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The Arcuate Fascicle Middle Temporal Gyrus Connection in Chimpanzees: A Missing Link in Language Evolution?

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Abstract

This forum article investigates the theoretical implications of the latest findings regarding the evolution of the arcuate fascicle (AF), the main white matter fibre tract for language. Thanks to ultra-high-resolution post-mortem tractography, a weak, left-lateralised connection between the inferior frontal gyrus and the middle temporal gyrus (MTG) connection was demonstrated in wild and captive chimpanzees. This proposed white matter substrate for the Faculty of Language in the Narrow sense (FLN) was previously thought to be unique to humans along with FLN itself. This finding suggests that the last common ancestor of humans and chimpanzees already possessed this neural architecture, casting into doubt the idea of a saltatory, human-specific emergence. The AF-MTG connection may therefore represent a missing link in language evolution, with strength and lateralisation that may have increased during human evolution, pointing to a more continuous evolution of language.

Keywords

language evolution, brain, primates, arcuate fasciculus, lateralization

The Concept of a Missing Link in Evolution

A missing link in evolution is a hypothesized transient fossil in a given evolutionary trajectory that explains how a specific trait has evolved in one species. For example, for decades, scientists wondered how humans achieved the upright stance. They hypothesized that an extinct species must have lived after the split between humans and great apes, possessing both ape- and human-like features. That species was discovered with

Lucy, the first identified Australopithecus, who possessed ape-like features, but was able to walk bipedally (Lewin, 1983).

A similar question might be asked about language evolution. Many scholars argue that language evolved uniquely about 100,000 years ago in the human species (Berwick & Chomsky, 2016). Others, however, propose a more continuous evolution, in which language can be decomposed into its building blocks and possible precursors of these building blocks can be studied (e.g., Arnon et al., 2025; Fitch, 2010). Therefore, it is possible to hypothesise missing links in this evolutionary trajectory. However, when studying language, it is first essential to clearly define the object of study. Indeed, many scholars diverge in their assessments of what exactly constitutes language.

Faculty of Language in the Narrow Sense Versus Faculty of Language in the Broad Sense

A highly influential framework, proposed by Hauser, Chomsky, and Fitch (2002), divides language into a so-called Faculty of Language in the Narrow Sense (FLN), which is a subset of a Faculty of Language in the Broad sense (FLB), the latter of which is further separated into two sub-systems. One FLB sub-system is crucial for the externalisation of FLN, the sensory-motor system. The other FLB sub-system is constituted by a cognitive conceptual-intentional system. The FLB systems are important components of language, but are not exclusive to it, and can exist on their own. Hence, language-independent precursors of these systems might be shared with other animals (Hauser, Chomsky, & Fitch, 2002).

In strong contrast stands the FLN, hypothesised to consist of a computation, which can be boiled down to a recursive syntactic operation (or MERGE), hypothesised to be unique to humans. Consequently, no parts of it are thought to be shared with other species in the animal kingdom. Berwick et al., (2013) define MERGE as follows: "In human language, the computational mechanism that constructs new syntactic objects Z (e.g., 'ate the apples') from already-constructed syntactic objects X ('ate'), Y ('the apples')".

A derived "tripartite" framework has also been proposed, in which FLN is equivalent to a "core language faculty", which engages with a sensory-motor interface for externalisation and with a conceptual-intentional interface which is internal (both equivalent to FLB sub-systems) (Berwick et al., 2013; Berwick & Chomsky, 2016). In this tripartite framework the core language faculty is decomposed into the same recursive MERGE operation combined with a lexical item (a word).

The repercussion of recursive MERGE is the unbound generative capacity of human language leading to infinite possibilities of sentences. By enabling unbounded hierarchical embedding, recursive MERGE provides a stack-like memory system that tracks long-distance dependencies and supports infinite generation through iterative self-application.

Nonhuman primates, like baboons, do not seem to have access to such an operation for their vocal communication and rarely combine more than two or three calls together (e.g., Kemp et al., 2017). They can however (in the visual domain) learn complex artificial grammar structures. In contrast to humans who learn these structures easily, nonhuman primates (like baboons) require extensive training to learn artificial grammar sequences with non-adjacent dependencies and a mirror structure which have a supra-regular generative power (Malassis et al., 2020). Furthermore, nonhuman primates have not yet been shown to process repeated structures, which may reveal a limitation to the generative power of sequence learning in nonhuman primates (Friederici, 2023). This limitation might also be related to a working-memory constrain (Malassis et al., 2020).

In order to maintain clarity for both primatology and neuroscience audiences, I will adopt the neuroscience-based definition of the core language faculty (e.g., Friederici, 2017), which focusses on "syntax" and certain aspects of semantics, particularly when syntactic rules are applied to lexical items (i.e. words) (following Berwick et al., 2013, see Figure 1). I acknowledge that this simplification may overlook nuances appreciated by linguists.

This FLN/FLB dichotomous view might be limited, and there is lack of research on precursors of FLN that could bridge the gap between these two language faculty systems.

The Comparative Approach

Soft tissues, like the brain, rarely fossilizes. How, then, can we study (language) evolution? A fruitful method is the comparative approach in which one compares contemporary living primate species with one another. For example, if we humans possess a certain trait that is also shared with a close primate relative, for example the chimpanzee, then our last common ancestor, who lived approximately 7-9 million years ago, likely already possessed this trait.

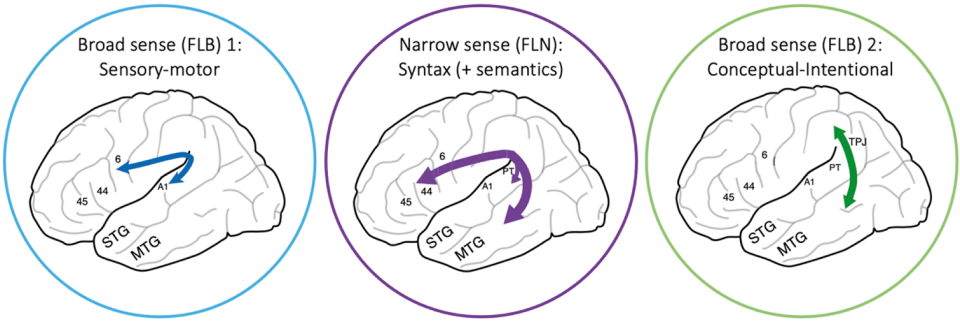
This approach allows to back trace the history of evolution and establish an evolutionary chronology. It is important to note that an apparently shared trait might actually be the result of convergent, independent evolution. For example, the wings of birds and insects serve the same function, which is flying. However, an analysis of the underlying structure of the wings reveals that they did not evolve from a common ancestor, but rather independently due to similar evolutionary pressures. Therefore, to reduce the uncertainty of such inferences, it is necessary to include both structure and function in the comparative approach (Becker & Trettenbrein, 2026).

Proposed Brain Bases of FLN and FLB and Its Evolution

The underlying structure for cognitive systems like language is the brain. Fortunately, potential brain bases for FLN and FLB have been proposed. In fact, the sensory-motor sub-system of FLB is centred around areas in the premotor cortex (Area 6) and the primary sensory areas, which is the primary auditory cortex (for the modality of speech), connected by dorsal white matter fibre bundles, the motor-sensory branches of the arcuate fascicle (Berwick et al., 2013; Fedorenko et al., 2024; Friederici, 2011; Friederici & Becker, 2025) (see Figure 1). The intentional conceptual FLB sub-system is proposed to be supported by the temporal-parietal junction and its white matter fibre connections, the indirect posterior segment of the arcuate fascicle (Catani & Bambini, 2014) (see Figure 1).

Figure 1

Schematical View of the Dorsal Neuroanatomy of the Faculty of Language in the Narrow Sense (FLN) (Middle) and Broad Sense (FLB) (Right and Left)



The underlying neural system for FLN is proposed to be supported by Broca's area in the inferior frontal gyrus, (specifically Areas 44 and 45, if defined cytoarchitecturally) and areas in the superior temporal gyrus (STG), such as the planum temporale (PT) and areas in the middle temporal gyrus (MTG) (Berwick et al., 2013; Fedorenko et al., 2024; Friederici, 2011; Friederici & Becker, 2025) (Figure 1). It is important to note that the neuroanatomy of FLN has key characteristics, not shared by FLB. In fact, this system is left-lateralised and connected by a white matter fibre bundle called the long and direct segment of the arcuate fascicle, hereafter simply the arcuate fascicle (AF), which connects the inferior frontal gyrus with the STG and MTG (Berwick et al., 2013; Fedorenko et al., 2024; Friederici, 2011; Friederici & Becker, 2025).

The AF's involvement in syntax and certain aspects of semantics, especially its connection to the MTG, has been extensively studied using functional MRI, and in aphasia research and developmental studies. However, it is challenging to pinpoint the

exact function of a white matter fibre tract, as it is often inferred from the function of the cortical regions it connects. fMRI studies have highlighted the role of Broca's area (and especially its posterior portion) in syntactic processes (for reviews see Hagoort, 2014; Goucha et al., 2017), and the posterior temporal cortex in sentence-level syntactic processes (Friederici, 2011) and the integration of semantic and syntactic information (Matchin et al., 2022). Therefore, the white matter fibre bundle connecting these regions has been proposed to heavily support syntactic operations (Friederici, 2017).

A second way to access function is through the study of a tract's loss. For example, in primary progressive aphasia, pathological degeneration of the AF in patients results in deficits in processing syntactically complex sentences (Wilson et al., 2011).

Developmental studies provide a third method of investigation. They have shown that the AF between IFG and posterior temporal lobe matures late in development, around 7 years of age, co-developing with the ability to process complex syntax (Brauer et al., 2013; Perani et al., 2011). Further, its growth between 3 and 10 years specifically predicts children's ability to comprehend syntactically complex sentences (Skeide et al., 2016). The individual microstructural values of the AF were significantly correlated with the individual performances (accuracy and reaction time) on object-first sentences in children aged 3 to 10 (Skeide et al., 2016).

When specifically examining the AF's function in its connections to the STG and MTG, Glasser and Rilling (2008) first used DTI to anatomically separate these connections and next compared the sites with activated regions from prior fMRI studies. The STG was found to be activated for phonological processes, while the MTG was activated for lexical-semantic processes. A more direct study from Janssen et al. (2023) demonstrated similar findings: fMRI with task-based peak activations served as seed regions for probabilistic tractography. Next the FA values of interindividual differences were then related to the reaction time on two tasks. The first task involved the overt repetition of binaurally presented pseudowords (testing sublexical phonological processes), while the second task consisted of the overt generation of verbs in response to binaurally presented nouns (testing lexical-syntactic integration, which is essential for recursive syntactic operations such as embeddings and long-distance dependencies). The AF-STG connection was found to support phonological mapping or repetitions of pseudowords, while the AF-MTG connection supported the generation of appropriate verbs to spoken nouns, in other words lexical syntactic mapping.

Regarding lateralisation, the language system is widely accepted to be functionally left-lateralised (e.g., Friederici, 2017). In addition, in humans, the AF is structurally left lateralised and there is evidence that its volume correlates with the leftward asymmetry observed in fMRI activations (Takaya et al., 2015; Vassal et al., 2016; but see also: Gerrits et al., 2021). This structural left lateralisation of the AF has also been linked crucial to language processes, as microstructural measurements of only the left AF correlated with word learning in adult subjects (López-Barroso et al., 2013). Additionally, a localized mi-

crostructural lateralization of the AF was found to be associated with syntactic sentence processing skills in children (Eichner, Berger, et al., 2024).

The AF, and specifically its MTG connection, is therefore the closest and most plausible white matter candidate for a distributed neurobiological basis (spanning inferior frontal and posterior temporal regions) of FLN, or the core language faculty as defined by Berwick et al. (2013). It should be noted that another plausible, yet less canonical view postulates a wider spread and distributed neural substrate for syntactic processing as highlighted by findings that include sub-cortical contributions such as those observed in agrammatism in cerebellar aphasias (Satoer et al., 2024; Silveri et al., 1994).

Discontinuous View of AF Evolution

The AF has undergone massive morphological changes during human evolution (Eichert et al., 2019; Friederici & Becker, 2025). Indeed, in monkeys and great apes, the AF has been described as connecting Broca's area to the STG only. In contrast, the human AF connects Broca's area to both the STG and the MTG (Rilling et al., 2008; for reviews: Becker et al., 2022a, 2022b).

If monkeys and apes lack a MTG connection, lexical-semantic and syntactic mapping through the AF cannot be achieved (Catani & Bambini, 2014; Rilling et al., 2008, 2012). In addition, studies have not found left lateralisation in either monkeys or apes (Balezeau et al., 2020; Bryant et al., 2020; Roumazeilles et al., 2020).

Numerous authors have cited the lack of AF-MTG connectivity in nonhuman primates as evidence that such a connection is linked to the human-specific FLN/core language faculty (Becker, 2025; Berwick & Chomsky, 2016; Dehaene, 2026; Fitch, 2018; Friederici 2017; Pulvermüller 2018). In particular, a discontinuous and sudden human-unique evolution of the AF has been put forward, in which the AF expanded massively into the MTG and became left lateralised. This neurophysiology is seen as a confirming basis for the conceptual view of a discontinuous and sudden human-unique FLN evolution in the last 100 000 years (e.g., Berwick & Chomsky, 2016; Friederici, 2017).

Interestingly, the seminal studies investigating the AF morphology between primate species (Rilling et al., 2008, 2012) did show a connection into the MTG in one chimpanzee subject. In addition, Rilling et al., (2012) is the only account thus far in the literature on the left lateralisation of the AF-STG connection in 22 female chimpanzees. However, subsequent investigation could not replicate these findings, establishing the consensus that the MTG connection and left lateralisation are absent in nonhuman primates (Balezeau et al., 2020; Barrett et al., 2020; Bryant et al., 2020; Eichert et al., 2019; Eichert et al., 2020; Rocchi et al., 2021; Roumazeilles et al., 2020; Sierpowska et al., 2022).

Revisiting AF Evolution Using Ultra-High-Resolution Post-Mortem Tractography

Due to the theoretical importance of morphological change to the AF in evolution, related to the FLN and the anecdotal finding of an AF-MTG connection in one subject as described above, we emphasized the need to reinvestigate how AF morphology has changed over the course of evolution. We hypothesized the existence of a missing link in AF evolution that might be shared with our primate relatives.

However, the only chimpanzee brain data previously available (chimpanzeebrain.org) has important limitations. While it has undeniably immensely advanced our understanding of brain evolution (and still does), the diffusion data is of low resolution and comes exclusively from captive, adult subjects, which may not be broadly representative.

In this regard, the Evolution of Brain Connectivity consortium, funded by the Max Planck Society (Friederici et al., 2024; Gräßle et al., 2023), is a game-changing initiative. A large network sources brains from wild and captive nonhuman primates across all age stages, obtained from naturally or unavoidably deceased subjects from zoos across Europe as well as sanctuaries and field sites across Africa. The brains are shipped to Germany for state-of-the-art scanning. Thanks to engineering advances and method development, this resource provides unparalleled post-mortem structural MRI data at a resolution of at least 500 μm, up to 46 times more detailed than previous analyses in apes (Eichner, Paquette, et al., 2024).

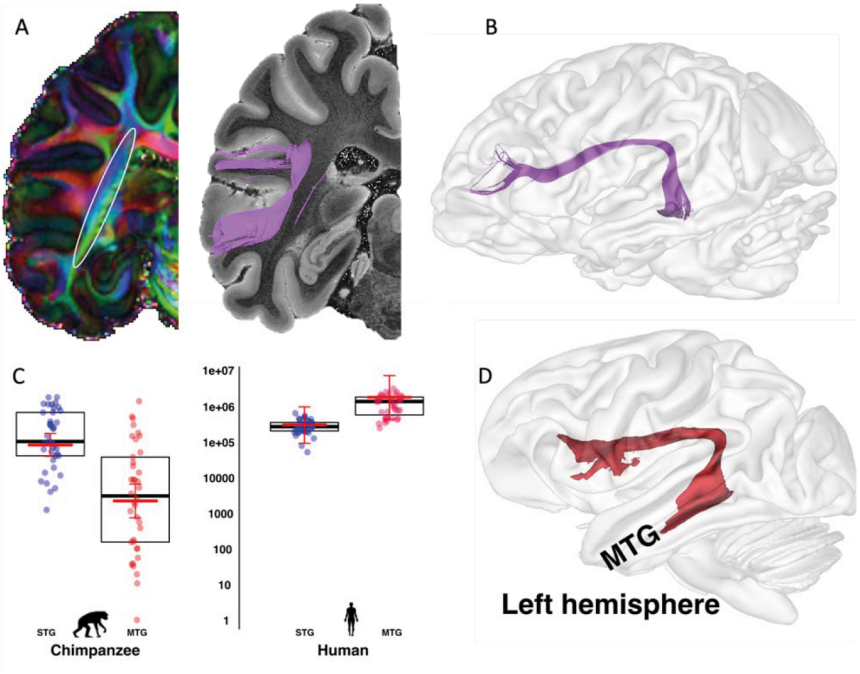
These efforts have paid off. Using three distinct methods, we have been able to show a weak but systematic AF-MTG connection in the chimpanzee (Becker et al., 2025), which I will summarise below:

An AF MTG Connection in Chimpanzees

First, the high-resolution diffusion images depict a blue strip in the coronal plane at the level of the closing of the sylvian fissure that runs through the STG and MTG, which can be seen in Figure 2A. In diffusion directions, the blue colour signifies diffusibility from inferior-to-superior. It might represent white matter that runs into the MTG. Importantly, this blue strip has been found in humans, but not previously in chimpanzees (Rilling et al., 2012).

Figure 2

Three Methods to Highlight the Existence of the AF-MTG Connection in Chimpanzees



Note. A) Colour FA image (left) depicting a blue strip indicating superior-inferior diffusibility. (Right) Deterministic tractography in the same location, showing a connection into the MTG. B) Lateral view of the same connection. C) Comparison of of probabilistic tractography connectivity strength between chimpanzees and humans. Note the opposite ratio of STG/MTG strength between the species. D) Probabilistic tractography between the inferior frontal gyrus and the MTG. A, B & D depict chimpanzee brains. Adapted from Becker et al. (2025).

Second, when virtually dissecting this white matter segment using deterministic tractography (see Figure 2A and B), streamlines that run from Broca's area homologue toward the STG and MTG become visible. From the lateral view, this resulting tract clearly represents an AF connecting the STG and MTG in one quarter of all hemispheres.

Third, we have used observer-independent, systematic, probabilistic tractography that is commonly used in chimpanzee studies (e.g., Balezeau et al., 2020; Bryant et al., 2020; Eichert et al., 2019; Eichert et al., 2020; Rilling et al., 2008, 2012). This more liberal technique allowed to visualize a clear AF-MTG connection in all subjects (Figure 2C, D).

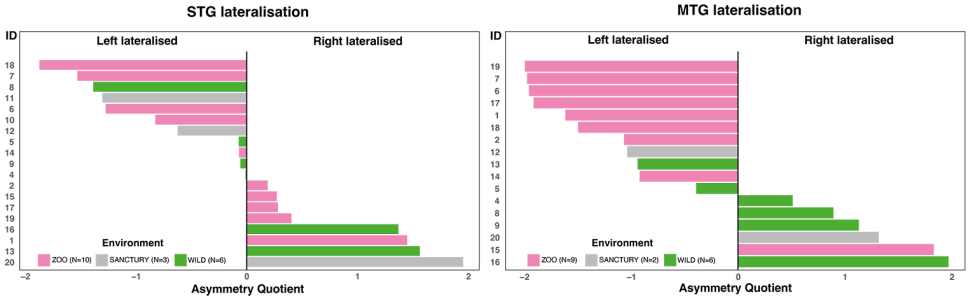
Interestingly, when comparing the connectivity strength of the AF-MTG connection to that of the AF-STG connection, it becomes apparent that the latter is much stronger than the former. Indeed, we found the AF-STG connection to be 14.3 and 45.3 times

stronger than the MTG connection for the left and right hemispheres, respectively. This contrasts with human connectivity strength, which was analysed from previously recorded Max Planck datasets, where a reversed ratio of STG to MTG connectivity exists. In humans, we found that the mean MTG connection is 6.32 and 2.5 times stronger than the STG connection for the left and right hemispheres, respectively, in agreement with the literature (Glasser & Rilling, 2008) (Figure 2C).

Regarding lateralisation, at both the individual and the group levels, and in agreement with the literature, we found no support for left lateralisation of the AF-STG connection in chimpanzees, contrary to humans (Balezeau et al., 2020; Bryant et al., 2020; Eichert et al., 2020; Hecht et al., 2025; Roumazeilles et al., 2020; Sierpowska et al., 2022; but see also Rilling et al., 2012). In contrast, for the AF-MTG connection we found weak support at the individual and group levels for a left lateralisation in chimpanzees, and no statistical difference between chimpanzee and human AF-MTG lateralisation, although the latter is numerically stronger. Interestingly, there may be plasticity in the AF-MTG pathway related to the living environment: 8 out of 9 zoo-housed chimpanzees show a left lateralisation of this connection, whereas wild individuals show a more diverse pattern (2 individuals are left lateralised and 4 are right lateralised) (Figure 3).

Figure 3

Asymmetry Quotients for Individual Chimpanzee Brains for the AF-STG (Right Panel) and AF-MTG (Left Panel) Connections Based on Living Conditions



Note. Zoo (pink), sanctuary (grey), wild (green). Adapted from Becker et al. (2025).

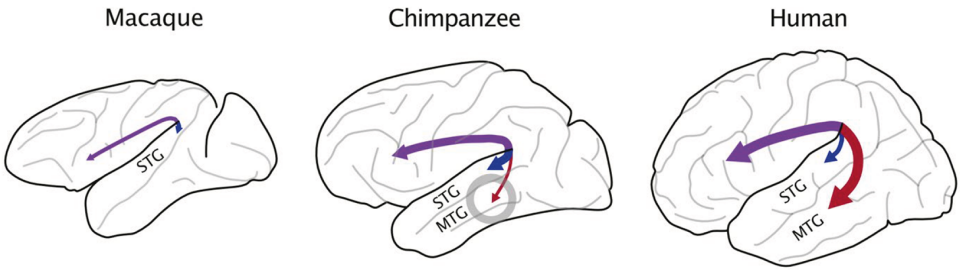
When virtually dissecting one high-resolution macaque monkey subject, no connection that reaches further than the superior-posterior tip of the STG could be found. It should be noted that monkeys lack a distinction between a MTG and inferior temporal gyrus. Therefore, direct comparisons with great apes are challenging due to the unknown structural homologies.

Discussion

The results from Becker et al. (2025) show, for the first time, a weak but systematic connection from the Broca's area homologue to the MTG via the AF in the chimpanzee (Figure 4). In addition, this connection seems to be left lateralised, especially in zoo subjects. Therefore, these findings might represent a missing neural link in the evolution of the Faculty of Language in the Narrow Sense (FLN). Because chimpanzees share this anatomy with humans, these findings indicate that at least the last common ancestor of chimpanzees and humans might already possessed this anatomy. Further studies must now determine whether other great ape species also possess this connection, in order to trace back its evolutionary onset.

Figure 4

Schematic View of the Evolution of the Arcuate Fascicle (AF)



Note. The temporal terminations of the AF (purple) in the STG (blue) and MTG (red) are shown in macaques, chimpanzees, and humans. Our findings confirm the STG connection in both chimpanzees and macaques and, for the first time, systematically highlight a human-like MTG connection in chimpanzees, though it is weaker than in humans (Figure 2). This MTG connection could be a key feature of the hominoid lineage and may have significantly increased during human evolution. Adapted from Becker et al. (2025).

One probable reason this observation has only been made now is the superior resolution and quality of the new dataset. Notably, the connection strength to the MTG is significantly weaker than that of the STG, a pattern that is opposite of what is observed in humans (Glasser & Rilling, 2008). In line with earlier research (Eichert et al., 2019, 2020; Rilling et al., 2012), it is plausible that AF-MTG connectivity expanded dramatically alongside the evolution of language in the human lineage.

With respect to the strong left lateralisation observed in humans, both in the literature (Catani et al., 2007; Dulyan et al., 2026) and in our own data, it is possible that AF-MTG connectivity has not only increased in strength but also in left lateralisation at the individual level throughout evolution. However, in our sample, most of the left-lateralised individuals are zoo-housed, and may be driving the group-level left lateralisation. On the behavioural side, captive chimpanzees show more intentional communication,

like pointing gestures or raspberry vocal sounds, than their wild counterparts, as these strategies develop specifically for communication with human caregivers (Leavens et al., 2005). Furthermore, captive individuals who communicate more effectively with humans—both vocally and gesturally—exhibit a stronger and more left-lateralised AF-STG connection (Hecht et al., 2025). In line with this idea, learning through imitation tasks has been shown to induce a leftward shift in fronto-temporal connectivity in captive chimpanzees (Pope et al., 2018). It is, in fact, not unlikely that captive subjects imitate and adapt behaviourally to human communication due to their dependency on human caregiving. A second hypothesis might propose that it's not the "human" nature of the caregiver but rather the fact that the caregiver is the only food source. In this case, attention-getting intentional communication (gestural and vocal) may be ritualised for imperatively demanding food. Our results may thus reflect neural plasticity supporting such behavioural adaptation. Further research is now needed to investigate the potential impact of living conditions on AF-MTG plasticity and lateralisation (Becker et al., 2026)

Interestingly, the regions connected by the AF-STG connection, such as Broca's area and the planum temporale, have been shown to be related to intentional communication in chimpanzees and baboons (Becker & Meguerditchian, 2022). In fact, in my previous work, thanks to the advances of large-scale monkey MRI acquisitions (Milham et al., 2020), we have demonstrated that the FLN left lateralisation for these grey matter areas is shared with the baboon (Becker et al., 2021; Becker, Phelipon, et al., 2022). Further, for Broca's homologue (Becker, Claidiere, et al., 2022) and the planum temporale (Becker et al., 2024) we found a link between the preferred hand for gestural communication and the regions' lateralisation. In addition, we have shown that the left planum temporale asymmetry is already present at birth in baboons and predicts their right-handedness for communication later in life, thus solving the chicken-and-egg problem (Becker et al., 2024).

Regarding the AF-STG connection which interconnects the aforementioned regions, we have also shown using a lower-resolution *in vivo* dataset from captive chimpanzees (*National Chimpanzee Brain Resource*, chimpanzeebrain.org) a link to intentional gestural and vocal communication. Specifically, chimpanzees who perform above average in intentional communicative gesture tasks exhibit greater white matter integrity in the AF (measured by fractional anisotropy) compared to those who perform below average. Furthermore, male subjects who produce intentional vocalisations towards a human caregiver show a left-lateralised connection, whereas those that do not produce these vocalizations have a right-lateralised bundle (Hecht et al., 2025).

The overall findings suggest that the human-specific AF morphology likely evolved by strengthening an existing brain connection, rather than appearing *de novo*. It is possible that such a neural scaffold was already present in the last common ancestor of humans and chimpanzees and enabled through gradual strengthening the evolution of Faculty of Language in the Narrow Sense processes in the human lineage. In terms of

cognitive computation, the findings may also suggest a more continuous evolution of MERGE (Martins & Boeckx, 2019; but see Berwick & Chomsky, 2019).

Crucially, future studies now need to investigate what behaviours the AF-MTG brain connection has evolved to support in chimpanzees. Could this be precursors to syntax and semantics, as it is the case in humans for the Faculty of Language in the Narrow Sense?

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