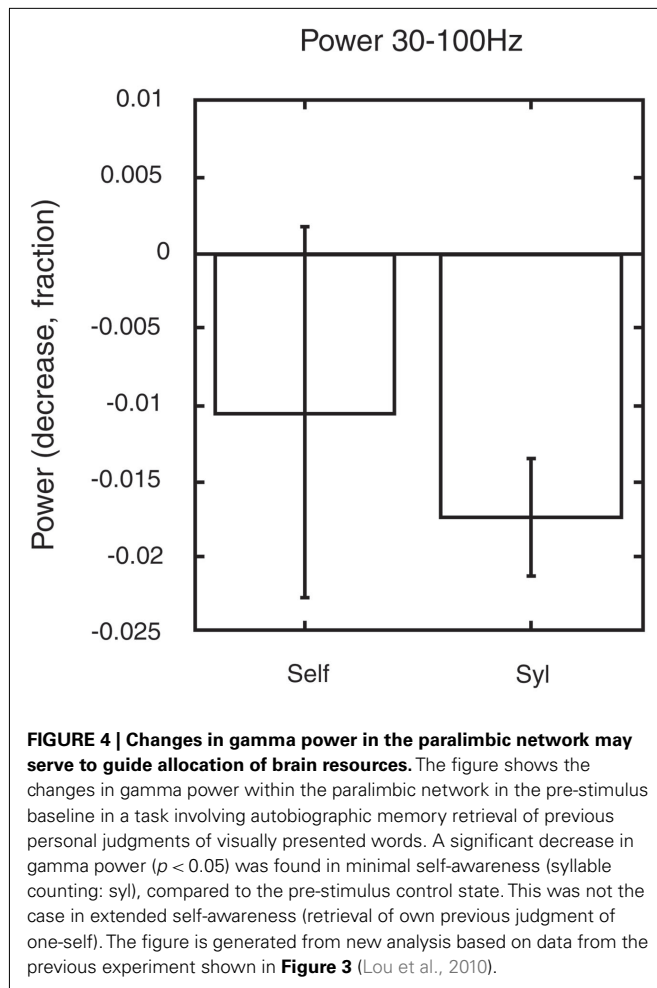
The hypothesized paralimbic network offers a solution to this apparent paradox. The evidence from MEG, which is a direct measure of brain activity, shows that paralimbic network becomes synchronized to varying degrees during experiences of both the outer world with only minimal self-reference, and more so in introspection during extended self-reference (Lou et al., 2010).

In contrast, we reanalyzed some of our data and found that the paralimbic network showed a significant reduction in gamma power only during a minimally self-related task (syllable counting, see **Figure 4**), while there were no significant change in gamma power during extended self-reference (retrieval of own judgment on one-self).

Compare this with the evidence from indirect measures of brain activity such as fMRI which shows that regions involved in the default mode network have reduced blood oxygenation level dependent (BOLD) signal during goal directed (non-self-referential) tasks relative to rest (Raichle et al., 2001). The reduction in gamma power as measured with MEG during an active task (syllable counting) could reflect the deactivation in the default mode network during active tasks. Some of the evidence suggests that changes in gamma power are indeed correlated with BOLD which is an indirect measure of the synaptic activity (Logothetis and Wandell, 2004).

In sum, the evidence from MEG studies show that the paralimbic network can provide the gamma synchrony needed for the global coherent workspace of consciousness, while also fulfilling the criteria of reduced activity (i.e., changes in gamma power in minimal self-reference) in the midline paralimbic regions of self-reference elicited by minimal self-reference.

Yet, general gamma synchrony on its own is not sufficient for consciousness but would also seem to require amplification of activity within recurrent networks. This is suggested by some



intriguing data gathered over 30 years ago, when (Libet, 1982) discovered that conscious sensations emerge as a function of both intensity and duration of electric stimulation of the human somatosensory cortices. They reported a delay of conscious experience of approximately 400 ms from onset of a sustained stimulus at threshold intensity and assumed that this latency reflected the need for maintaining the initial frequency and amplitude for an extended period of time. This suggests that amplification of perceptual processing is required to elicit conscious experience, a process which in the neuronal global workspace theory is termed “ignition.” In addition, evidence also indicates that high signal intensity in cortico-thalamic interaction is essential for emergence of consciousness. The possible nature of such amplification has been widely discussed in the literature. Several researchers have speculated that extensive recursive activity to bootstrap neuronal processing is a general mechanism for stimuli to become available for consciousness (Tononi and Edelman, 1998).

In spite of this long-standing interest in recurrent neuronal activity, beyond some demonstrations in primary visual cortices, such activity was only recently demonstrated in higher-order, modality non-specific regions using MEG and the so-called Granger causality analysis, a mathematical method initially developed to analyze econometric data but now also used to identify

the directionality of flow of information between brain regions (Granger, 1969).

Autobiographic memory retrieval of previous personal judgments of visually presented words was used to probe the temporal flow of activity within the paralimbic network (Lou et al., 2011a). It was demonstrated that the pre-stimulus condition is characterized by causal, recurrent oscillations which are maximal in the lower gamma range. When retrieving previous judgments of visually presented adjectives, this activity is dramatically increased during the stimulus task as ascertained by Granger causality analysis, demonstrating not only recurrent gamma activity in higher-order, modality non-specific regions but also how the paralimbic network serves to allocate brain sources.

CONSCIOUS EXPERIENCE UNDER THE INFLUENCE OF DOPAMINE

The paralimbic network described here does not only include mid-line structures in medial anterior and posterior regions which are continuously active in different states and traits of consciousness, but the evidence has also implicated the striatum. It is well-known that dopaminergic neurotransmission is abundantly present in the striatum. Therefore interest has recently focused on the possible role of dopaminergic neurotransmission in the regulation of conscious experience.

At the system level we now know that conscious experience is linked to interacting regions of parietal and prefrontal cortices, which are not only active, but also effective in self-reference (Lou et al., 2004). However, on the molecular level our knowledge has until recently merely been suggestive. Functional brain imaging has established that abnormal conscious experiences in schizophrenia, like hallucinations and delusions, are associated with abnormal dopaminergic neurotransmission (Changeux and Lou, 2011). For instance, striatal dopamine transporter availability is inversely correlated with hallucinations (Schmitt et al., 2006).

Furthermore, clinical evidence indicates that striatal dopamine might regulate conscious experience. One way to measure conscious experience is to approach the problem as one of probability of signal detection (and subsequent subjective interpretation). Following this approach, conscious experience can be determined by the setting of a criterion for when the sensory signal-to-noise ratio warrants sufficient subjective confidence that a stimulus is present. In schizophrenia, psychotic symptoms could be explained as a result of setting too liberal a signal-to-noise criterion. This is thought to be due to abnormally upregulated dopaminergic neurotransmission, an effect of dopamine on the cellular level being to influence the signal-to-noise ratio (Lou et al., 2011b).

Furthermore, in the previously mentioned study of Yoga-nidra meditation it was shown that such meditation is accompanied by a strong increase in sensory awareness, and that this phenomenon is linked to dopamine release in the nucleus accumbens in the ventral striatum, which has been implicated in the paralimbic network consistently active in different conscious states and traits (Kjaer et al., 2002a).

We directly examined the effect of increasing dopamine activation and showed that dopaminergic stimulation with the D_1 and D_2 receptor agonist pergolide is effective in increasing confidence in seeing words, a valid measure of awareness (Lou et al., 2011b).

These results demonstrate how dopamine can influence activity across the various nodes and hubs of the paralimbic network, giving rise to changes in both conscious states and content.

THE ROLE OF THE PARALIMBIC NETWORK IN LINKING REWARD, EMOTION, AND SELF-AWARENESS

The evidence presented above supports the hypothesis that the paralimbic network subserves self-processing in the human brain, and that specific changes in synchrony between the nodes and hubs of this network can regulate the dynamics of widespread connected brain networks. In addition, the evidence also suggests that dopamine has a special role in modulating activity in this network.

The evidence thus supports the overall notion that the paralimbic network plays a key role in the conscious brain resource allocation associated with predicting and selecting behaviors that ensures survival. The fundamental rewards afforded by evolution to ensure survival are food, sex, and conspecifics; and the time-courses of the associated behaviors are cyclical (Kringelbach and Berridge, 2009). There are distinct wanting, liking, and learning phases in the reward cycle, which have been shown to have partly dissociable neural substrates (Kringelbach, 2005).

Over time the human brain has to use attentional mechanisms to detect potential rewards which, depending on the current state of the organism, may (or may not) initiate a specific reward cycle. For example, after becoming aware of hunger signals, the food reward cycle is initiated and our attention invariably turns to finding potential food rewards.

We propose that the paralimbic network plays a key role in integrating awareness, attention, and emotion processing to optimize the brain resource allocation. The inputs from the senses such as vision, auditory, taste, smell, and touch (linked to survival-related rewards such as food and sex) and their subsequent evaluation have the potential to temporarily shift the focus of the brain networks to allow for efficient processing and control over behaviors (Berridge and Kringelbach, 2008; Kringelbach et al., 2008). The paralimbic network helps to ensure that the processing remains balanced over longer time periods.

Mounting evidence has demonstrated that frontal regions such as the medial orbitofrontal and the anterior cingulate cortices are situated anatomically at the crossroad between interacting networks of attention, awareness, and emotion as necessary nodes linking the networks (Tsuchiya and Adolphs, 2007; Kringelbach et al., 2011). It should, however, be noted that these regions are heterogenous regions with many sub-regions which have been implicated in different networks (Kringelbach and Rolls, 2004; Beckmann et al., 2009).

Direct causal evidence for the interaction has been given by studies showing that direct electrical stimulation of the anterior cingulate cortex can help to alleviate severe chronic pain in patients (Kringelbach et al., 2010). Recently, we further demonstrated that reward can directly impact conscious experience and this integration is directly reflected in the neural activity in the anterior cingulate cortex as measured by local field potentials (Rømer Thomsen et al., 2011).

In general, emerging evidence shows that perturbations to the paralimbic network may manifest in an unbalancing of widespread brain network as seen for example in the anhedonia associated with mental illness (Kringelbach et al., 2011).

CLINICAL CONSEQUENCES OF DEVELOPMENT IMPEDIMENT OF THE PARALIMBIC NETWORK

Development perturbations to the paralimbic network are not uncommon (Lou, 2011). Here we will briefly focus on an example of developmental dysfunction found in the Asperger syndrome (see **Box 1**).

Individuals with Asperger syndrome would appear to have problems with introspection and narrative self-awareness. In particular they have difficulty identifying and reflecting on their own emotional states. They also have peculiar concrete thought patterns and a tendency to focus on external events rather than inner experiences (Hill et al., 2004).

Given the hypothesis of the paralimbic network presented here, this failure of subjectivity may be predicted to be linked to dysfunction in the paralimbic loop and medial neocortical structures. While still scarce, some of the experimental data would seem to support this link. One neuroimaging study involved higher-order

Box 1 | Asperger syndrome.

Autism is a neurodevelopmental disorder of genetic origin, characterized by impaired social interaction and communication as well as repetitive behavior and restricted interests. The symptomatology being highly variable, the condition is often referred to as "autism spectrum disorder." Asperger syndrome is a subgroup where the affected individuals have normal language development and normal or above normal IQ, together with the typical social communication impairments, obsessions, and narrow interests, suggesting impaired binding of attention, awareness, and emotion.

Peter is a young boy 16 years of age. After a normal pregnancy and birth he was delayed in motor development and slightly delayed in development of language. He did not babble until he suddenly spoke perfectly correct. As a toddler he was always playing with construction toys and puzzles, but not with other children. At school he is marginalized, having special interests not shared by his classmates. He behaves oddly in social interaction where he is rigid and clumsy, with a very formal, monotonous language. He is unable to interpret moods or motives of others. He speaks without restraint about his special interests, in an exalted, gesturing, and noisy way. The psychological investigation shows that he is of normal intelligence, with high scores in memory of facts, especially meaningless facts, and he is eminent at puzzles and labyrinths. In contrast, he scores below normal in reasoning and social comprehension, in particular sequential understanding of social activities. He is unable to generate inclusive terms covering a variety of objects. He is characterized by orienting to details. He is diagnosed as having Asperger syndrome, a milder variant of autism.

consciousness based on linguistic information, sentence comprehension (Just et al., 2004). In autists compared to normal controls, higher activity was seen in the Wernicke region, while lower activity was found in Broca's region and in the medial paralimbic regions. This finding supports the hypothesis that the medial paralimbic circuitry could be defective in autism. Yet, some caution is needed given that the autists and the normal control participants were not compared directly, but only indirectly via a common reference to a fixation point.

Deficiency of the paralimbic loop of self-reference could potentially be explained by the evidence for volume reduction and reduction in glucose metabolism in the entire cingulate cortex in autism (Haznedar et al., 2000, 2004). In fact, related deficiencies may be seen in another disorder of self-awareness and higher-order consciousness: schizophrenia (Haznedar et al., 2004).

CONCLUSION AND PERSPECTIVE

There is a clear lesson for consciousness research initially emerging from studying the brain activity in experienced Yoga-nidra teachers during meditation but subsequently supported by a

wealth of other experiments: a common paralimbic network serves to regulate and balance the dynamic resource allocation needed to ensure survival. This process is guided by processes linked to awareness, attention, and emotion in order to support memory-dependent self-reference, which in narrative self-consciousness is extended into adjacent neocortical regions. Dire clinical consequences are linked to its impediment in pathological conditions. Yet, as a common reference of conscious experiences, it provides us with an adaptive tool for building a unified self and personality over the years by successfully balancing the allocation of brain resources for survival and procreation.

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The role of attention in conscious recollection

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Most research on the relationship between attention and consciousness has been limited to perception. However, perceptions are not the only kinds of mental contents of which we can be conscious. An important set of conscious states that has not received proper treatment within this discussion is that of memories. This paper reviews compelling evidence indicating that attention may be necessary, but probably not sufficient, for conscious recollection. However, it is argued that unlike the case of conscious perception, the kind of attention required during recollection is *internal*, as opposed to external, attention. As such, the surveyed empirical evidence is interpreted as suggesting that internal attention is necessary, but probably not sufficient, for conscious recollection. The paper begins by justifying the need for clear distinctions among different kinds of attention, and then emphasizes the difference between internal and external attention. Next, evidence from behavioral, neuropsychological, and neuroimaging studies suggesting that internal attention is required for the successful retrieval of memorial contents is reviewed. In turn, it is argued that internal attention during recollection is what makes us conscious of the contents of retrieved memories; further evidence in support of this claim is also provided. Finally, it is suggested that internal attention is probably not sufficient for conscious recollection. Open questions and possible avenues for future research are also mentioned.

Keywords: attention, consciousness, memory, recollection, retrieval, global neuronal workspace

INTRODUCTION

Although few would deny that consciousness and attention are intimately intertwined, their precise relationship remains unclear. Generally speaking, opinions about the nature of their relationship fall within one of three general views. The first view holds that attention is neither necessary nor sufficient for consciousness (Lamme, 2003; Koivisto et al., 2005). According to this perspective, even though attention and consciousness regularly occur in tandem, under specific circumstances they can be separated, suggesting that, in fact, consciousness and attention are dissociable processes (Koch and Tsuchiya, 2007). It follows from this view that it is possible to attend to something one is not conscious of, just as it is possible to be conscious of something while not attending to it. The second view, in contrast, holds that attention is necessary and sufficient for consciousness (Posner, 1994; Prinz, 2000, 2011). According to this perspective, the mechanisms of consciousness and attention are not entirely dissociable – although it remains an open question whether the precise relationship between such mechanisms is that of identity, causality, or constituency (Block, in preparation). A consequence of this view is that one cannot be conscious of something unless one attends to it, just as one cannot attend to something and fail to be conscious of it. Finally, there is an intermediate position according to which attention is necessary but not sufficient for consciousness (Moran and Desimone, 1985; Merikle and Joordens, 1997; Rensink et al., 1997; Dehaene et al., 2006; Dehaene and Changeux, 2011). It follows from this view that one cannot be conscious of something unless one attends to it, but attending to something is not enough to make one conscious of it, insofar as other processes are required. As such, this third view

agrees with the first one in that it denies that attention is sufficient for consciousness, while at the same time agrees with the second view in suggesting that attention is necessary for consciousness.

Since most research on attention has been limited to perception – which in turn is usually confined to vision and, to a lesser degree, audition – it is unsurprising to find that most of the discussion on attention and consciousness has focused on conscious perception. However, perceptual contents are not the only kind of mental contents of which we are ordinarily conscious. An important set of conscious mental states which has not been sufficiently addressed within this discussion, is that of memories. When we remember, we usually experience something akin to the reinstatement of the content of a previous experience, which may or may not have been perceptual¹. To be sure, memory enables us to recall past visual or auditory experiences, but it also brings to mind old nightmares and long-gone aspirations. Unlike perception, which allows us to be consciously aware of our present, memory allows us to be consciously aware of our past. As a result, it is natural to wonder whether or not attention plays a role during conscious

¹ Strictly speaking, when we remember we not only experience something akin to the reinstatement of the content of the original experience but also the sense of having experienced such a content in the past. In the philosophy of memory there is some debate as to whether this “double-consciousness” is to be understood as the belief that what content of the memory portrays occurred to us in the past (e.g., Locke and Russell) or rather as an emotion with no cognitive content (e.g., William James, see Locke, 1971). In psychology and cognitive neuroscience these issues are usually studied under the rubric “metamemory.” Since the purpose of the present paper is to understand the role of attention in the conscious recollection of memorial contents, this interesting metamemory issue will be sidestepped.

recollection, and also whether or not that role is analogous to the role it plays during conscious perception. Does conscious recollection depend in any way on attention or are they independent processes? More generally, what is the relationship between attention and consciousness during conscious recollection?

In this paper I want to defend the claim that attention is necessary, but probably not sufficient, for conscious recollection. However, unlike the case of conscious perception, I argue that the kind of attention required during recollection is *internal*, as opposed to external, attention. This makes the role of attention during conscious recollection significantly similar, but also importantly different, from the role it plays during conscious perception. More precisely, then, I argue that internal attention is necessary, but probably not sufficient, for conscious recollection. To that end, in Section “Varieties of Attention” I start by justifying the need for clear distinctions among different kinds of attention, emphasizing the difference between internal and external attention. In Section “Internal Attention and Episodic Memory Retrieval,” I review evidence from behavioral, neuropsychological, and neuroimaging studies suggesting that internal attention is required for the successful retrieval of memorial contents. Next, in Section “Internal Attention is Necessary for Conscious Recollection,” I argue that internal attention during recollection is what makes us conscious of the contents of retrieved memories. In turn, in Section “Internal Attention May Not be Sufficient for Conscious Recollection,” I briefly argue for the probable non-sufficiency of internal attention for conscious recollection. I conclude with some questions for future research.

VARIETIES OF ATTENTION

When James remarked that “everyone knows what attention is” (James, 1890), he was rather overconfident. In reality, there seems to be a substantial amount of disagreement as to what the nature of attention is (Styles, 1997). Part of the problem is that neither the folk nor the scientific use of the term “attention” is sufficiently precise. We usually employ the term “attention” in non-scientific contexts to refer to a wide array of phenomena. The word “attention” sometimes refers to the way in which we engage in certain cognitive tasks; like when we play chess attentively rather than distractedly. Other times “attention” means bringing something to the foreground of the mind, as when we mentally single out the player with the ball when watching a soccer game. Yet, on other occasions, we use the term “attention” to explain why we were not aware of certain information – as when we justify our failing to remember someone’s remark, or our inability to recognize a particular street when ambling absentmindedly, by simply saying that we were not paying attention. The problem is not with our use of the term “attention” in such circumstances. The trouble is rather that “attention” is *not* the only term we can employ to convey the same message. In certain contexts we use terms like “perceiving,” “noticing,” “being aware of,” and even “being conscious of” when we could have easily used the term “attending” instead. Given people often use these terms interchangeably (De Brigard, 2010), this lack of semantic precision between the words “consciousness” and “attention” becomes more problematic when trying to identify the relationship between the two folk psychological notions, “consciousness,” and “attention.”

Semantic consensus is not found in scientific circles either. On the one hand, there is disagreement as to whether “attention” refers to a personal or a sub-personal phenomenon (Watzl, 2011). Specifically, there is disagreement as to whether attention refers to a process one should expect to find a neural correlate for; or whether it refers to something the person does in virtue of having a brain, but for which it would be a category-mistake to try to find a neural correlate (Mole, 2010; Wu, 2011). On the other hand, there is disagreement as to whether or not attention names a natural kind. For instance, some suggest that attention does not name a single cognitive mechanism, but rather denotes particular ways in which certain cognitive processes can be carried out. Listening attentively and observing attentively are not two different processes (i.e., audition and vision) that share a common third mechanism (i.e., attention); they are simply two different cognitive processes, carried out in distinctly precise ways that may or may not share common properties (Parasuraman, 2000; Duncan, 2006). As such, it would be a mistake to try to find the neural correlate of attention *per se*, independently of other cognitive processes. In contrast, one could see attention as a unified cognitive process with either an identifiable sub-personal neural correlate (Prinz, 2011), or a set of personal-level phenomena such as behaviors (Wu, 2011) or subjective mental contents (Smithies, 2011; Watzl, 2011). Those who consider attention reducible to a neural process face the daunting task of identifying a single brain mechanism responsible for all forms of attentive behavior. Likewise, those who think that attention could be identified with a series of personal-level phenomena face the difficult task of discerning necessary and sufficient conditions for behaviors or subjective states to qualify as instances of attention.

Employing different methods, many cognitive neuroscientists working on attention adopt a reductionist approach. Critics of this approach claim that extant empirical evidence strongly suggests that there may *not* be a single neural mechanism responsible for all forms of attention (Wu, 2011). The lack of a common neural denominator for all forms of attention would make it tempting to advocate either for anti-reductionism – so that we are to find the essence of attention at the personal rather than the sub-personal neuronal level (Mole, 2010; Watzl, 2011) – or for eliminativism, ridding scientific psychology of the term “attention” (Allport, 1993; Anderson, 2011). But there is another alternative. “Attention” may not name a single unified neural mechanism. Indeed, it may not name a natural kind at all. Yet it may be worth keeping around in our scientific practice. After all, not all scientifically useful psychological terms refer to natural kinds, let alone single neural mechanisms. Consider memory. Memory researchers have struggled for decades to come up with a single unified definition of “memory”; something general enough to encompass different kinds of memory (i.e., semantic, episodic, implicit, etc.), but specific enough to separate it from other forms of cognitive and non-cognitive phenomena (Tulving, 2002). Additionally, extant scientific evidence conclusively shows that different forms of memory are subserved by different neural mechanisms (Schacter et al., 2000; De Brigard et al., in press). Nonetheless, despite longstanding disagreements as to what its essence may be, and despite its multiple and disjoint neural implementations, “memory” is still a useful term in scientific psychology as well as neuroscience.

I believe “attention” might be just like “memory.” In a recent review, Chun et al. (2011) put forth precisely this proposal. Consistent with the anti-reductionist spirit regarding attention, Chun et al. agree that there are multiple attentional systems that appear to be correlated with different neural mechanisms. But the fact that there may not be a single neural property shared by all attentional systems does not deter them from suggesting that all forms of attention share three essential properties at the *computational* level. First, according to Chun et al. (2011), attention is essentially a *filtering* process with limited informational capacity. Since the amount of information we live in exceeds our capacity to effectively process it, attention evolved to filter out irrelevant information detrimental to the ongoing cognitive or behavioral task (Pashler et al., 2001). Second, attention is essentially *selective*. In filtering out information for subsequent processing, attention necessarily selects informational items that will be further processed from those that will not. Finally, attention *modulates* the ease of processing of the selected information. Attended information is processed more efficiently and more deeply than information that is not selected by attentional mechanisms. Thus, according to Chun et al. (2011), all forms of attention share these three computational characteristics (i.e., filtering, selectiveness, and modulation), which may or may not be implemented by the same neural mechanism. Indeed, they suggest that trying to understand different kinds of attention in terms of their neural mechanisms may not be the best way to proceed. Instead, they suggest a taxonomy based on the type of information attention operates over; what they call “the targets of attention.”

According to Chun et al. (2011) proposed taxonomy, attention can be captured, first and foremost, either by targets in one’s surrounding environment (external) or within one’s own mind (internal). Thus, *external* versus *internal* attention constitute the first taxonomical division. External attention refers to the filtering, selection, and modulation of externally generated sensory information, whereas internal attention refers to the filtering, selection, and modulation of internally generated information – in the form of representations containing information not directly linked to objects in one’s immediate surrounding environment. It is worth noting that the division between internal and external attention is similar to, but also importantly different from, categorizations that have been proposed in the past. For instance, attention has been separated into exogenous and endogenous attention (Egeth and Yantis, 1997). Endogenous attention refers to the voluntary selection and modulation of information elicited by top-down mechanisms of orientation and control, such as one’s goals and intentions. Conversely, exogenous attention refers to the involuntary and bottom-up driven allocation of attention onto a target that is noted or otherwise cognitively highlighted for reasons outside of one’s control. Endogenous and exogenous attention, however, do not map onto the internal/external classification. After all, external objects can be attended both endogenously – as when we voluntarily and in a controlled manner direct our attention to a desired external target – and exogenously, as when a particular external target captures our attention involuntarily and in a mandatory fashion. Another popular division is between covert and overt attention (Wright and Ward, 2008). Overt attention refers to a shift in attentional allocation accompanied by noticeable

eye movements; whereas covert attention refers to a shift in attentional allocation with the eyes fixed on a certain target. However, as with the endogenous/exogenous dichotomy, the covert/overt distinction does not map squarely onto the internal/external categorization either. For one, as it has been shown experimentally, it is possible to divert attention from one target onto another without concomitant saccadic movements (Juan et al., 2004) – which, incidentally, evidences the fact that attention can be spread over a region of space and not only toward individual objects. Likewise, evidence shows that attention allocated to internally generated information is often times accompanied by eye movements (Hunt and Kingstone, 2003). Finally, it is extremely improbable that eye movements could provide a useful wedge to divide internal and external attention to non-visual stimuli. Therefore, mechanism-based dissociations such as endogenous/exogenous and covert/overt do not map onto the target-based distinction between internal and external attention suggested by Chun et al. (2011).

By embracing Chun et al.’s (2011) informational target- rather than a mechanism-based taxonomy for attention, I am committing to the very real possibility that internal and external attention may not share the same neural operations. This consequence already appears to be validated by recent studies showing dissociations between brain regions engaged during internal-monitoring tasks and brain regions involved in external orienting and detection tasks (e.g., Esterman et al., 2009). Moreover, it is also expected that more fine-grained distinctions within these categories, such as feature- versus object-based attention within external attention, will map onto different neural mechanisms. Given this variability in the neural implementation of different kinds of attention, it is difficult to assess general claims like “attention is necessary for consciousness” or “attention is sufficient for consciousness.” If either of these claims is supposed to capture something about the relationship between the mechanisms of attention and consciousness, they must be modified so as to specify the kind of attention to which they are supposed to apply. Since we are concerned here with conscious recollection, where the information of which we are aware is internally generated, the relevant kind of attention is internal. However, in order to understand the role of internal attention in conscious recollection, it is essential to first explore its role during episodic memory retrieval.

INTERNAL ATTENTION AND EPISODIC MEMORY RETRIEVAL

As mentioned above, external attention involves the filtering, selection, and modulation of sensory information (Chun et al., 2011). In addition, external attention can be allocated to one or to several sensory modalities, it can be focal or distributed spatially, and it can be transient or sustained. Each one of these forms of external attention activates distinct brain mechanism, some of which share certain features. For instance, visual attention enhances retinotopical activation in the visual cortex (Tootell et al., 1998), while auditory attention does so tonotopically in the auditory cortex (Woldorff et al., 1993). Thus, although the relevant cortical areas of enhanced activation differ across modalities, the specific processing elicited by attention appears to be similar. Likewise, external attention is known to recruit a fronto-parietal network of activation (Corbetta and Shulman, 2002). However,

it has been shown that the timing of this recruitment differs depending on whether attention is goal-directed or stimulus-driven. Goal-directed or “top-down” attention recruits frontal regions of the fronto-parietal network first; stimulus-driven or “bottom-up” attention recruits parietal regions first (Buschman and Miller, 2007). Thus, while both top-down and bottom-up attention recruit similar brain regions, the order in which these regions are recruited differs.

Unsurprisingly, the mechanisms responsible for internal and external attention have much in common. Internal attention, defined as the filtering, selection, and modulation of internally generated information, operates over representations of items and events that need not be in the subject’s immediate environment. Paradigmatically, internal attention operates over representations entertained during decision-making and working-memory tasks, but also – as I shall argue below – during retrieval of episodic information from long-term memory. Studies on task selection, in which competing options are filtered, chosen, and maintained, have shown specific capacity limitations expected from internal attentional processes. For instance, when choices are produced in rapid succession, the second response is delayed if presented less than half a second after the first choice – an effect known as “psychological refractory period” (Pashler, 1994). This bottleneck effect parallels well-known external attention effects, such as the attentional blink, in which a perceptual stimulus goes unnoticed if presented in close succession. Moreover, neuroimaging studies have shown common recruitment of regions engaged during attentional blink and the psychological refractory period (Wong, 2002; Marois and Ivanoff, 2005; Hesselmann et al., 2011; Marti et al., 2012), suggesting again the involvement of a common mechanism. Further neuroimaging studies on task selection have shown recruitment of several brain regions also associated with external attention, such as the prefrontal and anterior cingulate cortices (Botvinick et al., 2001). The overlap between internal and external attention mechanisms is even greater during working-memory tasks. For example, the maintenance of representations in working-memory modulates modality congruent sensory cortices (Serences et al., 2009) much the same way external attention modulates activation of sensory cortices during perception. Likewise, working-memory tasks are disrupted by material-congruent distraction tasks, suggesting – once again – recruitment of common mechanisms.

Despite their similarities, internal, and external attention differ in important respects. In an illuminating study, Nobre et al. (2004) directly compared brain activity associated with attentional orientation during a perceptual and a working-memory task. Although, as expected, both tasks recruited a common network of brain regions, some important differences emerged. In particular, the right inferior parietal cortex, extending onto posterior angular gyrus, was preferentially involved in the orientation of external attention. On the other hand, bilateral intraparietal sulcus, as well as right ventral and bilateral dorsolateral prefrontal cortices, were preferentially recruited in orientation shifts during the internal attention task. These results were corroborated and expanded upon by Esterman et al. (2009). Using multivoxel pattern classification (MVPA) analysis they trained a classifier that successfully identified subpopulations of neurons within the superior

parietal lobule preferentially associated with either internal or external attention-related activity. Finally, recent evidence showing differences between neural regions recruited during internal and external attention tasks comes from a study by Sestieri et al. (2010). In this study, participants engaged in top-down attentional search tasks looking for stimuli that were either retrieved or perceived. A direct comparison showed preferential activation in the angular gyrus, extending rostrally toward supramarginal gyrus and dorsally toward the intraparietal sulcus, precuneus, and posterior cingulate cortex for the memory search task. In contrast, the medial and ventral banks of the posterior intraparietal sulcus, as well as the superior parietal lobule, were preferentially associated with the perceptual search task. Taken together, the evidence just surveyed suggests that even though there is substantial overlap between internal and external attention, there are important differences as well (for a recent review, see Chun and Johnson, 2011).

Notwithstanding the substantial commonalities in the neural activations between internal and external attention, recent behavioral evidence is starting to suggest that internal rather than external attention may play a fundamental role during memory retrieval. Barring a few exceptions (e.g., Johnston et al., 1970; Trumbo and Milone, 1971), until the mid-1980s most memory researchers thought that, while attention was critical during memory encoding, it was not necessary for episodic memory retrieval. Neuropsychological evidence favored this claim, insofar as patients with attentional deficits due to parietal lesions showed no impairments during memory tasks (Critchley, 1953). Similar conclusions were reached by researchers conducting studies in which attention was manipulated during memory retrieval. In a classic paper, Baddeley et al. (1984) conducted a series of experiments using different attention-demanding secondary tasks during both encoding and retrieval. They found that, during encoding, all attention-demanding secondary tasks consistently impaired subsequent memory tests relative to conditions in which attention remained undisrupted. However, during retrieval, the same secondary tasks left memory performance unscathed. As a result, Baddeley et al. (1984) suggested that memory retrieval was a relatively automatic and mandatory operation that did not require the allocation of attentional resources. Since then, numerous studies have confirmed and clarified the essential role attention plays during episodic memory encoding (for a review, see Chun and Turk-Browne, 2007).

This dominant view has been recently challenged by a series of innovative studies showing that, under certain conditions, divided attention during episodic retrieval can actually affect memory performance. In a pioneer study, Fernandes and Moscovitch (2000) showed that when people engage in a material-congruent secondary task in a divided attention paradigm during retrieval, performance significantly decreases relative to a baseline in which the memory test is the only task. In a related study, Hicks and Marsh (2000) showed that under deep encoding conditions divided attention at retrieval significantly reduces successful recollection. Indeed, they argue that previous studies failed to find effects of divided attention during retrieval precisely because they used shallow as opposed to deep encoding strategies. As a result, Hicks and Marsh (2000) hypothesize that,

consistent with the dual-process theory of recognition memory², successful memory retrieval requires attention only when it is recollection- rather than familiarity-based (Yonelinas, 2002). The necessity of attention for material-congruent and recollection-based memory retrieval was nicely confirmed by Skinner and Fernandes (2008) who, employing a Remember/Know paradigm typically used to tap at differences between recollection and familiarity, showed that divided attention during retrieval only affected “Know” responses for material-congruent items. When the secondary task involved contents that differed from the target material (e.g., numerical tasks during retrieval of verbal information), and such materials were shallow versus deeply encoded, divided attention did not affect memory performance. Finally, Lozito and Mulligan (2006) extended these results by showing that, under conditions of strategic encoding (that need not be semantic) divided attention produces detrimental effects at retrieval. Taken together, the results of these – and related (e.g., Fernandes et al., 2005; Skinner et al., 2009) – studies suggest that divided attention affects recollection of strategic, deeply encoded information when attention is directed to material-congruent contents.

In addition to using shallow encoding strategies, previous studies failed to find an effect of attention during recollection for another reason: they either employed attention-diverting tasks with external targets (e.g., serial search) rather than internal targets, or they used material-incongruent tasks (e.g., number counting in verbal tasks) that did not demand the use of resources that internal attention was allocating to the process of recollecting memories. However, when the concurrent attention-diverting task employed during memory retrieval targeted internal and material-congruent contents, recollection was significantly impaired. Consequently, focusing one’s internal attention upon the to-be-retrieved material appears to be necessary for successful recollection of episodic memories. Indeed, this claim is further supported by recent neuropsychological studies on patients with parietal damage. As mentioned above, the traditional view is that patients with parietal lesions do not exhibit memory deficits. However, recent studies suggest that when recollection requires demanding internal maintenance and monitoring of retrieved information, patients with parietal damage show significant impairments relative to healthy controls. For instance, Berryhill et al. (2007) reported that, when compared with healthy controls, patients with bilateral ventral parietal lesions showed reduced levels of free-recall during autobiographical memory tasks as opposed to cued-recall, where they show no impairment. In addition, when compared with matched controls, patients

showed decreased levels of vividness and number of details in their recollections during free- as opposed to cued-recall.

Curiously, when considered from the point of view of free-recall, a classic study conducted by Bisiach and Luzzatti (1978) appears to be consistent with the claim that parietal damage impairs voluntary retrieval of stored information. Bisiach and Luzzatti (1978) asked a patient with a parietal lesion resulting in severe hemispatial neglect, to remember the main square in Milan, the city in which he had lived all his life. Despite claiming to know the square quite well, the patient’s report omitted the buildings to the left of the square when he tried to remember it facing one direction. When asked to imagine crossing the square and turning back, so he would be now facing the other direction from the opposite side, he omitted the buildings to his left even though he had just reported them. This surprising observation strongly suggests that damage to the parietal cortex, critical for the selection, and maintenance of visual information in external attention tasks, is also critical for the voluntary selection and maintenance of internal information during memory retrieval in conditions of free-recall.

The involvement of the parietal cortex during episodic memory retrieval has been a systematic finding in neuroimaging studies. For that reason, some theorists suggest that the role the parietal cortex may be playing during recollection is tantamount to the role it plays during visual perception. One of the most explicit articulations of this view has been put forth by Cabeza and colleagues (e.g., Cabeza, 2008; Cabeza et al., 2008). According to their “Attention to Memory” (AtoM) hypothesis, the dorsal parietal cortex, which is usually associated with top-down attention, is involved in voluntary, goal-directed attention, whereas the ventral parietal cortex, which is usually involved in bottom-up attention, appears to be associated with involuntary recollection (see Hutchinson et al., 2009, for some counter-evidence, but also Cabeza et al., 2011, for a response). Another hypothesis suggests that the parietal cortex may play a role analogous to the working-memory buffer suggested by Baddeley et al. (1998), insofar as it is required for gating stored information for decision-making and action (Wagner et al., 2005). Finally, one recent hypothesis – the Cortical Binding of Relational Activity (CoBRA) – suggests that the parietal cortex may modulate the reactivation of disaggregated sensory components during retrieval in order to bind them in the unified whole we experience during recollection (Shimamura, 2011). Although the jury is still out as to which of these views best captures the role of the parietal cortex during memory retrieval, for the present purposes it suffices to say that they all agree in that it plays a critical role in the selection (either voluntary or involuntary), modulation (either top-down or bottom-up), and maintenance of internally generated information – which, according to the operational definition used above, means that it plays a critical role during internal attention to memory representations.

In sum, the evidence reviewed in this section suggests that internal attention is required for the retrieval of episodic memories. Behavioral studies using divided attention paradigms show that when internal attention to material-congruent deeply encoded information is disrupted during retrieval, recollection is significantly impaired. In addition, neuropsychological studies in patients with parietal cortex damage, which usually results in attentional impairments to external stimuli, also suggest that

²According to the dual-process theory, recognition consists of two independent processes: recollection and familiarity. On the one hand, recollection involves the effortful retrieval of information about the encoded material plus contextual associations. Remembering the details of where you parked your car, its precise location and the visual layout of the surrounding environment constitute an example of a recollection-based memory. On the other hand, familiarity involves the mere feeling of having encountered the recognized item before, but without the capacity of conjuring up any details associated to such item. The feeling that you know someone you run into at a party without being able to place where you met her or what her name may be is an example of a familiarity-based memory (for a review, see Yonelinas, 2002).

under free-recall conditions they tend to retrieve less perceptual details from their autobiographical memories relative to both cued-recall and healthy controls. Finally, extant data coming from neuroimaging studies shows the involvement of attention-related parietal regions during episodic retrieval, further supporting the idea that internal attention plays a critical role during recollection. However, even if attention is required for episodic retrieval, there is still a further question as to whether it is necessary for conscious recollection – that is, the subjective experience of reliving the retrieved memory. In the next section I argue that this question should be answered in the affirmative.

INTERNAL ATTENTION IS NECESSARY FOR CONSCIOUS RECOLLECTION

The evidence reviewed so far suggests that internal attention is required for episodic memory retrieval. I now want to suggest that internal attention is also a necessary mechanism by means of which we become conscious of successfully retrieved memories. As mentioned before, episodic recollection requires the orchestrated operations of several brain regions. First, neuropsychological and neuroimaging studies show that the prefrontal cortex is involved in the initiation, monitoring, and maintenance of the retrieval attempt (Buckner and Wheeler, 2001). In particular, it has been suggested that the ventrolateral regions of the prefrontal cortex are involved in the initiation and maintenance of episodic memory retrieval, while the dorsolateral regions have been associated with the updating and manipulation of retrieved features (Wagner, 2002; Cabeza and St. Jacques, 2007). Second, recent evidence suggests that the medial-temporal lobes – previously thought to be involved only during memory encoding (but see Squire, 2004) – are also required for the successful binding and accessing of relational information from the neocortex during memory retrieval (Gilboa et al., 2005; Moscovitch et al., 2006). Finally, as mentioned in the previous section, it is now well accepted that the parietal cortex is involved in memory retrieval. Although its precise role remains elusive, extant theories suggest that it plays a role in the filtering and selection of information distributed in the sensory cortices (Shimamura, 2011).

It has also been suggested that this prefrontal/medial-temporal/parietal network of activation associated with episodic memory retrieval plays a critical role in the informational processing that gives rise to conscious awareness of mental contents. This suggestion has been thoroughly developed within the influential framework of the Global Neuronal Workspace (GNW) model suggested by Dehaene and Changeux (2000; see also Dehaene et al., 2003, 2006; Changeux and Dehaene, 2008; and Dehaene and Changeux, 2011). Briefly stated, the GNW model postulates two computational spaces in the brain, characterized by different patterns of connection. On the one hand, there is a *processing network*, which is seen as a set of local, informationally encapsulated, functionally specialized, and domain specific processors with limited numbers of medium-range connections. On the other hand, there is the GNW, which is characterized by distributed sets of cortical networks with long-range excitatory and inhibitory connections, allowing them to send and receive projections from distant areas in a global and flexible manner, so that the information these networks processes is neither encapsulated nor domain specific.

The projections that compose the GNW originate from pyramidal cells from layers II and III, the number of which is particularly high in lateral prefrontal, parietal, and medial-temporal cortices, specifically in the hippocampus, entorhinal, perirhinal, and parahippocampal cortices (von Economo, 1929; see also Changeux and Dehaene, 2008). Thus, according to the GNW hypothesis, informational inputs that enter the global neuronal workspace constitute the mental contents of which we are consciously aware.

The claim that attention is necessary for retrieved memories to become conscious becomes clear when it is considered from the point of view of the GNW hypothesis. Take the case of conscious recollection during free-recall. Assuming that what we know about the neural correlates of recollection is roughly accurate, the lateral prefrontal cortex would presumably initiate the process of retrieval (Rugg et al., 2002). Information is thus projected onto the ventral parietal cortex as well as the hippocampal and parahippocampal gyri, where stored indices of distributed sensory information would enable the binding of disaggregated memory traces (Nadel and Moscovitch, 2001). Then, dorsal regions of the parietal cortex would support the maintenance of the selected information via amplifying the signal from the local processing networks where it resides. When the signal reaches a certain threshold – most likely within the gamma frequency of 30–100 Hz (Jensen et al., 2007; see below) – the local sensory information that forms the memory trace would be broadcasted onto the global neuronal workspace which, by the GNW hypothesis, renders the memory not only conscious but also available for action. Since attention appears to operate via neural synchronization (e.g., Steinmetz et al., 2000), it follows that attention is the mechanism required to enhance gamma-band responses in local processing networks, which in turn renders them available for broadcasting onto the global neuronal workspace. Since these local processing networks represent stored rather than externally generated information from the immediate surrounding environment, the kind of attention required to render it available to the global neuronal workspace is internal instead of external attention. Thus, internal attention turns out to be necessary for conscious recollection.

Evidence in favor of the claim that internal attention permits the broadcasting of locally processed memory representations onto consciousness, comes from several electrophysiological and neuropsychological studies. As previously mentioned, attention appears to act upon local networks by modulating their synchronized firing (Steinmetz et al., 2000). Neuronal synchronization increases neuronal firing, which in turn promotes synaptic plasticity (Wespatat et al., 2004). Such neuronal changes have been correlated with increases in the gamma frequency of the relevant local network, which may explain why gamma-frequency activity predicts successful encoding during memory tasks, as confirmed by numerous EEG and MEG studies (e.g., Sederberg et al., 2003; Paller et al., 2009). Critically, increases in gamma activity have also been correlated with successful retrieval of old items versus correct rejection of new items (Gruber et al., 2004; Osipova et al., 2006; for a review see Jensen et al., 2007). Moreover, in a recent study involving intracranial electroencephalographic recordings in 52 patients with epilepsy, Sederberg et al. (2007) discovered that the same pattern of gamma-frequency activity that predicts successful encoding reappears at retrieval. Of note, this

oscillatory activity emerges in the prefrontal cortex and the hippocampus, and then spreads onto the sensory cortex – an observation consistent with several of the aforementioned neuroimaging results on memory retrieval. This finding, coupled with previous results showing the involvement of parieto-occipital regions in the modulation of gamma-frequency activity during recollection (Osipova et al., 2006), gives further support to the claim that the prefrontal/medial-temporal/parietal cortex plays a critical role in gating information from local sensory networks onto the global neuronal workspace.

Behavioral studies conducted with individuals who suffered parietal lesions give further support to the claim that internal attention gates memories into consciousness. If, as hypothesized, parietal regions modulate the availability of local sensory representations onto the global neuronal workspace, one should expect a diminished sense of “re-experiencing” or “autonoetic consciousness” in patients whose parietal lesions hinder such broadcasting. Indeed, this prediction has been recently confirmed. Berryhill et al. (2007) tested autobiographical recollection in patients with bilateral parietal lesions and showed that, during free-recall, these individuals exhibited fewer episodic details and reported lower levels of vividness in their recollections, suggesting that a reduced number of sensory representations were actually made available to their conscious experience. In a related study, Davidson et al. (2008) reported that patients with parietal lesions showed a reduced number of “remember” responses, which are associated with increased subjective experience of recollection, relative to both “know” responses and controls. Drowos et al. (2010) also found reduced levels of “remember” relative to “know” responses in patients with parietal lesions using the Deese/Roediger-McDermott (DRM) paradigm. Finally, Simons et al. (2010) found that patients with bilateral parietal damage showed lower confidence levels for source recollection tasks, a result they interpret as suggesting that parietal lobe lesions impair subjective experience of episodic recollection. The view that internal attention is required for conscious recollection is entirely consistent with their interpretation.

Finally, the claim that internal attention is necessary for conscious recollection also finds support when one considers cued-recall – albeit this foundation is perhaps more speculative. The fact that richer retrieval cues increase the likelihood of successful retrieval is at the heart of the notion of retrieval support, but it also suggests that these richer cues work precisely because they have a better chance of “highlighting” the relevant memory trace than poorer retrieval cues. This thought lies at the foundation of Tulving’s (1982) classic *synergistic ecphory* model, according to which the subjective sense of recollection occurs when the memory trace interfaces with the retrieval cue – a process he, following Semon (1904), called “ecphory.” Although little is known about the neural underpinnings of ecphory, research on memory reinstatement suggest that cued-recall facilitates the reactivation of regions engaged during encoding (Rugg et al., 1998, 2008). In a recent study, Manning et al. (2011) used electrocorticographic recordings in 69 patients during study and cued-recalled tests. They found that the recorded electrophysiological pattern of brain activity during encoding correlated with the pattern at retrieval. Critically, when successful reinstatement was evidenced it occurred within the gamma-band, suggesting the modulation of attentional

mechanisms. This activity may be related to bottom-up attention, as suggested by Cabeza’s (2008) AtoM model. It may also relate to the phenomenon of spontaneous autobiographical recollections that occur when unexpected stimulus, acting as powerful cues, manage to unintentionally trigger episodes from our past (Berntsen, 2010). Further research is needed to understand the precise ways in which bottom-up internal attention may render memories conscious. Nonetheless, the evidence reviewed in this section strongly suggests that internal attention is not only necessary to successfully retrieve episodic memories: it is also needed to render them conscious.

INTERNAL ATTENTION MAY NOT BE SUFFICIENT FOR CONSCIOUS RECOLLECTION

Although internal attention is necessary for retrieved contents to become conscious, recent evidence suggests that is not sufficient. There are two main reasons why this may be the case. The first reason is that successful episodic recollection requires that the memorial contents one internally attends to are effectively reinstated during retrieval. Striking evidence in favor of this claim comes from studies with patients suffering from visual amnesia. Rubin and Greenberg (1998) reported 11 cases of patients with focal lesions in occipital cortex. Although these patients did not exhibit retrograde or anterograde amnesia – as their medial-temporal lobes were preserved – they did show marked deficits in remembering visual details from their episodic autobiographical memories, the non-visual details of which they were still able to remember (Greenberg et al., 2005). Similar observations can be found in patients with certain kinds of visual agnosias, such as color and spatial location; these patients’ recollection of color and spatial details is impaired relative to their recollection of other preserved visual details, such as volume or directionality (Farah et al., 1988). If my rendition of the GNW model as it applies to conscious recollection is roughly correct, then we can find an explanation as to why these patients cannot access these particular informational contents consciously: it is not because they cannot attend to them, but rather because, when they try to, there is nothing to attend to. The damage in the occipital cortex makes it impossible to reinstate the sensory content which, had it been internally attended, would have been consciously recalled³.

Further support for this claim comes from a recent behavioral experiment conducted by Guerin et al. (2012). After studying a series of items, participants were presented with a recognition test in which they had to select one of three items. Critically, in one condition, participants saw two related items, both of the same kind as the studied item, plus a non-related item. None of the items was the studied item itself. In another condition, participants saw one non-related item and two related items, one of which was, in fact, the target item. Importantly, in the condition where the two

³In essence, this is the same explanation the GNW model offers to account for attentional blink (e.g., Dehaene et al., 2006). If the iconic memory of the masked stimulus in the occipital cortex has been erased and replaced by the masking item, when internal attention is reoriented toward the first content (i.e., the masked stimulus), it finds that such content is no longer available for conscious processing, so only the second content (i.e., the masking item) is broadcasted. I believe a similar phenomenon occurs during change blindness (for an explanation see De Brigard and Prinz, 2010).

related items that did not include the target item, participants' false alarm rate was at baseline level; whereas, in the condition in which one of the two related items was the target item, participant's false alarm rate was significantly reduced. Eye-tracking data collected during this study showed that in both cases participants were selectively attending to the perceptual differences between the related items. However, given the difference in false alarms, it appears as though the use of attention to perceptually discriminate between two related foils was not sufficient for the accurate retrieval of the target item. However, once the content was reinstated – as when the target item was actually seen next to a foil – it was more likely to capture internal attention, rendering it accessible for conscious recollection. This result suggests that, in addition to directing one's internal attention to stored contents, the presence of such contents is required for attention to render them conscious during recollection. As a consequence, internal attention appears to be necessary but perhaps not sufficient for conscious recollection.

The second reason attention may not be sufficient for conscious recollection has to do with the fact that attention is not an all-or-nothing process. It may be possible that, being a modulatory mechanism, attention can render contents conscious only if a certain threshold is reached. Indeed, this is a fall-out of the GNW model (Dehaene et al., 2003). It has also been proven experimentally in numerous studies showing that, under specific conditions, certain stimuli can exhibit attentional-cuing effects – even at the neuronal level – and yet those same stimuli go completely unnoticed by the subject (see, for instance, van Boxtel et al., 2010, for a review). The same may occur with memory traces that, for one reason or another, cannot reach the conscious threshold even when modulated by internal attentional mechanisms. In fact, it may be possible that unattended memory representations are responsible for certain priming effects as well as familiarity-based recognition judgments (Paller et al., 2009). Further research is needed to clarify the conditions under which internal attention to memory representations may suffice to render them conscious.

CONCLUSION

While this review only scratches the surface of a rather convoluted puzzle, I believe that the evidence surveyed in this paper strongly suggests that internal, as opposed to external, attention is necessary but maybe not sufficient for conscious recollection. There are still several open questions that deserve further scrutiny. Perhaps the most pressing one consists of defining the precise mechanisms involved in the kind of internal attention required for conscious recollection. Not only is there substantial disagreement as to the extent of the overlap between the neural correlates of external and internal attention (Chun and Johnson, 2011), there

is also disagreement as to the precise role each kind of attention plays during conscious experience. Another critical question concerns the role that attention plays during familiarity-based rather than recollection-based recognition (Yonelinas, 2002). As discussed, disturbing internal attention during retrieval affects recollection but not familiarity. Moreover, patients with parietal damage report significantly reduced numbers of “know” versus “remember” responses and lower confidence ratings, which are thought to track subjective feelings of remembering, suggesting that their recollective experience is impoverished (Davidson et al., 2008). Further research will be critical in illuminating the role that internal attention plays in differentiating recollection from familiarity.

Finally, it is also possible that the dispensability of internal attention during procedural memory performance could help us understand the difference between implicit and explicit memory (Schacter, 1992). Although much is known about the neural mechanisms responsible for these two kinds of memory, the precise role internal attention plays – if at all – during retrieval of implicit information is still understudied. In a pioneer study, Gooding et al. (1999) tested participants on an implicit word-stem completion test under divided attention conditions and found no differences in performance relative to full attention. Similar results were found using related paradigms, such as artificial-grammar learning tasks (Helman and Berry, 2003) and repetition priming (Clarke and Butler, 2008), supporting the hypothesis that attention does not play a critical role during the retrieval of implicit memory. Strong support in favor of this view comes from recent studies by Lozito and Mulligan (2010). Using a variety of implicit memory tasks – such as perceptual identification and category exemplar production tests – under divided attention conditions, Lozito and Mulligan (2010) found no effect of divided attention during implicit retrieval, and also no performance costs for the secondary task. To the best of my knowledge, the only study showing some reduction in priming during divided attention conditions at retrieval is Kinoshita (1999), who used a re-arranged word-stem completion task. As such, it remains a possibility that specific kinds of implicit tasks could require some level of attentional allocation. Further research is needed to understand this particular issue, and its relation to the more general question of the role of attention in conscious recollection.

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Rethinking the role of top-down attention in vision: effects attributable to a lossy representation in peripheral vision

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According to common wisdom in the field of visual perception, top-down selective attention is required in order to bind features into objects. In this view, even simple tasks, such as distinguishing a rotated T from a rotated L, require selective attention since they require feature binding. Selective attention, in turn, is commonly conceived as involving volition, intention, and at least implicitly, awareness. There is something non-intuitive about the notion that we might need so expensive (and possibly human) a resource as conscious awareness in order to perform so basic a function as perception. In fact, we can carry out complex sensorimotor tasks, seemingly in the near absence of awareness or volitional shifts of attention (“zombie behaviors”). More generally, the tight association between attention and awareness, and the presumed role of attention on perception, is problematic. We propose that under normal viewing conditions, the main processes of feature binding and perception proceed largely independently of top-down selective attention. Recent work suggests that there is a significant loss of information in early stages of visual processing, especially in the periphery. In particular, our texture tiling model (TTM) represents images in terms of a fixed set of “texture” statistics computed over local pooling regions that tile the visual input. We argue that this lossy representation produces the perceptual ambiguities that have previously been ascribed to a lack of feature binding in the absence of selective attention. At the same time, the TTM representation is sufficiently rich to explain performance in such complex tasks as scene gist recognition, pop-out target search, and navigation. A number of phenomena that have previously been explained in terms of voluntary attention can be explained more parsimoniously with the TTM. In this model, peripheral vision introduces a specific kind of information loss, and the information available to an observer varies greatly depending upon shifts of the point of gaze (which usually occur without awareness). The available information, in turn, provides a key determinant of the visual system’s capabilities and deficiencies. This scheme dissociates basic perceptual operations, such as feature binding, from both top-down attention and conscious awareness.

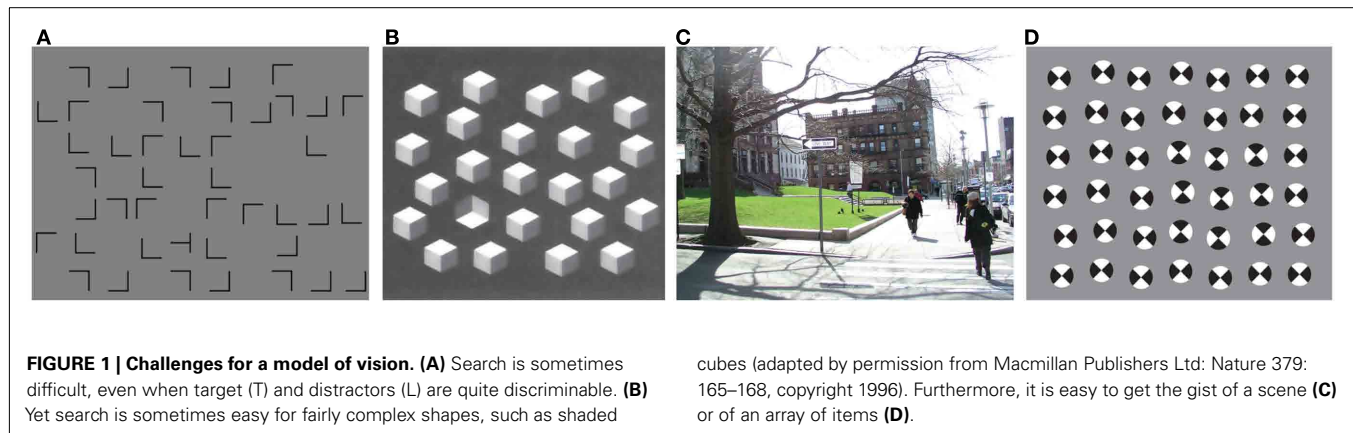
Keywords: selective attention, limited capacity, search, scene perception, model, peripheral vision, compression

INTRODUCTION

Our senses gather copious amounts of data, seemingly far more than our minds can fully process at once. At any given instant we are consciously aware of only a small fraction of the incoming sensory input. We seem to have a *limited capacity* for awareness, for memory, and for the number of tasks we can simultaneously perform. For example, our conscious experience when looking at a street scene (e.g., **Figure 1C**) consists of first noticing, perhaps, a one-way sign, then a pedestrian, then a tree next to the sidewalk. Subjectively, it seems as if we switch our awareness between them. The mechanism behind this experience of shifting the focus of our awareness has been called *selective attention*. Traditionally, selective attention has been intimately linked with conscious awareness. James (1890) said of attention that “focalization, concentration, of consciousness are of its essence.” However, the precise relationship between consciousness and attention has remained unclear.

Theories of selective attention vary, but in general it is presumed to operate by alternately selecting one of a number of competing subsets of the incoming sensory data for further processing. Unselected information is momentarily either unavailable, or available only for very limited processing. (*Attentional modulation*, by contrast, refers to effects of attention on existing visual processing, e.g., attenuation or enhancement of processing, or changes in the tuning or contrast sensitivity of a neuron.) Selective attention can be *bottom-up*, in which salient items draw attention by virtue of being unusual when compared to nearby items (Rosenholtz, 1999, 2000). Bottom-up selective attention is generally assumed to be largely automatic and independent of task (Wolfe, 2007). Much of selective attention, however, is assumed to be *top-down*, driven by the tasks and goals of the individual.

This framework raises the question which has occupied much of the study of attention for the last 50 years: at what stage does selective attention operate? In other words, what processing



occurs prior to selection – and is available to guide that selection process – and what processing occurs later, operating only on the selected information?

In vision, visual search has proved a rich experimental paradigm for investigating attention (**Figures 1A,B**). An observer's task consists of finding a *target* among competing *distractor* items. If attentional selection operates *late* in the processing pipeline, then all items in the display might be processed to the point of identification, but an observer might only be able to concentrate their awareness on one item at a time. Presumably if this were the case, visual search would be easy, so long as the target was visually distinct from the distractors; preattentive identification of the items would direct attention to the target. However, visual search is often quite difficult: it's surprisingly hard to find a rotated "T" among rotated "L"s, or search for a red vertical bar among red horizontal and green vertical distractors. These results have led to the conclusion that attention operates with *early selection*, i.e., that top-down selective attention is necessary even for so simple an operation as the *binding* together of pairs of features into a "T," "L," or red vertical bar. This conclusion dates back to Treisman and Gelade (1980). Despite some issues, discussed in the next section, this conclusion continues to pervade our thinking about visual perception.

The intimate relationship between consciousness and attention, coupled with the notion that attention strongly influences perception through early selection, is problematic. For one thing, consider the intertwined nature of consciousness and attention. It would seem straightforward to suggest that selective attention might be required as a gate to awareness (Treisman, 2003). However, an argument could also be made for the converse. "Top-down" implies goal-directed, volitional, and intentional, suggesting that some sort of conscious awareness might be a necessary precursor to top-down selective attention (Itti and Koch, 2001; Cavanagh, 2004). If selective attention, in turn, is required for feature binding, this is cause for concern. Surely so expensive (and possibly human) a resource as conscious awareness is not required for basic low-level perception. In fact, humans can perform many complex tasks, apparently with neither consciousness nor attention, such as driving home on a familiar route. Such "zombie behaviors" (Koch and Crick, 2001) would seem to imply that one can remove awareness and attention without a huge impact on task performance.

If awareness were required for top-down selective attention, could the visual system get around a need for consciousness by primarily processing "salient" regions of the image through bottom-up selective attention, and occasionally applying conscious, top-down selective attention? As Nakayama (1990) has previously argued, this does not seem like a viable strategy.

Dissociating awareness from attention (Nakayama, 1990; Levin and Simons, 1997; Koch and Tsuchiya, 2006; Wyart and Tallon-Baudry, 2008) can help resolve the issue of awareness being improbably coupled to basic perception. The notion of "unconscious inferences" (von Helmholtz, 1867) has certainly been popular in the study of human vision. This theory suggests that the brain might continuously, automatically, and often unconsciously postulate interpretations of the visual world (see Koenderink, 2011, for a recent formulation). Testing those hypothesized interpretations would involve some sort of top-down mechanisms, perhaps driving selective attention without awareness.

However, there are other issues with the awareness–attention–perception triad as well. As we will argue in the Section "Discussion," early selection may be incompatible with a number of theories of consciousness. Furthermore, the historical link between consciousness and attention may have biased us to think of limited capacity in a particular way, which is incompatible with reasoning about perception. We will argue that this has led to a complicated story about perception in a limited capacity system, where a simpler story will suffice.

We begin by reviewing research on early vs. late attentional selection in vision: the logic behind the experiments and conclusions, as well as issues that complicate the story. Next, we will review recent work on the nature of the lossy representation in early vision. This research attributes significant information loss not to a lack of selective attention, but rather to limitations of peripheral vision. Such a lossy representation predicts difficulties in visual search previously attributed to a lack of top-down selective attention (Rosenholtz et al., under review), including perceptual ambiguities often interpreted as a lack of feature binding. Nonetheless, this representation is sufficiently rich to explain performance in such complex tasks as scene gist recognition, pop-out search, and navigation. The result is a simple, coherent account of much of the evidence used to study selective attention in vision.

First, a bit of terminology: in this paper we use the term *selection* to refer to the momentary choice of a subset of the sensory input, *with the intent later, perhaps, to select a different subset*. While, for instance, having only three cone types in the retina might be thought of as representing only a subset of the input, we do not call this “selection,” as there is no plan to later use cones with different responsivity. On the other hand, moving one’s eyes to direct the highest density of photoreceptors to a particular location should certainly be thought of as involving a form of selection, but we do not refer to this as selective *attention*. Attention involves separate mechanism(s), a focus that may not agree with the point of fixation, and possibly different effects upon perception than shifting the point of gaze.

EARLY OR LATE ATTENTIONAL SELECTION IN VISUAL PROCESSING?

The visual system subjects the visual input to stages of processing, from basic feature measurements in early vision, through mid-level grouping, recognition, memory, and higher-level cognition. A number of initial processing stages are assumed to occur *preattentively* and in parallel across the visual field. At some point in the processing stream, selection occurs. What is selected is determined by the information available from the preattentive processing stages, as well as any task-relevant information such as likely location of a target (see also “Guided Search,” Cave and Wolfe, 1990). In the most straightforward version of the story, the selected information passes through a limited capacity channel to higher processing, e.g., semantic analysis, whereas the unselected information becomes unavailable for further processing and conscious awareness (Broadbent, 1958).

At what stage does attentional selection occur, i.e., what computations can occur without attention? To answer this question, one must first run experiments in which attentional selection is likely to matter, i.e., situations in which the sensory input contains multiple components competing for limited processing resources. For example, dichotic listening experiments simultaneously present two auditory stimuli, such as speech, one to each ear, and ask participants to attend to one or both. Easy tasks presumably use computations that happen before selection, whereas difficult tasks use computations that happen after attentional selection.

In audition, the early vs. late selection story at first seemed straightforward. Listeners can easily distinguish, in the unattended ear, tones from speech, and male from female voices. However, they have difficulty identifying even a single word or phrase presented to the unattended ear, determining whether the language is English or German, and even distinguishing forward speech from reversed (Cherry, 1953). Broadbent (1958) took these results to demonstrate early selection, in which only low-level “physical” characteristics – e.g., the frequency spectrum – of the signal can be processed without attention.

However, a number of empirical findings are at odds with Broadbent’s early selection theory, including the classic demonstration by Moray (1959) that people can recognize subjectively important “messages,” such as their own names, in the unattended stream of conversation. To accommodate these findings, Treisman (1960) proposed *attenuation theory*, which posits that unattended information, rather than being excluded from further

processing, instead has attenuated signal strength. At later stages processing occurs only if the signal falls above some threshold. An important message such as the listener’s name will be semantically processed, in this scheme, because even its attenuated signal strength will often fall above-threshold. By this theory, attentional attenuation happens early. The mere attenuation of unattended information does not obviously resolve issues of limited capacity at this early processing stage, though it does facilitate later selection of above-threshold signals for further processing.

In vision, the dominant experimental paradigm for studying early vs. late selection has been visual search, where the target and distractors are presumed to compete for limited processing resources. As discussed in the Section “Introduction,” initial results in visual search led researchers to conclude that selective attention operated early in visual processing, and to develop the highly influential feature integration theory (FIT, Treisman and Gelade, 1980). FIT suggests that spatially organized “maps” of basic features such as orientation, color, and size, can be preattentively extracted in parallel across the visual scene. However, any further processing requires attention, including the binding together of basic features. This theory predicts that searching for a target defined by a basic feature is efficient, parallel, and does not require attention. However, search for a target defined by conjunction or configuration of basic features requires the serial deployment of selective attention.

Although a number of search results support the early selection story, a number of issues arise; here we focus on only a few of the most critical. For one thing, the level at which attentional selection operates in visual search has seemed inconsistent. Studies have shown that some properties related to extraction of 3-D shape, direction of lighting, and apparent reflectance can be processed in parallel across the visual scene and thus enable easy search (Enns and Rensink, 1990; Sun and Perona, 1996). How could it be that processing of 3-D shape, lighting, and/or reflectance occurs preattentively, but not simple feature binding?

Furthermore, different paradigms have led to different conclusions about what processing occurs preattentively. Search for a scene containing an animal among non-animal scenes (VanRullen et al., 2004) or for a navigable scene among non-navigable scenes (Greene and Wolfe, 2011) seems to require a serial, attentive process. This is not surprising for FIT, since no single basic feature can identify an animal or a navigable path; search for these targets should require feature binding, which requires attention. FIT would also seem compatible with evidence from change-blindness that without attention the details of the scenes are murky (Rensink et al., 1997; Simons and Levin, 1997).

However, a number of studies have shown that natural scenes can be perceived preattentively in a dual-task paradigm. In this paradigm, the observer is given fewer competing sensory inputs than in a typical search display, but must complete both central and peripheral tasks. In this paradigm, observers can perform a peripheral task in which they identify whether a scene contains an animal or not, while simultaneously specifying whether letters presented at the center of the display are all “T”s, all “L”s, or mixed (Li et al., 2002). Furthermore, this result agrees with outcomes of rapid perception experiments. Rapid perception paradigms allow for brief attention to a scene, but minimal time to select multiple regions of that scene for further processing. Yet observers can

discern much information about the gist of a scene, sufficient to identify general scene categories and properties (Rousselet et al., 2005; Greene and Oliva, 2009) and perform basic object detection, for example determining whether an image contains an animal (Thorpe et al., 1996; Kirchner and Thorpe, 2006), vehicle (VanRullen and Thorpe, 2001), or human face (Crouzet et al., 2010). A brief (26 ms) glance at a scene is also sufficient to allow observers to distinguish specific types of animals (birds or dogs) from other animal distractors (Mace et al., 2009). How is this possible with minimal attention, when attention seems necessary to tell a “T” from an “L”?

The dual-task paradigm has also provided conflicting results for preattentive processing of 3-D shape. As mentioned above, findings from visual search have suggested that some 3-D properties can be processed preattentively. However, discriminating between an upright, shaded cube and an inverted one is a difficult, attention-demanding task in a dual-task paradigm.

In order to reconcile the above results, a number of researchers have postulated that certain visual computations, such as recognizing the gist of a scene, do not require selective attention (Rensink, 2001; Treisman, 2006), perhaps occurring in a separate pathway with no bottleneck limitations (Wolfe, 2007). Others have postulated a hierarchy of preattentive features, which includes not only simple features like color and orientation but also complex conjunctive features that respond to specific object or scene categories, like “animal,” “vehicle,” or “face” (VanRullen et al., 2004; Reddy and VanRullen, 2007). These authors reason that since the more complex features are processed by higher levels of the visual stream, which have larger receptive fields, they cannot preattentively guide visual search in the way that a low-level feature like color can. However, they do allow for preattentive processing of scenes in dual tasks. This theory, too, gives special status to processing of scenes; complex conjunctive features exist if and only if the brain has cells or brain regions specific to the particular type of discrimination. VanRullen et al. (2004) then, should predict easy dual-task performance for scene, face, and place tasks.

However, it is not merely scenes, faces, and places that afford easy preattentive processing of gist. It is easy to get the gist of a set of items (Treisman, 2006). **Figure 1D** can easily be seen to contain an array of circles split into quarters, alternating black and white. We have a rough guess as to their number. Yet it is surprisingly difficult to tell that a 3×3 sub-array consists of white “bowties,” whereas the rest are black bowties. How do we get a sense of the complex array of shapes, yet have difficulty discriminating between black and white bowties? Recently, researchers have suggested that, even without attention, the visual system can compute “ensemble statistics” of a set of items, such as mean size and mean orientation (see Alvarez, 2011, for a review). Clearly, however, the limited set of ensemble statistics which have been proposed is insufficient to capture the gist of **Figure 1D**.

As another way out of these conundrums, some researchers (e.g., Allport, 1993; Tsotsos et al., 1995) have argued that selection does not have a single locus of operation, but can occur throughout visual processing. Similarly, Nakayama (1990) and Treisman (2006) have suggested that one can attend to regions of varying size and complexity, and that the available processing depends upon the nature of the attended region. Attend to an object, and identify

that object, but perhaps not others. Attend to a set of objects, and extract set (“ensemble”) properties, but perhaps not the properties of individual objects. Attend to a scene, and get the scene gist.

Theories with ensemble statistics, special status for scene processing, or flexible representations which depend upon task may well prove correct (the last is certainly difficult to disprove). Until these theories are more fully specified, we fundamentally do not know what they can and cannot predict.

In this paper we propose a simpler, unified explanation, by re-conceptualizing early visual processing steps. Discriminating between early and late attentional selection fundamentally requires knowledge of the stages of processing, and that knowledge remains incomplete. In particular, if early stages include significant information loss not attributable to selective attention, this will profoundly affect our interpretation of the experimental results. We next review a recent model of just such an information loss in peripheral vision, and show that this lossy representation may be responsible for many of the puzzling results described above.

RECENT WORK: PERIPHERAL VISION

Peripheral vision is, as a rule, worse than foveal vision, and often much worse. Only a finite number of nerve fibers can emerge from the eye, and rather than providing uniformly mediocre vision, the eye trades off sparse sampling in the periphery for sharp, high resolution foveal vision. If we need finer detail (for example for reading), we move our eyes to bring the fovea to the desired location. This economical design continues into the cortex: the cortical magnification factor expresses the way in which cortical resources are concentrated in central vision at the expense of the periphery. However, acuity loss is not the entire story, as made clear by the visual phenomena of crowding. An example is given in **Figure 2**. A reader fixating the central cross will likely have no difficulty identifying the isolated letter on the left. However, the same letter can be difficult to recognize when flanked by additional letters, as shown on the right. An observer might see the letters on the right in the wrong order, perhaps confusing the word with “BORAD.” They might not see an “A” at all, or might see strange letter like shapes made up of a mixture of parts from several letters. This effect cannot be explained by the loss of acuity, as the reduction in acuity necessary to cause flankers to interfere with the central target on the right would also completely degrade the isolated letter on the left. (Lettvin, 1976, makes similar points about both the subjective experience and the infeasibility of acuity loss as an explanation.)

What mechanism could account for crowding? Recent research has suggested that the representation in peripheral vision consists of summary statistics computed over local pooling regions (Parkes et al., 2001; Levi, 2008; Pelli and Tillman, 2008; Balas et al., 2009). In particular, we have proposed that the visual system

A + **BOARD**

FIGURE 2 | Visual crowding. The “A” on the left is easy to recognize, if it is large enough, whereas the A amidst the word “BOARD” can be quite difficult to identify. This cannot be explained by a mere loss of acuity in peripheral vision.

might measure a fixed set of summary statistics: the marginal distribution of luminance; luminance autocorrelation; correlations of the magnitude of responses of oriented V1-like wavelets across differences in orientation, neighboring positions, and scale; and phase correlation across scale. This perhaps sounds complicated, but really is not: computing a given second-order correlation merely requires taking responses of a pair of V1-like filters, point-wise multiplying them, and taking the average over a “pooling region.” These summary statistics have been shown to do a good job of capturing texture appearance (Portilla and Simoncelli, 2000; Balas, 2006). Discriminability based on these summary statistics has been shown to predict performance recognizing crowded letters in the periphery (Balas et al., 2009).

What do we know about the pooling regions over which the summary statistics are computed? Work in crowding suggests that they grow linearly with eccentricity – i.e., with distance to the center of fixation – with a radius of ~ 0.4 – 0.5 the eccentricity. This has been dubbed “Bouma’s law,” and it seems to be invariant to the contents of the stimulus (Bouma, 1970). The pooling regions are elongated radially outward from fixation. Presumably overlapping pooling regions tile the entire visual input. We call our model, which represents images in terms of a fixed set of hypothesized “texture” statistics, computed over local pooling regions that tile the visual input in this fashion, the texture tiling model (TTM).

Representation in terms of a fixed set of summary statistics provides an alternative tool for dealing with a limited processing capacity in vision. Limited capacity, rather than implying a need for selective attention (Broadbent, 1958), may require our perceptual systems to “describe nature economically” (Attneave, 1954). Attneave suggested that “a major function of the perceptual machinery is to strip away some of the redundancy of stimulation, to describe or encode incoming information in a form more economical than that in which it impinges on the receptors.” Representation in terms of summary statistics provides a compressed representation of the visual input, which can capture detailed information at the expense of uncertainty about the locations of those details. **Figure 3** gives a demonstration. **Figure 3B** shows an image synthesized to have the same summary statistics as the original image in **Figure 3A**, using the texture synthesis algorithm of Portilla and Simoncelli (2000). This algorithm starts

with an image – usually random noise – and iteratively coerces it until it has approximately the same summary statistics as the original. We call these synthesized images “mongrels.” The results are intriguing. In order to coerce the noise “seed” image to share the same statistics as the original, apparently one must start making quadrisectioned circles! However, the statistics are not sufficient to distinguish between circles with black vs. white bowties; **Figure 3B** has the same statistics as **Figure 3A**, yet it contains both bowtie patterns, and the original contained only black. This may explain the difficulty segmenting the array in **Figure 1D**.

Figures 3C,D shows another example, in which we have synthesized a scene to have the same *local* summary statistics as the original. The statistics seem sufficient to categorize the scene, and even navigate down the sidewalk. The details – such as the number of cars on the street – are murky, in line with results from change-blindness.

While additional work is required to pin down the right statistical measurements, our present set provide a good initial guess. Certainly they seem quite plausible as a visual system representation. Early stages of standard models of object recognition typically measure responses of oriented, V1-like feature detectors, as does our model. They then build up progressively more complex features by looking for co-occurrence of simple structures over a small pooling region (Fukushima, 1980; Riesenhuber and Poggio, 1999; Deco and Rolls, 2004). These co-occurrences, computed over a larger pooling region, can approximate the correlations computed by our model.

Second, our summary statistics appear to be quite close to sufficient. Balas (2006) showed that observers are barely above chance at parafoveal discrimination between a grayscale texture synthesized with this set of statistics and an original patch of texture. More recent results have shown a similar sufficiency of these summary statistics for capturing the appearance of real scenes. Freeman and Simoncelli (2011) synthesized full-field versions of natural scenes. These syntheses were generated to satisfy constraints based on local summary statistics in regions that tile the visual field and grow linearly with eccentricity. When viewing at the appropriate fixation point, observers had great difficulty discriminating real from synthetic scenes. That the proposed statistics are close to sufficient for capturing both texture and scene appearance is impressive; much information has been thrown away, and yet



FIGURE 3 | (A) Original image. **(B)** We can visualize the information available in a set of summary statistics by synthesizing a new “sample” with the same statistics as the original. Here we constrain the statistics for a single pooling region (the whole image).

(C) Original photograph. **(D)** A new “sample,” which has the same *local* summary statistics as the original. The local regions overlap, tile the visual field, and grow linearly with distance from the fixation (blue cross).

observers have difficulty telling the difference between an original image and a noise image coerced to have the same statistics.

Finally, significant subsets of the proposed summary statistics are also necessary. If a subset of statistics is necessary, then textures synthesized without that set should be easily distinguishable from the original texture. Balas (2006) has shown that observers become much better at parafoveal discrimination between real and synthesized textures when the syntheses do not make use of either the marginal statistics of luminance, or of the correlations of magnitude responses of V1-like oriented filters.

To test the TTM, we make use of texture synthesis techniques (Portilla and Simoncelli, 2000, for local patches; Rosenholtz, 2011, for complex images) to generate new images – “mongrels” – that share approximately the same summary statistics as each original stimulus. Mongrels enable intuitions and the generation of testable predictions from our model. The general logic is essentially this: we can generate a number of mongrels (e.g., **Figure 3B**) which share the same local summary statistics as each original stimulus (e.g., **Figure 3A**). The model cannot tell these mongrels apart from the original, nor from each other. If these images are indistinguishable, how hard would a given task be? If we could not tell an image with all black bowtie circles from one with both white- and black- bowtie circles, it would be quite difficult to, say, find a white bowtie circle among black bowtie circles.

By synthesizing mongrel images which are equivalent to the original image, according to the model, we can generate testable model predictions for a wide range of tasks. Most powerfully, we can predict performance on higher-level visual tasks without needing a model of higher-level vision. We do not need to build a black vs. white bowtie discriminator to tell from mongrels (like **Figure 3B**) that our model predicts this task will be difficult. We do not need to model scene classification to tell from mongrels (like **Figure 3D**) that the model predicts easy discrimination between a street scene and a beach. In practice, we ask subjects to perform a discrimination task with a number of synthesized images,

and we measure their task performance with those mongrels as a measure of the informativeness of the summary statistics for a given task (see Materials and Methods.) We have previously used this methodology to make testable predictions of the model for a number of visual crowding tasks, and shown that the model can predict performance on these tasks (Balas et al., 2009).

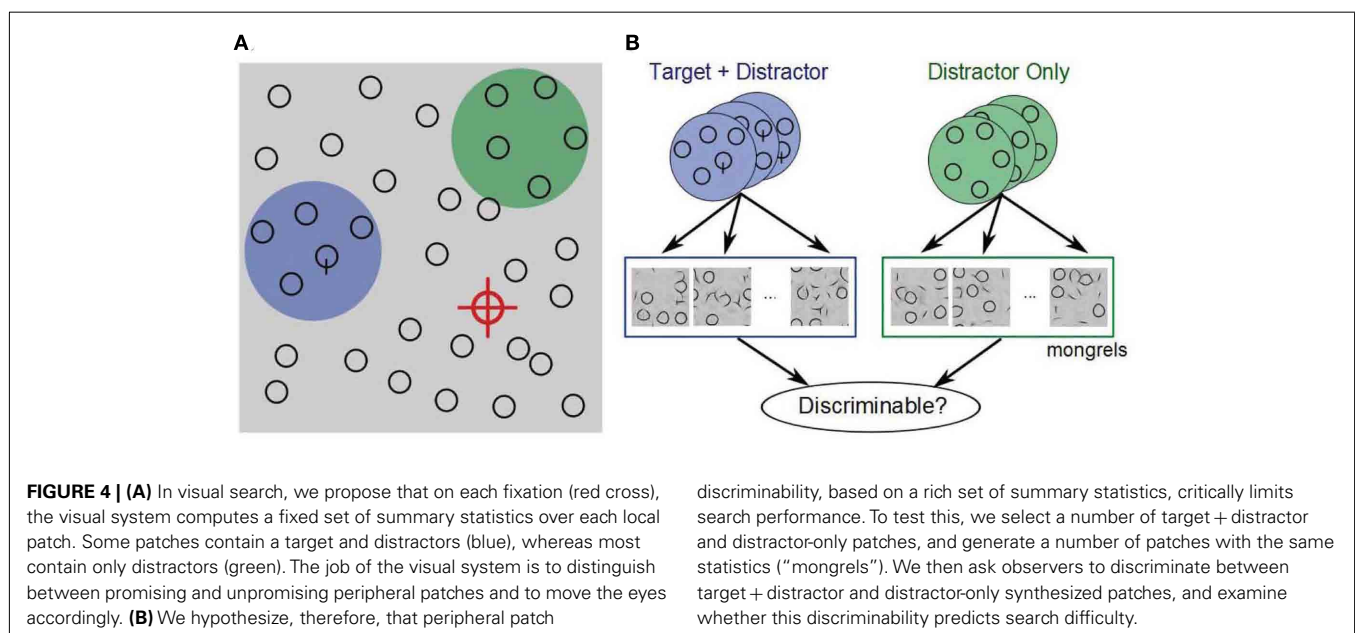
RESULTS: THE MODEL MAKES SENSE OF DIVERSE PHENOMENA

FEATURE, CONJUNCTION, AND CONFIGURATION SEARCH

Rethinking visual search in light of recent understanding of peripheral vision provides immediate insight. If early visual representation is in terms of a fixed set of summary statistics, computed over pooling regions that grow with eccentricity, then for typical search displays many of those pooling regions will contain more than a single item. This suggests that the visual system's real task as it confronts a search display is to discriminate between peripheral patches containing a target (plus distractors) from those containing only distractors. This is quite different from the usual formulation, in which the key determinant of search performance is whether an individual target is preattentively discriminable from an individual distractor.

In **Figure 4**, the target (“Q”) is not visible near the current fixation (red crosshairs), so the subject continues searching. Where to look next? A reasonable strategy is to seek out regions that have promising statistics. The green and blue disks represent two hypothetical pooling regions in the periphery, one containing the target (plus distractors), the other containing only distractors. If the statistics in a target-present patch are noticeably different from those of target-absent patches, then this can guide the subject's eyes toward the target. However, if the statistics are inadequate to make the distinction, then the subject must proceed without guidance.

The prediction is that to a first approximation, search will be easy only if the visual statistics of target-present patches are sufficiently different from those of target-absent patches.



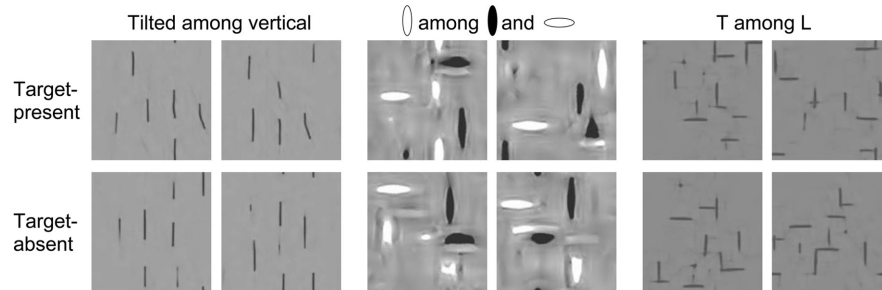


FIGURE 5 | Example mongrels for target-present (row 1) and target-absent (row 2) patches, for three classic search conditions. (A) tilted among vertical; (B) orientation-contrast conjunction search; (C) T among L. How discriminable are target-present from target-absent

mongrels? Inspection suggests that the summary statistic model correctly predicts easy search for tilted among vertical, more difficult conjunction search, and yet more difficult search for T among L, as validated by results in Figure 6.

(Two conditions with the same statistical discriminability might nonetheless lead to different performance due to peculiarities of later processing; e.g., stimuli like letters might be more effectively processed than non-letters at a later stage.) We can generate mongrels of target-present and target-absent patches, which share the same summary statistics as the corresponding original patches. Figure 5 shows examples for three conditions. To our model, these mongrels are indistinguishable from the original patches. How difficult would we expect a given search task to be?

Search for a tilted line among vertical is easy (Treisman and Gelade, 1980). The target-present mongrels for this condition clearly show a target-like item, whereas the distractor-only mongrels do not. Patch discrimination based upon statistics alone should be easy, predicting easy search.

Conjunction search for a white vertical among black verticals and white horizontals shows some intriguing “illusory conjunctions” (Treisman and Gelade, 1980; Treisman and Schmidt, 1982) – white verticals – in the distractor-only mongrels. This apparent lack of binding has previously been attributed to a need for selective attention for feature binding, but in our model is due to representation in terms of a rich set of image statistics. The inherent ambiguity in this representation makes it more difficult to discriminate between target-present and target-absent patches, and correctly predicts more difficult search.

Search for a “T” among “L”s is known as a difficult “configuration search” (Wolfe et al., 1989). In fact, the mongrels for this condition show “T”-like items in some of the distractor-only patches, and no “T”-like items in some of the target + distractor mongrels. Again, we note that the model predicts confusions which have previously been attributed to a lack of preattentive “binding.” Patch discrimination based upon summary statistics looks difficult, predicting difficult search.

Figure 6 plots search performance for five classic search tasks, vs. the discriminability of target-present vs. target-absent mongrels (see Materials and Methods). Results agree with the above intuitions. The data shows a clear relationship between search performance and visual discriminability of patch statistics as measured by human discrimination of the mongrels ($R^2 = 0.99$, $p < 0.01$; Rosenholtz et al., under review). Crucially, one can predict classic differences between feature, conjunction,

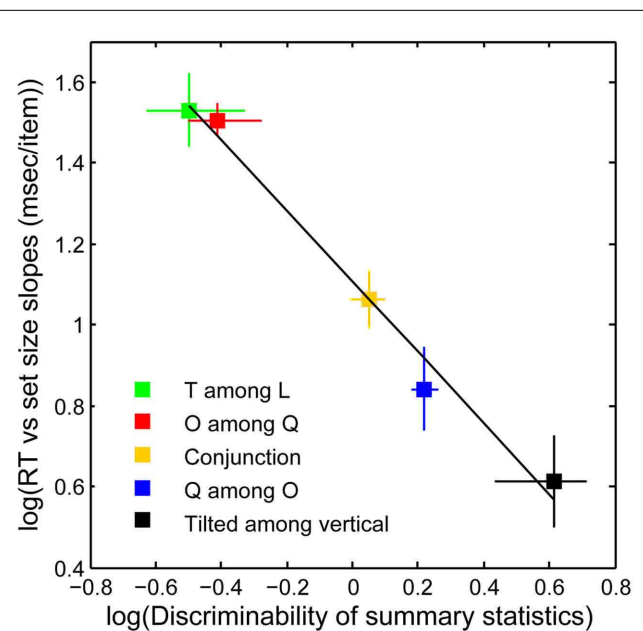


FIGURE 6 | Search performance vs. statistical discriminability. y-Axis: search performance for correct target-present trials, as measured by log 10 (search efficiency), i.e., the mean number of milliseconds (ms) of search time divided by the number of display items. x-Axis: “statistical discriminability” of target-present from target-absent patches based on the empirical discriminability, d' , of the corresponding mongrels. There is a strong relationship between search difficulty and mongrel discriminability, in agreement with our predictions. [y-axis error bars = SE of the mean; x-axis error bars = 95% confidence intervals for log 10 (d')].

and configuration search, with a model with no attentional selection.

SEARCH AND DUAL-TASK PERFORMANCE ON SHADED CUBES

The previous section demonstrated that the TTM can predict search results previously attributed to an early attentional selection mechanism. What about search results which are more problematic for early selection? Enns and Rensink (1990) demonstrated that searching for a side-lit cube among top-lit

shaded cubes is quite efficient (~ 8 ms/item), particularly when compared with search using “equivalent” 2-D targets and distractors (> 20 ms/item). This would seem to suggest that direction of illumination might be available prior to operation of selective attention. Other results from Enns and Rensink (1990) and Sun and Perona (1996) have suggested that 3-D orientation might be available preattentively. This work calls into question the early selection story, as surely 3-D orientation and lighting direction do not occur earlier in visual processing than piecing together vertical and horizontal bars to make a T-junction. The story has been further complicated by evidence that observers have difficulty distinguishing upright from inverted cubes in a dual-task setting (VanRullen et al., 2004).

We examined whether the TTM can shed light on these puzzling results. We generated a number of mongrels for target-present and target-absent patches for search for a side-lit cube among top-lit (Enns and Rensink’s Experiment 3A), as well as for some of their “equivalent” 2-D targets and distractors (Experiments 2B and 2C). As described in Section “Materials and Methods,” observers judged whether each mongrel came from an original patch that contained or did not contain the target.

Preliminary results demonstrate that the TTM can predict easier search for the 3-D condition ($d' = 2.44$) than for the 2-D conditions (mean $d' = 1.78$). Essentially what this means is that

there are 2-D pattern differences between the 3-D condition and the 2-D conditions, which show up in the summary statistics and make it easier in the 3-D condition to discriminate target-present from target-absent patches. The summary statistic information provides better search guidance in the 3-D case than in the 2-D conditions.

We then asked why distinguishing between an upright and inverted cube was difficult under dual-task conditions. For our model, this is actually an unsurprising result. Our summary statistic representation, *within a single pooling region*, is theoretically unable to tell an upright from an inverted figure (see **Figures 7A,B**), though constraints from multiple pooling regions may be able to do the discrimination. This is an odd consequence of our model, which nonetheless has correctly predicted performance in a peripheral discrimination task (Balas et al., 2009).

What sense can we make, then, of easy search (Enns and Rensink, 1990; Sun and Perona, 1996) for an inverted cube among upright cubes? Enns and Rensink reported slopes of 8 ms/item. For visual search, it matters not only what the target and distractor look like, but also what the search display looks like. **Figure 1B** shows an example display, adapted from Sun and Perona (1996). The cubes are so densely packed that they are almost regularly aligned with one another (Enns and Rensink (1990) used similar

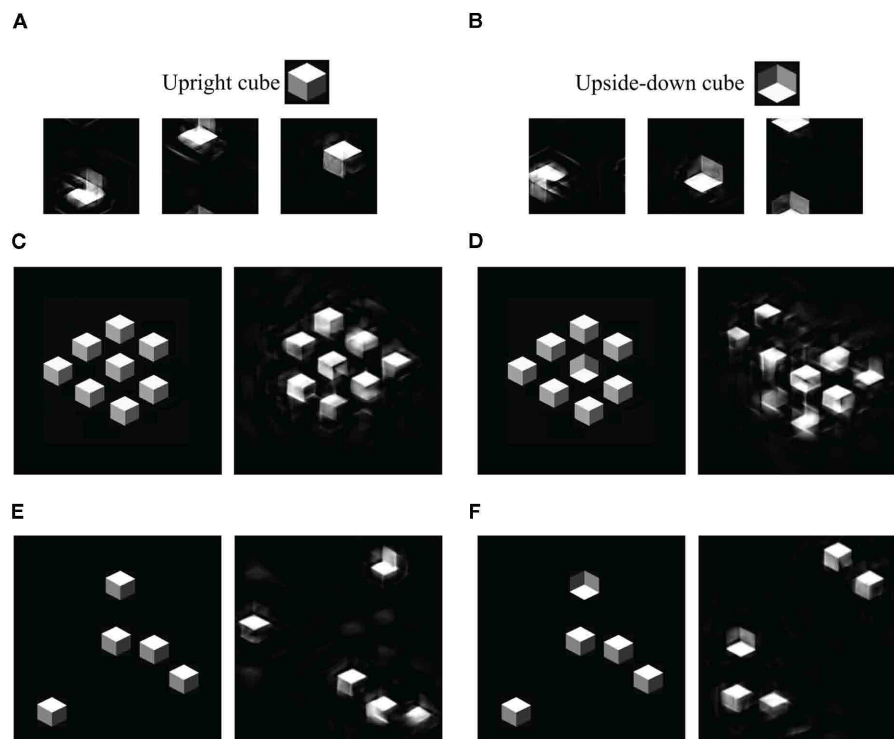


FIGURE 7 | Mongrels of shaded cubes. (A) Mongrels synthesized from an image containing a single upright cube (inset). **(B)** Mongrels of an image with a single inverted cube (inset). The statistics have difficulty discriminating an upright from inverted cube. **(C–F)** Original (left) and mongrel (right) pairs. **(C,D)** Patches from a dense, regular display. **(E,F)** Patches from a sparse display. For the dense display, the target-absent

mongrel shows no sign of a target, while the target-present mongrel does. For the sparse display, both mongrels show signs of a target. (Single pooling region mongrels wrap around both horizontally and vertically, so a cube may start at the top and end at the bottom of the image. The mongrels in **(C–F)** have been shifted to the middle, for easy viewing.)

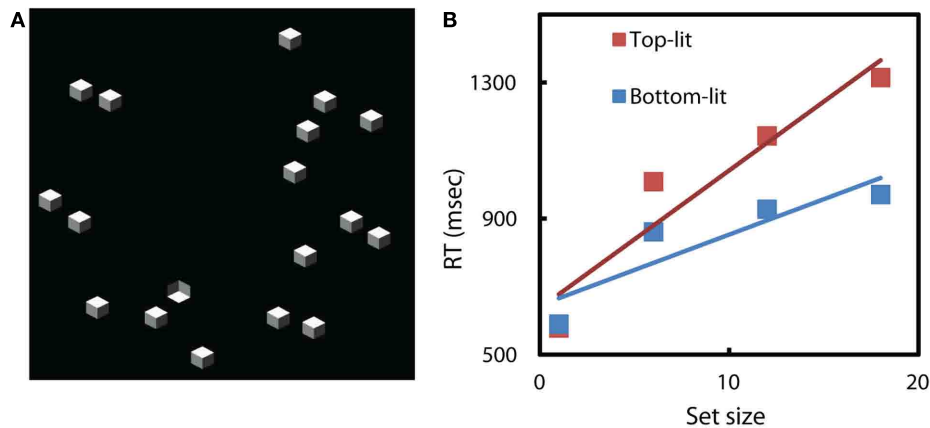


FIGURE 8 | (A) An example of our search displays. Target is an inverted cube; distractors are upright cubes. **(B)** More irregular search displays leads to less efficient search, for this task. Average response times on

correct target-present trials vs search set size. RT slope of searching for upright is 40 ms/item, the slope of searching for inverted cube is 21 ms/item.

but less dense displays). The dense, regular array of cubes may have introduced emergent features that could serve as cues to facilitate search. **Figures 7C,D** shows mongrels of dense vs. sparse displays. It appears from this demo that the dense regular arrangement contains features that favor recognition of homogeneous, distractor-only patches. (Future work is required to test whether the TTM can predict effects of item arrangement.)

To test the possibility of emergent features in the dense displays, we re-ran search conditions with upright and inverted cubes similar to those described by Sun and Perona (1996), but with the same random, less dense arrangement of elements as used in our previous search tasks (e.g., **Figure 8A**). As we expected, less dense and regular displays led to far less efficient search (**Figure 8B**). We conclude that earlier results demonstrating efficient search in these particular cube search conditions were efficient due to yet-unspecified emergent features of the displays.

Our TTM explains not only the basic visual search results, but also easier search for some 3-D cube stimuli than for “equivalent” 2-D stimuli. These results were problematic for an early selection story. Furthermore, we predict difficult dual-task performance discriminating upright vs. inverted cubes. Insights gained from the model led us to re-run search experiments on upright vs. inverted cubes, and to the conclusion that the original search displays may have enabled easy search due to an emergent feature.

SEARCH, DUAL-TASK, AND RAPID PERCEPTION OF SCENES

Other problematic results for the early selection story have involved scene perception. Scene perception is very fast, and people can do scene discrimination tasks, such as animal vs. non-animal, when attention is engaged elsewhere. However, searching for an animal scene among non-animal distractors is a slow, serial search that requires attention. If animals can be detected preattentively in a dual-task situation, why do not they “pop-out” in a search task (Li et al., 2002; VanRullen et al., 2004)?

VanRullen et al. (2004) suggest that any discrimination task can be preattentive if there is a dedicated population of neurons

in visual cortex that performs that task. With simple tasks, such as color discrimination, the dedicated neurons are located early in the visual system and these neurons can also guide visual search, producing “pop-out” effects. For more complex discriminations, such as animal vs. non-animal, the dedicated neurons are located higher in the visual stream, probably in inferotemporal cortex. These neurons cannot guide visual search, because their receptive fields are so large that they typically contain multiple items, so there is neural competition between target and distractors (Reddy and VanRullen, 2007).

Here we ask whether our model can explain the dichotomy between search performance and rapid/dual-task performance without needing to rely upon special neuronal populations dedicated to particular scene discrimination tasks. Earlier in this paper, we argued that the real task for the visual system in visual search is not to discriminate between a single target and a single distractor, but rather is often to discriminate between target-present and target-absent patches which may contain information from multiple items. With this reconceptualization of search, one expects search performance often to conflict with performance of tasks involving single items. We hypothesize that typical scene discrimination tasks (such as animal vs. non-animal) are easy with rapid presentation, even in a dual-task situation, because the summary statistic representation is sufficient to distinguish a single target from a distractor. However, when multiple images are presented in a crowded search display, the summary statistics mix features from nearby images, and it is no longer possible to clearly identify the region of the array which contains the target.

To test this hypothesis, we first had subjects perform one of two go/no-go rapid scene perception tasks (animal vs. non-animal or vehicle vs. non-vehicle) with image presentation either at fixation or 11° to the left or right of fixation (see Materials and Methods). Subjects were asked to respond to target images (animals or vehicles) as quickly as possible. We also synthesized “mongrel” versions of each of the images from the go/no-go tasks, using the TTM with fixation of the synthesis procedure set as in the go/no-go task (either in the center of each image, or 11°

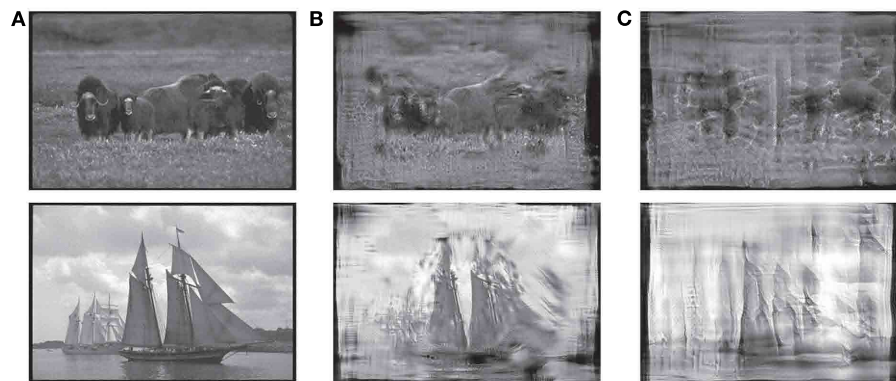


FIGURE 9 | Example stimuli from animal- and vehicle-detection tasks. (A) Target images used in the go/no-go task. **(B)** Mongrels synthesized with fixation in the center of the image. **(C)** Mongrels synthesized with fixation 11° left of the image center.

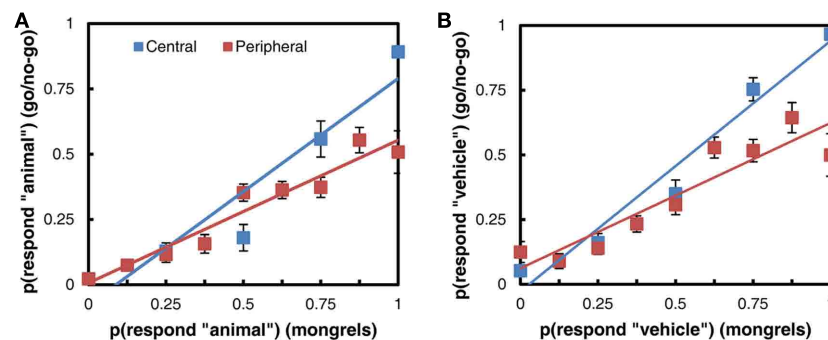


FIGURE 10 | Comparison of mongrel and go/no-go responses. (A) Animal vs. non-animal task. **(B)** Vehicle vs. non-vehicle task.

to the left or right of center). Examples of target images from the go/no-go task and their corresponding mongrels are shown in **Figure 9**. A separate group of subjects performed one of two mongrel-classification tasks: discriminating animal mongrels from non-animals or vehicle mongrels from non-vehicles.

Overall, subjects perform very well in the go/no-go tasks: averaging 94% correct detection at fixation, and 74 and 76% correct when detecting animals or vehicles, respectively, at 11° eccentricity. Performance is considerably lower with the mongrels: subjects average 85% correct in distinguishing mongrel animals from non-animals and 81% correct in distinguishing vehicles from non-vehicles. Performance with the peripheral mongrels is even lower, but still above chance: subjects average 60% correct in the animal/non-animal task and 62% correct in the vehicle/non-vehicle mongrel task. More work remains to determine the cause of this difference in performance, particularly on the peripheral tasks. These peripheral mongrels are challenging for our synthesis procedure, in terms of converging to a solution with the same statistics as the original. It is also possible that our model throws out a bit too much information, and that this was apparent in the scene task but not on crowding and search tasks with simpler displays.

Despite the overall difference in accuracy between the two tasks, target detection in the go/no-go rapid perception tasks correlates

with responses to the mongrel images. **Figure 10** shows a comparison of the responses to images in each task: images have been binned according to the proportion of target responses (“animal” or “vehicle”) they received in the mongrel sorting task, and points represent the average proportion of target responses to each image bin in the go/no-go task. The more strongly a mongrel is classified as “animal,” the more “animal” responses it receives in the go/no-go task, and the same is true of vehicles. The linear relationship between mongrel and go/no-go responses holds both when the image is presented centrally and when it is presented in the periphery. The fact that mongrel animal images can be distinguished from mongrel non-animals does not mean that search for animal among non-animal distractors should be an easy pop-out search. When multiple images are presented in a search display, features of the distractors may be combined with features of the target to mask its location, or combined features from two different distractors may create an illusory target. **Figure 11** illustrates this with a “mongrel” version of a scene search array, similar to the animal among non-animal search arrays used by VanRullen et al. (2004). The location of the animal image is not obvious in the mongrel array, even though this particular animal image’s mongrel is fairly easy to identify as an animal when it is synthesized as an isolated image in the periphery.

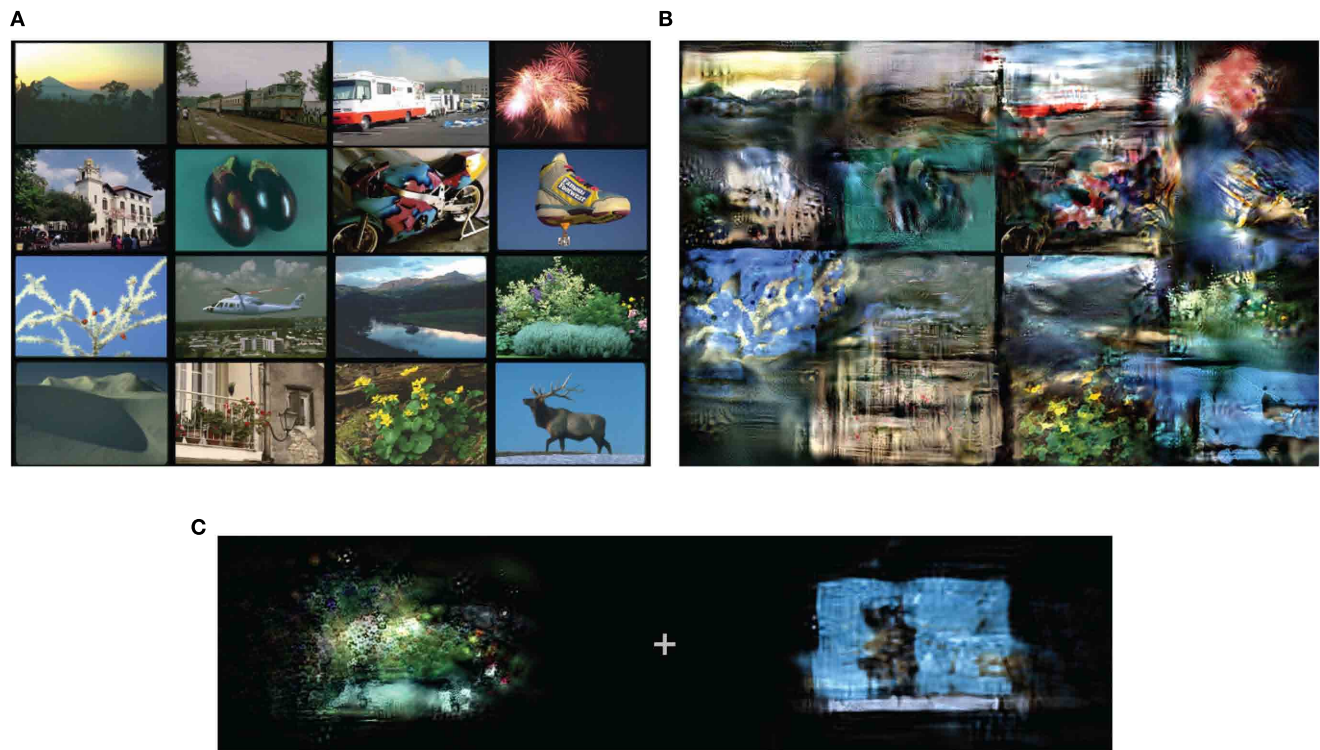


FIGURE 11 | (A) A scene search array in the style of VanRullen et al. (2004). **(B)** A mongrel version of the array, fixation at center. It is difficult to determine, from the mongrel, whether there is an animal. **(C)** Mongrels

generated from two scenes from the array (the elk and the hedge), shown in isolation in the periphery. In this case, it is easy to determine which image contains the animal.

DISCUSSION

This paper has focused on re-evaluating the role of top-down selective attention on perceptual processing. In the standard story, based on studies of visual search, such attentional selection occurs early in the processing stream. This conclusion was drawn from reasonable assumptions – at the time and even today – about early stages of processing, and reasonable experimental logic based upon those assumptions. Yet the resulting theories have been problematic, and had difficulty predicting a number of basic effects, such as extraction of gist from scenes and other displays, search for 3-D shaded cubes among differently lit cubes, zombie behaviors, and results from different experimental paradigms. We have suggested that these results can be explained more simply by a newer model of the processing in early vision, in which the visual system represents its inputs by a rich set of summary statistics.

For clarity, it is worth reformulating both the old and new ways of thinking in terms of strategies for dealing with limited capacity. The previous story assumes that the mechanism for operating with a limited capacity channel is selective attention. By this account, various parts of the input can be thought of as competing for use of that channel. These parts might be objects (e.g., the images of a one-way sign, a pedestrian, and a tree), feature bands (e.g., “red” or “vertical”), or locations (“upper left”). Selective attention is presumed to enable the different parts of the input to share the limited

capacity channel by taking turns using that channel. In digital communications – from which the “limited capacity” terminology in psychology derives – strategies for splitting up use of the channel so that multiple competing “senders” can access it are known as *multiplexing*, and the particular strategy of having the senders take turns using the channel is known as *time-division multiplexing*. (A number of other strategies exist; cell phone systems, for example, use an entirely different kind of multiplexing.) “Selection,” as defined in the Section “Introduction,” is equivalent to multiplexing, and common use of the term refers to time-division multiplexing.

When it comes to conscious awareness, the analogy to time-division multiplexing seems natural. We become aware, in a street scene (**Figure 1C**), of the one-way sign, then the pedestrian, then the tree; subjectively, we experience different objects, features, or locations competing for awareness. In perceptual processing, the analogy to multiplexing is far less obvious. A digital communications engineer, faced with the task of transmitting a street scene along a limited capacity channel, would be surprised at the suggestion that one should first transmit the one-way sign, then the pedestrian, then the tree. For one thing, finding each of the component objects in order to transmit their information requires a great deal of complicated processing. In terms of dealing with a limited capacity channel, there is lower-hanging fruit.

A more obvious choice to the engineer would be *compression*, also known as *source coding*¹. Compression consists of representing the input with as few “bits” as possible, while retaining as much fidelity of the original signal as possible. By compressing the input, one can push more information through a limited capacity channel, in less time. Compression can be *lossless*, i.e., such that one could perfectly reconstruct the original signal. Simply taking into account regularities of the world (e.g., in English text, some letter combinations are more likely than others) and redundancy in the signal (a patch of bright pixels in an image increases the chance of more bright pixels nearby) can reduce the number of bits necessary. Compression can also be *lossy*, in which one typically throws away “unimportant” information in order to obtain greater savings in the number of bits required. For example, JPEG image compression, in addition to taking into account regularities and redundancies in the input, typically represents high spatial frequency information more coarsely than low spatial frequency, as moderate loss of high spatial frequency information may be difficult for an observer to detect. Lossy compression “selects” what information to keep and throw away, but is theoretically distinct from selection as defined here, i.e., multiplexing. (Lossless compression, on the other hand, facilitates communication through a limited capacity channel, while involving no “selection” whatsoever.)

The notion of dealing with limited capacity by compressing the input has not been lost on perception researchers. Even as Broadbent (1958) was essentially talking about multiplexing, Attneave (1954), Miller (1956), and Barlow (1961) were talking about various forms of compression. However, the association between consciousness and attention may have biased the way that many researchers thought about limited capacity. In the attention literature, it is often stated without proof that limited capacity implies the need for selection. Certainly limited capacity does not obviously require selective attention, i.e., multiplexing. Multiplexing is necessary in digital communications only for certain situations; should images obviously be thought of as containing multiple senders competing for limited capacity? On the other hand, redundancies and regularities in the world make compression a clear choice of strategy for dealing with limited capacity.

If the visual system implements a lossy compression strategy, this creates problems for reasoning about early vs. late selection. In behavioral experiments, one can observe only the inputs to the visual system (images of the world), and the outputs (performance). If information loss due to compression is misattributed to multiplexing (selective attention), it becomes difficult to determine the stage at which selective attention operates.

Many of the hypothesized “fixes” to the standard early selection story amount to lossy compression strategies. Consider, for example, suggestions that the statistics of a set of items might be available preattentively (Treisman, 2006; see Alvarez, 2011 for

a review), and that image statistics might underlie preattentive recognition of the gist of a scene (Oliva and Torralba, 2006).

Our TTM incorporates both multiplexing and compression. The multiplexing mechanism consists of shifting one’s eyes in order to control what information gets through the “channel” at a given moment. For a given fixation location, the visual system has devised a general-purpose compression scheme, which represents the input with a fixed, rich set of local summary statistics, computed over regions that tile the visual field and grow with eccentricity. We have shown that this model can predict the difficulty of visual search tasks; it predicts the binding errors that have previously led researchers to conclude that attentional selection occurs early, while also predicting the ease of search for shaded cubes, which seems antithetical to early selection. Our model also shows promise in resolving a number of the conundrums surrounding the locus of attentional selection: the fact that observers can easily judge the gist of a scene or display, while being murky on the details, and the difference between scene search and dual-task performance. The TTM can more parsimoniously explain these phenomena than an early selection mechanism.

If selective attention occurs later, then there is no reason to assume that consciousness would be required for basic perceptual processing. This is some relief, and fits well with a number of functional theories of consciousness. Crick and Koch (1990), for instance, suggest that consciousness involves an attentional mechanism, and that “one of the functions of consciousness is to present the results of various underlying computations.” If one is presenting the results of only a select few computations, presumably one would want other useful computations to continue unconsciously, not stop at the stage of feature maps.

As another example, Dennett (1991) has proposed the Multiple Drafts theory of consciousness, in which multiple channels of “specialist circuits,” processes of interpretation, operate in parallel. Many of the “drafts” produced by these processes are short-lived, but some are “promoted to further functional roles.” It is unclear what role, if any, attention need play, unless perhaps it acts as a probe which asks questions of the parallel processing streams. Regardless, surely in this framework one would not want to be restricted to promoting drafts at such an early stage of interpretation as basic feature maps. Such “specialists” would not be very specialized, and would leave a great deal of interpretation to some other processing module. Both points seem antithetical to Multiple Drafts theory.

Finally, in Global Workspace theory, consciousness comes into play when information needs to be accessed by multiple brain systems, such as memory, motor control, verbal systems, and high-level decision-making systems (Baars, 2005). If we view selective attention as the mechanism that puts information into the “workspace,” then we would hardly expect attention to involve early selection. The visual system should not have to call a conference of multiple brain systems just to decide whether an image contains a corner.

Our rethinking of early visual representation seems to have eliminated a large role for attention in visual search, and perhaps in other tasks as well. Clearly attention does have measurable effects in both physiology and behavior (e.g., dual-task experiments). What might attention do? Attention seems to be able to

¹ A third part of the strategy for dealing with limited capacity is what digital communications refers to as “channel coding.” This is less relevant for the present discussion, and involves questions of how the system converts the information into a form which can be sent on the physical medium of the channel, be that wires, air, or neurons, in order to minimize transmission error. In the brain, details of spike rates and spike timing fall into this category.

modulate neuronal responses to produce increased firing rates, increase signal-to-noise, and narrow neuronal tuning curves (see Reynolds and Heeger, 2009, for a review). These effects, by themselves, seem unlikely to explain the difference between single- and dual-task performance. We suggest that different tasks (e.g., performing a covert discrimination of a peripheral stimulus with or without a simultaneous discrimination task at the fovea) allow more or less complicated communication within a population of neurons, enabling more or less complicated inferences. With minimal attention, the visual system might have access to local statistics from individual pooling regions across the visual field, but not be able to combine information from overlapping pooling regions to make more complex inferences. Intersecting constraints from overlapping pooling regions may not be needed for certain tasks, such as recognizing the general category of a scene (see Oliva and Torralba, 2006). However, more complex inference on the outputs of multiple pooling regions might make it possible to tell if an isolated cube were upright or inverted. Comparing the information from multiple overlapping pooling regions might explain the modest decrease in psychophysical pooling region size with attention (Yeshurun and Rashal, 2010), enable identification of an attended object when two are present within the receptive field of a given neuron (Desimone and Duncan, 1995), or allow an item to be localized with more precision than might be expected from a single large pooling region (as suggested by Rousselet et al., 2005).

The arguments presented in this paper should have a significant impact on discussions of the association between attention and awareness. If one attributes performance in a number of tasks to mechanisms of attention, when in fact performance is limited by lossy representation in early vision, this muddies questions of whether attention and awareness are the same thing and how they are linked. Just as one needs to properly understand representation to understand the impact of attention, one needs to understand attention to understand its relationship to awareness.

We have contributed to this discussion by presenting a predictive model of peripheral vision. Image synthesis techniques enable a methodology for making concrete, testable predictions of this model for a wide range of tasks. In developing such a model, it is important to understand not only that crowding occurs, perhaps because of “competition” between stimuli present in a receptive field (Desimone and Duncan, 1995), but also what information is available to the visual system in a crowded display. This information may be the elements from which perception is made, and be predictive of performance on a wide range of visual tasks.

MATERIALS AND METHODS

VISUAL SEARCH EXPERIMENTS AND CORRESPONDING MONGREL EXPERIMENTS

Subjects

Ten subjects (six male) participated in feature, conjunction, and configuration search experiments. The mongrel discrimination task for five classic search conditions was carried out by five other subjects (four male). A different group of nine subjects participated in the 3-D cube search experiment. The mongrel discrimination of 3-D cubes was carried out by a different group of eight subjects. Subjects' ages ranged from 18 to 45 years. All reported normal or corrected-to normal vision and were paid for their participation.

Stimuli and procedure: visual search experiments

Our visual search experiments resemble classic search experiments in the literature. We tested five search conditions: conjunction (targets defined by the conjunction of luminance contrast and orientation), rotated T among rotated Ls, O among Qs, Q among Os, and feature search for a tilted line among vertical lines. For 3-D cube search, we tested search for an inverted cube among upright, and vice versa.

Stimuli were presented on a 40-cm × 28-cm monitor, with subjects seated 75 cm away in a dark room. We ran our experiments in MATLAB, using the Psychophysics Toolbox (Brainard, 1997). The search displays consisted of either all distractors (target-absent trial) or one target and the rest distractors (target-present trial). Target-present and target-absent displays occurred with equal probability.

Each search task had four levels of the number of items in the display (the “set size”): 1, 6, 12, or 18. Stimuli were randomly placed on four concentric circles, with added positional jitter (up to one-eighth degree). The radii of the circles were 4°, 5.5°, 7°, and 8.5° of visual angle (v.a.).

Each search display remained on screen until subjects responded. Subjects indicated with a key press whether each stimulus contained or did not contain a target, and were given auditory feedback. Each subject finished 144 trials per search condition (72 target-present and 72 target-absent), evenly distributed across four set sizes. The order of the search conditions was counterbalanced across subjects, and blocked by set size.

Stimuli and procedure: mongrel discrimination of target-present vs. target-absent patches

To measure the informativeness of summary statistics for the search tasks, we first generated 10 target-present and 10 target-absent patches for each search condition described above. Then, for each patch, we synthesized 10 new image patches with approximately the same summary statistics as the original patch, using Portilla and Simoncelli's (2000) texture synthesis algorithm. This algorithm first measures a set of wavelet-based features at multiple spatial scales, then computes a number of summary statistics, including joint statistics that describe local relative orientation, relative phase, and wavelet correlations across position and scale. To synthesize a new texture, the algorithm then iteratively adjusts an initial “seed” image (often, as in this experiment, white noise, but any starting image may be used) until it has approximately the same statistics as the original image patch. The resulting “mongrel” is approximately equivalent to the original input in terms of the summary statistics measured by the model. **Figures 3B, 4, 5, and 7** all show mongrels generated using this procedure.

During each trial, a mongrel was presented at the center of the computer screen until subjects made a response. Each mongrel subtended 3.8° × 3.8° v.a. at a viewing distance of 75 cm. Subjects were shown examples of original patches, and examples of mongrels, and asked to categorize each mongrel according to whether the mongrel was synthesized from a target-present or target-absent patch. Subjects were instructed that they should look for any cues to help them perform the task, and that the target-present mongrels, for instance, might not actually contain a target. Subjects had unlimited time to freely view the mongrels.

Each of the conditions (corresponding to a search task, including the five classic search and four cube search-related conditions) had a total of 100 target + distractor and 100 distractor-only patches to be discriminated in this mongrel task, with the first 30 trials (15 target + distractor and 15 distractor-only) serving as training, to familiarize observers with the nature of the stimuli. Observers received auditory feedback about the correctness of their responses throughout the experiment.

GO/NO-GO RAPID SCENE PERCEPTION TASK AND CORRESPONDING MONGREL CLASSIFICATION TASK

Subjects

Twenty-four subjects participated in the rapid perception scene task, all 18–35 years old and reporting normal or corrected-to-normal vision. All subjects were paid for their participation.

A second group of 24 subjects participated in an online mongrel classification task on Amazon's Mechanical Turk service. All subjects gave written informed consent and were paid for their participation.

Stimuli and procedure: go/no-go task scene discrimination

Subjects were randomly assigned to either the animal-detection or vehicle-detection task (12 subjects completed each task). The stimuli were a randomly selected subset of the images used by Li et al. (2002). The target images for the animal-detection task were 240 scenes containing animals (including mammals, birds, reptiles, fish, and insects). The target images for the vehicle-detection task were 240 scenes containing vehicles (including cars, trains, boats, planes, and hot-air balloons). The distractor set for each task included 120 images from the other target category, plus 120 scenes which contained neither vehicles nor animals (which included images of plants, food, landscapes, and buildings). Stimuli were presented in grayscale at 384 by 256 pixels ($8.9^\circ \times 6.0^\circ$) on a 34-cm $\times$ 60-cm monitor, with subjects seated 75 cm away in a dark room.

We ran our experiments in MATLAB, using the Psychophysics Toolbox (Brainard, 1997). Subjects were instructed to hold down the left mouse button throughout the experiment. At the start of a trial, a central fixation cross appeared for 300 ± 100 ms, and was followed by an image presented for 20 ms. The image appeared either at the center of the screen or left or right of the fixation (center of the image at 11° eccentricity). If the image contained a target (animal or vehicle), subjects were to respond by releasing the left mouse button as quickly as possible (subjects made no response to non-target images). Subjects were given 1000 ms to make their response.

Subjects completed 10 blocks of 48 trials, with a break after each block. Each block contained an equal number of target and non-target images, and an equal number of images in each of the three presentation locations (left, center, and right).

Stimuli and procedure: mongrel scene classification

For the scene stimuli, we synthesized full-field mongrels based on the TTM. Given a fixation point, the full-field synthesis algorithm tiles the image with overlapping pooling regions. The size of the pooling regions increases with distance from fixation according to Bouma's Law. Within each pooling region, the model computes summary statistics using procedures similar to those described above for single pooling region mongrels, and as described in Portilla and Simoncelli (2000). Synthesis is initiated by assuming the foveal region (a small circle about fixation) is reconstructed perfectly. Then, moving outward, each subsequent pooling region is synthesized using the previous partial synthesis result as the seed for the texture synthesis process. The process iterates a number of times over the entire image. We use a coarse-to-fine strategy to speed convergence. **Figures 3D, 9B,C, and 11B,C** show example mongrels generated using this full-field procedure.

We generated mongrels for each image used in the rapid perception experiment. Pooling regions were placed to simulate fixation in either the center of the image or 11° left or right of center, to match the rapid perception task.

Subjects completed the task on their own computer, using a web interface on the Amazon Mechanical Turk website (www.mturk.com). The experiment consisted of 480 trials which exactly matched one the 24 sessions of the rapid perception experiment. On each trial, subjects were shown a mongrel version of an image from the rapid perception task. Mongrel images were always presented in the center of the screen, but had been synthesized to simulate the image's position in the rapid perception task (left of, right of, or at fixation). Subjects responded with a key press to indicate whether or not the mongrel corresponded to the target category for the experimental session ("animal" or "vehicle"). Instruction was otherwise similar to that in the above mongrel experiments. Subjects received feedback after each response. Subjects could study the mongrels for as long as they wished before making a response.

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Asynchrony in visual consciousness and the possible involvement of attention

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When subjects are asked to perceptually bind rapidly alternating color and motion stimuli, the pairings they report are different from the ones actually occurring in physical reality. A possible explanation for this misbinding is that the time necessary for perception is different for different visual attributes. Such an explanation is in logical harmony with the fact that the visual brain is characterized by different, functionally specialized systems, with different processing times for each; this type of organization naturally leads to different perceptual times for the corresponding attributes. In the present review, the experimental findings supporting perceptual asynchrony are presented, together with the original theoretical explanation behind the phenomenon and its implication for visual consciousness. Alternative theoretical views and additional experimental facts concerning perceptual misbinding are also reviewed, with a particular emphasis given to the role of attention. With few exceptions, most theories converge on the idea that the observed misbinding reflects a difference in perception times, which is in turn due to differences in neuronal processing times for different attributes within the brain. These processing time differences have been attributed to several different factors, attention included, with the possibility of co-existence between them.

Keywords: attention, color, consciousness, functional specialization, motion, perception, perceptual asynchrony, vision

FUNCTIONAL SPECIALIZATION AND PERCEPTUAL ASYNCHRONY IN VISION

A picture of functional specialization with respect to the processing of different visual attributes has emerged from studies in the visual system (Zeki, 1978, 1993). Such a specialization makes sense since, for example, the perception of color involves very different computations from the ones involved in perceiving motion: motion perception requires the calculation of the way in which an object changes position in space over time, whereas the task of a system generating color would be to compare the energy-wavelength composition of the light reflected simultaneously from different objects in the field of view and thus calculate their reflectances, irrespective of any changes in the illumination (e.g., Land, 1971). Functional specialization states that these different tasks are undertaken by different, functionally specialized systems, occupying topographically separate locations in the visual brain (Zeki, 1978, 1993). Specialized brain areas are created in this way, each one characterized by specialized neurons with different connection patterns, different conduction velocities and so on. Such architecture of the visual brain begs the question of whether these separate systems could “finish” their so different tasks at exactly the same time. The word “finish” is used here to refer to the time necessary for the corresponding visual percept to emerge – I will refer to this as *perception time*. Given this distribution of function and the reasons for it, it seems likely that different visual attributes could have different perception times and are therefore not perceived in synchrony. It should be noted that we are currently unaware of the spatiotemporal structure of the neurobiological events underpinning visual

awareness. Thus, perception time is regarded here as a property of the corresponding processing-perceptual system as a whole, free from any vague assumptions regarding particular visual areas and activation patterns in the brain. Since we are still far from understanding where or how a conscious visual percept arises in the brain, the exact relationship of the latter with activity reaching any certain levels in any particular brain areas (Moutoussis and Zeki, 2002; Moutoussis, 2009), back-projections and feedback (Lamme and Roelfsema, 2000), oscillations and synchronizations (Singer, 1999), etc., is beyond the interest of the general idea of perceptual asynchrony in vision.

The question of whether different visual attributes are perceived at exactly the same or at different times has been addressed experimentally (Moutoussis and Zeki, 1997a,b): If the perception time for a particular visual attribute, say color, is dt time shorter than that necessary for the perception time for another visual attribute, say motion, then the color which is present on the computer screen at time t will be perceived synchronously with the motion present on the screen at time $t - dt$. If this motion is different to the motion present on the screen at time t , then the color present on the screen at time t will not be perceived together with the motion with which it physically coexisted, but with a different one, which had occurred at time $t - dt$. Similarly, if the color changes at time $t + dt$ then also the motion present on the screen at time t will be perceived together with this new color rather than with the color with which it occurred together in reality. By presenting stimuli changing both in color (red/green) and in motion direction (up/down) rapidly and continuously, and instructing participants

to report which color-motion pairs were perceived as coexisting, color was found to be paired with the motion present on the computer screen ~ 100 ms earlier (Moutoussis and Zeki, 1997a). The observed misbinding between the two visual attributes was taken to suggest that the color of an object is perceived roughly 100 ms before its direction of motion. We have called this phenomenon *perceptual asynchrony* and have put forward the idea that it is due to the different processing times necessary for the two functionally specialized systems to “finish” their corresponding tasks. Binding color and motion belonging to the *same* object is not crucial, since identical results were also obtained when color and motion were made to belong to *different* objects (Moutoussis and Zeki, 1997b)¹. The perception of form (orientation) falls between that of color and of motion in time, with the estimated values of the three perception time differences adding up nicely (Moutoussis and Zeki, 1997b). The functionally specialized systems in vision thus seem able to create specific visual percepts in their own time and independently from each other, inspiring the so-called *micro-consciousness theory*, which states that conscious visual perception is not single and unified but rather made out of several, independent consciousnesses of the different visual attributes (Zeki and Bartels, 1999).

The color-motion misbinding illusion has been verified by several studies (Arnold et al., 2001; Viviani and Aymoz, 2001; Arnold and Clifford, 2002; Nishida and Johnston, 2002; Bedell et al., 2003; Clifford et al., 2003, 2004; Moradi and Shimojo, 2004; Arnold, 2005; Holcombe and Cavanagh, 2008). Particularly interesting is a study that controls for response bias, by combining perceptual asynchrony and the color-contingent motion-after-effect (MAE; Arnold et al., 2001). Continuous presentation of a rotating stimulus for a period of time will make a subsequent static stimulus appear to rotate in the opposite direction (Mather et al., 2008). This after-effect can be made contingent on color, by associating a particular direction of motion to a particular color and the opposite direction to a second color, during the same adaptation period (Favreau et al., 1972). Thus, if during adaptation red is associated with rightward motion and green with leftward motion, a static red pattern will appear to rotate leftwards and a static green pattern to rotate rightwards. In this way, the characteristics of the after-effect will directly reflect the perceptual associations between color and motion during the adaptation period. Arnold et al. have used our psychophysical paradigm to adapt subjects to rotational motion, and then checked for a color-contingent MAE. If the perception of color and motion were veridical, the maximum MAE in their experiment would have been obtained when the color and motion oscillations are in phase, with no MAE when the two oscillations are 90° out of phase (both color-motion pairs equally present). However, results from this experiment were in accord with the existence of a perceptual lag between motion and color perception, as originally reported by Moutoussis and Zeki (1997a,b). Since there was no binding-task involved, this novel setup has the

advantage of being protected against any possible response bias of the participants². In an attempt to account for the observed MAE without accepting the existence of perceptual asynchrony, Johnston and Nishida (2001) have suggested a hypothetical and somewhat far fetched mechanism, by which a change in the firing rate of neurons during the initial and the final stage of the color stimulus results to asymmetrical adaptation. Even if such a hypothetical mechanism exists, it is still not so clear why the binding should be stronger during the first part of the appearance of the new color rather than that of the new motion.

ALTERNATIVE VIEWS ON THE MISBINDING EFFECT

As noted above, since we do not yet know where, when and how in the brain a visual percept is created, the time taken from the presentation of a stimulus to its conscious perception is unknown. The psychophysical paradigm of Moutoussis and Zeki (1997a,b) can potentially measure *perception time differences* between different visual attributes, since *perception times per se* cannot be directly measured. What can be directly measured, however, is the *reaction time* to a visual stimulus. Different studies have used different methods to compare reaction times to color and motion stimuli, giving varying results: one study reports a quicker response to color than to motion (Barbur et al., 1998), whereas no difference was found in another (Nishida and Johnston, 2002). On top of that, there is the problem of whether one should expect reaction time data to reflect any underlying differences in perception time. It is not necessarily correct to use reaction time data to isolate the perceptual component of the delay, since these data are confounded with both the preparation and the execution of a motor response. For example, one could equate the second part of a theoretical *stimulation-perception-decision-reaction* model between color and motion reaction time data, in order to draw inferences regarding the first part. But it is far from clear whether different, functionally specialized, systems share common decision mechanisms or access the motor system in the same way and thus equating the *perception-decision-reaction* part is questionable. It is also possible that *stimulation-reaction* shortcuts might sometimes bypass the stage of conscious perception for a quicker response to, say, stimuli which are in motion. Thus, although the time necessary for conscious perception is usually part of the reaction time to a stimulus, a straightforward inference from the latter to the former is not always possible (see Arnold, 2010 for similar arguments). The suggestion that motor responses could be based on the first incoming spikes, whereas perception integrates over a longer time period (Eagleman, 2010) could be a possible explanation for the discrepancy observed between the timing of perception and action. Nevertheless, and despite the fact that negative results (i.e., *not* finding a difference) are of secondary importance in general, the failure of Nishida and Johnston (2002) to find any differences in the response times to *specific* colors and motion directions, remains an open question for the perceptual asynchrony theory.

¹It should be noted here that perceptual asynchrony occurs only when continuous changes are apparent as happening within clearly separate objects: perceptual misbinding was not produced by manipulations making the stimuli appear as (continuously present) transparent objects (Clifford et al., 2004; Moradi and Shimojo, 2004)

²In their original study, Moutoussis and Zeki (1997a) have used confidence ratings to protect their findings against any possible response bias explanation: participants were found to be most confident of their pairing response when color and motion were physically out of phase.

In addition to reaction time studies, the results on temporal order judgments (TOJ) between color and motion changes also vary³: some have found TOJs to be accurate (Nishida and Johnston, 2002; Bedell et al., 2003), whereas others have reported that color changes seem to precede synchronous motion onsets (Viviani and Aymoz, 2001; Aymoz and Viviani, 2004) or direction reversals (Adams and Mamassian, 2004). In general, the exact task performed by the subjects seems to be crucial: it has been shown that, using the exact same stimuli, TOJ tasks can yield no asynchrony when perceptual pairing judgments tasks do (Bedell et al., 2003; Clifford et al., 2003). Another issue is that of the rate of alternation: when participants were asked to judge which feature (color or motion) changed first, and the peak relative timing for synchronous judgment (TOJ choices equally split at 50% for each attribute) was taken as an indication of the perception time difference, the observed color-motion misbinding was diminished at slow alternations rates (Nishida and Johnston, 2002). But this result is perhaps not so surprising, since the nature of the task in the original experiment requires a moderately high alternation rate (1–2 Hz) for perceptual asynchrony to be revealed: only then does the perception time difference shift the temporal relation of the two percepts a significant proportion of the oscillation period, leading to a noticeable change in pairing. The phenomenon is thus diluted for very slow oscillations, but for moderate rates perception time difference is found to be independent from the rate of the oscillations (Moutoussis and Zeki, 1997a; Bedell et al., 2003; Holcombe and Cavanagh, 2008). If, on the other hand, the frequency of the oscillations is too high, perceptual pairing is an impossible task. This is the reason why, in a study using rapid alternation rates (between 3.6 and 5.3 Hz), delaying color changes was found to have no effect in color-motion pairing facilitation (Moradi and Shimojo, 2004). But if the rates used are within the range that makes the pairing task possible, delaying color with respect to motion facilitates perceptual pairing (Arnold, 2005).

In our original experiments (Moutoussis and Zeki, 1997a,b), both the color and the motion percept alternated between two values. Nevertheless, one could argue that, with respect to position, the motion change is “second-order” (a change in the way position changes over time – i.e., a change of a change) whereas the color change is “first-order” (just changing from one color to the other). It has been suggested that the observed misbinding is because the brain is slower in calculating a “second-order” change than it is in calculating a “first-order” change (Nishida and Johnston, 2002). Technically, two monitor-frames are necessary for a color change to take place, whereas a motion change needs three. This gives a ~14 ms time advantage to color, which is far less than the ~100 ms value observed experimentally. Furthermore, if memory is taken into account, the single next frame is enough to register a change for both color and motion. There is thus no big advantage for color in terms of the nature of the physical presentation, but perhaps brain mechanisms are internally biased (less sensitive?) against detecting a “second-order” change. Even so, it should be pointed

out here that motion changes are “second-order” with respect to position, not to motion (we have a first-order change in directional motion). It is questionable whether motion *perception* can be reduced to nothing more than perceiving position changes over time. There are instances when motion can be perceived without perceiving any particular object changing position, as in random dot stimuli (Newsome et al., 1989), or even without any object changing position at all, as in the MAE (Mather et al., 2008) or the Leviant illusion (Zeki et al., 1993). Stimulating area V5 can induce the perception of motion, again without any particular object being observed to change position (Salzman et al., 1990). Such studies suggest that motion perception is an autonomous perceptual entity, rather than the first derivative of position with respect to time (for a review see Nakayama, 1985). In a series of experiments manipulating the stimuli so as to make the position change a first-order change (here/there) and the color to gradually vary from red to green in a sine-wave manner, the sign of the perceptual misbinding was reversed (Nishida and Johnston, 2002). Although such a result at first seems to support the *first vs. second-order* hypothesis, the nature of this experiment is quite different from the original one: instead of reporting the perceptual pairing between two color and two motion percepts, numerous colors and no motion percept at all were involved, and participants had to pair the *position* of an object to the *direction of change* of its color. In our experiments, on the other hand, as far as motion perception is concerned, there is a bimodal perceptual switch between two different percepts, exactly as is the case with color. It should also be noted that, in the Nishida and Johnston study, when comparing color and position changes of the same order (either first or second), positions were found to be paired with colors which were presented at a slightly later time (Nishida and Johnston, 2002). This, together with reports of incorrect pairing between first-order (color and orientation) changes (Moutoussis and Zeki, 1997b; Clifford et al., 2003), as well as between second-order changes (Arnold and Clifford, 2002 – see next section) dilutes significantly the strength of the *order-of-change* account for perceptual misbinding.

It could be that the *perception of the time* at which a percept was perceived (*when* was that?) could be different from the real time at which *perception of the percept* took place (*what* is that?) If so, a misbinding could emerge as a result of the meta-analysis of salient temporal features, by a neural mechanism dedicated to code the timing of events, suggesting that the subjective time course of visual experience is the product of analysis beyond the temporal processing of the content of the events themselves (Dennett and Kinsbourne, 1992; Nishida and Johnston, 2002). It is not so clear whether the idea of perceptual asynchrony is totally abandoned in such a theory, i.e., whether color and motion take the same time to be perceived or not. The theory rather concentrates on the hypothetical existence of an independent system in the brain, responsible for the perception of the time of events, which is different from the mechanisms responsible for the perception of the events themselves. In such a scenario, the psychophysically observed misbinding (Moutoussis and Zeki, 1997a,b) is no longer considered to be the result of perceptual mechanisms *per se*, but an inaccurate judgment of the time of occurrence of perceptual events. It reflects the properties of a third mechanism, which uses temporal markers to reference the time a specific event occurs in

³ Rather than having to perceptually pair the perception of a particular color to that of a particular direction of motion, subjects in a TOJ task have to report whether a (usually) single change in color preceded a (usually) single change in motion or vice versa.

the world, rather than the time that the processing of the event is completed in the brain (Nishida and Johnston, 2002). An error-prone process of matching temporal markers of a different order (see above) could perhaps provide an alternative explanation to the perceptual misbinding observed. However, in addition to the ill-defined nature of temporal markers (see Arnold, 2010), one has to assume that, somewhere in the brain, a mechanism exists which is responsible and capable for timing perceptual events and providing the temporal order between them. Given functional specialization and no evidence for a terminal point of convergence in the brain (Shipp and Zeki, 1995), it would be a challenging task for this mechanism to have synchronous access to the output of several specialized processing-systems, in order to synchronize the perceived time of occurrence of percepts different in nature, and give an accurate picture of events in the real world.

Temporal markers are supposed to reference the time a specific event occurs in the world rather than the time the processing of this event completes in the brain. However, the idea of the perception of the time of a percept being different to the time that the actual percept is being perceived, seems quite awkward. It suggests a dissociation between the subjective time course of events, as it appears to the observer, and the times at which representations of those events are established in the observer's brain. Even more awkward seems the idea of the brain being able to know about the timing of things happening elsewhere (i.e., in the outside world), something necessary for a mechanism to be able to correctly synchronize different perceptual events in order to reflect physical reality. It is already difficult enough to imagine how such a mechanism could know the exact timing of different events *within* the brain. Even if such a mechanism exists, its function seems more appropriate for TOJ tasks, reporting the temporal order of events. But TOJ and perceptual pairing are two very different tasks, not least because in the former participants need to make a decision *after* the presentation of the stimuli, based on the memory of single, transient perceptual events (see Viviani and Aymoz, 2001 or Gauch and Kerzel, 2008 for examples). On the contrary, in perceptual-binding, decisions are not based on memory, since the stimulus is continuously present on the screen and the subject has to decide *online* which color is being perceived together with which direction of motion. It has been suggested that "postdiction"⁴ mechanisms could be involved in TOJs of single events, as for example in experiments investigating the flash-lag effect (Eagleman and Sejnowski, 2000). Therefore, using TOJ with respect to the instances at which color and motion changes occur, could potentially give misleading results with respect to the perception time of a particular visual attribute (see also the section on attention below). Finally, the independence of the apparent asynchronies on the oscillation rate (Moutoussis and Zeki, 1997a; Bedell et al., 2003) is problematic for a marker-mismatch account of the phenomenon (see Arnold, 2010 for a detailed argument), and it is far from clear why there should be a tendency to pair markers attached to first-order position transitions with markers attached to delayed

(rather than earlier) color changes. In conclusion, the temporal marker theory remains, at least to me, highly speculative as well as problematic⁵.

Based on a possible "postdiction" character of visual perception in general, yet another alternative explanation of perceptual misbinding has been suggested (Moradi and Shimojo, 2004). The basic idea is that a postdictive analysis determines the perceptual properties of new surfaces, by waiting for ~80 ms in order to integrate perceptual events taking place during this period and then allocating the result of this integration to its beginning. This time period is initiated by some sort of transient, like a direction reversal, which erases all previous information accumulated. The timing allocated by the brain to the result of perceptual integration is thus the commencement rather than the end of the integration period, something that could hypothetically compensate for the variability of neural transmissions (see Dennett and Kinsbourne, 1992). In this way, information from after an event is taken into account before committing to a visual interpretation (Eagleman and Sejnowski, 2000; Moradi and Shimojo, 2004). In an experiment using random dot stimuli with red and green dots, a particular group of dots suddenly turned gray and was set into motion, at the end of which these dots either returned to their original color or reversed color, and participants were found to report the color of the moving dots to be that *after* the motion was over (Moradi and Shimojo, 2004). This result was taken as an indication that the brain integrates perceptual events over a period of time, pairing together motion with a color that occurs at a later time, in a "postdiction" manner⁶. In the scenario in which a postdictive account of visual perception is combined together with the assumption that color is not treated evenly during the integration period (last part given more weight), perceptual asynchrony could perhaps find an alternative explanation (Moradi and Shimojo, 2004). However, an easy way to distinguish between this and the original brain-time explanation, is the fact that they predict different optimal conditions for making temporal judgments (see Arnold, 2005): postdiction gives a satisfactory explanation for the results observed at a phase difference of 90°, but cannot explain the results observed when the color and motion oscillations are in complete synchrony (i.e., at a phase difference of 0°). More specifically, if the appearance of a new direction of motion "resets" the system and makes the pairing between motion and color stronger during the later stage of this motion, then this could potentially explain why this motion is not equally paired with the two colors but more strongly with the second one at a phase difference of 90°. The same explanation would also predict, however, a perfect binding between motion and its corresponding color at a phase difference of 0°, something which is contrary to what has been observed (see text footnote 2). Perceptual asynchrony, on the other hand, not only explains equally well the result at a phase difference of 90°, but also predicts the misbinding observed at a phase difference of 0°. In a series of experiments in which the opposite direction of motion was replaced by a different transient (total

⁴This term is given to the idea that perception, rather than being online, accumulates evidence over small time intervals before committing to a given perceptual experience.

⁵For a recent defense of this theory, see Nishida and Johnston (2010)

⁶Note that these results can be equally well explained by perceptual asynchrony, a quicker perception time making color to be perceived together with motion that took place earlier in real time.

absence of the moving stimulus), color-motion misbinding was minimized and motion–motion misbinding was induced (Arnold, 2005). As proposed previously (Arnold and Clifford, 2002), the absence of the opponent direction of motion seems to result in faster processing within the motion system, reducing its lag with respect to the color system and introducing a perceptual advantage compared to a situation in which the opponent direction is present. Postdiction, on the other hand, would predict that any change in the motion status resets the system, irrespective of the particular characteristics of this transient.

THE EFFECTS OF PROCESSING TIME MANIPULATIONS

If perceptual asynchrony is due to a difference between the processing times of different functionally specialized systems, changes in the speed of processing should lead to changes in the magnitude of asynchrony. Along this line of thought, the role of the well known physiological effect of motion opponency has been examined (Arnold and Clifford, 2002). In our original setup, the two motion directions used (up and down) activate neuronal populations which inhibit each other maximally (Barlow and Levick, 1965; Snowden et al., 1991), possibly leading to a significant delay in processing time within the motion system. Indeed, Arnold and Clifford (2002) have found that the magnitude of the perception time difference between color and motion varies with respect to the angular difference between the two directions of motion which are present in the stimulus. The maximum difference was observed when the two directions were opposite, i.e., when the inhibition between the two neuronal populations responsible for the processing of the motion signal was at its maximum. However, while reduced, a robust perceptual asynchrony was still evident in the presence of a relatively slight angular difference in motion direction, suggesting that direction-selective inhibition is not the sole cause of perceptual asynchrony. These results pose a problem for the Nishida and Johnston (2002) temporal marker account, since it is not clear why the position of a temporal marker signaling a given direction of motion should depend on the magnitude of the preceding direction change. Furthermore, the fact that it takes different amounts of time to perceive two different motion pairs, which are nevertheless both second-order changes (Arnold and Clifford, 2002), speaks against the *first-* vs. *second-order* explanation of asynchrony (Nishida and Johnston, 2002). This finding also suggests that visual experience does not require the mediation of interpretive processes (Dennett and Kinsbourne, 1992; Eagleman and Sejnowski, 2000) or the aim of any specialized temporal coding system (Nishida and Johnston, 2002). Similar results, showing a dependence of perception time differences on the relative directions of motion, have been also found using random dot stimuli (Bedell et al., 2003 – but see Amano et al., 2007 for objections and an alternative view on the directional-effect).

There is further evidence for a direct relationship between the time courses of sensory processing in the brain and the timing of perceptual events, coming from experiments that show a dependence of the magnitude of perceptual asynchrony on factors such as the salience of the stimuli (Adams and Mamassian, 2004), their luminance (Bedell et al., 2006), as well as their contrast and speed (Lankheet and van de Grind, 2010). Clifford et al. (2004) have manipulated depth, speed, and transparency to show that

the phenomenology of binding parallels the physiological properties of area V5 (as is the case with direction-specific inhibition) and is thus a direct reflection of the time course of the underlying neural processing. It therefore seems that the magnitude of perceptual asynchrony varies in a manner that is broadly consistent with the known dynamics of sensory processing (see Arnold, 2010 for similar arguments). Within this neurobiological frame, a model explaining perceptual asynchrony with respect to feedback connections to V1 has been also proposed (Clifford, 2010), since the latter seems to be involved in both perceptual-binding (Hochstein and Ahissar, 2002; Shipp et al., 2009) and visual consciousness (Lamme and Roelfsema, 2000; Pascual-Leone and Walsh, 2001).

THE POSSIBLE INVOLVEMENT OF ATTENTION

Attention is joined at the hip with visual perception and consciousness, the link being so strong that it is sometimes difficult to distinguish between them (see Lamme, 2004). Several lines of evidence suggest that attention could be involved in the integration of visual information (Treisman and Gelade, 1980; Reynolds and Desimone, 1999). More specifically, it has been suggested that attention plays a crucial role in feature pairing, by associating features at a particular spatial location (Treisman and Gelade, 1980) and constructing neurons with dual selectivity to color and motion, as revealed by both anatomical (Shipp et al., 2009) and neurophysiological (Croner and Albright, 1999) findings. Psychophysically, rapid alternations of color and motion (above 5 Hz) prevent their correct pairing, despite the fact that both are still individually identifiable (Moradi and Shimojo, 2004; Arnold, 2005). Such a low temporal resolution nicely fits with the idea that feature binding might be under the control of a slow, high-level process like attention (Duncan et al., 1994).

Given the above, it is possible that perceptual asynchrony could be influenced by attention, or even totally explained in terms of attentional mechanisms. If this is the case, manipulating attention should modulate the magnitude, and perhaps the sign, of perceptual asynchrony. Experiments show that, although attended changes appear to precede unattended ones in temporal judgments (Sternberg and Knoll, 1973; Reeves and Sperling, 1986), the effects of endogenous feature attention on perceptual asynchrony (as measured via errors in perceptual pairing) are not robust. In a study in which subjects were instructed to attend to a particular color and pair it with one of two possible orientations in half of the trials, while in the other half of the trials attend to a particular orientation and pair it with one of two possible colors (Clifford et al., 2003), the perception time advantage of color over orientation was decreased in 2/3 subjects when attending to orientation (compared to when attending to color). Such a result suggests that attention might be able to modulate the magnitude of perceptual asynchrony, perhaps by speeding up the processing of the attended attribute (Sternberg and Knoll, 1973; Posner et al., 1980; Stelmach and Herdman, 1991; Carrasco and McElree, 2001). Unfortunately, the small sample used in this study does not allow for any strong conclusions to be drawn. In a similar study, in which half the subjects were instructed to attend to color and the other half to motion, no difference in perceptual pairing was found between the two conditions (Arnold, 2005). However, using exactly the same

methodology, an attentional effect has been reported in a meeting abstract some years ago (Enns and Oriet, 2004): asynchrony was found to reverse when subjects in one group were instructed to attend to color and then report the corresponding motion, compared to when subjects in a different group were instructed to attend to motion and report the corresponding color⁷. A weakness of this study is that only four phase differences between the color and the motion oscillations were used: 100% correlation (i.e., 0° and 180° phase differences) and 50% correlation (90° and 270° phase differences). The latter are quite difficult conditions (since color switches in the middle of the motion and vice versa) and a possible strategy to report the last segment of the non-attended stimulus could lead to the result reported. In a similar, recent study, in which many more phase differences were used and participants had to pair the color and the motion of peripherally presented random dot fields, attending to color vs. attending to motion did not alter perceptual misbinding in any significant way (Holcombe and Cavanagh, 2008). It therefore seems that, despite a few weak reports for the contrary, voluntary switching between feature dimensions cannot account for the better part of perceptual asynchrony.

Despite the fact that the effects of voluntary, endogenous attention are negligible, the possibility that involuntary, exogenous attention could play a role still remains. A straightforward way to modulate the ability of a stimulus to draw attention is to increase its saliency. Using a TOJ task, Adams and Mamassian (2004) showed that stimulus saliency can indeed influence perceptual asynchrony magnitude, with more salient changes being perceived faster. In this study, saliency was measured in terms of performance in a previous change-detection task. Interestingly though, when the contrasted stimulus-changes were matched in terms of detection ease, color changes were still perceived as occurring before physically synchronous changes in direction. Thus, although exogenous attention seems able to modulate the magnitude of perceptual asynchrony, it cannot provide an adequate and complete explanation for it (Adams and Mamassian, 2004).

In a different study, strong external transients (known to be very effective in engaging attention – see Posner, 1980) were used, in order to modulate exogenous spatiotemporal attention (Holcombe and Cavanagh, 2008). It seems odd why spatial attention alone would give an advantage to any particular feature of the ones present in the particular spatial location, especially since it has been previously reported to be ineffective in changing perceptual asynchrony (Paul and Schyns, 2003). The temporal component seems to be more important here: perhaps a strong transient signal sent down both the color and motion pathways could somehow serve as a cue for synchronization, eliminating the asynchrony observed otherwise (Holcombe and Cavanagh, 2008). Generalizing this finding to the perceptual asynchrony reported by others (e.g., Moutoussis and Zeki, 1997a,b), Holcombe and Cavanagh argue that the latter could be due to unbalanced effects of intrinsic transients in the stimuli. Although they do not make absolutely clear what they mean by this, my personal understanding is that

color changes could perhaps be more salient than motion ones, attracting attention first and thus leading to a more rapid processing of this attribute. Alternatively, they could simply mean that color changes are being processed more quickly than motion changes. Both of these explanations are not that far from the idea that, for one reason or the other, color is being processed faster than motion (Moutoussis and Zeki, 1997a,b). It is also not clear whether these authors discard functional specialization as the reason behind any differences in processing time of the two attributes, and their main point that attention operates on independent processing streams does not seem to be at odds with the functional specialization argument.

A distinction between the perception of the transients and the perception of the attributes themselves should be made here: in variations of our original experiment, in which subjects were asked to judge whether a color or a motion direction change occurred first, no perceptual asynchrony was observed (Nishida and Johnston, 2002; Bedell et al., 2003). The same is true for color and orientation changes: despite color showing a perception time advantage in the perceptual pairing task, no time difference was found between the perception of color changes and that of the orientation changes (Clifford et al., 2003). If anything, such findings suggest that both transients are made available to perception equally fast, and it is the actual calculation of what follows the change which takes longer in the case of motion. Also, if perceptual asynchrony results because of attention giving a start-advantage to color, do these authors implicitly suppose that the processing of color and motion take equal time? Given the difference between both the nature of these attributes and the properties, topographical distribution and organization of the brain mechanisms responsible for their processing, it is rather unlikely. A compromise would be to assume that there is a perception time difference due to different processing times, on top of which a modulatory role of (exogenous) attention is possible.

In addition to the theoretical issues discussed above, there are also some methodological ones in the Holcombe and Cavanagh (2008) study. In their experimental setup, random dot fields were arranged in a circular array around fixation. In each field the dots were oscillating between red and green, and between moving toward and away the fixation point, at various phase differences. While maintaining fixation, the attention of the subjects was automatically captured by the appearance of a luminance ring surrounding one of the fields. The task was to report the color and direction of motion of the dots inside this field, *during the presence of the ring*. What was found is that asynchrony was lost, and that report probability was independent for each feature and determined by how synchronized this feature was with the cueing ring. The authors concluded that the exogenous transient is much stronger than both the color and the motion transients and is thus the determining factor of what will be perceived and when. However, the cueing ring was presented very briefly (for half a period) and participants reported on the color and motion present during this short interval. Given the simultaneous presence of several stimuli, each one could be individually perceived only via (voluntary or involuntary) attentional selection. Stimuli were thus virtually presented only for a brief interval, during which a maximum of one change for each attribute took place – in

⁷ It should be noted here that this abstract was never followed up by a proper journal article. In a recent publication by Enns et al. (2010), it is actually acknowledged that perceptual asynchrony is not simply the result of a “sluggishness” in attentional shifts from one attribute to the other.

most cases one of the colors or motion directions did not appear at all, leaving one of the attributes without a transient. In order to misbind something that is presented now to something that was presented earlier, you need something that was presented earlier! It is therefore not surprising that no misbinding is observed in cases where there are not enough stimuli present for misbinding to occur. It is possible that subjects perceived (not equally fast) the two attributes which were mostly available during this brief period, and reported them from memory (see below) when asked afterward, without any involvement of perceptual-binding whatsoever.

Another objection is that the task was *not* an *online perceptual pairing* between color and motion, but a *recall from memory* of the *presence* of color and of motion during this very brief period⁸. Experiments reporting perceptual asynchrony give participants ample of time to observe the continuously alternating stimuli, and are asked to report on the perceptual co-existence of color and motion *at the time they are experiencing it*, since reporting *after* the completion of a perceptual event is vulnerable to post-perceptual biases. It is very difficult to perceptually pair attributes at single brief presentations, and there is only one such reported case (Linares and López-Moliner, 2006) but with presentations which are still quite longer than the ones used by Holcombe and Cavanagh. What can be accurately reported in such brief presentations is the order of the *single changes* in motion direction and color (Nishida and Johnston, 2002; Bedell et al., 2003), a task which is very different since TOJs on attribute-changes can be accurate even when continuous presentations lead to false perceptual pairings (Bedell et al., 2003; Clifford et al., 2003). Not surprisingly, when participants in the Holcombe and Cavanagh (2008) study were allowed to attend to the stimulus throughout the whole presentation, a perceptual asynchrony between color and motion was reported. In another variation of their experiment, asynchrony was also eliminated when the flash was continuously presented but stepping from one dot field to the other. However, the part of the oscillation “illuminated” each time by the flash was always the same, and was also presented at different spatial locations, making this setup perceptually equivalent to (several repetitions of) the single-flash condition⁹. These methodological issues, together with the fact that the main finding of Holcombe and Cavanagh (2008) is based on a *negative result*, from only 3 subjects that did not show much consistency between them (see Figure A1 in their manuscript), unfortunately weaken the conclusive strength of the potentially interesting effects reported.

PHILOSOPHICAL ISSUES REGARDING PERCEPTUAL ASYNCHRONY

The theoretical context in which these psychophysical results are put is based on two, perhaps simplified, assumptions. Firstly, that

there is a given (objective) time¹⁰ at which the processing of visual information leads to the creation of a conscious visual percept. Secondly, the time at which a subject is having a perceptual experience, is also the time that the experience is perceived to happen, i.e., each time I have a percept, I also perceive that it is happening *now*. Both these assumptions have been questioned (Dennett and Kinsbourne, 1992; Johnston and Nishida, 2001), but the alternative “solutions” offered are even more vague and unsatisfactory than the problems they are trying to solve¹¹. Given these two assumptions, the fact that we perceive different visual attributes at different times, raises some interesting theoretical implications regarding visual consciousness and consciousness in general. Since the experiments were initially conceived as a consequence of functional specialization in the visual brain it was natural, given the results, to suppose that perceptual asynchrony reflects a difference in processing time between the different, functionally specialized, systems. Furthermore, the fact that these different visual attributes are perceived independently and in their own times, supports the possibility for these systems to be not only processing but also perceptual ones. Functional specialization is in this way extended to the world of phenomenology and qualia, giving rise to the idea of multiple visual consciousnesses coexisting in vision (see Zeki and Bartels, 1999 for a theoretical expansion of this idea). However, the introspective unity of consciousness begs the question of how do these visual percepts, which arise at topographically different parts of the brain, come together as a single experience. The problem goes beyond vision, as it also applies to the way in which different sensory modalities, as well as mental events in general, are combined into a single, unified consciousness. An obvious solution would be to assume the existence of some “executive” brain area to which all other areas report, a central stage at the end of a hierarchical chain of “importance.” Such a solution arises from the old intuitive assumption of a “spirit,” “ghost in the machine,” “single-self,” etc., existing above and supervising over the rest of the brain, spending its time by comfortably inspecting mental events projected for its delight on the stage of a “Cartesian Theater.” Against such an intuition, a series of interesting philosophical arguments fighting this essentially dualistic approach, as well as fighting against the illusion of the existence of a single “self,” have been made by Dennett (1991) and Dennett and Kinsbourne (1992). Additionally, the neuroanatomical reality does not support the presence of such a “brain within the brain,” where all the parallel distributed processing eventually comes together. There are, of course, examples of convergence and cross-talking in the brain, an example related to this discussion being the existence of cortical and subcortical regions that receive multisensory input. What is missing is an area where everything comes together – both function and thus information seem to be dispersed throughout the brain¹². Thus there seems to be no terminal station in the brain,

⁸Note that, since there was enough presentation time for a single color-motion “pair” only, participants chose between four possible response buttons (rather than between two, as in most previous perceptual pairing experiments).

⁹The authors claim that an apparent asynchrony was also observed when color and motion sequences were presented only during a ring flash period (but without the ring). This would be an important finding but, unfortunately, no data is presented to support it.

¹⁰This time is probably not dimensionless – it should be considered as a range rather than as a time-point.

¹¹The basic idea is that perhaps ‘the representation of sequence in the stream of consciousness is the product of the brain’s interpretive processes, not a direct reflection of the sequence of events making up these processes’ (Dennett and Kinsbourne, 1992).

¹²Even if such an area existed, an interesting philosophical game is the idea that, if different parts of it carried different bits of information, there would have to be

the architecture of which is characterized by a segregated organization principle, containing several functionally specialized modules that remain more or less separate (Zeki, 1974, 1978; Fodor, 1983). The perceptual asynchrony results support such a view and extend it to the specific domain of visual consciousness.

The question, however, remains: in order to perform the task, subjects need to combine together their color and motion percepts. Doesn't this mean that the corresponding two pieces of neuronal information need to also *physically* come together at a common brain area? If not, does this imply that we are looking for a solution outside the neural substrate (see Johnston and Nishida, 2001)? On the one hand, the way in which localized activation contributes to and affects the prevailing brain state and thus consciousness, remains unknown. On the other hand, the prevailing brain state is nothing more than the collection of these activations, what is happening *now* at various parts of my brain. We have previously proposed a bold, perhaps extreme solution (Moutoussis and Zeki, 2004), suggesting that there is no binding at all in consciousness but rather that different experiences are phenomenally "bound" together in virtue of an external factor, namely the time at which they occur. In this way, brain-time is still important for the when of a percept, without the necessity of a single brain structure that is critical is critical for perceptual-binding. It is perhaps an illusion that I am the same person perceiving both color and motion, and it is perhaps even more wrong to make a distinction between the "person" and the "percept." If we instead assume that a "person" is nothing but a temporary composition of different mental events coexisting at a given point in time, would the problem be solved? One would still have to explain the way mental events are grouped and experienced together – why isn't the color I perceive now bound to the motion that you perceive now? It probably has something to do with the fact that some groups of mental events (*my* mental events) are sharing a common brain (*my* brain), but as long as the relationship between the latter and the so-called "mind" remains a mystery, questions like this will also remain unresolved. However, it is important to point out that these problems do not

arise because of assuming the presence of functional segregation in visual consciousness. Alternative views, suggesting that everything is done everywhere (Schiller, 1997), or that special areas supervise mental events and assign temporal markers to them (Nishida and Johnston, 2002), are equally subject to the problem of implementation with respect to this marvelous physical entity living inside our head.

CONCLUSION

There seems to be good evidence for a relationship between the time courses of sensory processing in the brain and the perceived timing of perceptual events. Most accounts of the perceptual misbinding between color and motion accept this idea, the difference between them being the question of what it is that causes these processing time differences to occur. Even the temporal marker-matching theory, which began as a totally different approach, accepts in its latest, modified version (Amano et al., 2007) the existence of processing time differences at the heart of the phenomenon, and thus transforms the temporal marker account of perceptual asynchrony into yet another form of "brain-time" (see Arnold, 2010). With respect to attention in specific, no strong conclusion regarding its significance in the misbinding observed between different visual attributes can be drawn. Most studies have found weak (if any) effects, and the ones showing an effect are confounded by methodological issues. Furthermore, the finding that implicit processing manifests a similar asynchrony to conscious report (Arnold et al., 2001), argues against an explanation of perceptual asynchrony based entirely on attentional mechanisms. Thus, attention does not seem to be responsible for the best part of perceptual asynchrony in vision. The idea that the latter emerges as a direct consequence of functional specialization in the visual system, comes out as the most attractive explanation of the asynchrony phenomenon. Attention might be able to slightly alter the magnitude of the effect in favor of one or another attribute, and the differentiation between perceptual asynchrony being caused by differences in processing time vs. attention seems arbitrary, as the latter could very well influence the former. A model in which several factors (attention included) could influence the time necessary for neuronal processing, seems to be the most appropriate explanation for the perceptual asynchrony observed. However, the question of how different visual attributes, which are processed independently, are perceptually bound together to form a coherent conscious percept, remains open.

yet another round of convergence, everything coming together to an even smaller part of this area and so on. When is one satisfied that all has come together? Is a new grandmother-cell type solution, where all information available in the brain would converge to a single "hyperneuron," what we really want here? Therefore, it seems that a convergence-type solution to the binding problem creates nothing more than vicious cycles, and should perhaps be abandoned as a theoretical approach altogether.

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Color improves speed of processing but not perception in a motion illusion

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When two superimposed surfaces of dots move in different directions, the perceived directions are shifted away from each other. This perceptual illusion has been termed direction repulsion and is thought to be due to mutual inhibition between the representations of the two directions. It has further been shown that a speed difference between the two surfaces attenuates direction repulsion. As speed and direction are both necessary components of representing motion, the reduction in direction repulsion can be attributed to the additional motion information strengthening the representations of the two directions and thus reducing the mutual inhibition. We tested whether bottom-up attention and top-down task demands, in the form of color differences between the two surfaces, would also enhance motion processing, reducing direction repulsion. We found that the addition of color differences did not improve direction discrimination and reduce direction repulsion. However, we did find that adding a color difference improved performance on the task. We hypothesized that the performance differences were due to the limited presentation time of the stimuli. We tested this in a follow-up experiment where we varied the time of presentation to determine the duration needed to successfully perform the task with and without the color difference. As we expected, color segmentation reduced the amount of time needed to process and encode both directions of motion. Thus we find a dissociation between the effects of attention on the speed of processing and conscious perception of direction. We propose four potential mechanisms wherein color speeds figure-ground segmentation of an object, attentional switching between objects, direction discrimination and/or the accumulation of motion information for decision-making, without affecting conscious perception of the direction. Potential neural bases are also explored.

Keywords: attention, consciousness, awareness, color, motion, vision, illusion, perception

INTRODUCTION

In the study of attention and consciousness it is important to operationally define the terms as there are multiple definitions in the literature. We define attention as the preferential processing of a subset of visual information selected either by bottom-up (stimulus-driven) features or through goal-driven top-down processes. Top-down or goal-driven attention is dependent on task demands which require attending to a location, feature, or object, and is dependent on fronto-parietal networks (Corbetta et al., 1993; Nobre et al., 1997; Corbetta, 1998; Shulman et al., 1999; Yantis and Serences, 2003; Serences et al., 2004; Kelley et al., 2008; Ozaki, 2011) that modulate visual processing areas. Attentional selection by bottom-up or stimulus-driven factors has also been called pre-attentive processing or early (versus late) selection. All three nomenclatures describe feature differences that are rapidly and easily processed, such as differences in contrast, hue, orientation, form, or motion. Bottom-up attention is thought to give rise to a map of attentional priority for each object in the field of view, either as a master salience map (Treisman and Gelade, 1980; Koch and Ullman, 1985; Neibur and Koch, 1996; Itti and

Koch, 2001; Thompson and Bichot, 2005) or at individual stages of visual processing (e.g., Selective Tuning Model of attention, Tsotsos et al., 1995). Bottom-up and top-down mechanisms work together in driving attentional selection. The effects of attention are often measured as either speeded processing which produces faster reaction times in detection tasks (e.g., Posner, 1980) or as improved visual sensitivity producing lower perceptual thresholds (Mueller and Humphreys, 1991), smaller just-noticeable differences in feature processing (Nakayama and Mackeben, 1989), or better signal-to-noise discrimination (Doshier and Lu, 2000).

Consciousness is the internal awareness, from near-threshold awareness (Marks and Stevens, 1968; Azzopardi and Cowey, 1997; Kunimoto et al., 2001) to full conscious experience, of visual input, which is different than unconscious visual processing (as in blindsight, Weiskrantz, 1986; Azzopardi and Cowey, 1997, 1998; Stoerig and Cowey, 1997). This definition is supported by studies that quantify the strength of the conscious experience through confidence ratings (Kolb and Braun, 1995; Kunimoto et al., 2001; Boyer et al., 2005; Wilimzig et al., 2008). Conscious awareness occurs when a stimulus reaches a threshold and can then be focused upon

or queried. At that stage, the features of the object can be processed and bound into the object. It has been shown that different features take differing amounts of time to be processed and reach awareness: orientation is processed faster than color (e.g., Bodelon et al., 2007) and color is processed faster than motion (Moutoussis and Zeki, 1997). As each feature is processed, that feature of the object reaches consciousness. Therefore being conscious of an object is not a unitary experience: you can be conscious of different features of the same object at different times (Dennett and Kinsbourne, 1992; Noe and O'Regan, 2002). Conscious awareness of an object does not wait for the slowest feature of that object to be processed (Bodelon et al., 2007). Thus there are two parts of consciousness that can be queried: awareness of the stimulus existing and the conscious perception of the feature. Much of our conscious perception is driven by visual processing as evidenced in a myriad of visual illusions such as the waterfall illusion (Anstis et al., 1998), moon illusion (Kaufman and Rock, 1962), McCollough effect (McCollough, 1965), Land effect (Land and McCann, 1971), and Titchener circles (Pavani et al., 1999). These visual elements not only reach conscious awareness, but are also consciously perceived as being different than the veridical visual input. In multi-object tracking (MOT), target objects can be tracked as they move amongst distractors but the features and identity of the objects are not well processed (Scholl and Pylyshyn, 1999; Bahrami, 2003; Pylyshyn, 2004). Thus, conscious awareness of an object and perception of its features can be dissociated from each other.

We can relate consciousness to the attentional literature: a simple detection task queries awareness whereas a discrimination task queries perception. A number of paradigms including attentional blink (Broadbent and Broadbent, 1987; Raymond et al., 1992), change blindness (Rensink et al., 1997), inattention blindness (Rock et al., 1992), load-induced blindness (Lavie, 1995), and visual neglect (Driver and Mattingley, 1998) have shown an apparent failure of conscious awareness in the absence of attention (for review see van Boxtel et al., 2010a). Attention also affects objects that easily reach awareness: attentional effects on detection tasks are often measured by speed of response, i.e., reaction time (e.g., spatial cueing paradigm: Posner, 1980). Other studies have suggested that attention does not affect conscious awareness directly, but instead affects the sensitivity of the visual system. The presence of spatial attention improves contrast sensitivity (Lee et al., 1999a; Carrasco et al., 2000; Reynolds et al., 2000; Di Russo et al., 2001; Moore and Fallah, 2001, 2003, 2004). The absence of attention results in a decrease in discrimination of luminance and color contrasts, orientation, and spatial frequency (Lee et al., 1999b; Morrone et al., 2002, 2004). Furthermore, spatial attention and increased contrast have similar effects on neuronal firing (Mangun et al., 1998; Boynton et al., 1999; Reynolds and Desimone, 2003). However, it should be noted that the effects of attention on visual sensitivity and neuronal responses only occur when there are multiple stimuli to be simultaneously processed (Spitzer et al., 1988; Desimone and Duncan, 1995; McAdams and Maunsell, 2000; Martinez-Trujillo and Treue, 2004; Reynolds and Fallah, 2004; Fallah et al., 2007; Sundberg et al., 2009) and attention has little effect on single stimuli (Luck et al., 1997; Moore and Fallah, 2004; Tsuchiya and Braun, 2007). While these studies suggest that attention and

consciousness can be dissociated, it is still in contention which attentional mechanisms give rise to awareness and which affect perception.

Perceptual illusions have an advantage in the study of consciousness in that the conscious percept is dissociated from the physical stimulus and is instead created by neural processing (de Gardelle et al., 2009, 2010). Instead of using *post hoc* confidence ratings, the strength of the illusion can be used to measure consciousness. For example, prior research has used the strength of the afterimages (Suzuki and Grabowecky, 2003; Hofstoetter et al., 2004; van Boxtel et al., 2010b) to study the relationship between attention and consciousness. Similarly, that relationship is also studied with motion illusions (motion aftereffect: van de Grind et al., 2001; Castelo-Branco et al., 2009; Kaunitz et al., 2011; Murd and Bachmann, 2011; motion-induced mislocalization: Tse et al., 2011). We used a different perceptual motion illusion, direction repulsion (Marshak and Sekuler, 1979), to investigate the relationship between attention and consciousness. In this illusion, observers perceive the directions of motion of two superimposed surfaces as being repulsed away from each other. The conscious experience of this event is a misrepresentation of the actual motion directions, and occurs with superimposed random dot kinetograms (Marshak and Sekuler, 1979; Mather and Moulden, 1980; Hiris and Blake, 1996; Braddick et al., 2002; Curran and Benton, 2003) or superimposed gratings (Kim and Wilson, 1996). The illusion is strong, producing a percept that is repulsed up to 20° away from the real direction of each surface (Marshak and Sekuler, 1979; Braddick et al., 2002). While the direction of a sole surface is accurately perceived, the superimposition of two surfaces is thought to produce a competition between the representations of the two directions, a process termed mutual inhibition which results in repulsion (Marshak and Sekuler, 1979; Mather and Moulden, 1980). As stated previously, the effects of attention on visual sensitivity are generally seen with multiple stimuli as single stimuli are processed with full resources. Similarly, the competition between the two surfaces' directions interferes with their processing (Braddick et al., 2002) producing the repulsion. In the standard direction repulsion illusion, all features of the surfaces are identical except for the direction. So the ability to select one of the surfaces is based solely on the direction information which is what produces the repulsion. Additional feature differences between the surfaces would provide other handles by which to select a surface. So attentional mechanisms should reduce the interference between the two directions and attenuate the repulsion, resulting in a more veridical percept. A reduction in repulsion does in fact occur due to bottom-up saliency produced by differences in speed (Marshak and Sekuler, 1979; Curran and Benton, 2003) or spatial frequency (Kim and Wilson, 1996). When the surfaces are distinguished by speed or spatial frequency differences, selection can work through those features to reduce the illusion. However, a real depth difference produced by stereoscopic viewing does not attenuate direction repulsion (Hiris and Blake, 1996). When the two surfaces are in the same depth plane, they are already perceived to be in different apparent depth planes (Hiris and Blake, 1996). Therefore, the addition of stereoscopic depth does not add additional features to select by.

Speed and spatial frequency, as well as direction and depth, are all components of motion processing in the dorsal stream (Maunsell and Van Essen, 1983a,b; Albright, 1984; Mikami et al., 1986a,b; Van Essen and Gallant, 1994; Bradley and Andersen, 1998; DeAngelis and Newsome, 1999). Thus this bottom-up attentional effect could be limited to concurrently processed motion features processed by local circuitry within motion areas. Since reporting a second feature on the same object has been shown to not require additional resources (Duncan, 1984), we asked whether the addition of a motion-irrelevant feature processed in the ventral stream, such as color, could also attenuate direction repulsion. A salient color difference allows for selection of the objects, not just the concurrently processed motion information. Thus, we tested whether bottom-up attention (in the form of color segmentation) reduces direction repulsion in local motion circuits or at the level of binding color to motion. In the unicolor condition, participants reported the two directions of motion (similar to the procedure in Braddick et al., 2002, Experiment 2). In the color-segmented condition, participants reported the combination of color and direction, thus also activating top-down mechanisms involved in selecting objects by color. We tested whether bottom-up segmentation and top-down task demands involving one feature of an object would affect the conscious perception of other features of the object.

Both the unicolor and color-segmented conditions required top-down attention to the direction of the objects. We activated bottom-up attentional mechanisms by the use of color segmentation cues and also added the top-down attentional demand of linking each direction to the color of the surface. Note that bottom-up attention is not as often studied with regard to consciousness as it requires comparison between conditions that have different physical stimulus properties, whereas top-down attention can be allocated differently to the same visual scene, either as spatial (Jonides, 1981; Egeth and Yantis, 1997; Driver, 2001; Rodriguez-Sanchez et al., 2007; Tsotsos, 2011), feature-based (Treue and Martinez-Trujillo, 1999; Saenz et al., 2002; Tsotsos, 2011), or object-based attention (Valdes-Sosa et al., 1998, 2000; O'Craven et al., 1999; Fallah et al., 2007). Bottom-up attention is therefore expected to be linked with conscious perception, which is likely why the addition of speed or spatial frequency differences attenuate direction repulsion (Marshak and Sekuler, 1979; Kim and Wilson, 1996; Curran and Benton, 2003). Furthermore the ventral stream which processes color has the function of processing vision for perception, i.e., consciousness (Goodale and Milner, 1992; Milner and Goodale, 1993). For these reasons, we expected that the addition of color segmentation cues would also attenuate direction repulsion. Surprisingly, we found that the addition of color differences did not affect direction repulsion. While not affecting the conscious perception of surface direction, this attentional cueing did in fact have an effect on visual processing: color decreased the time needed to process both directions of motion. While speeded reaction time is a well-studied effect of visual attention (Posner, 1980; Jonides, 1981; Driver, 2001, for review see Egeth and Yantis, 1997), here we have shown that speeded visual processing can be dissociated from the perceptual outcome of that processing. Finally, we relate these findings to possible underlying mechanisms and attentional networks.

MATERIALS AND METHODS

PARTICIPANTS

In Experiment 1, six participants (ages 21–47, two female) completed the unicolor: white paradigm, six participants (age 18–31, one female) completed the unicolor: red or green paradigm, and six participants (ages 20–26, two female) completed the color-segmented paradigm. In Experiment 2, an additional 24 naïve individuals participated: 12 in the unicolor paradigm (ages 18–27, three female) and 12 in the color-segmented paradigm (ages 19–26, 10 female). All participants had normal or corrected-to-normal visual acuity, and none tested positive for color blindness using Ishihara plates. The research was approved by York University's Human Research Participation Committee. Informed consent was obtained from all participants.

PROCEDURE

Participants sat in a darkened, quiet room, 57 cm away from a computer monitor (21" ViewSonic, 1280 × 1024 resolution, 60 Hz) with their head position stabilized by a headrest (Headspot, UHCotech). They wore a head-mounted, infrared eye tracker (Eyelink II, SR Research Ltd., 500 Hz) monitoring right eye position. Stimuli were created using Matlab (The Mathworks Corp.). Experimental control was maintained by Presentation (Neurobehavioral Systems). Data was analyzed using Matlab and SPSS (SPSS Inc.).

Participants fixated a white cross centered on a black screen (see **Figure 1**). After 200 ms, a circular aperture appeared in the lower right quadrant. The aperture consisted of two superimposed, 100% coherent random dot kinetograms (RDks: dot size = 0.04°, aperture size = 5°, dot density = 1.54 dots/degree², velocity = 3°/s) moving in two different directions. We tested all combinations of one direction drawn from the vertical axis ($\pm 2^\circ$, 6° , and 10° from either up or down) and the other from the horizontal axis ($\pm 2^\circ$, 6° , and 10° from either left or right). While all directions appeared with equal frequency, this created differences between the two directions that ranged from 70° to 110° . If fixation was broken the trial was aborted and randomly reinserted into the remaining trials. After a period of time (Experiment 1: 1000 ms, Experiment 2: variable, see below), the aperture was replaced with a circular outline (response circle) on which the participants indicated the directions of motion of each surface by mouse clicks. In the unicolor: white paradigm, both surfaces were white (24.4 cd/m²) as was the response circle. In the unicolor: red or green paradigm, both surfaces were either red or green (red: $x = 11.97$, $y = 24.37$; green: $x = 46.37$, $y = 24.38$; isoluminant, 24.4 cd/m²), pseudorandomly interleaved. In the color-segmented paradigm, one surface was red and the other was green (red: $x = 11.97$, $y = 24.37$; green: $x = 46.37$, $y = 24.38$; isoluminant, 24.4 cd/m²). Participants responded on sequential colored circles whose order was randomly interleaved across trials.

In Experiment 1, the unicolor: white paradigm resulted in a 12 (Surface 1 Direction) × 12 (Surface 2 Direction) experimental design. The unicolor: red or green paradigm resulted in a 12 (Surface 1 Direction) × 12 (Surface 2 Direction) × 2 (Surface Color) design. The color-segmented paradigm resulted in a 12 (Surface 1 Direction) × 12 (Surface 2 Direction) × 2 (Surface Color) × 2

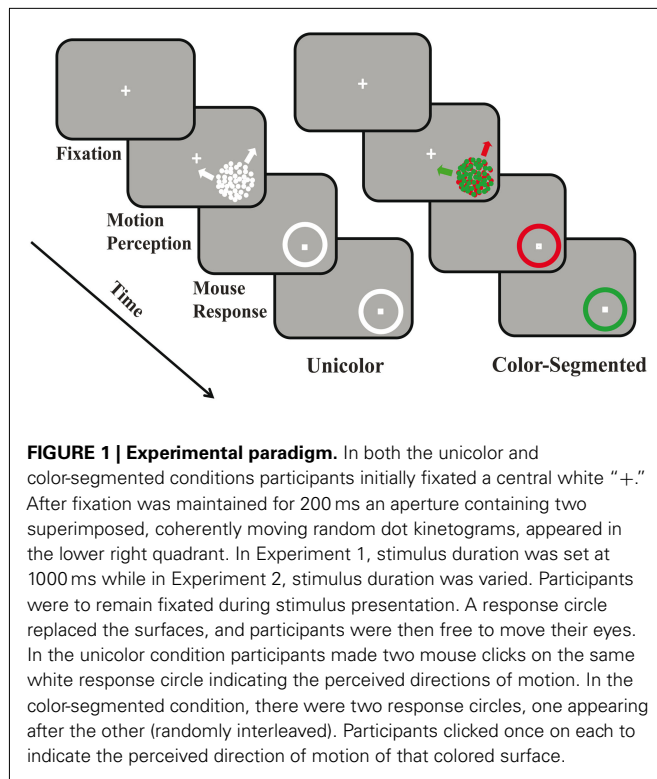


FIGURE 1 | Experimental paradigm. In both the unicolor and color-segmented conditions participants initially fixated a central white “+.” After fixation was maintained for 200 ms an aperture containing two superimposed, coherently moving random dot kinetograms, appeared in the lower right quadrant. In Experiment 1, stimulus duration was set at 1000 ms while in Experiment 2, stimulus duration was varied. Participants were to remain fixated during stimulus presentation. A response circle replaced the surfaces, and participants were then free to move their eyes. In the unicolor condition participants made two mouse clicks on the same white response circle indicating the perceived directions of motion. In the color-segmented condition, there were two response circles, one appearing after the other (randomly interleaved). Participants clicked once on each to indicate the perceived direction of motion of that colored surface.

(Response Order: green then red, or red then green) design. Participants completed a practice block of 10 trials, and then performed 288 trials in one of the unicolor paradigms or 576 trials in the color-segmented paradigm.

In Experiment 2, stimulus duration was varied using a staircase design. Based on pilot data, the starting unicolor stimulus duration was 2000 ms and the color-segmented stimulus duration was 1000 ms. Each block contained eight trials at a given stimulus duration. If performance was $\geq 87.5\%$ (7/8), the stimulus duration was decreased in the next block. Otherwise the duration was not long enough to perform the task at criterion, and the stimulus duration increased. The staircase had two stages; in the first the stimulus duration increased or decreased by a step size of 500 ms. Upon a double reversal, the staircase switched to stage two with a 100-ms step size. The staircase ended when stage two produced a double reversal or the 1 h session was completed. The time required to process both directions correctly was taken as the average between the final two durations at the staircase plateau.

DATA ANALYSIS

Correct perceptual responses for directions one and two were defined as being those that fell within a range that extended from halfway between the two directions to 45° away from the real directions (Figure 2). This was to account for variability in participant's responses due to repulsion effects. In order to compare them, correct responses in the color-segmented paradigm were computed the same way as in the unicolor paradigms: the two direction responses were deemed correct or incorrect without regard to whether the directions matched the correct color surface. In essence, this was analyzing performance in the

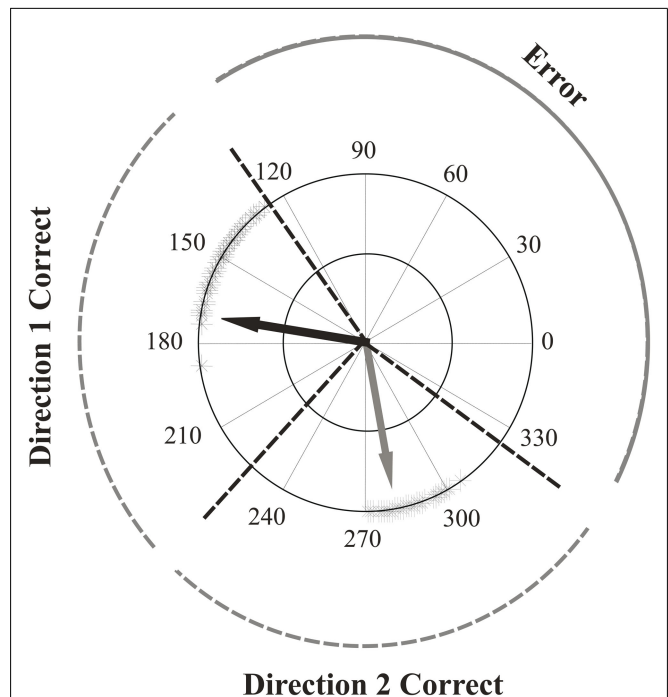


FIGURE 2 | Response range of an example participant with correct and error ranges indicated. Shown are all the both-correct responses one participant made to surfaces that were moving at between 170° – 190° and 260° – 280° . Note that the responses are repulsed away from each other and from the real directions. Overlaid are the ranges used to determine the both-correct, one-wrong and both-wrong rates for surfaces moving at 170° and 280° . Correct ranges were defined as halfway between the two directions to $\pm 45^\circ$. One-wrong rates then were trials in which participants clicked on the response circle within the correct range for either direction one or direction two, and made a second response within the error range. Both-wrong rates were based on trials in which participants made both clicks on the response circle within the error range.

color-segmented paradigm as if the color of the surfaces were irrelevant. For all paradigms, only trials in which both directions were correct were included in the direction repulsion analysis. The perceived angle was the difference between the two response directions. Direction repulsion was computed as the difference between the perceived angle and the actual angle difference between the two directions of motion. Positive values indicated direction repulsion.

In Experiment 1, performance was also calculated, measuring the rate at which participants: responded correctly to both surfaces (both-correct), responded correctly to one surface (one-wrong), and were unable to respond correctly to either surface (both-wrong). We also calculated total error rate which included all trials in which participants got either one response or both responses incorrect (total error rate = $1 - \text{both-correct rate}$).

Means were calculated for each variable: direction repulsion, both-correct, one-wrong, both-wrong, total error, and stimulus duration. Independent *t*-tests were performed for direction repulsion and stimulus duration analyses comparing means in the unicolor versus the color-segmented paradigms. As the error rates may violate the normality assumptions underlying the *t*-test, we

performed Wilcoxon rank-sum tests on both-correct, one-wrong, both-wrong, and total errors between the paradigms.

RESULTS

EXPERIMENT 1

We hypothesized that direction repulsion would be attenuated with the addition of a different color to each of the surfaces as this would further segment the surfaces making them more distinct from one another. We expected no difference between the two unicolor paradigms.

It is important to remove errors caused by guessing from our repulsion analysis, because guesses, as outliers, would be independent of the repulsion effect but would skew the distribution means. Therefore, correct ranges were set *a priori* based on previous literature (Marshak and Sekuler, 1979; Mather and Moulden, 1980; Hiris and Blake, 1996; Braddick et al., 2002) which showed peak single surface repulsions of $\sim 20^\circ$ with an angular difference between the two real directions of 22.5° . In our range of $70\text{--}110^\circ$ angular differences, those studies found a mean repulsion of $3\text{--}9^\circ$. In addition, if a participant did not fully process one of the directions of motion, they were still required to respond, thus forcing guesses. As we presented directions $\pm 2^\circ, 6^\circ, 10^\circ$ from each of the four cardinal directions, guesses should therefore be clustered around the cardinal directions. We used a cutoff of $+45^\circ$ (half the distance between the correct direction and the closest cardinal direction) which encompasses the mean repulsions seen in prior research and excludes guesses at the remaining cardinal directions. **Figure 2** depicts the correct and error ranges for an example pair of directions. To determine if the cutoff was appropriate, we plotted the distribution of responses for an example participant from each of the unicolor and color-segmented conditions (**Figure 3**). The responses show multiple distinct distributions. The distribution around the actual direction of motion (normalized to 0°) falls within the 45° cutoff and is shifted to the right, consistent with direction repulsion. Trials outside this range, considered error trials in our analysis, show clustering around repulsion magnitudes of 90° and 180° , consistent with guessing around the remaining cardinal directions.

The motion processing system is generally considered to be color-blind (Maunsell and Van Essen, 1983a,b; Shipp and Zeki, 1985; Zeki et al., 1991), however a few recent studies have suggested that color and motion processing may be linked (Croner and Albright, 1997, 1999; Tchernikov and Fallah, 2010). Therefore, we first tested whether the addition of color itself affected direction processing by comparing the unicolor: white and unicolor: red or green paradigms. We found no significant differences in any of our measures: Direction Repulsion [$t(10) = 0.84$, $p = 0.42$], Both-Correct rates ($W_s = 31.00$, $z = -1.28$, $p = 0.24$), One-Wrong rates ($W_s = 30.00$, $z = -1.44$, $p = 0.18$), Both-Wrong rates ($W_s = 33.5$, $z = -0.89$, $p = 0.39$), and Total Error rates ($W_s = 31.00$, $z = -1.28$, $p = 0.24$). We collapsed the two unicolor paradigms for the remaining analyses.

We next compared the color-segmented paradigm to the combined unicolor paradigms. On correct trials, mean direction repulsion in the unicolor paradigm ($7.32 \pm 1.45^\circ$) did not differ significantly from the color-segmented paradigm [$7.45 \pm 3.50^\circ$, $t(16) = -0.04$, $p = 0.97$ – see **Figure 4**]. The addition of color segmentation cues did not affect motion perception, specifically the illusory direction repulsion. However, participants' performance, that is their ability to correctly determine both directions, was significantly higher in the presence of color segmentation cues ($93.3 \pm 0.75\%$) versus the unicolor condition ($80.48 \pm 2.74\%$; $W_s = 83.00$, $z = -2.90$, $p = 0.002$). This is also shown in the total error rate (proportion of trials in which the participant responded incorrectly to either one or both of the directions – see **Figure 5**). There was a significant decrease ($W_s = 26.00$, $z = -2.90$, $p = 0.002$) in the total error rate in the color-segmented condition ($6.67 \pm 0.75\%$) compared to the unicolor condition ($19.52 \pm 2.74\%$). To determine what was driving the difference in performance, error trials were broken down into two categories: when only one direction was incorrectly determined (One-Wrong) or when both were incorrectly determined (Both-Wrong). There was a significant difference in Both-Wrong error rates ($W_s = 31.00$, $z = -2.45$, $p = 0.013$) between the unicolor ($1.97 \pm 0.57\%$) and the color-segmented ($0.17 \pm 0.06\%$) conditions (**Figure 5**). The Both-Wrong error rates

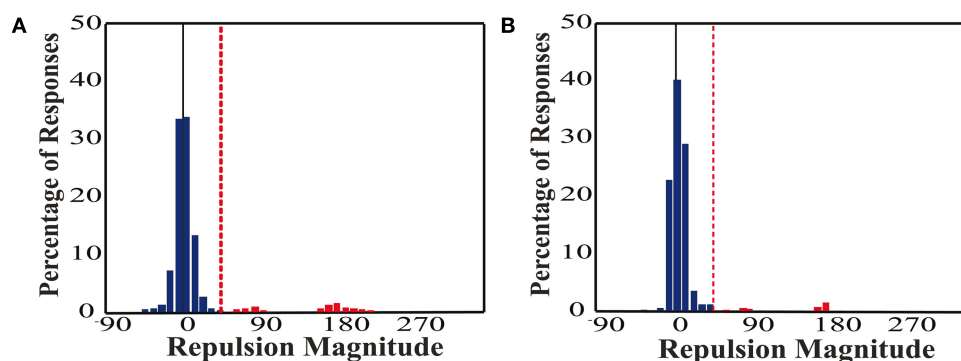
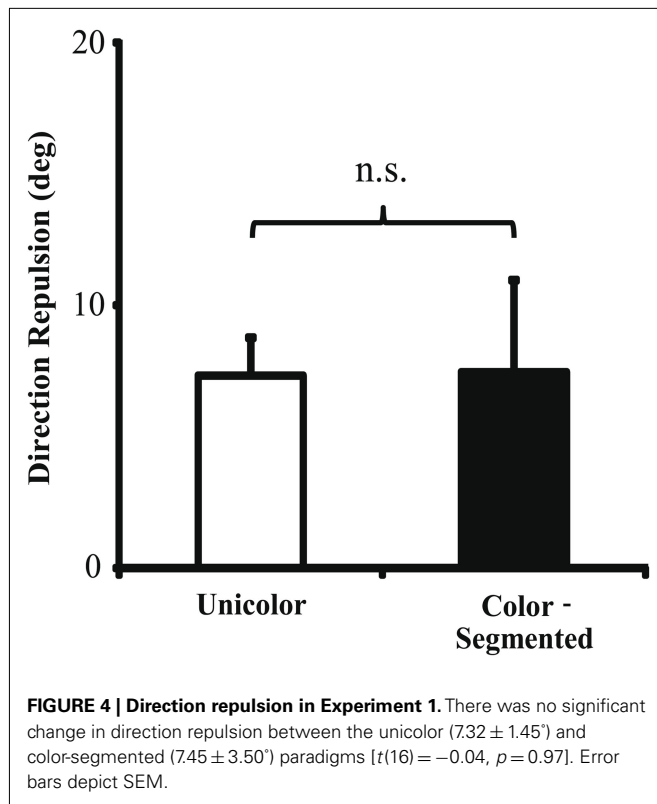


FIGURE 3 | Example distributions of repulsion magnitude. (A) Unicolor, **(B)** Color-segmented. Responses are plotted for one participant in each paradigm. The real direction of motion was normalized to 0° repulsion (black vertical line). The $+45^\circ$ cutoff is depicted by the red dashed

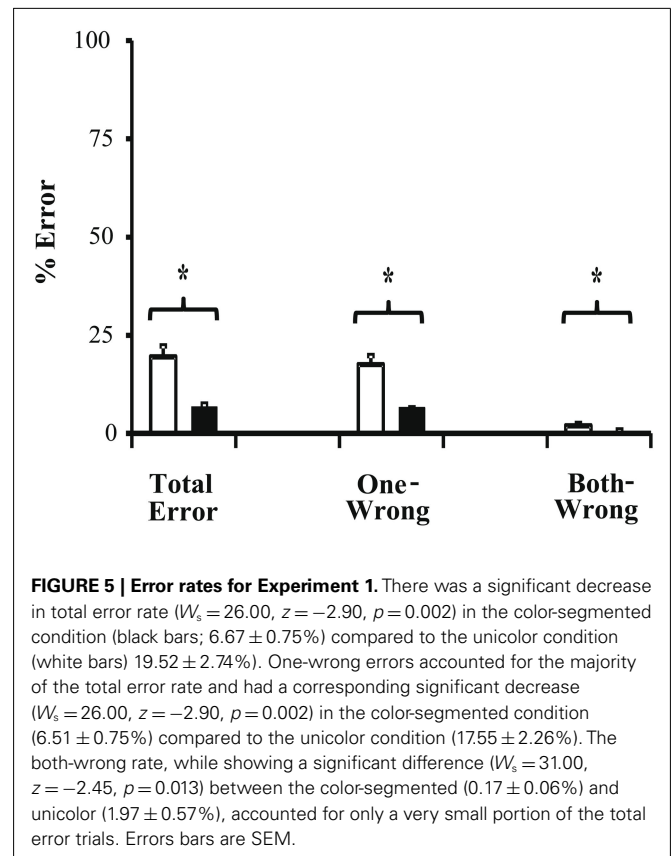
line. Responses outside of this range are indicated in red and were classified as errors. Note the majority of responses fall within the correct range. The errors are distributed around 90° and 180° , consistent with guessing the remaining cardinal directions.



were under 2%, thus participants were able to process at least one of the directions on nearly every trial (Unicolor: 98.03%, Color-Segmented: 99.8%). Note that the $\sim 2\%$ difference in Both-Wrong error rates between the conditions was a small proportion of the difference in overall performance (Unicolor: 80.48%, Color-Segmented: 93.3%). Instead, the addition of color segmentation cues improved performance by significantly reducing the One-Wrong error rate (Unicolor: $17.55 \pm 2.26\%$, Color-Segmented: $6.5 \pm 0.75\%$; $W_s = 26.00$, $z = -2.90$, $p = 0.002$; **Figure 5**). While direction repulsion was not affected by the presence of color segmentation cues, the ability to process not just one but both directions was significantly improved.

EXPERIMENT 2

In Experiment 1, participants were able to correctly determine the direction of one of the surfaces whether or not color differences were present. The addition of color segmentation cues significantly improved participants' ability to process the second direction of motion, without affecting the direction repulsion illusion. We hypothesized that the addition of color may have speeded processing without affecting perception, even though there was the added task demand of associating direction with color. In Experiment 1, the stimuli were presented for 1000 ms, which was sufficient time to perform the task when the surfaces were segmented by color, but apparently not enough time to process both unicolor surfaces. In Experiment 2, we varied the duration of stimulus presentation to determine how much time was necessary to process both directions with and without color segmentation cues. We predicted that without color segmentation cues, a presentation



time of greater than 1000 ms would be necessary to process both directions of motion.

Consistent with Experiment 1, there was no significant difference in direction repulsion between the unicolor ($14.02 \pm 1.39^\circ$) and color-segmented ($13.79 \pm 1.54^\circ$) conditions [$t(22) = 0.12$, $p = 0.91$ – see **Figure 6A**]. We performed an omnibus direction repulsion analysis using a 2 (Experiment 1 versus 2) $\times 2$ (Segmentation: Unicolor versus Color-segmented) ANOVA. There was a significant main effect of Experiment ($p = 0.001$), but no main effect of Segmentation ($p = 0.82$) nor a significant interaction ($p = 0.87$). It is also possible that due to the between-subjects design, the repulsion magnitude difference is based upon group differences between the participants in Experiments 1 and 2. However, it is unlikely that random assignment of 42 participants would result in such a large and significant difference. The repulsion magnitude difference is more likely due to differences in the two experimental paradigms. In Experiment 1, the timing is set and known, whereas in Experiment 2, it is variable. We can only speculate that this may produce different levels of alertness and/or arousal resulting in the magnitude differences. It is important to note that while there is a difference in direction repulsion magnitude between the two experiments, the addition of color segmentation, within each experiment, did not affect direction repulsion.

As expected, participants required less than 1000 ms to process both directions when the surfaces were segmented by color (841.7 ± 150.5 ms). In the unicolor condition, participants on

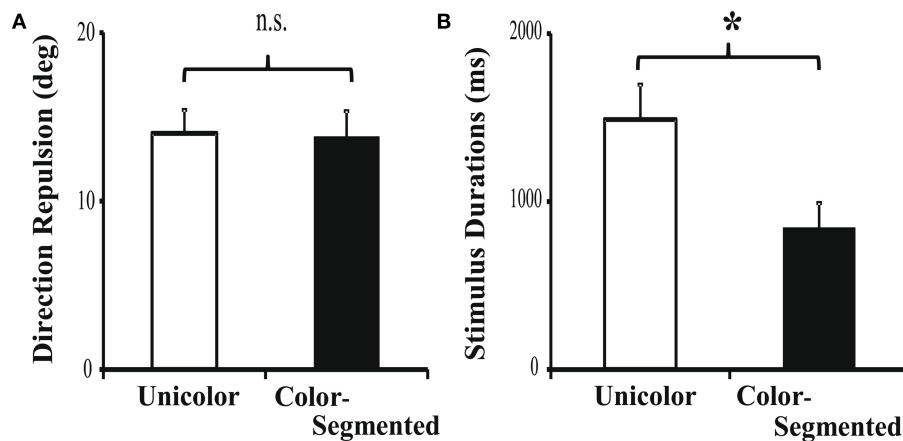


FIGURE 6 | Direction repulsion and stimulus duration results for Experiment 2. (A) As in Experiment 1, there was no significant modulation of direction repulsion with the addition of color ($13.79 \pm 1.54^\circ$) when compared to the unicolor ($14.02 \pm 1.39^\circ$) condition [$t(22) = 0.12$,

$p = 0.91$]. **(B)** Participants required significantly less time in the color-segmented paradigm (841.7 ± 150.5 ms) than in the unicolor paradigm (1487.5 ± 208.5 ms) to correctly process both directions [$t(22) = 2.51$, $p = 0.02$]. Error bars are SEM.

average required 1488 ms to process both directions of motion (1487.5 ± 208.5 ms). The presentation time required in the unicolor condition was significantly longer than in the color-segmented condition [$t(22) = 2.51$, $p = 0.02$ – see **Figure 6B**]. This difference in timing supports the results of Experiment 1. Color segmentation enabled processing both directions of motion within 1000 ms (93% performance), but in the unicolor condition, participants were not always able to process the second surface's direction (80% performance). Thus, the addition of color segmentation cues, providing an additional feature by which to select a surface, significantly speeded processing in the motion discrimination task without affecting conscious perception of the direction repulsion illusion.

DISCUSSION

In the direction repulsion illusion, previous work has shown that conscious misperception of motion direction can be altered through the use of bottom-up segmentation cues, which are thought to reduce the effect of mutual inhibition between the superimposed objects. When the objects were distinguished from each other by differences in speed (Marshak and Sekuler, 1979; Curran and Benton, 2003) or spatial frequency (Kim and Wilson, 1996), direction repulsion was reduced resulting in a more realistic conscious experience. Note that speed and spatial frequency are co-processed with direction in motion-sensitive visual areas, such as area MT, in the dorsal visual processing stream (for review, see Born and Bradley, 2005). Evidence suggests that motion processing is segregated along different speed (Edwards et al., 1998) or spatial frequency channels (Kim and Wilson, 1993). Thus, direction repulsion could be attenuated by segregating the objects by different speed (Curran and Benton, 2003) or spatial frequency channels (Kim and Wilson, 1996). As superimposed transparent surfaces are automatically perceived as being at different apparent depths, additionally segmenting the surfaces by stereoscopic depth does not attenuate direction repulsion (Hiris and Blake, 1996). We hypothesized that distinguishing two superimposed objects by a

feature processed outside of the dorsal stream, providing both bottom-up segmentation cues and an additional top-down task demand, should also attenuate direction repulsion. Such a finding would be consistent with attention to an object strengthening the conscious representation of all the features of that object. In contrast, our findings show that conscious perception of motion direction is unaffected: direction repulsion was no different when the objects were additionally segmented by color versus when they were the same color. This result suggests that color cues had no effect on motion processing: computing direction was blind to the color of the moving object. While illusory perception of the direction repulsion was not affected, we did find that participants' ability to process both objects' directions of motion in a set period of time was improved with the addition of color. When the surfaces were only segmented by direction (unicolor condition), one of the directions of motion did not always reach conscious awareness. But color segmentation brought both directions of motion into conscious awareness. We hypothesized that color sped processing in the task, similar to how attentional facilitation speeds reaction times. Speeded processing would allow the direction computation to complete and enter conscious awareness, without affecting the perceived direction. In Experiment 2, we varied the presentation duration to test this hypothesis and determine how much time was necessary to process both objects' directions with and without color cues. Color segmentation did indeed speed visual processing, resulting in participants requiring less time (color-segmented: ~840 ms; unicolor: ~1490 ms) to fully process the directions of motion of both objects. These timings were consistent with the results of Experiment 1 that used a set 1000 ms stimulus duration. Therefore, while determining the global motion direction of colored, coherently moving dots requires a hierarchical object representation, attention to one feature of the object (color) did not modify the conscious percept of other features of the object (direction of motion). However, segmentation by that feature did speed processing of other features, allowing them to enter conscious awareness more quickly.

SPEEDED PROCESSING AND REACTION TIME STUDIES

Our results suggest that the representation of an object's features in conscious perception is independent of the speed at which the neural circuitry processes that sensory input. A number of spatial attention studies have focused on detection tasks where performance is at ceiling (e.g., the precueing paradigm, Posner, 1980). The effect of spatial attention is then measured as changes in the speed of response, termed reaction time. As the strength and quality of the sensory input is already high, attention is thought to speed visual processing in these paradigms. Behavioral studies of non-spatial object-based attention using superimposition (e.g., Duncan, 1984; Valdes-Sosa et al., 1998, 2000; Reynolds et al., 2003) have generally measured accuracy of discrimination judgments and thus have not investigated effects on processing speed (but see Tipper, 2001, for a review of negative priming: slower reaction times resulting from distractor inhibition). Our results are consistent with attentional speeding of visual processing, but we also show that it is not limited to spatial attention because the surfaces are superimposed. In fact, we recently performed a reaction time precueing study using superimposed surfaces (Fallah et al., under review). In that study, non-spatial object-based attention modulated response times, supporting the point that speeded visual processing is not limited to spatial attention.

PRE-ATTENTIVE PROCESSING

We have suggested that color segmentation speeds motion processing due to attentional mechanisms because attention has been shown to speed visual processing (e.g., reaction times). However, it is also possible that color segmentation increased the speed of motion processing through pre-attentive mechanisms. That is, the effects of color segmentation could have been due to feed-forward pre-attentive processing of the motion direction and not been reliant on attentional feedback. This would occur if color and motion are bound prior to or during motion processing. As additional time is required to bind different features together (Bodelon et al., 2007), linking color and motion pre-attentively would need to provide a larger speed advantage than that cost. Due to the magnitude of the benefit seen with color segmentation in this task, it is possible that more than one mechanism is in effect. In the following discussion of the different stages of visual processing wherein color segmentation could potentially speed motion processing, we will highlight which mechanisms rely on pre-attentive or attentive processing.

TIMING MODELS

This task required top-down and bottom-up attention along with visual processing, working memory and hierarchical object processing. As such, there are a number of stages of processing required to perform the task, but we are only focusing on the stages necessary during the presentation of the stimuli and not the memory retrieval and response stages. We propose two possible models: one based on serial processing and another based on parallel processing. The serial model is based on prior studies that have shown people are impaired at simultaneously processing features on two different, superimposed objects (Neisser and Becklen, 1975; Duncan, 1984; Blaser et al., 2000), and thus may select and process one object before switching and processing the

other object. Alternatively, the directions of both objects could be processed in parallel. **Figure 7A** depicts the necessary stages of processing in the serial model. Participants first need time to separate the dots into two different objects (SG: segmentation time), in order to process the direction of the first object (D1: direction discrimination of object 1). Note that processing the direction includes motion processing, decision-making and storage in working memory. The time to complete these two stages is the time needed to completely process the first object (T1: time to process direction 1). Once the first object is processed, participants need to disengage attention from this object and switch their attention to the second object (SW: switch). Then the direction of the second object can be determined (D2). T2 is the time needed to accomplish these two (SW and D2) stages. Completing all of the stages is the time needed to determine the direction of both objects. In the parallel model (**Figure 7E**), the dots are also initially segmented into two separate objects (SG). Then both directions are processed in parallel (D1 and D2). The parallel direction processing may occur at equal rates or one may complete before the other, consistent with our one-correct rates. Whether the process is serial or parallel, color segmentation may increase the speed of processing at one or more of these stages. We propose three models wherein different stages of processing may be speeded by the addition of color cues. We also review possible anatomical underpinnings of each.

Segmentation

The first model is based on color speeding segmentation (SG) of the dots into two superimposed objects, resulting in a decrease in the total time required to perform the task. This could occur through pre-attentive processing and affect both the serial (**Figure 7B**) and parallel (**Figure 7F**) mechanisms. In this paradigm, segmentation is mainly dependent on the Gestalt principle of common fate: items that move together are grouped together (e.g., Blake and Lee, 2005). Two fields of dots that are superimposed but not moving appear as a single surface, whether or not they differ in color. It is the motion of the dots that segments them into two superimposed objects. It is at this stage that the two superimposed objects, but not the directions of motion, enter conscious awareness. The addition of color cues increases the strength of segmentation between the two objects. It may be that in addition to increasing the segmentation strength, color cues also speed the segmentation process by grouping the dots into two objects more efficiently. Color and motion are processed separately, starting with different photoreceptors in the retina and continuing through separate functional areas in cortex (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992; Milner and Goodale, 1993). In cortical visual processing the ventral stream is sensitive to color, whereas the dorsal stream is sensitive to motion. Color could affect motion segmentation through the anatomical links between area V4, which represents perceived color, and area MT, which processes motion (Ungerleider and Haxby, 1994). As color is processed faster than motion (Moutoussis and Zeki, 1997), it therefore would be available to aid in grouping the dots and segmenting the objects by motion. Such color–motion interaction would occur during early pre-attentive visual processing. While prior research has suggested that area MT may use color

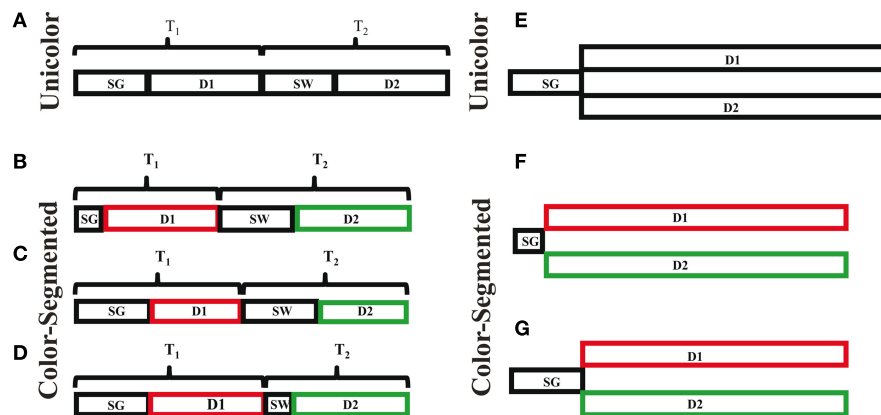


FIGURE 7 | Task processing and timing models. Serial models are depicted in (A–D). (A) Shows the time components involved in processing the directions of both surfaces. T₁, the time to process the direction of one surface, is divided into the time needed to segment the surfaces (SG), and the time to discriminate the direction (D1). T₂, the time to process the direction of the other surface, is divided into the time needed to disengage attention from surface one and instead attend to the other surface, i.e., switch (SW), and the time required to distinguish the direction of surface two (D2). (B) Faster segmentation hypothesis; the time needed to segment (SG) the surfaces decreases with the addition of a color difference, thus decreasing the amount of time to process surface one (T₁), and the total time needed to

perform the task. (C) Faster motion processing hypothesis; the addition of color reduces the time needed to process the direction of each surface. Again, the total time needed to perform the task decreases. (D) Faster attentional switch hypothesis; color reduces the amount of time required to disengage attention from surface 1 and switch to processing surface 2 (SW), thus reducing the time needed to process the second surface (T₂), and the total time needed to perform the task. Parallel models are depicted in (E–G). This would eliminate the need to switch attention between objects, leaving decreased segmentation time (F), and faster motion processing (G), as possible mechanisms through which decreased processing time in the color-segmented paradigm could occur.

to segment moving dots (Croner and Albright, 1997; Born and Bradley, 2005), this study suggests that color may also speed the segmentation by motion process. Since increased discriminability of a texture-defined object only speeds segmentation time by up to 25 ms (Caputo and Casco, 1999), it is not likely that color affecting SG alone can account for the total difference in processing time.

Sensory processing

The second model is based on color speeding motion processing, resulting in a decrease in both D1 and D2. This would affect both the serial (Figure 7C) and parallel (Figure 7G) mechanisms. Historically motion processing was thought to be color-blind (Maunsell and Van Essen, 1983a,b; Shipp and Zeki, 1985; Zeki et al., 1991), especially since the dorsal stream that processes motion only receives magnocellular (rod) input and not parvocellular (cone) input. More recently, evidence is accumulating that color can affect motion processing, possibly through cross-talk connections between areas V4 and MT (Ungerleider and Desimone, 1986). For example, Croner and Albright (1997, 1999) found that direction discrimination was enhanced when distractors were distinguished by color. More recently, Tchernikov and Fallah (2010) found that color modulated the speed of smooth pursuit eye movements, thought to be dependent on motion processing in area MT (Lisberger and Ferrera, 1997; Recanzone and Wurtz, 1999). Thus color processing within the ventral stream has both anatomical and functional connectivity with motion processing in the dorsal stream. The outstanding question is how do those connections speed processing without affecting the perception of motion?

In order to process motion, MT first needs to associate the identity of each dot across two frames (aliasing – Snowden and

Braddick, 1990), and then use Gestalt rules of common fate to group dots with common motion directions into the two global objects. The common color of dots within the same object may speed processing by reducing the aliasing options; each dot has half as many possible matches across frames of motion in the color-segmented than in the unicolor condition. This could either occur through pre-attentive processing if color segregates motion input early in the visual processing stream, by top-down attentional selection through color filtering (Croner and Albright, 1997, 1999), or by bottom-up attention as surfaces provide an advantage over lower-level features in visual search (He and Nakayama, 1992). Concurrent direction judgments of superimposed surfaces are based on the global motion representations of each surface (Braddick et al., 2002). We suggest that it is the global motion processing of each surface that is affected by color segmentation. Then, once each surface's direction is determined, mutual inhibition between the populations of neurons representing each direction shifts the perceived directions away from each other. Thus, time to process may be affected by color segmentation in this task, without affecting the conscious misperception of the directions of the objects.

Alternatively, it may be possible to speed the decision-making process. Direction judgments have been shown to be based on area MT processing motion information (Albright, 1984; Mikami et al., 1986a,b; Newsome and Pare, 1988; Salzman et al., 1992) and passing the information along to area LIP which accumulates the evidence to reach a decision threshold (accumulator model: Shadlen and Newsome, 1996, 2001; Huk and Shadlen, 2005; Palmer et al., 2005). LIP also receives color information directly from area V4, an intermediate stage of feature processing in the ventral visual stream (Ungerleider and Haxby, 1994). In this model, area MT contains

direction processing circuitry, including that of mutual inhibition which produces direction repulsion, and passes the two misperceived directions to LIP which accumulates this information over time. In the unicolor condition, segmentation occurs solely on the basis of motion direction and thus the direction of one surface interferes with the accumulation of direction information for the other surface. This leads to a “noisy walk” toward threshold (e.g., Palmer et al., 2005). When the motion information is separated by color, focusing on a single color reduces the noise produced by the other surface’s direction which increases the slope of accumulation, resulting in a faster approach to the decision threshold. Note that this would occur after mutual inhibition in area MT produces the misperceived directions. The accumulator model can account for differences in reaction time based on the strength of the motion stimulus (motion coherence) and for speed–accuracy tradeoffs (Palmer et al., 2005). We hypothesize that attention, using color segmentation, gates direction information after motion processing which leads to speeded decision-making (accumulator model) without affecting conscious perception (direction repulsion). While our experiments cannot determine whether motion processing or decision-making occur faster, future studies can test these hypotheses by performing neuronal recordings in areas MT and LIP.

Attentional switching

The third model is based on color differences producing faster attentional switching between objects; seen as a decrease in SW and thus T2 time. This model only affects the serial mechanism (Figure 7D), as there is no attentional switching in the parallel model. Switching attention between objects at a given location has best been studied in the attentional blink paradigm. In attentional blink, it has been shown that being able to switch one’s attention between serially presented objects is limited when the objects appear within ~100–500 ms of each other (Shapiro et al., 2009). Color segmentation provides an additional feature by which to select a surface, which could produce an advantage of up to a few hundred milliseconds.

Attentional control is thought to be mediated by distinct ventral and dorsal attention networks (Corbetta and Shulman, 2002; Shulman et al., 2002; Sridharan et al., 2007). The dorsal attention network is involved in top-down control of attention to locations, objects, and features (Corbetta et al., 1993; Nobre et al., 1997; Corbetta, 1998; Shulman et al., 1999; Yantis and Serences, 2003; Serences et al., 2004; Kelley et al., 2008; Ozaki, 2011). The dorsal attention network has also been shown to be driven by bottom-up attentional cues relating to motion but not by color cues (Shulman et al., 2002; d’Avossa et al., 2003), whereas color saliency activates occipitotemporal regions instead (Kincade et al., 2005). While attentional switching activates both attention networks (Corbetta and Shulman, 2002; Serences et al., 2004), it has been suggested that attentional switching is in fact facilitated by the ventral attention network acting as a “circuit breaker” (Marois et al., 2000; Corbetta and Shulman, 2002; Shulman et al., 2002, 2007; Chambers et al., 2004) whose function is to interrupt an ongoing cognitive task to reorient attention to different behaviorally relevant sensory information (Serences et al., 2005) even at the same spatial location (Greenberg et al., 2010). Therefore, color segmentation would

aid in disengaging from one surface and reorienting to the other surface, speeding the attentional switch. In this model, the ventral attention network affects the speed of visual processing, whereas the dorsal attention network is instead linked to conscious perception as it likely mediates attenuation of direction repulsion due to increased segmentation from bottom-up motion features such as speed and spatial frequency.

CONSCIOUSNESS

Pre-attentive processing could subserve color effects on the segmentation and direction discrimination stages. Attentional mechanisms could underlie color effects on the direction discrimination, decision-making, and attentional switching stages. Based on the magnitude of the color segmentation effect, it is likely more than one stage is affected. These potential attentional mechanisms add to the growing body of evidence that, under certain circumstances, attention and consciousness can be dissociated (Braun and Sagi, 1990; Braun and Julesz, 1998; Kentridge et al., 1999a,b, 2004; Tsushima et al., 2006, 2008; van Boxtel et al., 2010a for a full review). For example, in blindsight, attention can be directed to a stimulus even though the stimulus is not consciously perceived (Kentridge et al., 1999a,b, 2004). In fact, an unseen distractor in the blind field inhibits saccades to consciously perceived targets in the intact visual field (Rafal et al., 1990) similar to a visible distractor in normal participants, i.e., the oculomotor distractor effect (Walker et al., 1995, 1997). As another example, Tsushima et al. (2006, 2008) showed that subthreshold motion coherence (consciously invisible direction) was more distracting in an RSVP task than was suprathreshold motion coherence. Those studies have used stimuli that do not reach conscious awareness to produce a dissociation between attention and consciousness. In the current study, color segmentation did not alter conscious perception of direction, suggesting that in this case processing speed and conscious perception are somehow dissociated even when the stimuli do reach conscious awareness. With or without color segmentation, participants were consciously aware of one of the directions on nearly every trial. Furthermore, with increased presentation time (~1500 ms) of the two surfaces, participants were aware of both directions of motion even when they were the same color (Experiment 2, unicolor condition). Thus, color segmentation only sped the entry of motion information into awareness without altering the illusory percept, even though the task required attending to both the color and direction of each surface. This may be due to pre-attentive bottom-up mechanisms, attentional mechanisms, or a combination of the two.

CONCLUSION

We find that adding color segmentation cues to superimposed objects speeds motion processing, without affecting the misperception of their directions in the direction repulsion illusion. This is in contrast to features within the dorsal stream, specifically speed and spatial frequency, which do affect conscious perception of motion direction, as measured by a reduction in the illusory repulsion. It remains unknown whether those dorsal stream features also speed motion processing or just affect motion perception. Color segmentation affects the speed but not the quality of the direction computation. Speed and spatial frequency affect the

quality of the direction computation (and may or may not affect the speed of processing). So for color segmentation there is a dissociation between speed of processing, i.e., the time required to reach conscious awareness, and the conscious percept in that awareness. We propose four stages at which color segmentation may speed processing: segmentation, switching, direction discrimination, and decision-making. The dissociation seen between color segmentation and the conscious perception of the direction repulsion illusion is likely due to color and motion being processed separately by the dorsal and ventral visual streams, whereas the

cross-talk between the streams still allows for speeded processing. In summary, we have shown that a consciously perceived feature of an object can speed the processing of other features of the same object without affecting the outcome of their perceptual processing.

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Motor consciousness during intention-based and stimulus-based actions: modulating attention resources through mindfulness meditation

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Mindfulness-Based Stress Reduction meditation (MBSR) may offer optimal performance through heightened attention for increased body consciousness. To test this hypothesis, MBSR effects were assessed on the simple task of lifting an object. A dual task paradigm was included to assess the opposite effect of a limited amount of attention on motor consciousness. In a stimulus-based condition, the subjects' task was to lift an object that was hefted with weights. In an intention-based condition, subjects were required to lift a light object while imagining that the object was virtually heavier and thus, adjust their grip voluntarily. The degree of motor consciousness was evaluated by calculating correlation factors for each participant between the grip force level used during the lift trial ("lift the object") and that used during its associated reproduce trial ("without lifting, indicate the force you think you used in the previous trial"). Under dual task condition, motor consciousness decreased for intention- and stimulus-based actions, revealing the importance of top-down attention for building the motor representation that guides action planning. For MBSR-experts, heightened attention provided stronger levels of motor consciousness; this was true for both intention and stimulus-based actions. For controls, heightened attention decreased the capacity to reproduce force levels, suggesting that voluntary top-down attention interfered with the automatic bottom-up emergence of body sensations. Our results provide strong arguments for involvement of two types of attention for the emergence of motor consciousness. Bottom-up attention would serve as an amplifier of motor-sensory afferences; top-down attention would help transfer the motor-sensory content from a pre-conscious to a conscious state of processing. MBSR would be a specific state for which both types of attention are optimally combined to provide experts with total experiences of their body in movement.

Keywords: grip force, sensation, consciousness, attention, dual task, mindfulness, motor planning, intention

INTRODUCTION

Mental skills are crucial in ensuring great performances at world championships and Olympic Games (Werthner, 2002). The often-referenced study by Orlick and Partington (1988), an extensive study of 235 Canadian athletes, revealed that mental readiness was a significant factor in determining which athletes were able to perform their best under the pressures and stresses of the Olympics. The ability to focus attention and control performance imagery was later found to be the key factors in successful performances (Werthner, 2002). What a person directs his or her attention to while preparing to execute a skill determines in fact how fluid the motion, how consistent the movement and in general, how accurate the outcome is (for a review, see Wulf et al., 2010b).

In the past 20 years, mindfulness-based stress reduction (MBSR) meditation has been adopted by many athletes especially those evolving in individual sports for which self-awareness of body performance is a key to success (skiing, gymnastics, swimming). Acquired through long periods of months, some athletes

are convinced of its usefulness for filtering in only those positive thoughts needed for the task at hand, thus augmenting concentration capacities. Others are more sensitive to the role of mindfulness to heighten the *sensory experiences* of their body during performance execution. The aim of the present study was to develop a simple lab-based methodology to assess objectively the effects of mindfulness meditation through the manipulation of the nature of the task (automatic vs. controlled) and of the quantity of available attention (simple vs. dual task) during the planning of a simple grip to lift action. More specifically, we wanted to gain a better understanding of the role played by meditation for the allocation of attention resources in relation to the emergence of the consciousness of body in action.

MEDITATION FOR HEIGHTENED MOTOR ATTENTION

Even if grip force (GF) is a motor parameter that is scaled automatically, it appears that during some fine manipulative tasks (e.g., threading a needle), we can make a conscious effort to orient more attention to modulate muscle contraction output

(Delevoeye-Turrell and Wing, 2004). As such, it is possible to increase our levels of body consciousness of even the smallest body part (*while reading this sentence, orient in the present moment your attention to your left big toe. . .*). With practice, it has been shown that body consciousness can become so vivid and intense that certain experts report having experienced what is called the flow state of consciousness – an optimal performance state that is most searched for by athletes (Bianco et al., 1999) and by music maestros (Glise, 2011). During flow state, the modified state of attention can increase body consciousness to such an extent that performers experience loss of temporal awareness, a calm loss of emotional and physical tension as well as an increase sensitivity to sound, light, and tactile stimuli (Williams and Krane, 1993). Because of these observations, it has been suggested that MBSR meditation techniques may help individuals gain control on those brain mechanism leading to the emergence of the flow state of body consciousness.

In current research contexts, MBSR meditation is typically defined as non-judgmental attention to experiences in the present moment (Shapiro et al., 2008). Bishop et al. (2004) have suggested a two-component model of mindfulness where the first component is the regulation of attention in order to maintain it on the immediate experience, and the second component involves approaching one's experiences with an orientation of curiosity, openness, and acceptance. As such, the practice of mindfulness meditation encompasses *paying attention on purpose, in the present moment, on the experience of thoughts, emotions, and body sensations simply observing them as they arise and pass away* (Kabat-Zinn, 1994). Attentional training and improvement are in fact core elements in traditional meditation practices, and meditation types are often defined according to their attentional characteristics (Andresen, 2000; Lutz et al., 2008).

Nevertheless, it is also known that paying “too much attention” to our movements can disrupt performance, especially if the skill is well practiced and performed following an automatic *routine* (Flegal and Anderson, 2008). For example, being conscious of our feet when quickly walking down a flight of stairs can make one trip and fall. There is hardly an athlete, a musician, or a public speaker who could not give an example of “choking,” especially when he or she was trying hard to concentrate and do well (Beilock et al., 2002). It is thus possible that heightened attention to body movements through MBSR techniques may be good for certain types of movements only.

TWO MODES OF ACTION PLANNING FOR ADAPTED INTERACTION WITH THE WORLD

It is the case that there are two principal ways in which one can interact with the environment. One may carry out movements to manipulate the environment in order to produce desired environmental effects. In such an intentional state, one may grasp a plastic cup to squash it intentionally before placing it in the bin. In such *intention-guided* case, the force level applied through the fingertips is increased voluntarily to reach the desired state of a *flattened cup*. On another hand, actions may be carried out to accommodate environmental demands: grasp the cup to move it and make place for a hot dish. In this *stimulus-driven* case, the force level applied through the fingertips is increased automatically, without

further thought. There is now convincing scientific evidence that intention-guided actions, on the one hand, and stimulus-driven actions, on the other hand, are controlled by different neural-psychological pathways (Herwig et al., 2007; Tubau et al., 2007; Casal et al., 2009).

The activity of these pathways has been shown to rely on different kinds of memory traces (Elsner and Hommel, 2001). The stimulus-based control mode represents a case of a “prepared reflex” (Hommel, 2000), for which the cognitive system is prepared to respond to particular, typically highly response compatible stimuli in a more or less automatic fashion. Accordingly, not much of the sequence is actually learned and little attention resources are thought to be required. In contrast, actions following an internal desire will produce a selected series of actions, and it has been suggested that the intention-based control mode relies on the construction of an action plan (Luria, 1962; Maasen et al., 2003), which consists in the planning of ordered sequences of representations of action effects (Hommel, 1996). Intention-based control implies that plan-related representations (i.e., action-triggering signals) are internally generated (Zelazo et al., 1999) and as such, require attention for optimal preparation and fluent execution.

CONTRASTING LEVELS OF MOTOR ATTENTION IN FUNCTION OF ACTION MODE

To gain a direct insight on exactly what aspects of movement planning or executing required attention resources, we used a dual task paradigm to probe the levels of attention needed for gripping actions (Delevoeye-Turrell et al., 2006). In an implicit scaling condition (stimulus-driven), subjects were required to reach for an object and move it across the table. Because there was an objective to the task, the subjects' focus of attention was oriented toward the final goal of the task and thus, GF was automatically scaled to the object's weight. In the explicit scaling condition (intention-based), the subjects' task was to reach for the object and grip it harder, i.e., increase explicitly the level of GF applied to the surfaces of the object. An auditory probe could occur before or during action execution, and subjects were instructed to react as fast as possible to the probe (with their foot) without interrupting the hand-task. This dual task paradigm provided the means to evaluate the amount of attention used for motor *planning* (with a probe that occurred between the start of the trial and movement onset) and for motor *execution* (with a probe that occurred during the movement) as a proportion of reaction time augmentation (Kahneman, 1973). Results showed that there was a significant increase in reaction times for all types of actions under dual task compared to single task conditions, suggesting that all grip actions required a minimal amount of attention both for planning and execution. Nevertheless, less attention was overall required for the planning of stimulus-driven actions compared to that used for intention-based actions.

Following the idea that more attention should lead to increased levels of motor consciousness (i.e., the explicit knowledge of physical responses), we predicted in the present study that intention-based actions would be associated to a higher level of motor consciousness compared to stimulus-driven actions. Under the effects of MBSR meditation, motor consciousness should be maximal as subjects focus more attention resources during action planning

and execution, with however lower reproducing capacities in the stimulus-based mode of action planning. Finally, because attention is required for even the simplest gripping task, the decrease in attention availability (through the use of a dual task paradigm) should impair the levels reached of motor consciousness by all our participants in both modes of action planning.

MATERIALS AND METHODS

PARTICIPANTS

Participants were recruited in the different departments of the University of Lille3 (psychology; musicology; arts) and at the symphony orchestra of Lille (*Orchestre Nationale de Lille*). They were divided in two groups in function of their knowledge and expertise in mindfulness MBSR meditation technique. The group of MBSR-experts were 10 right-handed professional or amateur musicians who practiced daily mindfulness meditation (six males; mean age 40.8 years, SD 11.2, range 23.6–56.2; years of education 14.9, SD 2.6). The mean level of mindfulness meditation experience was high (mean period of 12.2 years, SD 5.2, range 3.0–23.5). Twenty right-handed professional or amateur musicians (eight males; mean age 36.0 years, SD 16.1, range 19.3–62.4; years of education 13.9, SD 3.0) also took part in this study as controls; none had any experience in mindfulness meditation. There were no statistical differences between Groups for Age [$t(1, 28) = 0.841$; $p = 0.407$], years of education [$t(1, 28) = 0.898$; $p = 0.379$], and years of musical practice [$t(1, 28) = 0.871$; $p = 0.436$]. All subjects were naïve to the specific purpose of the experiment.

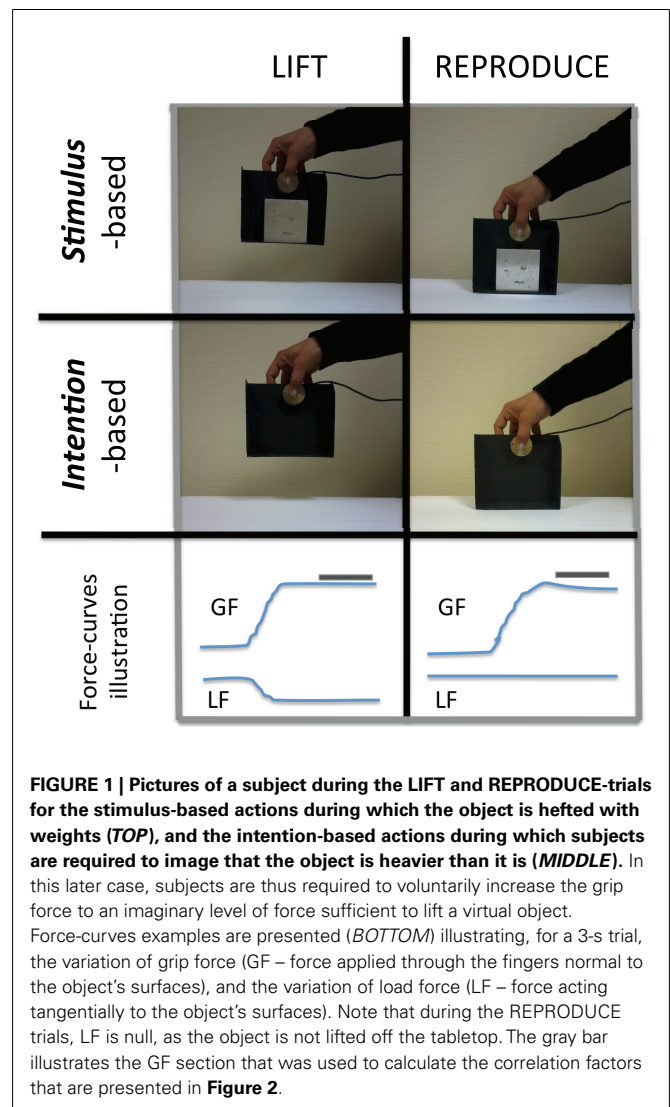
None of the participants had any known psychological or neurological deficits. They had normal or corrected-to-normal vision. The local ethics committee approved the experimental protocol and all participants provided written informed consent after the procedure had been fully explained. Participants were tested individually, in an isolated room and participated in a single experimental session lasting approximately 45-min.

APPARATUS

Subjects were seated facing a table on which was placed an object. With their dominant right hand, subjects used a precision grip with thumb on one side opposed by three fingers to lift and hold the object (weight: 65 g) that had metal-surfaced plates (see **Figure 1**). A circular load cell (*TIA Mini 40 Force/Torques* transducer; weight: 50 g; diameter: 40 mm; width: 15 mm) was mounted within this object to measure the GF (in Newton) produced by the digits normal to the vertical grasp surfaces. This six-axis load cell also provided the means to measure load force fluctuations (LF in Newton) that acted tangential to the object's surfaces, induced by gravity. The load cell was connected to a laptop computer and the data collection was run through custom-made *Labview* software at a sampling frequency of 1000 Hz.

EXPERIMENTAL PROCEDURE

On each trial, participants were required to lift the object and hold it immobile, in mid air, for approximately 3 s (**Figure 1** – left). After this LIFT trial, they were instructed to reproduce the GF level they thought they had used on the previous trial to hold the object in mid air (**Figure 1** – right). For this REPRODUCE trial, participants were required to maintain the object on the table,



thus applying only forces normal to the object's surfaces. After each pair of trials, the experimenter checked the LF curves to verify that the subjects had followed instructions, i.e., had not lifted the object, even slightly, during the REPRODUCE trial. When the conditions had not been met (LF varied above 0.5 N – see curves in the bottom panel of **Figure 1**), the pair of trials was discarded; the trial was represented to the participant at the end of the block. The start of each trial was signaled by an auditory beep. The time interval between the end of the LIFT and the start of the REPRODUCE trials was 1.5 s; the time interval between pairs of trials was 5 s.

To gain an insight in the role played by the subjects' mode of action planning on motor consciousness, two modes of action planning were proposed. In the *stimulus-based* mode, subjects lifted an object that was hefted with a light, a medium-heavy, or a heavy weight in order to afford objects of 200, 400, and 800 g. Hence, the level of active GF required to lift the object depended directly on the levels of passive force induced to the object by the environment (gravity). In the *intention-based* mode, the subjects'

task was to lift the very light object (115 g was the mass of the empty object) and to imagine that the object was light, medium-heavy, or heavy. Hence, under this condition, the active GF scaling depended solely on the force scaling that subjects voluntarily decided to apply. The order in which the two modes were performed was randomly assigned to the subjects who then maintained the same order for the three attention blocks.

To manipulate the quantity of attention resources allocated for the planning phase of the LIFT trial, subjects performed the task in three different attention block conditions. In the *Neutral* condition, subjects performed the LIFT/REPRODUCE pairs of trials without further constraints. For all participants, this was the first condition experienced. Then, either a Heightened (A++) or a Diminished (AA--) attention block was performed. Under the *Diminished* condition, subjects performed a dual task situation for which they were required to count backward by 7 starting from a three-digit number (e.g., 231). Subjects were required to count as fluently as possible at a tempo of 1 countdown per second, without making a mistake. This count down procedure was performed on the LIFT trial only. The REPRODUCE trial was performed without further constraints. Subjects performed the countdown in their native language to facilitate the task. In this study, five MBSR-experts and two controls performed the task in English. The other participants performed the countdown in French.

Prior to the *Heightened* condition, subjects were asked to relax and become aware of the environmental noises (people walking in the hallway; water dripping in the pipes; airplane passing) in order to anchor themselves in the present moment. Then, the experimenter encouraged all participants to close their eyes and to use the *dominant hand* as specific target of meditation on which to focus attention. If the mind started to wander, subjects were encouraged to simply direct the mind back toward the object of attention with a sense of “friendliness” without judgment. A 5-min meditation program was proposed in order to provide the necessary time for all subjects to become calmer with a slowing down of breathing rhythm and of discursive thought. Without talking, when subjects felt ready to pursue, they opened the eyes and the experimental block was launched.

Subjects performed five pairs of trials for each mass (light; medium-heavy; heavy), in each action mode (stimulus-based; intention-based) under each attention condition (neutral; diminished; heightened) for a total of 90 trials. Prior to the start of the experimental session, it was emphasized that there would be quite a large number of trials to perform (a minimum of 100 trials), and that subjects should relax their grip as best they could to minimize muscle fatigue during the LIFT trials. Subjects were assigned to one of the two experimental groups in function of their knowledge in mindfulness meditation.

At the end of the session, participants were asked to fill in a brief questionnaire to report on their subjective experience of the different attention conditions. In addition, they were asked to score between 1 and 10 the accuracy of reproduction of the force level they thought to have reached, distinguishing between the action modes as well as the attention conditions. Finally, subjects were briefed about the overall aim of the experiment and were thanked for their participation.

DATA ANALYSIS

To describe general performance, mean GF levels applied 1.5 s after the start of each trial for a 500 ms-duration was calculated. In the LIFT trials, this time period fell during the time interval for which the object was held immobile in mid air; in the REPRODUCE trials, this time period fell within the time interval for which subjects were indicating force levels used in the previous LIFT trial (see gray horizontal bar in **Figure 1** – bottom). To analyze the level of motor consciousness reached by each subject, Pearson correlation analyses were then conducted between the GF level measured for each pair of LIFT and REPRODUCE trials. Finally, these correlation measures were submitted to a 3 by 2 repeated measures Analysis of Variance with Attention (Neutral; Diminished; Heightened) and Mode (Stimulus-based vs. Intention-based) as within subject factors. When required, corrected Scheffé *post hoc* analyses were used. The significance level was set at $p = 0.05$.

RESULTS

All participants performed the motor tasks under the different attention conditions without apparent difficulty. They also expressed pleasurable experiences in the heightened attention condition, reporting having experienced “calmness” and “control” during the action of lifting.

ANALYSIS OF THE GF LEVELS USED IN THE LIFT TRIALS

Statistical analysis on the mean GF used in the LIFT trials revealed an absence of Group differences [$F(1, 42) = 2.725$; $p = 0.106$], with similar force levels for the controls (14.7 SD 0.7 N) and the MBSR-experts (12.2 SD 1.4 N). Furthermore, subjects distinguished well between the three object masses [$F(2, 42) = 33.584$; $p = 0.001$]. For all masses, GF levels were slightly higher in the intention-based mode compared to that observed in the stimulus-based mode but this slight over estimation did not reach significance [$F(1, 42) = 1.186$; $p = 0.282$]. Finally, similar GF levels were used under the different attention conditions [$F(2, 42) = 1.561$; $p = 0.216$]. The detailed values for these results are presented in **Table 1**.

EFFECTS OF ATTENTION AND PLANNING-MODE ON MOTOR CONSCIOUSNESS

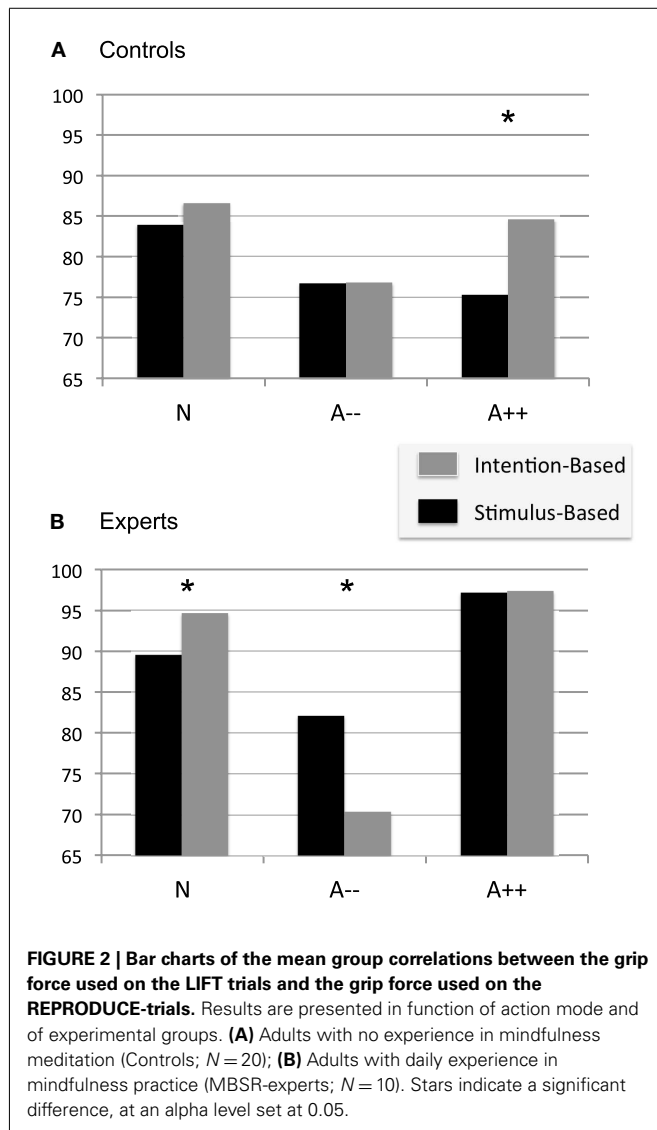
In the second series of analyses, we considered the correlation between the GF levels used during the LIFT trial and the motor judgment that was given by the subjects immediately afterward, during the REPRODUCE trial. The closeness of fit was taken as an indicator of the level of motor consciousness reached by each participant and thus, correlation values were calculated at an individual level for each experimental condition. A repeated measures ANOVA was then used to reveal the effects of Mode (stimulus-based; intention-based) and Attention (Neutral; Diminished; Heightened) on the levels of motor consciousness in function of expertise in MBSR meditation techniques. Correlation values (r^2) are reported in % of variance explained, and are presented in **Figure 2A**, for the controls and **Figure 2B** for the MBSR-experts.

Participants were able to reproduce movement kinetics with similar force modulation patterns in the LIFT and in the REPRODUCE trials, under all conditions. However, their level of motor consciousness varied significantly from one individual to another

Table 1 | Details of the mean results obtained for the grip force levels (in Newton) used for the different action modes and under the different attention conditions.

	Neutral (A)		Diminished (A--)		Heightened (A++)	
	Stimulus	Intention	Stimulus	Intention	Stimulus	Intention
Light	5.9 (2.8)	5.8 (3.4)	8.8 (3.3)	8.5 (3.3)	5.9 (3.2)	4.6 (3.9)
Medium	10.7 (1.3)	13.7 (1.5)	13.7 (1.5)	13.0 (1.5)	11.7 (1.4)	12.2 (1.7)
Heavy	17.8 (1.5)	23.0 (1.8)	20.0 (1.7)	23.5 (1.7)	20.4 (1.6)	22.3 (2.0)

There were no significant differences between the groups. Thus, results for the 30 participants are presented here averaged together.



with correlation values ranging from $r^2 = 43.1\%$ (lowest of the controls) to $r^2 = 98.9\%$ (the highest of the MBSR-experts). Motor consciousness was overall greater in the MBSR-experts ($r^2 = 87.4$ SD 2.2%) than in the controls ($r^2 = 80.1$ SD 4.3%). Results are thus presented for each group separately in the following section.

For the controls, motor consciousness was similar for the two action modes [$F(1, 38) = 2.302$; $p = 0.146$], and the effect of

attention failed to reach significance [$F(1, 38) = 2.807$; $p = 0.073$]. But if anything, motor consciousness was worse in both Heightened and Diminished attention conditions compared to that seen in the Neutral condition (see **Figure 2A**).

For the MBSR-experts, both the effects of Attention [$F(2, 18) = 23.466$; $p = 0.001$] and the interaction Mode $\times$ Attention were significant [$F(2, 18) = 7.570$; $p = 0.004$]. In the Neutral condition, motor consciousness was greater in the intention-based mode (94.6 SD 1.0%) than in the stimulus-based mode (89.5 SD 1.8%). With Heightened attention, motor consciousness in the stimulus-based mode increased and there was then an absence of differences between intention-based (97.3 SD 0.9%) and stimulus-based modes of action planning (97.1 SD 0.5%). This result suggests that, contrary to the controls, mindfulness-based meditation helped participants increase the level of motor consciousness even for those actions that were programmed in a more automatic fashion (see **Figure 2B**). Finally, the dual task paradigm led to a significant loss of motor consciousness in both types of action modes, but the loss was significantly more drastic for those actions performed in the intention-based mode (70.4 SD 4.4%) than those planned in the stimulus-based mode (82.1 SD 4.3%). Under this Diminished condition, motor consciousness was of similar degree in the controls and the MBSR-experts.

SELF-EVALUATION OF MOTOR CONSCIOUSNESS

When asked to provide a self-evaluation of their capabilities to perform the REPRODUCE trials, all subjects thought that they had performed under the stimulus-based mode rather well (7/10 on a Likert-type rating scale; range 5–9). All subjects reported having great doubts for those trials performed under the intention-based mode (3/10 on a Likert-type rating scale; range 2–5). For the effects of attention, the self-evaluation reports followed a similar pattern of results in both experimental groups. Whatever the level in MBSR meditation technique, participants thought to have done worse in the Diminished condition and best in the Heightened condition. To note, is the fact that professional musicians ($N = 12$) were those who were overall the most accurate in the self-evaluation exercise.

These results suggest that whatever the level of MBSR-expertise, one can reach a certain degree of motor consciousness of movement kinetics without being self confident about the accuracy of the judgment. These findings suggest a pre-reflective nature to the mechanism and stress furthermore the importance of using non-verbal tasks to investigate levels of consciousness reached for motor-sensory body experiences.

DISCUSSION

Considering the pre-reflective nature of body experiences, reports in the literature have defended the idea that only limited aspects of motor acts can be consciously perceived. Nevertheless, when using appropriate methods, i.e., non-verbal, it was possible here to show that individuals have in fact access to a significant extent of the motor-sensory content of motor actions. Our main findings are that (1) with free allocation of attention (neutral condition), adult individuals can remarkably reproduce force levels that are automatically scaled to an object's weight. (2) The level of motor consciousness is severely impaired when attention is withdrawn. (3) Increasing the focus of top-down attention (heightened condition) does not increase motor consciousness in controls; on the contrary, in the case of automatic motor adjustments (stimulus-based actions), increased top-down attention can hinder the emergence of body awareness. (4) Contrasting results are obtained for mindfulness experts with enhanced motor consciousness under Heightened focus of attention for motor adjustments that were both voluntarily (intention-based) and automatically scaled (stimulus-based). These later results suggest that MBSR meditation is not simply an increased state of attention but may also play on the threshold of conscious perception for bottom-up motor-sensory information. In the following sections, we detail these results by considering the role of attention, intention, and mindfulness meditation, respectively in the theoretical context of a *tripartite model of consciousness*.

AN IMPLICIT MEASURE TO EVALUATE MOTOR CONSCIOUSNESS

Motor consciousness is by definition an “inner subjective state” (Searle, 2000) and thus, “it is not directly accessible from a third person viewpoint.” Following this idea, we asked subjects to focus on the dynamical rather than on the observational aspect of their motor output. The basic assumption of such a reproduction paradigm was that the movement characteristics that can be reproduced are those of which we are aware of, at a pre-reflective level, and that the modulation of attention resources will help emerge to consciousness only those body motor-sensory experiences, which possess a constructed representational content.

With freely oriented attention (neutral condition), participants were able to reproduce the force levels used with correlations (r^2) greater than 70% of total variance. This observation indicated that the reproduction task was based on a true content of body experience. It has been assumed in the literature that subjects' perceptual awareness (their explicit knowledge of *action goal*) is equivalent to their motor awareness (their explicit knowledge of their *physical response* – for further discussion, see Coello and Delevoye-Turrell, 2007; Johnson et al., 2002). But, this is not the case as we demonstrated in the present study that all subjects had good reproduction capabilities without explicit knowledge of action outcome. This important result confirms a previous study that also used manual responses to assess motor consciousness more accurately (Johnson and Haggard, 2005).

THE IMPORTANCE OF ATTENTION FOR MOTOR CONSCIOUSNESS

Our findings confirmed the hypothesis that attention resources are required to reach good levels of motor consciousness. In a dual task paradigm, subjects were required to perform a cognitive highly

demanding count down task while preparing and performing the lift action. GF levels were reproduced with greater errors under this dual task condition (70–75%) compared to that observed under the single task condition (85–95%). These results suggest that attention allocation during action preparation and execution is required in order to access the content of body motor-sensory experiences, at a later moment. Without these cognitive resources, one loses in our simple case up to 25% of information content. This may explain why pathologies associated to attention deficits are often characterized by abnormal conscious experiences, e.g., schizophrenia (Davie and Freeman, 1961; Sass and Parnas, 2003; Voss et al., 2010) and bipolar patients (Bartolomeo, 2007; Lanyon and Denham, 2010).

Interestingly, and contrary to that hypothesized, subjects did not take advantage of the augmented attention allocation for better motor consciousness. If anything, augmented attention lead to a decrease in the accuracy of force reproduction. These results confirmed the conclusions reached in many sports oriented studies that declare that motor routines must be learned and performed without attention allocated to motor planning (Forkstam and Petersson, 2005; Janacek and Nemeth, 2012). As such, it has been established that attention must be geared to external goals for high motor performance in order to maintain all attention away from those brain mechanism that automatically organize and execute action sequences (Wulf and Prinz, 2001; Wulf et al., 2010a). Hence, heightened attention for motor planning – through for example MBSR meditation techniques – may not be adequate for those actions that depend on brain processes that are by nature automatic and unconscious.

MOTOR CONSCIOUSNESS DEPENDS ON THE INTENTIONAL STATE OF ACTION PLANNING

It is the case that the negative effect of heightened attention on motor consciousness was observed in the controls only for those actions that required an automatic scaling of GF, on the basis of the true weight of the object, i.e., for stimulus-based planned actions (Figure 2A). Indeed, in those cases for which force scaling was set on the basis of an intentional and explicit motor goal, augmented attention to the task-preparation and execution did not interfere with the overall process; The content of body experiences was accessed in the following trial as well as that observed in the neutral condition. These results confirm that (1) the mechanisms for the planning and execution of motor actions are of a different nature depending on the intentional state of the subjects and that (2) attention to action will have a different effect on motor consciousness depending on the explicit level in which the performer is engaged.

Other studies have also reported that the degree of motor consciousness depends on the subjects' intentional state (Castiello et al., 1991; Beilock et al., 2002, 2006). For example, using a movement reproduction paradigm in a double-step pointing task, Johnson et al. (2002) had subjects follow a target (*pointing*) or voluntarily move in the opposite direction (*anti-pointing*). After each initial trial, an indicator of the subjects' awareness was obtained by asking subjects to reproduce the movement they thought they had previously executed. Results confirmed that subjects were able to make rapid corrections to an ongoing pointing movement, in

response to a target shift. For anti-pointing trials, the corrections occurred later than the corrections toward the target in standard pointing. This pattern of results is consistent with the idea that two different mechanisms are involved: (1) a relatively slow neuronal circuit via the frontal cortices for intentional corrections, (2) a faster parietal connection for automatic corrections (Day and Lyon, 2000).

The interesting finding however was that subjects were able to perceive and reproduce the trajectories of the pointing corrections even in absence of a conscious perception of a target shift, indicating once more a significant difference between perceptual and motor consciousness. In addition, there was a net difference in the quality of the content of motor awareness. Indeed, for standard pointing (automatic pointing), subjects systematically underestimated their correction-capabilities, with important time delays (>30 ms) and diminished awareness of the spatial characteristics of the correction. In contrast, for the anti-pointing trials (intentional pointing), subjects reproduced the corrections close to that truly performed with very little awareness time-delay. Thus, subjects had a better conscious recollection of those corrections made in the intention-based mode of action correction. Our findings lead to a similar conclusion but in the force domain of motor control, during a highly ecological task of manipulating an object with a precision grip. Hence, it is possible to suggest a generalization principle that subjects possess different levels of motor consciousness of their body in action, depending upon the nature of the planning-mode used to prepare and execute that action. More specifically, intention-based actions would be sub-conscious but would be more accessible to a conscious state of processing than the more automatically triggered movements.

MINDFULNESS IS NOT ALLOCATION OF ATTENTION TO THE CONTENT OF BODY EXPERIENCES

An often-cited definition of mindfulness is *paying attention in a particular way*: on purpose, in the present moment and non-judgmentally (Kabat-Zinn, 1994). It has been proposed that this definition embodies three principle axioms (Shapiro et al., 2006): (1) *on purpose or intention*, (2) *paying attention or attention*, (3) *in a particular way or attitude*. As such, intention, attention, and attitude would be three interwoven aspects of a single cyclic process and would occur simultaneously. Mindfulness would be this moment-to-moment process. Very little work has been geared to the proposal of a comprehensive theoretical model of what happens under mindfulness meditation. Nevertheless, Hölzel and collaborators have recently proposed that mindfulness meditation would play upon several components and would especially change the cortical relation between (1) the anterior cingulate cortex for attention regulation (Hölzel et al., 2007) and (2) gray matter concentration in the temporo-parietal junction (Hölzel et al., 2011), which may modify the levels of body awareness.

Experimentally, meditation has shown to provide individuals with the capacity to increase cognitive resources both in healthy subjects (Jain et al., 2007; van den Hurk et al., 2010) and in pathological patients (Britton et al., 2010; Crane-Okada et al., 2012). Meditation has also revealed to increase body awareness (Kerr et al., 2008). In the present study, results are in line with these general ideas and showed that already in the neutral condition, participants with high experience in MBSR meditation techniques

revealed greater capacities in reproducing a force level than those who had no meditation expertise.

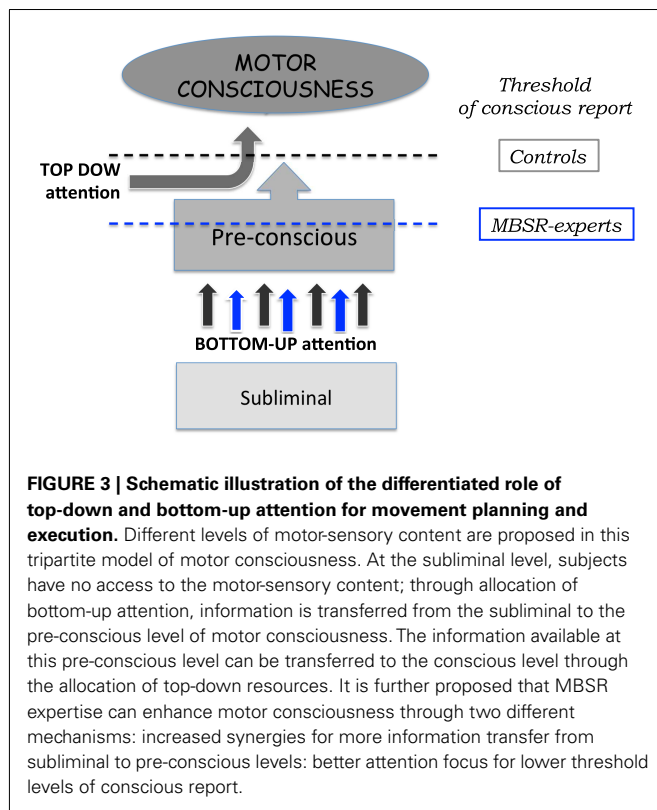
Interestingly, even for MBSR-experts, when attention resources were reduced through dual task manipulation, subjects revealed weaker levels of motor consciousness than that measured in the neutral condition. This effect was drastic for the intention-based mode that impaired motor awareness to such an extent that controls and MBSR-experts revealed similar levels of motor consciousness under this condition only. Finally, in the heightened attention condition. Results revealed that the effect of *paying attention in a particular way* increased motor consciousness both in the intention-based mode and in the stimulus-based mode of action planning. This was possible to such an extent that performances reached almost perfection, with correlation values being all over 90%, and reaching 99% in 2 of the participants. It would now be important in forthcoming studies to further confirm the present results (1) by testing a larger group of meditation experts and (2) by controlling the type and level of meditation expertise developed on a daily basis.

In the final section, we discuss our results in the light of a possible neuro-cognitive model that may help gain a better understanding of the contrasting effects of attention and meditation on motor consciousness.

A TRIPARTITE MODEL TO EXPLAIN THE EFFECTS OF MEDITATION ON THE EMERGENCE OF SUBLIMINAL SENSORY INFORMATION

Instead of the classical binary separation between non-conscious and conscious processing, Dehaene et al. (2006) introduced a tripartite distinction between subliminal, preconscious, and conscious processing. More specifically, the key idea is that, within non-conscious states, it makes a major difference whether the stimuli invisibility is due to a limitation in bottom-up stimulus strength, or by the temporary withdrawal of top-down attention. The first case corresponds to subliminal processing; the second to preconscious processing. Following this idea, motor consciousness would be the resultant of the interaction between bottom-up mechanism for body sensations (depending on the strength of motor-sensory content) and the amount of top-down attention allocated to the task, at a given moment in time.

It has been proposed that the subliminal level of processing (etymologically “below the threshold”) would be a condition for which information is inaccessible to consciousness because this bottom-up activation is insufficient to trigger a large-scale reverberating state, in a global network of neurons, with long-range axons. The preconscious level would be a neural process that potentially carries enough activation for conscious access, but is temporarily buffered in a non-conscious store because of a lack of top-down attentional amplification, e.g., owing to transient occupancy of the central workspace system during dual task conditions (Sigman and Dehaene, 2005, 2008). Even strong sensory stimuli could remain temporarily preconscious. With top-down attention focus, these preconscious stimuli could become conscious and thus, be explicitly reported by a subject. At the neurocomputational level, preconscious processing is proposed to involve resonant loops within medium range connections, which maintain the representation of a motor-sensory content temporarily active in a sensory buffer for a few hundred milliseconds. A preconscious stimulus might ultimately achieve conscious



access once the central workspace is freed. It might however never gain access to conscious processing if the preconscious buffer is erased before receiving sufficient top-down attention. An illustration of this tripartite distinction is proposed in **Figure 3**.

We propose that the experimental data reported in the present study can be placed within this framework of consciousness. For actions performed in the stimulus-based mode, GF is automatically scaled to the object weight. Little bottom-up attention is geared to the task and thus, motor-sensory afferences from the gripping fingers arrive and remain primarily in the subliminal state. When during the REPRODUCE trial, subjects try to indicate the level of GF used in the previous LIFT trial, large reproducing errors are performed because little motor-sensory content has reached levels of explicit motor consciousness, even after focusing top-down attention to the task. This mechanism would explain why subjects know that they are agent of the action, and they know what final goal they achieved (*"I lifted the object to this height"*) but they have very little sensation content of the acting fingers upon the object. Because of the automaticity of the gripping action, with heightened top-down attention, large interferences occur between top-down and bottom-up attentional systems, which in turn affects the transition of motor-sensory information from subliminal to the preconscious state of processing.

For actions performed in the intention-based mode, top-down attention is used to scale voluntarily the GF levels in accordance to the internal representation of the weight of the imaginary object. In this case, in addition to bottom-up attention for muscle activation, top-down attention is also used to maintain a vivid representation to guide action planning and execution. This double attention activity would allow for a rich motor-sensory

content to be buffered in the preconscious level of processing. With larger and more precise content, the REPRODUCE trial would be performed more accurately. As confirmed by our data, the heightened attention condition may not change performance outcome as top-down attention is allocated to the task whether explicitly through instruction or implicitly due to task demands. In the present study, the absence of differences in the controls between motor consciousness for intention and stimulus-based actions in the neutral condition may be due to the simplicity of the gripping task. Hence, our interpretations need now to be verified by replicating the present findings in a larger sample group and especially, using a more complex task that associates new experiences of whole body movements.

Finally, the power of meditation would lie within the possibility to increase both types of attention in order to optimize the quantity and quality of motor-sensory content. For the bottom-up circuit, meditation would lead to increased synergies during muscle activation, which in turn would code sensations directly into the preconscious level of information processing. As such, movements that are planned in the stimulus-based mode would be associated to sensory contents that are as vivid than that obtained for those actions planned intentionally. With more focused energies in the top-down areas of the brain, a lowering of the threshold level of conscious report could in addition occur in the most experts (**Figure 3** – right), leading to a global level of motor consciousness close to perfection. Using a combination of attention paradigms, Jensen et al. (2012) have recently suggested a similar interpretation of MBSR-enhancement in reaction time based measures.

CONCLUSION

The results reported here confirm that mindfulness increases the sensory experiences of body during motor action execution. The intentional state in which the action is produced plays an important role in the level of motor consciousness that subjects can achieve. This is probably due to the fact that intention-based actions require that plan-related representations be internally generated. With more top-down attention, greater amounts of sensory information are buffered at a preconscious level of motor-sensory processing. As described in the tripartite model of consciousness (Dehaene et al., 2006), top-down attention would play the role of an amplifier of bottom-up sensations that remain nevertheless preconscious in most everyday activities. Meditation techniques significantly enhance bottom-up sensory information processing of ongoing movements, enabling sensory information to transfer directly from subliminal to preconscious levels of the brain. When top-down attention is then directed toward these preconscious senses of body experiences, total consciousness of our body in action can emerge for even the simplest of movements.

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Spatial frequency tuning during the conscious and non-conscious perception of emotional facial expressions – an intracranial ERP study

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Previous studies have shown that complex visual stimuli, such as emotional facial expressions, can influence brain activity independently of the observers' awareness. Little is known yet, however, about the "informational correlates" of consciousness – i.e., which low-level information correlates with brain activation during conscious vs. non-conscious perception. Here, we investigated this question in the spatial frequency (SF) domain. We examined which SFs in disgusted and fearful faces modulate activation in the insula and amygdala over time and as a function of awareness, using a combination of intracranial event-related potentials (ERPs), SF Bubbles (Willenbockel et al., 2010a), and Continuous Flash Suppression (CFS; Tsuchiya and Koch, 2005). Patients implanted with electrodes for epilepsy monitoring viewed face photographs (13° × 7°) that were randomly SF filtered on a trial-by-trial basis. In the conscious condition, the faces were visible; in the non-conscious condition, they were rendered invisible using CFS. The data were analyzed by performing multiple linear regressions on the SF filters from each trial and the transformed ERP amplitudes across time. The resulting classification images suggest that many SFs are involved in the conscious and non-conscious perception of emotional expressions, with SFs between 6 and 10 cycles per face width being particularly important early on. The results also revealed qualitative differences between the awareness conditions for both regions. Non-conscious processing relied on low SFs more and was faster than conscious processing. Overall, our findings are consistent with the idea that different pathways are employed for the processing of emotional stimuli under different degrees of awareness. The present study represents a first step to mapping how SF information "flows" through the emotion-processing network with a high temporal resolution and to shedding light on the informational correlates of consciousness in general.

Keywords: consciousness, emotional facial expressions, spatial frequency

INTRODUCTION

The look on someone's face can speak volumes. Emotional facial expressions convey a wealth of information, such as cues about a person's state of mind or warning signs of potentially threatening situations (e.g., reflected by fear) or materials (e.g., reflected by disgust). Human faces and brains are thought to have co-evolved to be efficient transmitters and decoders of emotional signals, respectively (Smith et al., 2005; Schyns et al., 2007, 2009). Moreover, it has been claimed that emotional information from a face can be extracted without the observer's awareness (see Tamietto and De Gelder, 2010, for a review). Numerous studies have shown that face stimuli rendered "invisible" using techniques such as backward masking (e.g., Smith, in press), binocular rivalry (e.g., Williams et al., 2004), or Continuous Flash Suppression (CFS; e.g., Tsuchiya and Koch, 2005; Jiang and He, 2006; Jiang et al., 2009) can be processed sufficiently for the healthy brain to distinguish neutral from emotional expressions, including fear, disgust, and happiness. Differential brain responses to both invisible and visible

facial expressions have been measured, for instance, using functional magnetic resonance imaging (fMRI; e.g., Williams et al., 2004; Jiang and He, 2006) and surface event-related potentials (ERPs; e.g., Jiang et al., 2009; Smith, in press). Thus, it is now widely thought that facial expressions can influence neural activity and behavior independently of awareness, and that they constitute a stimulus class well suited for investigating differences between conscious and non-conscious perception in the human brain.

One fundamental question, which is the focus of the present article, concerns which "low-level" aspects of facial-expression signals modulate brain responses as a function of awareness. Faces are complex stimuli that contain information at various spatial frequencies (SFs). Broadly speaking, low SFs represent the coarse information in an image (e.g., luminance blobs), whereas high SFs represent the fine-grained information (e.g., fine wrinkles in a face). It is well known that the visual system filters any retinal input with multiple quasi-linear band-pass filters, each tuned to a specific range of SFs (see De Valois and De Valois, 1990,

for a review). The contribution of different SFs to the perception of facial expressions has been investigated in a number of fMRI (Vuilleumier et al., 2003; Winston et al., 2003b; Morawetz et al., 2011) and surface ERP (Holmes et al., 2005; Pourtois et al., 2005; Schyns et al., 2007, 2009; Vlamings et al., 2009) studies. However, the studies led to mixed findings and were limited in several respects. For instance, the low temporal resolution of fMRI and the low spatial resolution of surface ERPs did not allow for conclusions to be drawn about the precise temporal dynamics of SF processing in specific brain regions. Moreover, the SF filtering methods that were employed (low-pass, high-pass, or band-pass filtering) provided only a crude estimate of SF tuning. Also, the studies were restricted to consciously perceived face stimuli. Therefore, not much is known yet about the “informational correlates” of consciousness in this context – i.e., precisely which SFs are correlated with localized brain signals during the conscious vs. non-conscious perception of emotional expressions.

The aim of the present study was to examine which SFs are correlated with brain signals in specific regions of the emotion-processing network under different awareness conditions. We had the opportunity to record intracranial ERPs from the insula and, to a lesser extent, from the amygdala of patients undergoing monitoring for medically intractable epilepsy. The insula and amygdala have previously been associated with the processing of disgust and fear, respectively (e.g., Adolphs et al., 1994, 1995; Phillips et al., 1997, 1998, 2004; Krolak-Salmon et al., 2003, 2004; but for evidence that the insula also responds to fear, see, e.g., Morris et al., 1998, and for evidence that the amygdala also responds to disgust, see Winston et al., 2003a; Fitzgerald et al., 2006; Van der Gaag et al., 2007). Here, we traced which SFs in disgusted and fearful faces modulate activation in these two interconnected brain structures over time. Our study employed a novel combination of CFS (Tsuchiya and Koch, 2005), intracranial recordings, and the SF Bubbles technique (Willenbockel et al., 2010a). We will elaborate on the three methods in the following paragraphs and briefly review some of their applications in previous studies.

CFS is a powerful method to render visual stimuli invisible (Tsuchiya and Koch, 2005). One of its main strengths is that it allows for suppressing stimuli from awareness for a long duration (i.e., up to several seconds). A second strength of CFS is that the onset of the suppression can be precisely timed. CFS involves presenting a static image to one of the observer's eyes, while dynamic high-contrast noise (e.g., Mondrian patterns flashed at 10 Hz; Tsuchiya and Koch, 2005) is presented to the other eye. As a result of this dichoptic stimulation, typically only the noise is consciously perceived; the static stimulus is suppressed from the observer's awareness but nevertheless processed in the brain (e.g., Tsuchiya and Koch, 2005; Jiang and He, 2006; Jiang et al., 2009). Using CFS and fMRI, Jiang and He (2006) found that suppressed fearful compared with scrambled faces elicited significant activation in the fusiform face area, superior temporal sulcus, and the bilateral amygdalae. The amygdalae were also more activated by fearful than by neutral faces, independently of awareness. Using CFS in combination with surface ERPs, Jiang et al. (2009) observed significant amplitude differences to suppressed fearful vs. scrambled faces beginning at 140 ms and to suppressed fearful vs. neutral

faces starting at 220 ms after stimulus onset. Overall, combining CFS with fMRI, which has a high spatial resolution, or with surface ERPs, which have a high temporal resolution, has provided important insights into the “where” or “when” of non-conscious facial expression processing – but not both aspects simultaneously. In the present study, we combined CFS with intracranial recordings, which combine some of the advantages of fMRI and surface ERPs.

It has been argued that intracranial recordings currently provide the best combination of high temporal *and* high spatial resolution, plus large anatomical field-of-view and wide frequency bandwidth (Tsuchiya et al., 2008). A number of previous intracranial ERP studies with patients undergoing epilepsy monitoring investigated the temporal dynamics of conscious emotional facial expression processing in the insula and amygdala (Krolak-Salmon et al., 2003, 2004; Pourtois et al., 2010). Krolak-Salmon et al. (2003) found amplitude differences to disgusted vs. neutral, fearful, and happy expressions in the ventral anterior insula. This “disgust effect” started at approximately 300 ms post stimulus onset when observers were engaged in an expression task and approximately 100 ms later when they performed a face-gender task. In a similar study, a “fear effect” was observed in the amygdala, starting at 200 ms in an expression task and later (after 600 ms) in a face-gender task (Krolak-Salmon et al., 2004). Pourtois et al. (2010) observed earlier amplitude differences to fearful vs. neutral faces in the amygdala, starting at 140 ms post stimulus onset. This early effect was not affected by attention but an attentional modulation of emotional responses occurred at longer latencies (after 700 ms). Intracranial ERPs were also used to study amygdala activation to masked emotional words (Naccache et al., 2005). Differences between invisible threatening and neutral words were found after 800 ms post stimulus onset. In the current study, we combined intracranial recordings with CFS to investigate the temporal dynamics of non-conscious emotional expression processing in these brain regions. Furthermore, we went beyond previous studies by examining precisely which SFs in fearful and disgusted faces modulate brain signals over time by combining intracranial recordings with the SF Bubbles technique (Willenbockel et al., 2010a).

The Bubbles method (Gosselin and Schyns, 2001) is a classification image technique that can be used to reveal which stimulus information modulates observers' behavioral (e.g., Adolphs et al., 2005; Smith et al., 2005) or brain (Schyns et al., 2003, 2007, 2009; Smith et al., 2004, 2007) responses. SF Bubbles (Willenbockel et al., 2010a) is a variant of the technique that can be employed to examine which information in the SF domain correlates with observers' responses. SF Bubbles involves randomly sampling the energy of visual stimuli at different SFs on a trial-by-trial basis and then performing a multiple linear regression on the information samples and the response measure of interest to precisely reveal the SF tuning curves for a given task. For example, Willenbockel et al. (2010a) used the technique to compare the SF tuning of upright and inverted face identification, and Thurman and Grossman (2011) employed it to investigate SF tuning for discriminating videos of human actions. In the latter study, the results obtained with SF Bubbles were directly compared with those from a more traditional band-pass filtering approach. The results from both methods were consistent but the authors stressed that SF Bubbles

offers several advantages. Specifically, SF Bubbles allows for deriving SF tuning curves – spanning the whole SF spectrum – at a much higher resolution and based on a smaller number of trials. A second strength of the method is that randomly sampling multiple SFs simultaneously on a trial-by-trial basis minimizes the risk that participants adapt to a predictable stimulus manipulation (e.g., band-, low-, or high-pass filtering or critical band masking; see Sowden and Schyns, 2006, for evidence of “channel surfing”). Moreover, SF Bubbles is unbiased in that no cutoff frequencies have to be chosen – a parameter that differs considerably between previous experiments using traditional filtering methods (for examples from the emotion-processing literature, see, e.g., Vuilleumier et al., 2003; Vlamings et al., 2009; Morawetz et al., 2011).

The combination of SF Bubbles with intracranial recordings employed in the current study allowed us to map the SF tuning of the insula and amygdala over time. In one condition, we used CFS to render SF filtered disgusted and fearful faces invisible (i.e., dynamic Mondrian patterns were presented to one eye while an “SF bubbled” emotional face was presented to the other eye). In the other condition, the filtered faces were visible (i.e., an “SF bubbled” face was presented to both eyes). Overall, this study represents a unique opportunity to shed light on the neural processing dynamics for ecologically important visual information as a function of awareness.

MATERIALS AND METHODS

PARTICIPANTS

Three patients with medically intractable epilepsy gave their written informed consent and participated in this experiment. The patients were undergoing epilepsy monitoring at the Hôpital Notre-Dame, Montréal, to guide neurosurgical treatment. For this purpose, they had electrodes implanted under a clinical protocol; the electrode locations were chosen solely based on medical considerations. Our study was approved by the CHUM (Centre Hospitalier de l’Université de Montréal) ethics committee and took place at the hospital approximately 6–10 days after the electrode implantation. The participants were naïve to the awareness aspect of the study until the debriefing after the experiment. All of them had normal or corrected-to-normal vision; further participant information is summarized in Table 1.

ANATOMICAL LOCATION OF THE ELECTRODES OF INTEREST

All patients had depth electrodes (Ad-Tech Medical Instrument Corporation, Racine, WI, USA) implanted in the insula, and additional grid, strip, or depth electrodes in other regions. One of the

patients had a depth electrode implanted in the amygdala. The implantation schemes are described in detail in a previous article (Surbeck et al., 2011). Patient 1 underwent an open microdissection of the Sylvian fissure (Type I implantation). In the anterior, medial, and posterior insula each, she had a Spencer depth electrode with a diameter of 1.1 mm, which featured four contacts along its length. The contacts were of 2.3 mm in length and spaced 5 mm apart from center to center. Two contacts per electrode ended up in the insular cortex. In the amygdala, she also had a depth electrode with four contacts (1.1 mm diameter, 2.3 mm length, 10 mm spacing). Patient 2 underwent the combined Yale-Grenoble stereotactic implantation (Type II). In the anterior and posterior insula each, he was implanted with a 10-contact Spencer depth electrode (1.1 mm diameter, 2.3 mm length, 10 mm spacing). Patient 3 underwent a Type I implantation with a new hybrid operculo-insular electrode (Ad-Tech Medical Instrument Corporation, WI, USA), among other regular subdural electrodes. The hybrid electrode combined the design of a depth and a subdural strip electrode. The depth component featuring two contacts was implanted into the insular cortex. The length of that segment was 10 mm and the diameter 1.1 mm. The length of each contact was 2.4 mm. Further information can be found in an article by Bouthillier et al. (2012).

High-resolution MRIs with 1 mm-thick slices were obtained after the implantation to determine the exact position of the electrodes (Figure 1). A 3D representation of the electrodes with respect to the patient’s brain was generated using Grid View software (Stellate Systems Inc., Montreal, QC, Canada; see also Wang et al., 2005). In the analyses presented here we included two contacts per electrode implanted either in the anterior insula (Participants 1–3) or in the amygdala (Participant 1).

ELECTROPHYSIOLOGICAL RECORDING AND STIMULUS DISPLAY

Intracranial EEG was recorded at 2 kHz using a Stellate Harmonie system (Stellate Systems, Inc., Montreal, QC, Canada). Either a subdural parietal contact (Participant 1), a subdural temporal contact (Participant 2), or the mastoids (Participant 3) served as a reference. This heterogeneity was not a concern to us because we were interested in the correlations between random SF filters and trial-by-trial voltage variations, which are robust to reference changes. The timing of the stimulus onsets was determined based on the recording of digital trigger signals by the Stellate eAmp using the eAMP Trigger Interface. A dual core 2.19 GHz PC (AMD Athlon 64 X2 4200+) and a 17” LCD display (VE700, ViewSonic, CA, USA) were used for presenting the stimuli. The gamma parameter was set to 1, to linearize the relationship between the

Table 1 | Participant information.

ID	Gender	Age (years)	Handedness	Seizure focus	Hemisphere recorded from	Number of trials
1	Female	39	Ambidextrous	Frontal operculum Temporal operculum Insula Superior temporal gyrus	Left	1920
2	Male	34	Ambidextrous	Hippocampus	Left	1823
3	Male	35	Right	Inferior frontal gyrus	Right	2007

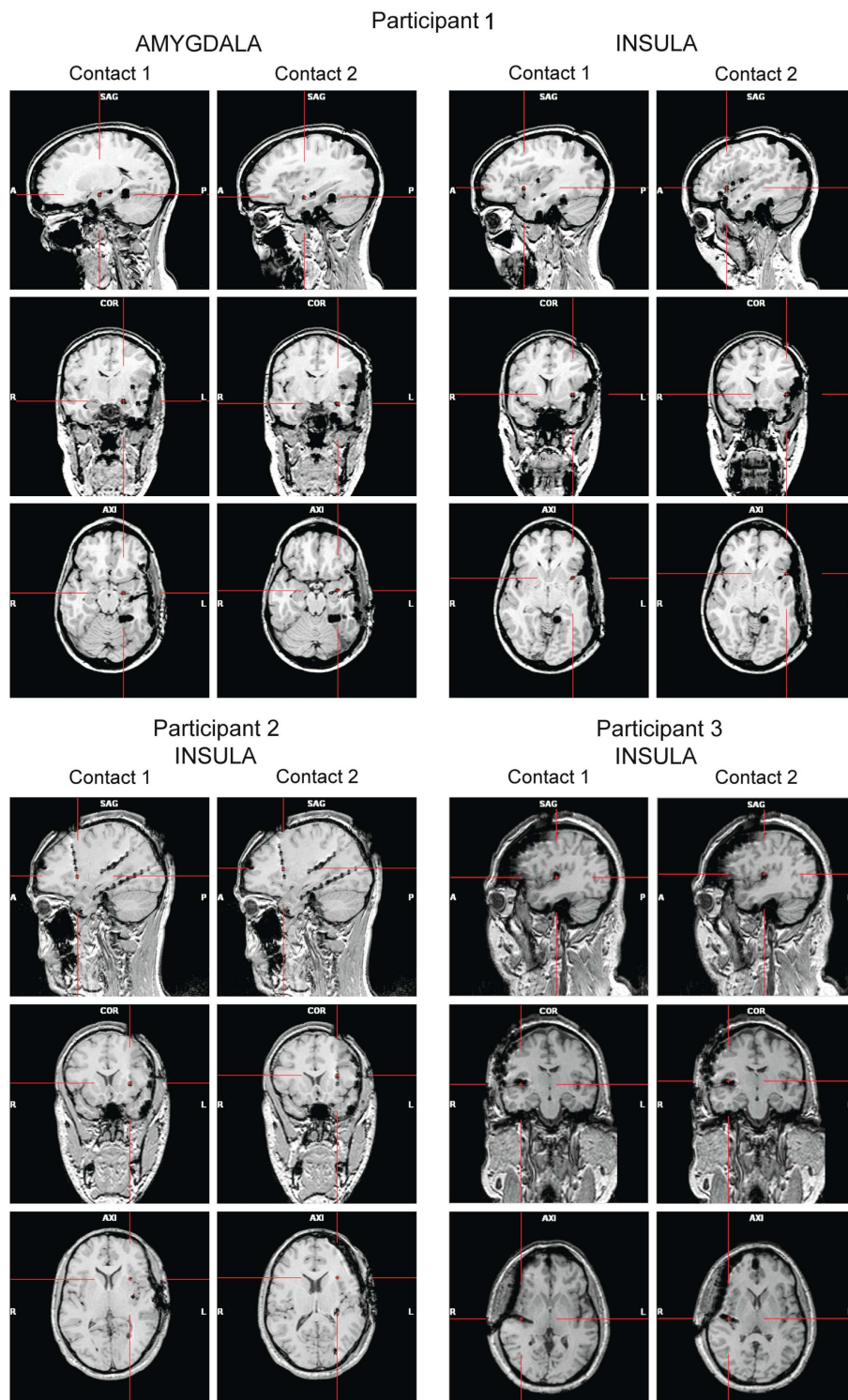


FIGURE 1 | Panels show the locations of the electrode contacts of interest for each participant based on post-implantation MRIs (A, anterior; P, posterior; L, left; R, right).

RGB values and corresponding luminance values. The refresh rate was 60 Hz and the resolution 1024×768 pixels. The luminance range in the green channel was diminished to match the

red channel, which typically has a lower maximum luminance (min = 0.4 cd/m^2 , max = 33.3 cd/m^2). All stimuli were shown on a gray background (13.57 cd/m^2) using the Psychophysics toolbox

(Brainard, 1997; Pelli, 1997) for MATLAB (Mathworks, Natick, MA, USA).

STIMULI

Twelve grayscale face photographs (256×256 pixels) from the STOIC database (Roy, Roy, Éthier-Majcher, Fortin, Belin, and Goselin, submitted) served as base stimuli. The photographs depicted three male and three female faces, each with a disgusted and a fearful expression (Figure 2). The faces were cropped to exclude non-facial cues, and they were equated in mean luminance and contrast [root mean square (RMS) contrast of 0.2] using the SHINE toolbox (Willenbockel et al., 2010b).

The SFs of the base images (see Figure S1 in Supplementary Material for a plot of the spectral content of the base faces) were randomly sampled trial-by-trial using the SF Bubbles technique (Willenbockel et al., 2010a). In brief, the to-be-filtered base image was padded with a uniform gray background and then subjected to a fast Fourier transform. The amplitude spectrum of the padded image was multiplied element-wise with a filter constructed in the following way: A vector consisting of randomly distributed binary elements (45 ones among 10,195 zeros) was convolved with a Gaussian kernel, referred to as an “SF bubble” ($\sigma = 1.8$). This yielded a smoothed sampling vector. The sampling vector was subjected to a logarithmic transformation to take into account the fact that the human visual system is more sensitive to low than to high SFs (e.g., De Valois and De Valois, 1990). To obtain a two-dimensional filter, the log-transformed, smoothed sampling vector was then “rotated” about its origin. After multiplying the two-dimensional filter element-wise with the amplitude spectrum of the base image, the result was back-transformed into the image domain via an inverse fast Fourier transform. The “SF bubbled” image contained a random subset of the base image’s SF content (see Figure 3 for sample stimuli; for an illustration of the filtering procedure, see Figure 1 in Willenbockel et al., 2010a).

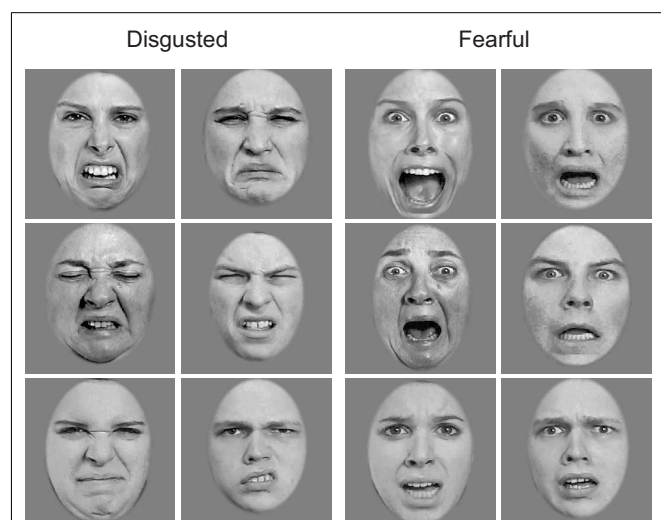


FIGURE 2 | Base face images with disgusted and fearful expressions used in the experiment.



FIGURE 3 | Example of a face image filtered with the SF Bubbles technique on six hypothetical trials.

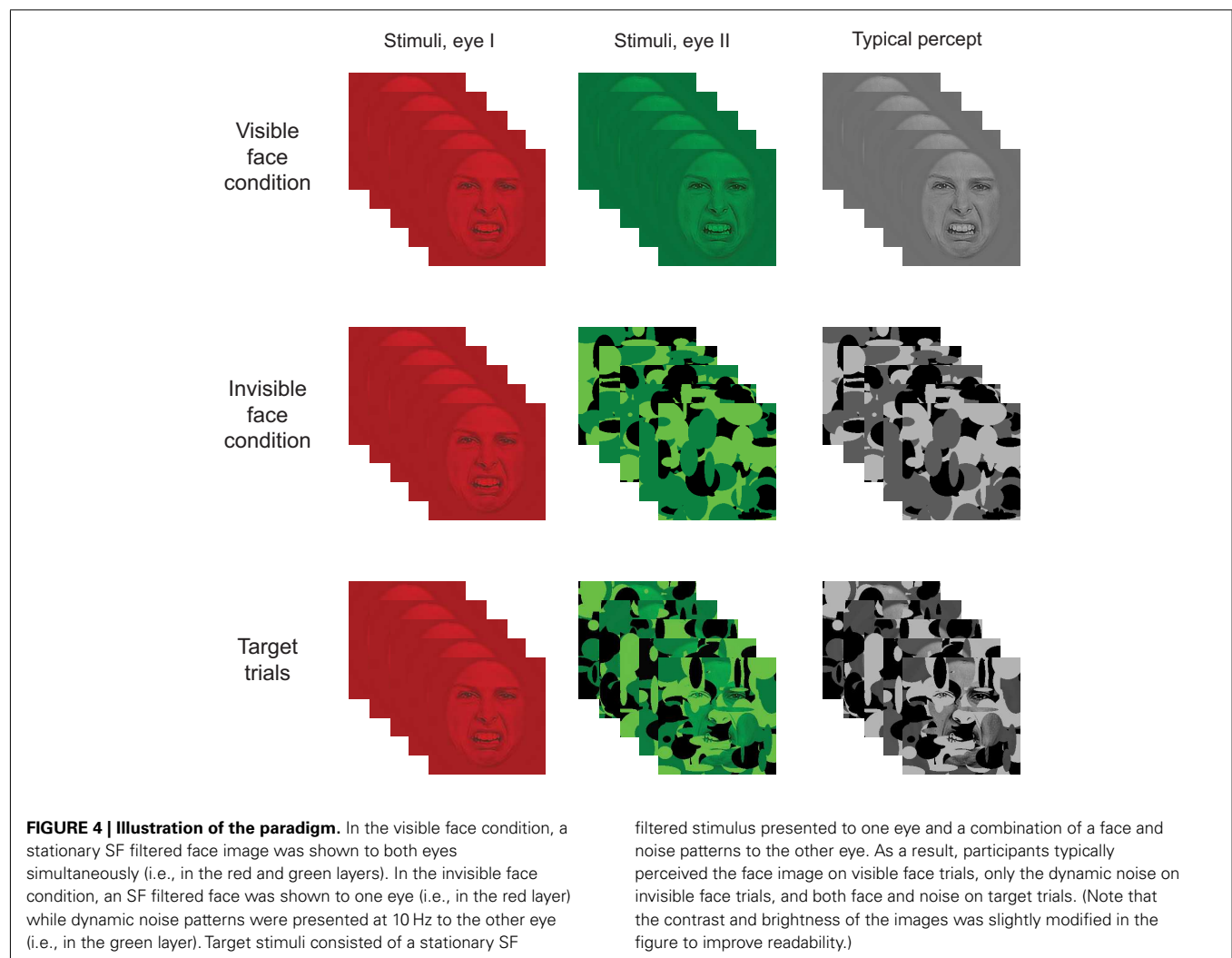
The contrast level of the SF sampled stimuli was kept constant across experimental conditions but was adjusted for each participant so he/she reported being able to recognize the facial expressions in the *visible face* condition (see Procedure) but did not detect the faces in the *invisible face* condition. For Participants 1 and 2, this resulted in a mean RMS contrast of 0.019 and for Participant 3 of 0.024. To be able to display stimuli with low contrast, we used Floyd-Steinberg dithering (Floyd and Steinberg, 1976), which enhances the luminance resolution (see also Allard and Faubert, 2008). The face stimuli subtended visual angles of approximately 7.1° horizontally and 12.8° vertically.

The high-contrast noise used for CFS (Tsuchiya and Koch, 2005) consisted of random elliptical Mondrian patterns (Figure 4; see also, e.g., Tsuchiya et al., 2009). The mean RMS contrast of the Mondrians was 0.80 ($SD = 0.11$). The noise fields were of 256×256 pixels and subtended horizontal and vertical visual angles of approximately 10.6° and 13.7° , respectively (see Figure S1 in Supplementary Material for a plot of the spectral content of the Mondrians).

Target stimuli consisted of face/Mondrian composites (Figure 4). A composite was constructed by multiplying the pixel values of an SF sampled face image (RMS contrast = 0.04) element-wise with those of a Mondrian noise field and then adjusting the contrast so it matched the Mondrians. For each target trial, five Mondrian/face composites were constructed using the same face image but different Mondrian patterns.

PROCEDURE

The participants took part in the experiment while sitting comfortably in their dimly lit hospital room. All stimuli appeared at the center of the computer screen and were viewed from a distance of 56 cm through red-green anaglyph glasses. The glasses allowed us to simultaneously present distinct information to each eye of the participant (i.e., one eye with information in red and the other with information in green). Each trial began with a fixation cross presented for 500–900 ms (to both eyes), followed by a blank screen for 500–900 ms. Then, a face stimulus was



displayed for 500 ms in one of three conditions: the *invisible face* condition, the *visible face* condition, or the *target* condition (Figure 4).

In the invisible face condition, we employed CFS to suppress the face stimulus from awareness. The static SF sampled face image was presented to one eye (by showing it in the red layer of the RGB image) while the other eye was presented with suppression noise (i.e., Mondrians were presented in the green layer). The Mondrians changed at a rate of 10 Hz (see also Tsuchiya and Koch, 2005). As a result, only the dynamic Mondrians were consciously perceived. In the visible face condition, both eyes were presented with the same SF filtered face by displaying it in both the red and green layers. On target trials, a face was shown to one eye (i.e., in the red layer) while a Mondrian/face composite was shown to the other eye (i.e., in the green layer) at 10 Hz.

The participants were instructed to look at all images carefully and to press the space bar on a regular computer keyboard if they perceived Mondrian patterns and a face together on a given trial. The detection task allowed us to see if participants were paying attention to the stimuli and to evaluate for each CFS trial whether the faces were successfully suppressed. The interstimulus interval

was adjusted for each participant to ensure that he/she had enough time for the keypress (see also Jiang and He, 2006).

One experimental session typically consisted of five 105-trial blocks (plus one practice block in the first session), with breaks in between. After each session, the red and green lenses were swapped. 45.7% of the trials were invisible face trials, 45.7% were visible face trials, and 8.6% were target trials. The different trial types were randomly intermixed within each block. We recorded four sessions per participant (with a maximum of two sessions per day, depending on the patient's willingness for research participation and on clinical constraints). In total, Participant 1 completed 20 blocks, Participant 2, 19 blocks, and Participant 3, 21 blocks.

ANALYSIS

The intracranial EEG data from all contacts of interest for each participant were segmented from 200 ms before stimulus onset until 1500 ms after stimulus onset and baseline corrected using Brain Vision Analyzer 2.0.1 (Brain Products GmbH, Munich, Germany). The following analyses were carried out with custom MATLAB programs. Target trials and all other trials on which a keypress

was made were excluded from the SF analysis. **Table 1** provides the exact number of trials included in the analyses for each participant.

To trace which SFs modulate the EEG amplitudes recorded from the insula or amygdala over time, we ran multiple linear regressions on the SF filters from each trial and the transformed EEG amplitudes within time bins of 20 ms (separately for each participant, brain region, condition, and session). EEG amplitudes within a given time bin were transformed as follows: First, we averaged the recorded EEG amplitudes within the time bin and across the two contacts of interest from each electrode. Then we performed a median split across trials: we set the amplitude from a given trial to 1 if it was greater than or equal to the median of all trials or to -1 if it fell below the median. This way, the impact of any abnormal amplitudes (e.g., due to epileptic spikes) was minimized without having to rely on a subjective trial rejection criterion. We then summed the filters from all trials weighted by the transformed amplitudes, which, here, is equivalent to a multiple linear regression. This was done separately for each of the 85 bins between 200 ms before stimulus onset and 1500 ms after stimulus onset.

The vectors of regression coefficients obtained for each time bin were stored in a time segment $\times$ SF sampling points matrix and smoothed using Gaussian kernels with a standard deviation of 4.0 time bins and 300 sampling points. The result was transformed into Z -scores – henceforth called classification images (CIs). We focus here on the overall CIs for each brain structure (insula and amygdala) and for each awareness condition to maximize the signal-to-noise ratio. Separately for the visible and invisible face conditions, we summed the CIs across sessions and divided the result by the square root of the number of sessions (i.e., $\sqrt{4}$). We then summed the resulting CIs across emotional expressions and divided by the square root of the number of expressions (i.e., $\sqrt{2}$). In addition, to compute the insula CIs, we summed the respective CIs across participants and divided by the square root of the number of participants (i.e., $\sqrt{3}$). Statistical significance was evaluated using the Pixel test from the Stat4Ci toolbox ($p < 0.05$, $S_r = 870400$, FWHM = 99.91, $Z_{crit} = \pm 3.78$; Chauvin et al., 2005).

RESULTS

BEHAVIORAL RESULTS

The detection task served two purposes: (a) to ensure that participants stayed alert during the experiment, and (b) to check on each CFS trial whether the face broke through the suppression noise. The percentage of correctly detected targets for the three participants was very high ($M = 97.07\%$, $SD = 1.13\%$), suggesting that the participants paid attention to the stimuli. The percentage of detected non-targets was small ($M = 0.30\%$, $SD = 0.43\%$), which confirmed that the faces were successfully suppressed from awareness in the invisible face condition.

SPATIAL FREQUENCY RESULTS

Figure 5 depicts the significant pixels (regardless of polarity) for each SF and time bin, up to 1.5 s after stimulus onset for the overall insula and amygdala CIs (see Figure S2 in Supplementary Material for the raw, non-thresholded, CIs). The purple pixels correspond to the visible face condition, the green pixels to the invisible face

condition, and the black pixels indicate overlaps between the conditions. We will focus on the SFs that reached significance during stimulus presentation (0–500 ms). Note, however, that for both regions and visibility conditions, we found multiple other low-, mid-, and high-SF clusters to be significant after the offset of the stimulus.

Figure 5A shows the results for the insula (Participants 1–3). In the visible face condition, SFs around 8.75 cycles per face width (cpf) reached significance at approximately 340 ms after stimulus onset. In the invisible face condition, SFs around 9.40 cpf became significant at approximately 140 ms, followed by very low SFs around 2.27 cpf. The latter attained significance at approximately 200 ms and again at 420 ms. The significant pixels of the two visibility conditions overlap for SFs around 9.04 cpf between 340 and 400 ms.

Figure 5B displays the results for the amygdala (Participant 1). In the visible face condition, SFs around 6.48 cpf attained significance at approximately 240 ms. In the invisible face condition, SFs around 5.51 cpf became significant at about 140 ms. Then, at approximately 260 ms, very low SFs (1.95 cpf) reached significance.

The line graphs (summation plots) on top of the CIs depict the number of significant pixels for each SF, collapsed across time. For both the insula and amygdala, they show quite clearly that processing in the invisible face condition relied on low SFs more than processing in the visible face condition. Likewise, the graphs on the right of the CIs show the number of significant pixels for each time bin, collapsed across SFs. For both regions, they indicate that significant correlations between SFs and brain signals occurred earlier for the invisible than for the visible face condition.

DISCUSSION

The aim of the present study was to shed light on the informational correlates of consciousness in the context of emotional facial expression perception. Specifically, we examined which SFs in consciously and non-consciously perceived stimuli are correlated with brain signals in two key structures of the emotion-processing network – the insula and the amygdala. We employed a novel combination of three techniques: intracranial recordings in awake human participants, SF Bubbles (Willenbockel et al., 2010a), and CFS (Tsuchiya and Koch, 2005). To our knowledge, this is the first study that mapped the time course of SF tuning for specific regions of the emotion-processing network and as a function of awareness. In the following, we will put our findings into context by focusing, in turn, on (a) emotional expression perception and awareness, (b) awareness and SF processing (during face perception in general), and (c) SF processing and emotional expression perception. We will then briefly discuss our findings in light of theories on the neural pathways involved in emotion perception.

Disgusted and fearful faces were used as stimuli because previous work has shown that the insula and amygdala are implicated in the processing of these facial expressions. In particular, numerous studies led to the conclusion that the anterior insula is important for the processing of disgust (e.g., Phillips et al., 1997, 1998; Krolak-Salmon et al., 2003), and the amygdala for the processing of fear (e.g., Adolphs et al., 1994, 1995; Morris et al., 1996; Phillips et al., 1998; Krolak-Salmon et al., 2004); taken together,

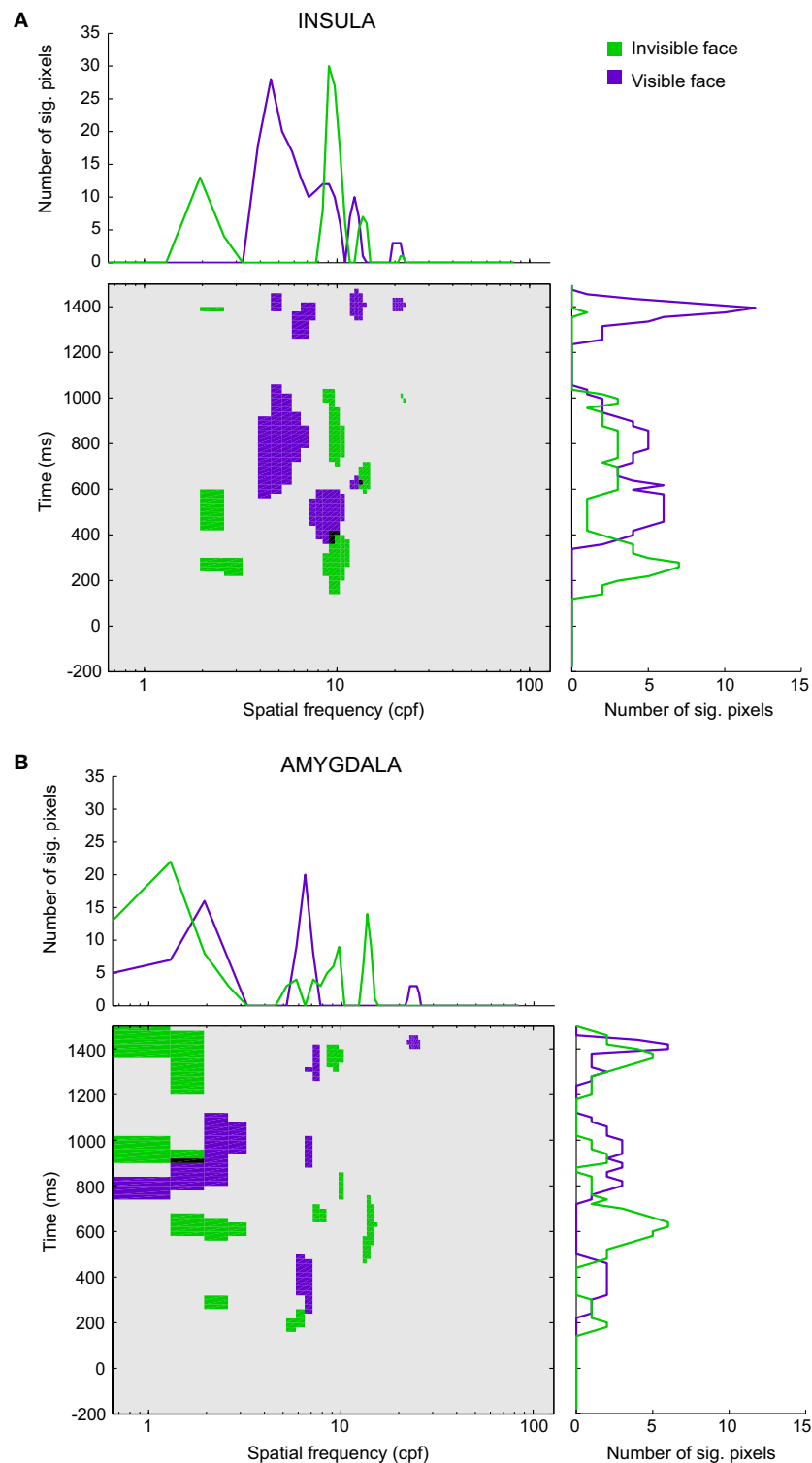


FIGURE 5 | Classification images for (A) the insula and (B) the amygdala.

The classification images show the significant pixels for the invisible face condition (green) and the visible face condition (purple) for each spatial frequency (in cpf, cycles per face) and time segment between 200 ms before

stimulus onset and 1500 ms after stimulus onset. Black regions indicate the overlap between the awareness conditions. The line graphs (summation plots) show the number of significant pixels across time for each spatial frequency (top) or across spatial frequencies for each time segment (right).

other studies indicated that these brain regions respond to both disgusted and fearful faces (e.g., Morris et al., 1998; Winston et al., 2003a; Fitzgerald et al., 2006; Van der Gaag et al., 2007; see also Anderson et al., 2003). Our results replicate these findings. However, the emotion-specificity of the responses in these regions goes beyond the scope of this article.

Previous work has also shown that both disgusted and fearful expressions can be perceived independently of awareness (e.g., Smith, *in press*). Using various methods to render stimuli invisible, neuroimaging studies demonstrated that the amygdala is involved in the non-conscious processing of emotional faces (e.g., Whalen et al., 1998; Morris et al., 1999; Pasley et al., 2004; Williams et al., 2004, 2006; Jiang and He, 2006; but see Phillips et al., 2004). Scarce studies found support for an involvement of the insula in the non-conscious processing of emotional stimuli (e.g., Sabatini et al., 2009; but see, Anderson et al., 2003, and Phillips et al., 2004, for results that speak against automatic facial expression processing in the insula). The present results indicate that both structures play a role in perceiving emotional expressions, consciously and non-consciously.

In our visible face condition, the first significant correlations between stimulus information and brain signals occurred at approximately 340 and 240 ms after stimulus onset in the insula and amygdala, respectively. In our invisible face condition, they were present as early as 140 ms in both regions. Moreover, in both visibility conditions, we found significant correlations at long latencies, up to 1500 ms after stimulus onset. These temporal dynamics appear largely consistent with the results from previous intracranial ERP studies on conscious emotional facial expression perception, although a direct comparison is difficult due to important methodological differences. In line with our finding that the response of the insula occurred later than that of the amygdala, previous results revealed emotional effects as early as 300 ms post stimulus onset in the insula (Krolak-Salmon et al., 2003), and as early as 140 (Pourtois et al., 2010) or 200 ms (Krolak-Salmon et al., 2004) in the amygdala.

Furthermore, long-latency effects were present in previous intracranial ERP data as well. For instance, Krolak-Salmon et al. (2004) observed differential responses to fear vs. neutral or happy faces until 1100 ms after stimulus onset in the amygdala of one patient. Pourtois et al. (2010) found late emotional effects in the amygdala that were modulated by attention, starting at approximately 700 ms after stimulus onset and lasting more than 300 ms. Finally, such late effects were seen in response to invisible emotional words in the amygdala (after 800 ms after stimulus onset; Naccache et al., 2005), suggesting that considerable time is needed for extracting emotional meaning. Naccache et al. (2005) speculated that top-down influences might amplify non-conscious amygdala activation in this context, without making information accessible to conscious report. Possibly, the late significant correlations with low-level information that we found also reflect feedback or top-down influences that amplify certain aspects of the stimuli later on.

Our CIs show complex patterns of SF tuning over time, for both the insula and the amygdala. A comparison of the CIs between awareness conditions revealed that invisible face processing relied on very low SFs (<3 cpf) more than visible face

processing, especially within the first 600 ms after stimulus onset. The idea that SF processing and awareness interact during face perception has come up repeatedly in the literature but has, as far as we know, only been investigated in one published study (De Gardelle and Kouider, 2010). The authors employed a masked priming paradigm with hybrid prime stimuli – composed of the low SFs of one face and the high SFs of another face – and a fame judgment task. Using behavioral measures, they discovered that both low SFs (<12 cpf) and high SFs (>12 cpf) could be processed without awareness. The influence of high SFs correlated with prime visibility (i.e., prime duration), whereas the influence of low SFs did not. De Gardelle and Kouider's results are consistent with ours inasmuch as we also found a broad range of SFs to be processed non-consciously. The qualitative differences that we observed between our awareness conditions, however, were not seen in their data. This discrepancy could be due to several methodological differences between the studies.

Whereas not much work has been done on SF processing and awareness, several studies have looked at SF processing during the conscious perception of fearful faces. The majority of studies imply that low SFs are particularly important for the perception of fear (Vuilleumier et al., 2003; Winston et al., 2003b; Pourtois et al., 2005; Vlamings et al., 2009; but see Holmes et al., 2005; Morawetz et al., 2011). For instance, in an fMRI study, Vuilleumier et al. (2003) observed larger amygdala responses to fearful than to neutral faces when stimuli were unfiltered or low-pass filtered (<6 cpf), but not when they were high-pass filtered (>24 cpf). In a recent surface ERP study (Vlamings et al., 2009), it was found that fearful relative to neutral faces elicited a larger P1 component (i.e., a positive deflection around 100 ms post stimulus onset) and a larger N170 (i.e., a negative deflection around 170 ms), also only for low-pass (≤ 12 cpf), not for high-pass (≥ 36 cpf), filtered faces. These findings are in line with our amygdala CI: many pixels reached significance for SFs under 6 cpf but very few attained significance for SFs above 24 cpf [see the summation plot in **Figure 5B** (top)]. However, as discussed above, we did not find any significant SFs for latencies below 200 ms in our visible face condition, suggesting that the early emotional effects observed using surface ERPs (Vlamings et al., 2009; see also Pourtois et al., 2005) are probably not driven by the amygdala or insula.

The SF tuning patterns we found raise the question about the underlying neural mechanisms of SF processing as a function of awareness. Specifically, through which pathways does SF information arrive at the insula and amygdala? Currently two theories are discussed in the emotion-processing literature, namely the subcortical pathway hypothesis (for recent reviews see Tamietto and De Gelder, 2010; De Gelder et al., 2011) and the multiple waves model (Pessoa and Adolphs, 2010, 2011). According to the former, low-SF information from emotional stimuli is conveyed quickly and automatically via a subcortical route through the superior colliculus and the pulvinar nucleus of the thalamus to the amygdala, whereas high SFs are processed more slowly along a cortical route. The multiple waves model, in contrast, suggests that emotional information is processed in parallel by multiple cortical pathways, without reliance on a direct subcortical route to the amygdala. Our study was not designed to test these theories; however, our results

appear to be consistent with the multiple waves model, while they challenge the subcortical pathway hypothesis in at least two ways. The first hurdle for the subcortical pathway hypothesis is that the early low-SF clusters revealed to be significant in the invisible face condition are *not* present in the visible face condition. The second hurdle is that the latencies we found in both awareness conditions (140 ms in the invisible face condition, and 340 ms or 240 ms in the visible face condition for the insula and amygdala, respectively) do not appear faster than cortical visual processing (see Pessoa and Adolphs, 2010, for a review). More work will be needed to test these two theories.

One limitation of the current study is that since we recorded brain signals from patients with epilepsy, we cannot be entirely sure that our data are representative of the healthy population. For Participant 1, epileptic spikes were found in the insula; we therefore recomputed our CIs without her data for the insular contacts. However, we did not find any changes in the main results (see Figure S3 in Supplementary Material). The structures we recorded from in all participants were structurally normal-appearing on high-resolution MRI. Thus, we think it is reasonable to assume that the results we report here can be generalized. Intracranial recordings from volunteers with epilepsy have previously been used in several studies (e.g., Oya et al., 2002; Krolak-Salmon et al., 2003, 2004; Naccache et al., 2005; Tsuchiya et al., 2008; Pourtois et al., 2010) because they bear a number of advantages – specifically, a millisecond temporal resolution combined with a high spatial resolution – and are thus considered to provide an important window into the workings of the human brain.

A second drawback is that in creating the two awareness conditions, we introduced differences in physical stimulation. In the visible face condition, a static face was presented to both eyes, whereas in the invisible face condition, dynamic high-contrast noise replaced the face presented to one eye. This has the disadvantage that we do not know to what extent and how the flashing of the noise patterns influenced our SF results (see Yang and Blake, 2012). We chose suppression noise that was used in several previous studies and found to be very effective (i.e., high-contrast Mondrian patterns; e.g., Tsuchiya and Koch, 2005; Jiang and He, 2006; Jiang et al., 2009). The spectral energy of our Mondrians was highly correlated with that of our base faces (see Figure S1 in Supplementary Material; the correlation between the average across faces and the average across noise patterns was $r = 0.95$). Our Mondrians consisted of elliptical elements (see also Tsuchiya et al., 2009; Adams et al., 2010) and thus contained energy at all orientations. It is not yet known what the optimal suppression noise would be, and basically all methods used to render visual stimuli invisible for normal-sighted observers introduce differences in stimulation. Therefore, this problem is difficult to overcome (see, e.g., the review by Tamietto and De Gelder, 2010). We used CFS because it results in longer suppression than other techniques, such as backward masking or binocular rivalry. Also, it has the advantage that the suppression can be precisely timed.

Investigating the informational correlates of consciousness from several angles – i.e., with different awareness-manipulating techniques and paradigms (e.g., Faivre et al., 2012; for a review see Kim and Blake, 2005) – might currently be the best approach to overcome the limitations of the present study. For example,

one could combine the SF Bubbles technique with masked priming to examine which SFs of visible vs. invisible primes influence observers' responses to a visible target. It might also be a good idea to use SF Bubbles together with a crowding paradigm, which has recently been emphasized as a more ecologically valid approach than masking or CFS (Faivre et al., 2012). Furthermore, it might be insightful to combine SF Bubbles with an attentional blink (e.g., Raymond et al., 1992) paradigm, where physical stimulation remains constant but stimuli can be rendered invisible by diverting the observers' attention. This could represent a promising avenue for contrasting SF tuning between conscious and *preconscious* processing (see Dehaene et al., 2006). The present study is meant as a first step toward gathering converging evidence about the informational correlates of consciousness.

CONCLUSION

Using state-of-the-art techniques, we mapped the SF tuning of the insula and amygdala as a function of awareness. Our results are consistent with the idea that a wide range of SFs plays a role in the conscious and non-conscious perception of emotional facial expressions, with SFs between 6 and 10 cpf appearing particularly important early on (for faces subtending approximately 7°). That being said, qualitative differences in SF tuning were observed between our awareness conditions – particularly in the early processing of very low SFs – that are consistent with the idea that different neural pathways are employed for conveying visual information to the amygdala and insula under different degrees of awareness. The present study paves the way for future work that investigates the temporal dynamics of SF processing in specific structures of the emotion-processing network and for elucidating the informational correlates of consciousness in general.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at http://www.frontiersin.org/Consciousness_Research/10.3389/fpsyg.2012.00237/abstract

Figure S1 | Rotational average of the power spectra of the 12 base faces and the suppression noise (540 Mondrian patterns).

Figure S2 | Raw classification images for the two regions (top: insula; bottom: amygdala) and awareness conditions (left: visible face; right: invisible face).

Figure S3 | Insula classification images [(A), thresholded; (B), raw] computed from the data of Participants 2 and 3 only.

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