



# Language as a mental capacity

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While bonding and stress signals are widespread across species, symbolic computation is a uniquely human capacity. This article examines the intricate relationship between the evolving primate brain and the emergence of the mental language capacity in the human lineage, focusing on the neural circuits instantiated by mental agents. By integrating neurobiological and eco-cultural evidence, we identify a punctuated step at around 1.8 Ma with the appearance of *Homo erectus* and propose a corresponding neural threshold for symbolic representations and processes. The critical increase in internal computational capacity may reflect interactions between behavioral dynamics and neurogenetic properties. We argue, in particular, that the rise in social interactions and learning, the adoption of an energetically richer diet, and increased mobility exerted mutually reinforcing effects on cortical reorganization, enhancing neural connectivity and ultimately supporting symbolic language processing. We therefore suggest a scaled mental capacity for language and emphasize the importance of incorporating neurobiological factors when defining the evolution of the language capacity and its functions.

### KEYWORDS

internal thoughts, language capacity, mental agents, neural structures, origin of language, scaled mental capacity, language evolution

## 1 Introduction

Owing to our own biological makeup, complex mental computations occur effortlessly. Only partially we become aware of this intrinsic power when we express it through symbolic concepts. The ability to acquire and use these concepts, in turn, depends on our innate mental readiness. In constructing mental models, we employ these symbolic concepts to represent various mental activities, including language, music, mathematics, navigation, or games. A critical question is how to best model these intrinsic computations. For instance, it remains unclear to what extent these models should incorporate domain-specific or domain-independent structures to adequately represent these computations. Additionally, while it is an ambitious goal, modeling a correspondence between mental computations and neural signaling activities is highly sought after (Churchland and Sejnowski, 1992; Piccinini and Bahar, 2013; Colom et al., 2010).

Our approach seeks to interpret mental computations as changes in neural signaling within and between cortical circuits. These changes can be contextually unique in timing and setting, yet fundamental principles likely apply universally across all mental computations. This distinct human capacity is rooted in our species-specific genetic makeup. Additionally, comparative research shows that some basic mental computations and neural structures are shared with other primates and mammals, underscoring a broader evolutionary continuum (Cantlon and Brannon, 2007; Tomasello and Herrmann, 2010; Ardesch et al., 2019; van den Heuvel et al., 2023; Spocter et al., 1691; Sousa et al., 2017; Margulies et al., 2016).

Our understanding of “what language is” is fundamentally shaped by our mental and neural frameworks. In particular, when language research includes an evolutionary perspective, it becomes evident that many controversial discussions in the field stem

from varying definitions of language. Here our approach integrates introspective and behavioral data with critical neurobiological insights to understand better the cortical circuits responsible for linguistic and symbolic computations. They underpin modern language, a capacity uniquely human yet evolved from our primate and hominin ancestors. We advocate an incremental perspective, suggesting that the mental capacities enabling language were, to some extent, present in our biological predecessors.

Discerning this innate predisposition is crucial for defining language as a mental capacity. Specifically, the focus is not on *how* language manifests specific typologies such as sound patterns, syntactic roles, lexical categorizations, phrasal structures, semantic frames or pragmatic expressions. Instead, our interest is the speaker's mental capacity to acquire and employ these structures. The standard view is that we share 98.8% of our genes with panins (chimpanzees and bonobos), but a recent study reports differences between 12.5 and 13.3% (Yoo et al., 2025). Apart from these reports, the gaps responsible for different mental capacities are gene sequences (the precise order of bases), changes in protein-noncoding DNA and significant differences in gene regulations. Due to those species-specific gene regulations, the human brain undergoes significant maturation within the first 4 years of life. By means of directed linguistic input and contextually relevant self-reinforcing cycle, synaptic pruning actively shapes and refines neural circuits. Setting aside speculations about the linguistic and mental capacities of our extinct hominin relatives, the human brain is genetically predisposed to acquire a symbolic system for expressing inner mental states such as feelings, ideas, or opinions.

We discuss how the network of neural circuits brings about *mental agents* in modern humans. Specifically, regarding the language capacity, we discuss what sets the human brain apart of other primates. We draw conclusions how this language capacity may have evolved in the hominin lineage. Neural circuits emerged in context of specific ecocultural conditions, implying that the language capacity may have changed over time in the human lineage. Hence, the discussion will further outline major distinctions between the human language system and the semiotic signal system of other animals, further clarifying language as a mental system.

## 2 Neural circuits as mental agents

A species' neural circuits can be viewed as a composition of *mental agents* that employ strategies in response to socioecological challenges. These circuits internally compute mental representations to create beliefs, goals, intentions and creates specialized mental systems (Davidson, 1963; Dennett, 1987). The human language system is one of these specialized systems. It shares to some extent neural circuits with other, non-linguistic systems such as visuospatial working memory, hierarchical action planning, tool-use sequencing, or theory of mind (ToM; Baddeley, 2003; Badre and D'Esposito, 2009; Fedorenko and Duncan, 2013). It operates like a specialized agent that forms conceptual representations and generates linguistic computations (Fodor, 1983; Baron-Cohen, 1995; Chomsky, 2000). As we discuss below, some inference-based evidence indicates that

language-related brain circuits evolved incrementally in the lineage of higher primates.

Drawing on the evolutionary perspective: the more adaptable a mental agent the better equipped for survival (Emery and Clayton, 2009; Uddin, 2021). The rise of mental agents in evolution are caused by the increase of neural network communication, including recurrent loops (re-entrant). Some factors are brain mass ( $M_{BR}$ ), structural properties, neuron numbers (N) and their density and packing properties. The human mind consists of numerous mental agents that cooperate—or sometimes compete—to carry out mental tasks (society of mind theory; Minsky, 1986). The brain organ of our extinct hominin ancestors is essentially unknown to us. We can only draw indirect conclusions from fossils, including endocasts, and to some extent from behavioral proxies to fill the evolutionary gap since the divergence from panins about 7–6 Ma. One approach is to use endocasts volumes to interfere N and match them against behavioral adaptiveness to offer insight into mental capacity of an extinct species. However, since other significant neural factors such as cortical connectivity or neuron density cannot be considered, we are confined to describing broad tendencies about how human mental agents evolved.

While mice and other rodents' mental agents excel at memorizing food source locations, higher primates generally exhibit more complex mental agents. Gibbons (*Hylobatidae*), for example, have a relative (r) $M_{BR}$  of about 1.82% (brain-body ratio of 100:5,500 g), which is similar to modern humans who exhibit an r $M_{BR}$  of about 1.9% (1,350:70,000 g). However, the average r $M_{BR}$  of modern humans is about three times larger than that expected for non-human primates of equivalent body size (Passingham, 1975). Thus,  $M_{BR}$  and body mass does not consistently inform about a species' mental capacity. Instead, absolute  $M_{BR}$  has been shown to be a more accurate predictor of mental capacities (Gibson et al., 2001; Roth and Dicke, 2005; Deane et al., 2007).

Substantial mental differences between humans and other primates are undoubtedly influenced by  $M_{BR}$ , yet the question remains: what specific neuronal factors endow humans with unparalleled mental abilities? The predisposed sheer N and their extensive interconnectivity likely contribute to our mental capacity, including our ability to acquire a modern-type language.

The African elephant (*Loxodonta africana*), for instance, with r $M_{BR}$  of 0.07%, has approximately 257 bn (billion) N, with a large portion located in the cerebellum, primarily dedicated to motor control (Herculano-Houzel et al., 2014). Despite their modest r $M_{BR}$ , elephants are noted for their high social and emotional skills and self-awareness (Herculano-Houzel, 2009, 2012). In contrast, the human brain, which is densely packed, has, as mentioned above, an r $M_{BR}$  of 1.9% and contains about 86 bn N. This structure supports advanced mental abilities such as symbolic thinking, complex social interactions, and technological innovations. While total N is an important factor in determining a species' mental capacity, the critical element is the neural composition, which enables relatively efficient and flexible signal processing. Ultimately, each species' brain is adapted to its unique ecological niche, and the mental capacity is just one component that contributes to a species' survival strategy.

Terrestrial ecosystems typically feature a broader diversity of competitive scenarios among species compared to aquatic or

aerial environments. Within these ecosystems, hominids not only developed tools but also transformed their environments through increased social interactions. On various scales, this may have spurred the development of cortical structures that supported expanded mental capacities, including language and memory. However, can we identify one or several critical neural factors that underpinned the emergence of language-readiness? Moreover, what was the evolutionary driving force behind this capacity?

A species genotypic traits interact with ecological and cultural niches and in form of mutual reinforcing feedback loops, known as *triadic niche construction* (Deacon, 1997; Fuentes, 2017; Odling-Smeel et al., 2003). Phenotypic traits are, for instance, shaped by survival pressures, tool use, shared intentionality, ToM and semiotic practices and determine a species' brain architecture, including neural circuits associated with mental agents (Premack, 1978; Frith, 2003). Hominins are active niche constructors and not passive recipients, and their mental agents emerged in context of such an increasingly triadic environment. We report evidence that supports the view of scaled mental capacity for language in the human lineage. This mental capacity underlies various cognitive domains. It has been argued that computations supporting manual tool production and use may have been co-opted for another domain, such as language (Corballis, 2002; Stout and Chaminade, 2007; Arbib, 2012; Fitch and Martins, 2014). From a capacity-based perspective, one may posit that new neural circuits and mental agents draw on domain-general cortical resources rather than arising through cross-domain fertilization, while acknowledging that both processes may interact.

### 3 A scaled mental capacity

Humans possess an innate capacity to create and manipulate symbols, a product of an evolving mental capacity (Traugott, 2011). In the domain of language, this capacity manifests as the linguistic properties that a child acquires with relative ease within the first 3–4 years of life, encompassing sound patterns, the formation and manipulation of syntactic groups, and the generation of structured, contextually relevant meanings. This capacity for storing and manipulating extensive symbolic information is unique to modern humans.

The emergence of this internal capacity is widely debated, with some theorists positing that it coincided with the advent of modern human behaviors around 65 ka, propelled by increases in social complexity and genetic mutations (Corballis, 2002; Miyagawa et al., 2025). While this scenario is plausible, it remains speculative, has only limited neurobiological backing and is not universally accepted (Hillert, 2015; Mcbrearty and Brooks, 2000; Billard, 2002).

Based on fossil evidence, the average  $M_{BR}$  of 350 g for *Pan troglodytes* (emergence: ~6.5 Ma) and of 400 g for *Australopithecus* (4 Ma) are marginally different. The C-copy (*srGAP2C*) is associated with  $M_{BR}$  of 600 g for *Homo (H.) habilis* (2.8 Ma),  $M_{BR}$  of 775 g for *H. rudolfensis* (2.4 Ma), and 930 g for *early H. erectus* (1.8 Ma), 1,029 g for *late H. erectus* (~0.75 Ma) and the D-copy mechanism with  $M_{BR}$  of 1,250 g for *H. heidelbergensis* (0.6 Ma), 1,487 g of *H. neanderthalensis* (0.4 Ma) and 1,350 g for *H. sapiens* (0.3 Ma; Sporny et al., 2017). While the initial B-copy is relative inactive and the D-copy is a pseudogene lacking regulatory

elements for gene expressions, *srGAP2C* may have been a critical factor for facilitating the development of complex neural networks and synaptic genesis (Charrier et al., 2012).

*H. naledi* (538 g  $M_{BR}$ ; 0.34 Ma) and *H. floresiensis* (380 g  $M_{BR}$ ; 0.19 Ma) represent notable exceptions to the general trend toward larger brain and body sizes in the human lineage. The neural architecture of *H. naledi* may have been similar to *early H. erectus*, while *H. floresiensis* might have shared characteristics with *late H. erectus*, with its smaller size potentially resulting from insular dwarfism. Despite their smaller brains, both species seem to exhibit relatively complex behaviors (Holloway, 2012; Brumm et al., 2016).

Research has shown that the human brain conforms to the *cellular scaling rules* observed in other primate brains (Azevedo et al., 2009). These rules are derived from the isotropic fractionator method, which involves direct processing of brain tissue to count the number of neuronal and non-neuronal nuclei such as glia, ependymal cells, and pericytes. The sampled volume is then scaled up to estimate N in the entire brain (Herculano-Houzel and Lent, 2005). According to scaling rules for primate brains, relatively close similarities have been observed between the *generic primate brain* and that of a *male human*. This comparison includes N and non-N with the following measurements:  $M_{BR}$  (1,500/ 1,508 g),  $N_{BR}$  (93/ 86 bn; non- $N_{BR}$  (112/85 bn);  $M_{CX}$  (cortex; 1,412/1,233 g);  $N_{CX}$  (25/16 bn);  $rM_{BR}$ : 94/82%,  $rN_{CX}$  (27/19%);  $M_{CB}$  (cerebellum; 121/154 g);  $N_{CB}$  (61/69 bn);  $rM_{CB}$  8/10% (Gibson et al., 2001).

Recently, the brain of a fruit fly (*Drosophila melanogaster*), comparable in size to a grain of sand, was analyzed using a manually corrected machine learning 3D image reconstruction algorithm (Shiu et al., 2024). This brain comprises 140,000 N across 8,400 different types and possesses about 54.5 M syn (synapses). Although these figures appear vast, they are minuscule when compared to the scale of the human brain. However, despite advances in technology, directly quantifying the neural connections in a human brain remains a challenge, akin to counting leaves in a vast forest. Based on histological sampling and extrapolation techniques, it is estimated that a typical human brain, containing about 86–100 bn N, harbors between 100 trillion (tn: 10e12) and 1 quadrillion (qtn: 10e15) syn. This amounts to approximately 1,000–10,000 syn per N (Drachman, 2005). Thus, a human brain with a  $M_{BR}$  of around 1,350 g has on average about 88 bn N and 484 tn syn.

These estimates, though bold, must be considered with caution since the potential neural connections are not simply an exponential function of N. Biological constraints, such as variations in synaptic density influenced by factors like age and health, complicate these calculations (Samu et al., 2017). The range of N in the human brain, which overlaps with those found in *H. heidelbergensis* or Neanderthals (76–90 bn N), suggests that these ancient humans possessed mental capacities comparable to those of modern humans (Berwick and Chomsky, 2016; Herculano-Houzel and Kaas, 2011). This alignment is not surprising, given that some taxonomies classify both *Homo* species as variations of modern humans rather than distinct species (Bräuer, 2021; Stringer, 2012; Hillert, 2021).

An average *early H. erectus* brain with  $M_{BR}$  of 930 g would have possessed about 59 bn N and an estimated 333 tn syn, while a *late H. erectus* with an  $M_{BR}$  of 1,029 g about 66 bn N and 370 tn syn. For several reasons, we assume *late H. erectus*' cortical composition may have approximately achieved a significant portion of the

metrics found in archaic humans such as Neanderthals or *H. heidelbergensis*, and in modern humans (Berwick and Chomsky, 2016). The mental agents that reflect the language capacity likely hinge on a neural complexity threshold, best estimated by  $N$  and neural network connectivity (Tallerman and Gibson, 2012; Hillert, 2023). The mere increase in  $N$  and alterations in cellular composition in response to ecological pressures might have spurred the necessary neural reorganization for mental agents supporting symbolic thoughts.

As a result, we project a scaled mental capacity for internal thought processes throughout the primate lineage. Endocranial and archaeological evidence suggests that *H. erectus*' brain reached a neural threshold for symbolic capacity around 1.8 Ma (see Figure 1). In essence, the expansion of the primate brain, coupled with subcortical and cortical reorganization in various areas, laid the groundwork for complex symbolic computations. Furthermore, endocranial and genetic evidence indicates a significant increase in  $M_{BR}$  within the hominin lineage (Du et al., 2018).

Recent studies have pinpointed a series of genes that contribute to cortical expansion in hominins, notably through the copy mechanisms of the ancestral *srGAP2* gene (Slit-Robo Rho GTPase activating protein 2; Dennis et al., 2012). For example, great apes, including members of the genus *Pan*, possess a *B*-copy of this gene, a trait shared with extinct early hominins. This genetic endowment underscores the evolutionary continuity and genetic factors driving cortical growth across various hominin species.

Fossils and artifacts provide evidence for how the human mental capacity evolved and came to be used in our hominin ancestors. It should be stressed that we discuss a mental capacity fundamentally grounded in a neurobiological predisposition. Although niche construction processes may have gradually cultivated more specialized mental agents, a species' neurobiological makeup remains the essential prerequisite and must be sufficiently flexible to allow further refinements. The appearance of artifacts indicating visuospatial, aesthetic or symbolic computation can offer partial insight into the species' mental capacity. Nevertheless, such manifestations are always contingent on prior biological prerequisites that enable new adaptive behaviors. We argued here that the neural threshold for a symbolic capacity may be associated with *early H. erectus* about 1.8 Ma due to genetic changes such as *C*-copy of *srGAP2* and cortical growth ( $M_{BR}$  reached ca. 930 g). Prehistoric hominin endocasts and artifacts support this timeline although the evidence is suggestive rather than conclusive. It is said that *H. habilis* endocasts indicate an expansion and reorganization of the neural circuits involved in language, in particular prefrontal and parietotemporal regions (Falk, 1983; Tobias, 1987).

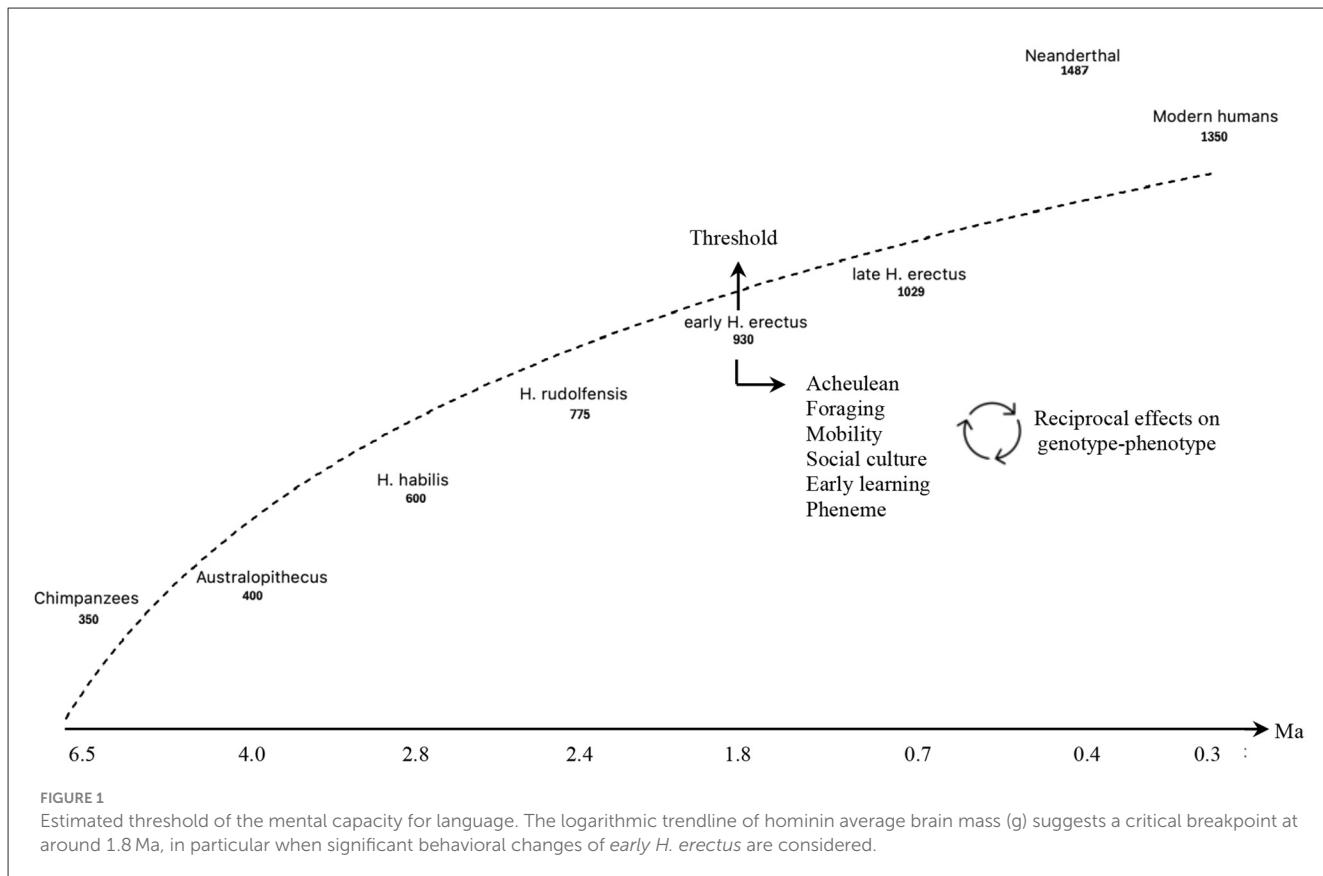
The earliest known tool industry, including the Lomekwi 3 assemblage dated to approximately 3.3 Ma, associated with *Kenyanthropus platyops* and possibly *Australopithecus afarensis*, whereas later Oldowan tools are linked to *H. habilis*. The refinement of tools did not emerge abruptly but can be traced back to the simpler Oldowan and early Acheulean tools, which were primarily crude bifaces or choppers. The earliest Acheulean assemblages, so far known, appeared around 1.76 Ma at Konso (Ethiopia) and West Turkana (Kenya). They reflect hierarchical action sequencing, learning strategies and cultural transmission. These

finds were taken as evidence for early forms of speech or gestural communication (Tobias, 1971; Holloway, 1981; Falk, 2009, 2014; Holloway, 2008). Other candidates are even older and refer to Oldowan paleoart (Bednarik, 2003; Harrod, 2014).

For example, in the Kenyan East Turkana at the Koobi Fora formation (site FxJ1), a 1.8 Ma broken core with inner diamond-shape was found, typically produced by (intentional) flake removal; or in the East African Rift Valley at Olduvai Gorge in Tanzania (site Frida Leakey Korongo North), a 1.87 Ma grooved and pecked cobble was discovered indicating an intentionally altered surface structure. Oldowan artifacts seem to reflect constructive visuospatial processes, including basic hierarchical sequences with subroutines. There are, however, no signs for aesthetic symmetry or symbolic representations as found for Acheulean bifacial tools (Wynn, 2002; D'Errico and Villa, 1997; Miyagawa et al., 2025). The transition from early to late Acheulean marking a particularly significant cognitive advancement beyond the preceding Oldowan phase (Wynn, 1985). The continuous expansion of mental computational capacities supports the hypothesis of transformative shifts in neuronal composition and integration of cortico-subcortical networks, acknowledging that merely expanding  $M_{BR}$  is insufficient to signify the emergence of symbolic cognition (Semendeferi et al., 2002; Rilling and Seligman, 2002; Schoenemann et al., 2005). Alongside increasing mental computations, adaptive neuroplasticity might have driven neural changes to enhance both mass and connectivity, accommodating complex internal and symbolic processing.

The specific ecological and cultural factors that influences cortical expansion in the human lineage are unknown. However, *H. erectus* seemed to have crossed a qualitative leap through coordinated high-return foraging diets (Potts, 2012). In turn, this led to reduced energy constraints on brain growth and to a smaller digestive system (Aiello and Wheeler, 1995; Pontzer, 2012; Bramble and Lieberman, 2004). Thus, more complex behaviors were possible such as inhabiting variable and new environments, forming stable social structures and accumulated tool innovations more rapidly. Cortical expansion and mental complexity mutually amplified each other and generated a niche construction feedback loop. These changes were supported by shifts of the life cycle such as prolonged juvenile learning (DeSilva and Lesnik, 2008). By contrast, many contemporaneous hominins, including *H. habilis*, *H. rudolfensis* or species of the *Paranthropus* lineage, were confined to relatively specific ecological niches. Their mobility and social structure was limited and lacked the energetic benefits due to lower caloric diets. Those hominins did not attain the trajectory required for increasingly complex mental capacities (Rightmire, 2013). *H. erectus* became therefore the only lineage to survive, spread and give rise to later *Homo* species, including our own species.

In conclusion, the mental capacity for language is a scaled product that already begun in its basic forms in *H. erectus*' ancestors, including the genera *Australopithecus* and *Pan*. Neural changes associated with active tool making imply a growing awareness of the self, others, and the environment, and an increased ability to act on that awareness. For reasons discussed above, a threshold toward symbols and basic syntax may have reached with the appearance of *H. erectus* (Bickerton, 2014; Wynn, 1985). According to one *primordial language hypothesis*, phenemes are



the onset building blocks for early spoken language. They are speech sounds produced along with gestures expressing meaning. At a later stage, phenemes were desemanticized and replaced by meaning-neutral phonemes (Foster, 1978). Even though early *Homo* species might have used a combination of phenemes and gestures, their mental capacity may have already met the threshold for symbolic processing due to isometric increase in N, connectivity, and reorganization.

Research into the mental capacity for language typically does not necessarily explore cultural-linguistic differences since it does not inform about the underlying computations. Arguing that speakers of different languages think differently is a superficial argument since they can describe meanings non-lexicalized in their respective culture. Figuratively speaking, the structure of a house is governed by the laws of statics, while the choice of materials and design is influenced by factors like climate and personal preference. One may choose different aesthetics but needs to comply to the principles of physics.

While it is both intriguing and compelling to explore typological styles of thinking, a deeper understanding of what thinking entails and its evolutionary origin requires us to examine the shared mental computational capacities within a species or even across species. The mental capacity for language pertains to these inherent mental dispositions and computations. The philosophical underpinning of the mentalistic paradigm provides a comprehensive framework for addressing these issues (Chomsky, 1968; Berwick and Chomsky, 2016). Since only humans possess the ability to acquire and use an internalized symbolic system to decode and encode thoughts, this capacity is likely an integral component of the human genotype, one that enables neural circuits supporting language. We posit that this mental capacity or organ evolved over time, suggesting that our ancestors must have been partially equipped with this capacity (Hillert, 2026).

It is often debated whether the mental capacity for language primarily arose from the need to enhance communicative efficiency (Wilson and Sperber, 2004; Tomasello, 2008; Fedorenko

## 4 Language as a mental organ

Empirical and theoretical approaches to studying language are diverse and often subject to vigorous debate. A significant portion of human interaction relies on spoken or signed language, supplemented by non-verbal cues ranging from eye contact to body posture and facial expressions. Analyzing the structure and pragmatic use of individual languages represents a research approach fundamentally different from investigating the underlying mental capacity for language. Even in these seemingly clear contexts, debates continue to stir in the murky waters. For example, proponents of the strong version of the linguistic relativity hypothesis argue that language profoundly influences how we think, what we focus on, and how we perceive the world. They suggest that speakers of different languages do not merely express themselves differently but may also think differently (Boroditsky, 2011; Whorf, 1956).

et al., 2024) or if its principal function was to expand mental capacities for various reasons (Fodor, 1975; Chomsky, 2007; Pinker, 2007; Fujita, 2014). While both perspectives emphasize different aspects of communication and cognition, there is consensus, as discussed above, that the selection of advantageous traits leading to increased cortical size is not arbitrary (Darwin, 1859; Dawkins, 1976). For several reasons, the *internal thought hypothesis* is a plausible scenario, although it does not undermine the communicative function of language (Traugott, 2011). It states that thinking occurs via an innate mental language (mentalese) that manipulates symbols and representations. Moreover, mental representations of syntactic structures would reflect the logical structure of the propositions they represent, with a key property being compositionality. This approach suggests that much of our thinking is analogous to linguistic computations, a claim for which there is limited evidence. Reasoning, for instance, can be based on non-symbolic processes, including holistic or statistical computations, as observed in motor learning, visuo-spatial reasoning, or heuristic-pragmatic decision-making.

The generative-linguistic approach highlights discrete infinity as a critical criterion for the development of the human mental capacity, asserting that a language-specific binary operation (Merge) generates tree-like sentence structures (Chomsky, 1995). For example, internal Merge is demonstrated in questions like *What<sub>x</sub> did you say that you bought<sub>x</sub>?* Here, the interrogative pronoun *what* is moved from the embedded canonical structure to the beginning of the sentence. It should be noted, though, that while most known languages utilize such an extended syntax, including embedding phrases within phrases (recursion), exceptions exist. They include, for example, Pirahã (indigenous Amazonian language), Warlpiri and Jingulu (Australian aboriginal language), Hua (Papua New Guinea language) or Dani (New Guinea language; Everett, 2005, 2008; Simpson, 1991; Haiman, 1980; Pensalfini, 2003; Heider, 1972). Despite their limited use of extended syntax in everyday communication, speakers of these languages undoubtedly possess the mental capacity to acquire and use these structures. Cultural lifestyle factors may influence the grammatical complexity metric observed in these languages compared to more wide-spread languages.

Furthermore, recursive operations are not restricted to syntax in language. The formation of vertical concept formations, mediated through symbolic representations, involves recursive processes. The origin of these abstract concepts can be linked to the idea to specify or generalize beyond perceptual entities, such as “harmful vs. non-harmful animals (Rosch, 1978).” Semantic recursion, in the form of lexical grouping, may represent an early stage in language evolution where syntactic rules were not yet prominent (Jackendoff, 1999; Hillert and Fujita, 2023). Moreover, recursive patterns are not confined to linguistic domains; they are prevalent in areas such as mathematics, music, and reasoning (Corballis, 2011; De Martins, 2012). Thus, the definition of “what language is” should not hinge on typological complexity or communicative efficiency but must be linked to the evolving mental capacities.

As discussed, a crucial argument is that an increase in critical M<sub>BR</sub> enhanced capacities across various domains in the human lineage, not merely in sensory-motor modalities related to language. The generation of internal images based on perception and enhanced long- and short-memory systems exemplifies this.

Abstract thinking and reasoning represent language-independent mental computations. In the early stages of hominin evolution, individuals may have modified their kinetic behaviors to optimize survival strategies, sharing this knowledge with conspecifics through non-verbal means, including facial expressions, body posture or vocalizations (Donald, 1991; Zlatev et al., 2005; Arbib, 2012). Although this communication style might be regarded as an incipient stage of language, kinetic interactions are primarily the result of enhanced internal computations.

Language disorders provide further evidence for the independence of thought from language. Aphasic disorders and specific language impairments in children typically do not impact general aspects of cognition, often referred to as intelligence (Broca, 1861; Wernicke, 1874; Jackson, 1878; Head, 1926; Orton, 1937; Bishop, 1997; Leonard, 1998). However, defining intelligence remains challenging. Individuals whose neural circuits are impaired for lexical production or spatial orientation, may still utilize multiple specific or broad-scaled cortical and subcortical networks (Aguirre and D'Esposito, 1999; Goodglass and Wingfield, 1997). Such individuals retain sufficient access to alternative mental agents, possibly redundant memory systems, even though they may be unable to perform specific tasks. A dissociation between specific language-related aspects (e.g., circuits related to motor-sensory or lexical processes) and predefined non-linguistic circuits, as evidenced by neuroimaging, does not negate the internal thought hypothesis. Language-related circuits are not only modularly organized but also distributed, tapping into various memory systems such as social-pragmatic aspects, cognitive control, or ToM (Arbib, 2012; Graci and Capone, 2023). From an evolutionary perspective, it is plausible that language and its associated memory systems evolved from the need to enhance internal mental computations. Although the distinction between a narrow and broad language system has been introduced, focusing on linguistic syntax, we find similar computations in non-syntactic linguistic and non-linguistic domains (Hauser and Chomsky, 2002; Katz and Pesetsky, 2011; Wakita, 2014; Levinson, 2014; De Martins et al., 2015; Nasukawa, 2017).

Linguistic encoding of thoughts likely played a critical role. Refined concept formations, scaffolded by symbolic representations and their manipulations, may have enhanced mental abilities within and across domains, improved self-awareness, and facilitated social interactions, including communication. The properties of the human brain that enables the sharing of thoughts through rules and representations making it the most efficient mental system for interpreting the world and communicating ideas.

## 5 Conclusions

We contend that language, as a form of symbolic processing, represents a scaled mental capacity in evolutionary terms. Due to competitive pressures in terrestrial environments, hominin brains evolved to enhance internal computations, thereby increasing mental versatility and survival rates against competitors for resources. This mental capacity developed along with cortical growth in the hominin lineage, providing the necessary capacities for enhanced mental computations as ultimately evidenced in extended rules and representations across and within domains. Hence, from a phylogenetic perspective, language primarily

functions as a system for expressing thoughts, encoded into motor activity that manifests as either covert or overt speech.

Neurobiological evidence indicates that while mental activities related to bonding and stress responses are observed in non-human primates, mammals, and birds, symbolic computations remain a uniquely human capacity. Fossil finds, behavioral relics, and neural properties in terms of brain mass, neuron count, and estimated synaptic connections across various hominins suggest that language is a scaled mental capacity. Although our final assumptions are based on inferences from various datasets, we predict that the critical neural threshold for the mental language capacity was reached by 1.8 Ma with the emergence of early *H. erectus*.

## Author contributions

DH: Conceptualization, Writing – original draft, Writing – review & editing.

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## References

Aguirre, G. K., and D'Esposito, M. (1999). Topographical disorientation: a synthesis and taxonomy. *Brain* 122, 1613–1628. doi: 10.1093/brain/122.9.1613

Aiello, L. C., and Wheeler, P. (1995). The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36, 199–221. doi: 10.1086/204350

Arbib, M. (2012). *How the Brain got Language: The Mirror System Hypothesis*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780199896684.001.0001

Ardesch, D. J., Scholten, L. H., Li, L., Preuss, T. M., Rilling, J. K., and van den Heuvel, M. P. (2019). Evolutionary expansion of connectivity between multimodal association areas in the human brain compared with chimpanzees. *Proc. Natl. Acad. Sci.* 116, 7101–7106. doi: 10.1073/pnas.1818512116

Azevedo, F. A., Carvalho, L. R., Grinberg, L. T., Farfel, J. M., Ferretti, R. E., Leite, R. E., et al. (2009). Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain. *J. Comp. Neurol.* 513, 532–541. doi: 10.1002/cne.21974

Baddeley, A. D. (2003). Working memory: looking back and looking forward. *Nat. Rev. Neurosci.* 4, 829–839. doi: 10.1038/nrn1201

Badre, D., and D'Esposito, M. (2009). Is the rostro-caudal axis of the frontal lobe hierarchical? *Nat. Rev. Neurosci.* 10, 659–669. doi: 10.1038/nrn2667

Baron-Cohen, S. (1995). *Mindblindness: An Essay on Autism and Theory of Mind*. Cambridge, MA: The MIT Press. doi: 10.7551/mitpress/4635.001.0001

Bednarik, R. G. (2003). The earliest evidence of paleoart. *Rock Art Res.* 20, 89–135.

Berwick, R. C., and Chomsky, N. (2016). *Why only us, Language and Evolution*. Cambridge, MA: MIT Press. doi: 10.7551/mitpress/9780262034241.001.0001

Bickerton, D. (2014). *More than Nature Needs: Language, Mind and Evolution*. Cambridge, MA: Harvard University Press. doi: 10.4159/9780674728523

Billard, A. (2002). “Mirror neurons and the neural basis for learning by imitation: Computational modeling,” in *Mirror Neurons and the Evolution of Brain and*

*Language*, eds M. I. Stamenov, and V. Gallese (Amsterdam: John Benjamins), 344–352. doi: 10.1075/aicr.42.27bil

Bishop, D. V. M. (1997). *Uncommon Understanding: Development and Disorders of Language Comprehension in Children*. Hove: Psychology Press.

Boroditsky, L. (2011). How language shapes thought. The languages we speak affect our perceptions of the world. *Sci. Am.* 304, 62–65. doi: 10.1038/scientificamerican0211-62

Bramble, D. M., and Lieberman, D. E. (2004). Endurance running and the evolution of Homo. *Nature* 432, 345–352. doi: 10.1038/nature03052

Bräuer, G. (2021). The origin of modern anatomy: by speciation or intraspecific evolution? *Evol. Anthropol.* 17, 22–37. doi: 10.1002/evan.20157

Broca, P. (1861). Remarks on the seat of the faculty of articulated language (following an observation of aphemia (loss of speech)). *Bull. Soc. Anat. Paris* 6, 330–357.

Brumm, A., van den Bergh, G. D., Storey, M., Kurniawan, I., Alloway, B. V., Setiawan, R., et al. (2016). Age and context of the oldest known hominin fossils from Flores. *Nature* 534, 249–253. doi: 10.1038/nature17663

Cantlon, J. F., and Brannon, E. M. (2007). Basic math in monkeys and college students. *PLoS Biol.* 5:e328. doi: 10.1371/journal.pbio.0050328

Charrier, C., Joshi, K., Coutinho-Budd, J., Kim, J. E., Lambert, N., de Marchena, J., et al. (2012). Inhibition of SRGAP2 function by its human-specific paralogs induces neoteny during spine maturation. *Cell* 149, 923–935. doi: 10.1016/j.cell.2012.03.034

Chomsky, N. (1968). *Language and Mind*. New York, NY: Harcourt Brace Jovanovich, Inc. doi: 10.1037/e400082009-004

Chomsky, N. (1995). *The Minimalist Program*. Cambridge: MIT Press.

Chomsky, N. (2000). *New Horizons in the Study of Language and Mind*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511811937

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Chomsky, N. (2007). "Approaching UG from Below. Interfaces+Recursion = Language?" in: *Chomsky's Minimalism and the View from Syntax-Semantics*, eds. U. Sauerland, and H.-M. Gärtnner. Berlin: Mouton de Gruyter, pp. 1-29. doi: 10.1515/9783110207552.1

Churchland, P. S., and Sejnowski, T. J. (1992). *The Computational Brain*. Cambridge, MA: MIT Press. doi: 10.7551/mitpress/2010.001.0001

Colom, R., Karama, S., Jung, R. E., and Haier, R. J. (2010). Human intelligence and brain networks. *Dialogues Clin. Neurosci.* 12, 489-501. doi: 10.31887/DCNS.2010.12.4/rcolom

Corballis, M. (2011). *The Recursive Mind: The Origins of Human Language, Thought, and Civilization*. Princeton, NJ: Princeton University Press.

Corballis, M. C. (2002). *From Hand to Mouth: The Origins of Language*. Princeton, NJ: Princeton University Press. doi: 10.1515/9780691221731

Darwin, C. R. (1859). *On the Origin of Species by Means of Natural Selection (or the Preservation of Favoured Races in the Struggle for Life)*. 1st ed. London: John Murray. doi: 10.5962/bhl.title.68064

Davidson, D. (1963). Actions, reasons, and causes. *J. Philos.* 60, 685-700. doi: 10.2307/2023177

Dawkins, R. (1976). *The Selfish Gene*. Oxford: Oxford University Press.

De Martins, M. D. (2012). Distinctive signatures of recursion. *Philos Trans R Soc Lond B Biol Sci.* 367, 2055-2064. doi: 10.1098/rstb.2012.0097

De Martins, M. J., Muršič, Z., Oh, J., and Fitch, W. T. (2015). Representing visual recursion does not require verbal or motor resources. *Cogn. Psychol.* 77, 20-41. doi: 10.1016/j.cogpsych.2015.01.004

Deacon, T. (1997). *The Symbolic Species: The Co-evolution of Language and the Brain*. New York, NY: Penguin Press.

Deaner, R. O., Isler, K., Burkart, J., and van Schaik, C. (2007). Overall brain size (and not encephalization quotient) best predicts cognitive ability across non-human primates. *Brain Behav.* E70, 115-124. doi: 10.1159/000102973

Dennett, D. C. (1987). *The Intentional Stance*. Cambridge, MA: MIT Press.

Dennis, M. Y., Nuttle, X., Sudmant, P. H., Antonacci, F., Graves, T. A., Nefedov, M., et al. (2012). Evolution of human-specific neural SRGAP2 genes by incomplete segmental duplication. *Cell* 149, 912-922. doi: 10.1016/j.cell.2012.03.033

D'Errico, F., and Villa, P. (1997). Holes and grooves: the contribution of microscopy and taphonomy to the problem of art origins. *J. Hum. Evol.* E33, 1-31. doi: 10.1006/jhev.1997.0141

DeSilva, J. M., and Lesnik, J. J. (2008). Brain size at birth throughout human evolution: a new method for estimating neonatal brain size in hominins. *J. Hum. Evol.* 55, 1064-1074. doi: 10.1016/j.jhevol.2008.07.008

Donald, M. (1991). *Origins of the Modern Mind: Three Stages in the evolution of Culture and Cognition*. Cambridge, MA: Harvard University Press.

Drachman, D. A. (2005). Do we have brain to spare? *Neurology* 64, 2004-2005. doi: 10.1212/01.WNL.0000166914.38327.BB

Du, A., Zipkin, A. M., Hatala, K. G., Renner, E., Baker, J. L., Bianchi, S., et al. (2018). Pattern and process in hominin brain size evolution are scale-dependent. *Proc. R. Soc. B* 285:20172738. doi: 10.1098/rspb.2017.2738

Emery, N. J., and Clayton, N. S. (2009). Comparative social cognition. *Annu. Rev. Psychol.* 60, 87-113. doi: 10.1146/annurev.psych.60.110707.163526

Everett, D. L. (2005). Cultural constraints on grammar and cognition in Pirahã: Another look at the design features of human language. *Curr. Anthropol.* 46 621-646. doi: 10.1086/431525

Everett, D. L. (2008). *Don't Sleep, there are Snakes: Life and Language in the Amazonian Jungle*. New York, NY: Pantheon Books.

Falk, D. (1983). Cerebral cortices of East African early hominids. *Science*. 221, 1072-1074. doi: 10.1126/science.221.4615.1072

Falk, D. (2009). *Finding our Tongues: Mothers, Infants and the Origins of Language*. New York, NY: Basic Books.

Falk, D. (2014). Interpreting sulci on hominin endocasts: old hypotheses and new findings. *Front. Hum. Neurosci.* 8:134. doi: 10.3389/fnhum.2014.00134

Fedorenko, E., and Duncan, J. (2013). Broad domain-generality in focal regions of frontal and parietal cortex. *Proc. Natl. Acad. Sci. USA* 110, 16616-16621. doi: 10.1073/pnas.1315235110

Fedorenko, E., Piantadosi, S. T., and Gibson, E. A. F. (2024). Language is primarily a tool for communication rather than thought. *Nature* 630, 575-586. doi: 10.1038/s41586-024-07522-w

Fitch, W. T., and Martins, M. D. (2014). Hierarchical processing in music, language, and action: Lashley revisited. *Ann. N. Y. Acad. Sci.* 1316, 87-104. doi: 10.1111/nyas.12406

Fodor, J. A. (1975). *The Language of Thought*. Cambridge, MA: Harvard University Press.

Fodor, J. A. (1983). *The Modularity of Mind: An Essay on Faculty Psychology*. Cambridge, MA: MIT Press. doi: 10.7551/mitpress/4737.001.0001

Foster, M. L. (1978). "The symbolic structure of primordial language," in *Human Evolution: Biosocial Perspectives*, eds S. L. Washburn, and E. R. McCown (Menlo Park, CA: Benjamin/Cummings), 77-121.

Frith, U. (2003). Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. B Biol. Sci.* 358, 459-473. doi: 10.1098/rstb.2002.1218

Fuentes, A. (2017). Human niche, human behaviour, human nature. *Interface Focus* 7:20160136. doi: 10.1098/rsfs.2016.0136

Fujita, K. (2014). "Recursive merge and human language evolution," in *Recursion: Complexity in Cognition*, eds T. Roeper, and M. Speas (Dordrecht: Springer), 243-264. doi: 10.1007/978-3-319-05086-7\_11

Gibson, K. R., Rumbaugh, D., and Baren, M. (2001). "Bigger is better: primate brain size in relationship to cognition," in *Evolutionary Anatomy of the Primate Cerebral Cortex*, eds D. Falk, and K. R. Gibson (Cambridge: Cambridge University Press), 79-97. doi: 10.1017/CBO9780511897085.007

Goodglass, H., and Wingfield, A. (1997). *Anomia: Neuroanatomical and Cognitive Correlates*. San Diego, CA: Academic Press.

Graci, R., and Capone, A. (2023). Perspectives on the semantics/pragmatics debate: insights from aphasia research. *Front. Psychol.* 14:1250170. doi: 10.3389/fpsyg.2023.1250170

Haiman, J. (1980). *Hua: A Papuan language of the Eastern Highlands of New Guinea*. Amsterdam: John Benjamins. doi: 10.1075/scls.5

Harrod, J. B. (2014). Palaeoart at two million years ago? A review of the evidence. *Arts* 3, 135-155. doi: 10.3390/arts3010135

Hauser, M. D., and Chomsky, N. (2002). The faculty of language: what is it, who has it, and how did it evolve? *Science* 298, 1569-1579. doi: 10.1126/science.298.5598.1569

Head, H. (1926). *Aphasia and Kindred Disorders of Speech*. Cambridge: Cambridge University Press.

Heider, K. G. (1972). *Dani Ethnography*. Cambridge, MA: Harvard University Press.

Herculano-Houzel, S. (2009). The human brain in numbers: a linearly scaled-up primate brain. *Front. Hum. Neurosci.* 3:31. doi: 10.3389/neuro.09.031.2009

Herculano-Houzel, S. (2012). The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. *Proc. Natl. Acad. Sci. USA* 109(Suppl 1):10661-10668. doi: 10.1073/pnas.1201895109

Herculano-Houzel, S., Avelino-de-Souza, K., Neves, K., Porfirio, J., Messeder, D., Mattos Feijó, L., et al. (2014). The elephant brain in numbers. *Front. Neuroanat.* 8:46. doi: 10.3389/fnana.2014.00046

Herculano-Houzel, S., and Kaas, J. H. (2011). Gorilla and orangutan brains conform to the primate cellular scaling rules: implications for human evolution. *Brain Behav. Evol.* 77, 33-44. doi: 10.1159/000322729

Herculano-Houzel, S., and Lent, R. (2005). Isotropic fractionator: a simple, rapid method for the quantification of total cell and neuron numbers in the brain. *J. Neurosci.* 25, 2518-2521. doi: 10.1523/JNEUROSCI.4526-04.2005

Hillert, D. (2021). How did language evolve in the lineage of higher primates? *Lingua* 264:103158. doi: 10.1016/j.lingua.2021.103158

Hillert, D. (2026). *The Birth of Language*. London: Routledge. doi: 10.4324/9781003667995

Hillert, D. G. (2015). On the evolving biology of language. *Front. Psychol.* 6:1796. doi: 10.3389/fpsyg.2015.01796

Hillert, D. G. (2023). On how 'early syntax' came about. *Front. Lang. Sci.* 2:1251498. doi: 10.3389/flang.2023.1251498

Hillert, D. G., and Fujita, K. (2023). Pragmatic language in genus Homo. *Biolinguistics* 17:e11911. doi: 10.5964/bioling.11911

Holloway, R. L. (1981). Culture, symbols, and human brain evolution: a synthesis. *Dialect. Anthropol.* 5, 287-303. doi: 10.1007/BF00246207

Holloway, R. L. (2008). The human brain evolving: a personal retrospective. *Annu. Rev. Anthropol.* 37, 1-19. doi: 10.1146/annurev.anthro.37.081407.085211

Holloway, R. L. (2012). Language and tool making are similar cognitive processes. *Behav. Brain Sci.* 35:226. doi: 10.1017/S0140525X11002019

Jackendoff, R. (1999). Possible stages in the evolution of the language capacity. *Trends Cogn. Sci.* 3, 272-279. doi: 10.1016/S1364-6613(99)01333-9

Jackson, J. H. (1878). On affections of speech from disease of the brain. *Brain* 1, 304-330. doi: 10.1093/brain/1.3.304

Katz, J., and Pesetsky, D. (2011). *The identity thesis for language and music*.

Leonard, L. B. (1998). *Children with Specific Language Impairment*. Cambridge, MA: MIT Press. doi: 10.7551/mitpress/1810.001.0001

Levinson, S. C. (2014). "Pragmatics as the origin of recursion," in *Language and Recursion*, eds F. Lowenthal, and L. Lefebvre (New York, NY: Springer), 3-13. doi: 10.1007/978-1-4614-9414-0\_1

Margulies, D. S., Ghosh, S. S., Goulas, A., Falkiewicz, M., Huntenburg, J. M., Langs, G., et al. (2016). Situating the default-mode network along a principal gradient of macroscale cortical organization. *Proc. Natl. Acad. Sci. USA* 113, 12574–12579. doi: 10.1073/pnas.1608282113

McBrearty, S., and Brooks, A. S. (2000). The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* 39, 453–563. doi: 10.1006/jhev.2000.0435

Minsky, M. (1986). *The Society of Mind*. New York, NY: Simon & Schuster.

Miyagawa, S., DeSalle, R., Nóbrega, V. A., Nitschke, R., Okumura, M., and Tattersall, I. (2025). Linguistic capacity was present in the *Homo sapiens* population 135 thousand years ago. *Front. Psychol.* 16:1503900. doi: 10.3389/fpsyg.2025.1503900

Nasukawa, K. (2017). Extending the application of merge to elements in phonological representations. *J. Phonetic Soc. Jpn.* 21, 59–70. doi: 10.24467/onseikenkyu.21.1\_59

Odling-Smeel, F. J., Laland, K. N., and Feldman, M. W. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton University Press.

Orton, S. T. (1937). *Reading, Writing, and Speech Problems in Children*. New York, NY: W. W. Norton and Company.

Passingham, R. E. (1975). The brain and intelligence. *Brain Behav. Evol.* 11, 1–15. doi: 10.1159/000123620

Pensalfini, R. (2003). *A Grammar of Jingulu: An Aboriginal Language of the Northern Territory*. Pacific Linguistics. Canberra: Pacific linguistics, Research School of Pacific and Asian Studies, Australian National University

Piccinini, G., and Bahar, S. (2013). Neural computation and the computational theory of cognition. *Cogn. Sci.* 37, 453–488. doi: 10.1111/cogs.12012

Pinker, S. (2007). *The Stuff of Thought: Language as a Window into Human Nature*. New York, NY: Viking.

Pontzer, H. (2012). Ecological energetics in early hominins: the “costs” of being human. *Curr. Anthropol.* 53, S449–S458. doi: 10.1086/667402

Potts, R. (2012). Evolution and environmental change in early human prehistory. *Annu. Rev. Anthropol.* 41, 151–167. doi: 10.1146/annurev-anthro-092611-145754

Premack, D. (1978). Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* 1, 515–526. doi: 10.1017/S0140525X00076512

Rightmire, G. P. (2013). *Homo erectus* and Middle Pleistocene hominins: brain size, skull form, and facial evolution. *Evol. Anthropol.* 22, 247–262. doi: 10.1016/j.evanthol.2013.04.008

Rilling, J. K., and Seligman, R. A. (2002). A quantitative morphometric comparative analysis of the primate temporal lobe. *J. Hum. Evol.* 42, 505–533. doi: 10.1006/jhev.2001.0537

Rosch, E. (1978). “Principles of categorization,” in *Cognition and Categorization*, eds E. Rosch, and B. B. Lloyd (Hillsdale, NJ: Lawrence Erlbaum Associates), 27–48. doi: 10.4324/9781032633275-4

Roth, G., and Dicke, U. (2005). Evolution of the brain and intelligence. *Trends Cogn. Sci.* 9, 250–257. doi: 10.1016/j.tics.2005.03.005

Samu, D., Campbell, K. L., Tsvetanov, K. A., Shafto, M. A., Cam-CAN consortium, and Tyler, L. K. (2017). Preserved cognitive functions with age are determined by domain-dependent shifts in network responsiveness. *Nat. Commun.* 8, 1–14. doi: 10.1038/ncomms14743

Schoenemann, P. T., Sheehan, M. J., and Glotzer, L. D. (2005). Prefrontal white matter volume is disproportionately larger in humans than in other primates. *Nat. Neurosci.* 8, 242–252. doi: 10.1038/nn1394

Semendeferi, K., Lu, A., Schenker, N., and Damasio, H. (2002). Humans and great apes share a large frontal cortex. *Nat. Neurosci.* 5, 272–276. doi: 10.1038/nn814

Shiu, P. K., Sterne, G. R., Spiller, N., Franconville, R., Sandoval, A., Zhou, J., et al. (2024). A *Drosophila* computational brain model reveals sensorimotor processing. *Nature* 634, 210–219. doi: 10.1038/s41586-024-07763-9

Simpson, J. (1991). *Warrupi Morpho-Syntax: A Lexicalist Approach*. New York, NY: Springer. doi: 10.1007/978-94-011-3204-6

Sousa, A. M. M., Meyer, K. A., Santpere, G., Gulden, F. O., and Sestan, N. (2017). Evolution of the human nervous system function, structure, and development. *Cell* 170, 226–247. doi: 10.1016/j.cell.2017.06.036

Spocter, M. A., Hopkins, W. D., Garrison, A. R., Bauernfeind, A. L., Stimpson, C. D., Hof, P. R., et al. (1691). (2010). Wernicke's area homologue in chimpanzees (*Pan troglodytes*) and its relation to the appearance of modern human language. *Proc. R. Soc.* 277, 2165–2174. doi: 10.1098/rspb.2010.0011

Sporny, M., Guez-Haddad, J., Kreusch, A., Shakartzi, S., Neznansky, A., Cross, A., et al. (2017). Structural history of human SRGAP2 proteins. *Mol. Biol.* E34, 1463–1478. doi: 10.1093/molbev/msx094

Stout, D., and Chaminade, T. (2007). The evolutionary neuroscience of tool making. *Neuropsychologia* 45, 1091–1100. doi: 10.1016/j.neuropsychologia.2006.09.014

Stringer, C. B. (2012). The status of *Homo heidelbergensis* (Schoetensack 1908). *Evol. Anthropol.* 21, 101–104. doi: 10.1002/evan.21311

Tallerman, M., and Gibson, K. R. (2012). “Introduction: the evolution of language,” in *The Oxford Handbook of Language Evolution*, eds M. Tallerman, and K. R. Gibson (Oxford: Oxford University Press), 1–35. doi: 10.1093/oxfordhb/9780199541119.01.30001

Tobias, P. V. (1971). *The Brain in Hominid Evolution*. New York, NY: Columbia University Press. doi: 10.5962/bhl.title.15880

Tobias, P. V. (1987). The brain of *Homo habilis*: a new level of organization in cerebral evolution. *J. Hum. Evol.* 16, 741–761. doi: 10.1016/0047-2484(87)90022-4

Tomasello, M. (2008). *Origins of Human Communication*. Cambridge, MA: MIT Press. doi: 10.7551/mitpress/7551.001.0001

Tomasello, M., and Herrmann, E. (2010). Ape and human cognition: what's the difference? *Curr. Dir. Psychol. Sci.* 19, 3–8. doi: 10.1177/0963721409359300

Traugott, E. C. (2011). Linguistics: the study of the language capacity and its functions. *Diogenes* 58, 20–34. doi: 10.1177/0392192112441910

Uddin, L. Q. (2021). Cognitive and behavioural flexibility: neural mechanisms and clinical considerations. *Nat. Rev. Neurosci.* 22, 167–179. doi: 10.1038/s41583-021-00428-w

van den Heuvel, M. P., Ardesch, D. J., Scholtens, L. H., de Lange, S. C., van Haren, N. E. M., Sommer, I. E. C., et al. (2023). Human and chimpanzee shared and divergent neurobiological systems for general and specific cognitive brain functions. *PNAS USA* 120, 1–8. doi: 10.1073/pnas.2218565120

Wakita, M. (2014). Broca's area processes the hierarchical organization of observed action. *Front. Hum. Neurosci.* 7:937. doi: 10.3389/fnhum.2013.00937

Wernicke, C. (1874). *The Symptom Complex of aphasia: A Psychological Study on an Anatomical Basis*. London: Cohn and Weigert.

Whorf, B. L. (1956). *Language, Thought and Reality*. Cambridge, MA: Technology Press of MIT; New York, NY: John Wiley & Sons, Inc.

Wilson, D., and Sperber, D. (2004). “Relevance theory,” in *The Handbook of Pragmatics*, eds L. R. Horn, and G. Ward (Malden, MA: Blackwell), 607–632.

Wynn, T. (1985). Piaget, stone tools and the evolution of human intelligence. *World Archaeol.* 17, 32–43. doi: 10.1080/00438243.1985.9979948

Wynn, T. (2002). Archaeology and cognitive evolution. *Behav. Brain Sci.* 25, 389–402. doi: 10.1017/S0140525X02000079

Yoo, D., Rhie, A., Hebbar, P., Antonacci, F., Logsdon, G. A., Solar, S. J., et al. (2025). Complete sequencing of ape genomes. *Nature* 641, 401–18. doi: 10.1038/s41586-025-08816-3

Zlatev, J., Gärdenfors, P., Persson, T., and Lindblom, J. (2005). *Bodily mimesis as “the missing link” in human cognitive evolution*. Lund University Cognitive Studies 121.