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Review

Structural Brain Asymmetries for Language: A Comparative Approach across Primates

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Abstract: Humans are the only species that can speak. Nonhuman primates, however, share some 'domain-general' cognitive properties that are essential to language processes. Whether these shared cognitive properties between humans and nonhuman primates are the results of a continuous evolution [homologies] or of a convergent evolution [analogies] remain difficult to demonstrate. However, comparing their respective underlying structure—the brain—to determinate their similarity or their divergence across species is critical to help increase the probability of either of the two hypotheses, respectively. Key areas associated with language processes are the Planum Temporale, Broca's Area, the Arcuate Fasciculus, Cingulate Sulcus, The Insula, Superior Temporal Sulcus, the Inferior Parietal lobe, and the Central Sulcus. These structures share a fundamental feature: They are functionally and structurally specialised to one hemisphere. Interestingly, several nonhuman primate species, such as chimpanzees and baboons, show human-like structural brain asymmetries for areas homologous to key language regions. The question then arises: for what function did these asymmetries arise in non-linguistic primates, if not for language per se? In an attempt to provide some answers, we review the literature on the lateralisation of the gestural communication system, which may represent the missing behavioural link to brain asymmetries for language area's homologues in our common ancestor.

Keywords: hemispheric specialization; language evolution; lateralization; MRI; baboon; development; language areas

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1. Introduction

"Human being: n. a man, woman, or child of the species Homo sapiens, distinguished from other animals by superior mental development and language . . . " [The Oxford Pocket Dictionary of Current English, Oxford University Press 2009].

This definition states the obvious: humans are the only species able to speak, and thus, this fascinating cognitive faculty is considered as a key feature which divides us from other animals [1]. However, in recent years, the conception of one holistic language faculty has been contrasted with an alternative view that language may be the result of an assembly of cognitive properties that are domain-general and not specific to language [2,3]. Therefore, since nonhuman animals, especially primates, have been shown to share some of these domain-general cognitive properties, the research on nonhuman primates was reconsidered as a critical model to investigate language evolution [3–5]. Whether these shared cognitive properties between humans and nonhuman primates are the result of a continuous evolution (homologies) or of a convergent evolution (analogies) remains difficult to demonstrate. However, comparing their respective underlying structure—the brain—to determinate their similarity or divergence across species is critical to help increase the probability of either of the two hypotheses, respectively. In humans, language models congruently describe a few key hubs of language processing, namely Broca's and

Wernicke's area, and their interconnection, the Arcuate Fasciculus [6–9]. However, in recent years, data have expanded to more distributed models, taking into account several different fibre tracts and regions crucial for language processing, as demonstrated by clinical cases [10] and questioned a localisationist viewpoint of language specialisation [11]. For example, the importance of regions in the interface between social cognition and communication like the Superior Temporal Sulcus and Geschwind's territory in the Inferior Parietal Lobe are highlighted [12], as well as the anterior Insula cortex [13] and the anterior and mid-Cingulate Sulci [14]. Most of these structures share one fundamental feature: they are functionally and structurally specialised towards one hemisphere, mostly the left [7,13,14]. Specifically, 'functional lateralisation' refers to a more pronounced activation in one hemisphere than the other. 'Structural lateralisation' refers to a more pronounced volume, size, surface measurements, or neuron density of a given region in one hemisphere than the other. Although the link between structural and functional asymmetry remains in question [15,16], most authors usually consider that structural asymmetry (the size of the roads) of these regions might reflect the functional asymmetry (the traffic) for language tasks [13,17,18].

Thus, the fundamental question of 'how language lateralisation has evolved' is more relevant than ever in the light of the aforementioned findings about language organisation in the brain. This is where comparative studies on our primate cousins are of importance. In this view of language evolution, the different cognitive components of language could have evolved gradually, in opposition to a saltatory emergence [19]. In this evolutionary process, it is not excluded that 'exaptation' phenomena, where an opportunistic selective adaptation is piggybacked onto preexisting structures, could have played a crucial role [3]. Because brain tissue hardly fossilises, one fruitful way to look for intermediate steps is the comparison of brains between primate species, including humans, in order to infer potential features inherited from their shared common ancestors [20]. In other words, one can determine which brain architectures and behaviours are shared between us and other primates, suggesting its pre-existence before the emergence of our species. Comparative brain approaches for primate species have particularly focussed on neuroanatomy, given the well-known limitation for functional studies in apes and monkeys (e.g., techniques, ethics, sample size, reproductivity). The advent of non-invasive techniques such as Magnetic Resonance Imaging (MRI) favours in-vivo acquisitions on anesthetised subjects, allowing no limitation in terms of sample sizes and species diversity [21]. As a result, primate brain research has benefited in recent years from considerable increase in available MRI databases on large cohorts in many primate species, including macaques: Prime-De [22] and chimpanzees: www.chimpanzeebrain.org (accessed on 12 April 2022) [23]. Just as in human brain research, research on primate brain anatomy allows morphological quantification of regions in each hemisphere and determination of possible interhemispheric asymmetries. In this quest, an increased body of evidence highlights that different nonhuman primate species, such as chimpanzees or baboons, show human-like structural brain asymmetries for areas homologous to key language regions [20,24].

Thus, the question arises: for which function have these asymmetries in non-linguistic primates developed, if not for language per se? In humans, handedness for manual actions was for a long time considered a behavioural reflection of language-related brain lateralisation [25]. However, more recent studies indicate that the direction of handedness for manual actions poorly predicts language lateralisation, especially in left-handed humans. Indeed, 96% of right-handers and 70% of left-handers have their left hemisphere functionally specialised for most language functions [25]. In fact, handedness for manual actions was shown to be associated with the contralateral lateralisation of the motor hand area within the Central Sulcus, rather than key language areas [26]. Altogether, it is now acknowledged that direction of handedness might be independent from direction of language lateralisation [27–29]. As a result, comparative research on handedness for manual actions across primates might not be suitable for investigating phylogenetical origins of hemispheric language specialisation. To do so, it has been suggested that studying the

manual lateralisation of gestural communication in nonhuman primates—and not handedness for manipulative actions—might constitute a more fruitful approach [30]. In fact, following the evolutionary framework on the gestural origins of language [31], the gestural communication system in nonhuman primates was found to share key features of domain-general processes, important for language, such as intentionality, referentiality, and learning flexibility [32–34]. Interestingly, production of communicative manual gestures has been found highly lateralised in favour of the right hand in both baboons and chimpanzees. In contrast, the handedness patterns for non-communicative manual actions in chimpanzees and baboons were found to be different from those found for communicative gestures at both the populational and individual levels [30]. These findings supported the idea that gestural communication in nonhuman primates may be related to a specific lateralised system for communication, which might be different from handedness for manipulative actions [33].

In addition, the sequential and hierarchical motor actions that underlie tool-use behaviours have been used as the basis for the emergence of communicative systems [35–38], and share neural substrates with the human language network [39]. A recent functional MRI study with human subjects showed that the use of learning tools improved a language syntax task and there is neural overlap of both behaviours in the basal ganglia [40].

Therefore, there is the necessity to take stock of what the work on neuroanatomical correlates of gestural communication and tool-use in nonhuman primates has provided, in order to test its supposed continuity with language lateralisation.

In this paper, we aimed to review the literature comparing structural brain asymmetries across primates for areas related to language in humans. We focus on the classical perisylvian language regions, namely the Planum Temporale, Broca's Area, and the white matter tract that interconnects these two regions—The Arcuate Fasciculus. In this review, it is of importance to take also into account other key regions of the large, distributed language network beyond the perisylvian regions, such the Insula, the Cingulate Sulcus, and the Superior Temporal Sulcus (STS) as novel grey matter areas of interest. Finally, we consider the Central Sulcus (CS), which delimitates the primary motor from the primary somato-sensory cortex and include thus the mouth and lips motor areas as well as the motor hand area related to handedness (see Figure 1). After briefly describing their functions, we first review their structural and functional lateralisation in humans, including infants, to discuss whether structural markers can predict the functional lateralisation of language. In the next step, we compare these findings with nonhuman primates and discuss whether this asymmetric organisation is shared between species. Finally, we address the following question: If such brain lateralisation is shared with our non-linguistic primate cousins, for what behavioural functions did it evolve, if not for language? In an attempt to provide some elements of responses, we propose to review the literature about the lateralisation of the gestural communicative system, which could potentially constitute the ideal missing behavioural link with brain asymmetries for language in our common ancestor.

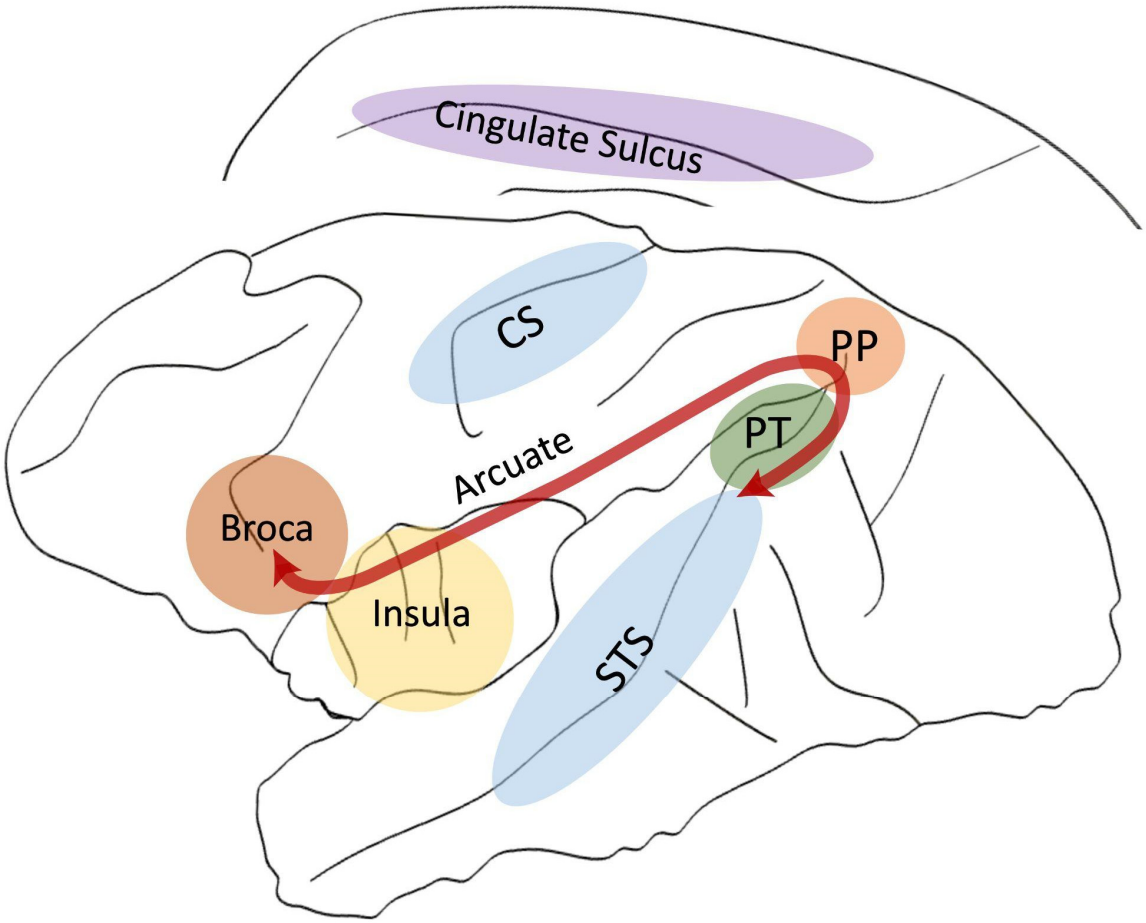

Figure 1. Illustration of the reviewed key structures in a monkey brain. In brown: Broca's area, in yellow: the Insula, in red: the Arcuate Fasciculus, in blue: the Central Sulcus, in green: the Planum Temporale, in light red: the Planum Parietale, in grey: the Superior Temporal Sulcus, in purple: the Cingulate Sulcus. Arcuate: Arcuate Fasciculus, CS: Central Sulcus, PT: Planum Temporale, PP: Planum Parietale, STS: Superior Temporal Sulcus.

2. Planum Temporale

The most emblematic marker of the lateralised language organisation is the Planum Temporale (PT), which is located within the Sylvian fissure and is part of the auditory association cortex [41] and Wernicke's area [42]. In adults, left hemispheric lesions in this region result in severe language comprehension and production deficits [43–45]. Therefore, many studies have shown the particular functional significance of the PT in the left hemisphere for a variety of auditory language processing [46], including the main perception component of the audio–motor loop for phonological processing [47]. Interestingly, in preverbal newborns, the functional implication of the left PT was highlighted from birth [17,48,49].

In a pioneering work by Geschwind and Levitsky [50], the PT was shown to be anatomically asymmetric: in 100 post-mortem brains, 65% of the left PT was larger than the right, which was confirmed by in-vivo MRI studies [46] and also highlighted in early development (Post-mortem Infants: [51,52]; in-vivo MRI infants: [53–56]; foetuses: [57,58]). These asymmetries later increase during development and are associated with language development [17,48,49,51]. PT asymmetry, is, therefore seen as a marker for human unique innate readiness to acquire language [17].

Indeed, in adults, a direct relationship was shown between the left PT's size and functional asymmetry of language tasks [59]. In addition, an absence or reversed PT asymmetry has been linked to several language-related pathologies like dyslexia [60,61]. This function-structure relationship is however debated [13,15,16,62–68]. For example,

Greve et al. [65] showed that regardless of the functional hemispheric dominance for language, the structural PT volume asymmetry is left biased. In contrast, Ocklenburg et al. [68] found that a higher density at a microstructural level of the left PT was associated with faster processing of auditory speed in the same area, as shown in EEG. More recently, Tzourio-Mazoyer et al. [16] demonstrated that, although the structural PT asymmetry is not predictive of its functional counterpart in a language task, an adjacent auditory area at the end of the Sylvian fissure is.

Several studies in nonhuman primates also showed striking human-like PT asymmetries in their homologous regions. Manual delineation of post-mortem brains [69], in-vivo MRI scans [70,71] as well as voxel-based morphology on MRI scans [23], showed larger left PTs in chimpanzees and in apes in general [72]. Recently, in-vivo MRI studies on adult and newborn baboons with manual PT delineation extended this finding to a shared feature between Old World monkeys and humans [24,73,74]. Interestingly, the asymmetry strength increased with age in this longitudinal study [74]. These results are questioning the PT asymmetry: (1) to be unique in humans and (2) to be marker for language development in newborns. Rather, the PT asymmetry might have evolved for a cognitive function shared between Old World monkeys, apes, and humans, which is at the core of language processing in humans. A potential candidate related to such a function may be communicative gesture. Indeed, Meguerditchian et al. [75] highlighted a relation between Planum Temporale grey matter volume asymmetry and hand preference for communicative gesture in chimpanzee. Moreover, the left PT asymmetry was also found related to handedness for tool-use but not for handedness for manipulative actions in chimpanzees, which required no structured sequence of motor actions [76].

3. Broca's Area

Broca area and its left hemispheric specialisation was historically considered as the center of speech production [77]. This modular view of the neuronal basis of language was progressively questioned by the view that language involves a plastic and large distributed network [11,78] and even implicates the two hemispheres. However, it is still well acknowledged that Broca's area in the left hemisphere remains a key component for language specialisation within its distributed neural network [79]. Interestingly, complementary work thereby highlighted Broca's area as a lateralised interface between speech and multimodal motor integration, including gesture and mouth movements [80]. Broca's area is also known for its involvement in motor planning, sequential and hierarchical organisation of behaviours, including syntax [81], tool-use [39,82], and sign language production, thus including manual and oro–facial gestures [83,84]. In infants, speech perception activates Broca's area from very early development on as highlighted in MEG or functional MRI studies [48,85,86]. This activation before the babbling stage suggested that activity of this area is not due to motor learning but might drive the learning of complex sequences [86].

In contrast to the PT [see section above], a clear structural leftward asymmetry has not been reproducibly demonstrated [87,88], which may be due to natural variability between subjects in sulcal contours defining this area [87,89]. Cytoarchitectonic analyses, however, reported a leftward asymmetry of some parts of area 44 and/or area 45, which together form Broca's area [90–92]. In contrast, other accounts state a rightward asymmetry for area 45 grey matter, which gets reduced during aging, especially due to a loss in the right hemisphere [93]. In development, an early structural primacy of right-sided dendrite systems shortly after birth and a progressive shift to left-sided primacy during years three to six was highlighted and related to critical periods for language acquisition [94]. A second study found leftward asymmetries on the cellular level very early from 1-year old infants on [92], which increased into an adult-like leftward asymmetry at 5 years for area 45 and 11 years for area 44. This maturational effect was suggested to be influenced by language practice and thus, the interhemispheric asymmetry of this area would continue to change throughout life [92]. Interestingly, because area 45 supports semantic processes and area 44

subserves syntactic processes in adults, some see in this maturational difference a neural underpinning of the earlier onset of semantics than syntax in children [79].

In great apes, a homologous region was documented in several studies, which described the precentral inferior sulcus, the inferior frontal sulcus, and the fronto-orbital sulcus as common borders of Broca's homologue [95–97]. Like in humans, inquiries about Broca's area's structural asymmetry on a population-level remain inconsistent in apes due to interindividual variation in location and cytoarchitecture [98]. Leftward lateralisation was found at a macrostructural level [95] but not at a cytoarchitectonic level in a relative smaller sample size ([98]; but see also [99]). In monkeys, no data of structural asymmetry for this region has been reported so far. In fact, determining Broca's homologue is challenging because the common borders of Broca's homologue in apes are absent in monkeys. Nevertheless, we know from few detailed cytoarchitectonic studies in macaques that the two parts of Broca's area 44 and 45 are respectively located in the fundus and lower caudal/posterior bank, and on the rostral/anterior side, of the most ventral part of the inferior arcuate sulcus IAS [100–102]. Electric stimulation of this region elicited oro-facial and finger movements. Therefore, together with cytoarchitectonic similarities, the region anterior to the ventral part of the IAS was proposed as an equivalent area 44 in macaques [101]. Recent studies even reported that Broca's homologue's activation preceded voluntary trained production of a vocalisation after intensive operant conditioning in juvenile rhesus monkeys [103]. Moreover, the use of positron emission tomography (PET) in three captive chimpanzees has revealed that begging food from a human by using either gestures, novel species atypical attention-getting sounds, or both simultaneously, activated a homologous region of Broca's area (IFG) predominantly in the left hemisphere [104]. Some functions associated with Broca's homologue's lateralisation in nonhuman primates have been proposed in relation to tool-use processing and communication gesture production. Regarding tool-use, chimpanzees that performed better a tool-use task with their right hand showed a greater left-lateralisation of Broca's homologue [105]. Such a link might be attributed to the typical Broca's function described in humans, namely hierarchical organisation of behaviours involved in tool-use [81,82]. Regarding gestural communication, Meguerditchian et al. [75] highlighted a relation between Broca's homologue grey matter volume asymmetry and hand preference for communicative gesture in chimpanzees. Similarly, in a recent study in baboons, we showed that variation in hand preference for communicative gesture—but not for non-communicative manipulative actions—is related to the anatomical variation of Broca's homologue. Indeed, the right Broca's portion of the IAS is deeper than the left for baboons communicating with their left hand and vice versa [106].

4. Arcuate Fasciculus

The Arcuate Fasciculus (AF) is a bundle of white matter, which arches dorsally around the Sylvian fissure, interconnecting Broca's area in the frontal lobe with the Planum Temporale in the temporal lobe [107]. It was highlighted that the connectivity between language areas, due to the AF, is crucial. For example, the integrity of the AF might be more important for lesion recovery (e.g., strokes) than the integrity of grey matter regions that it is connecting [11]. In addition, as neurological cases have shown, the AF plays a key role in language processing in the left hemisphere, with lesion of the direct pathway also causing conduction aphasia [10] in deaf signers [108]. The AF is already present at birth [109] but matures slowly until late childhood [109,110]. In contemporary language models, the AF (or also called Dorsal Pathway) is often opposed to the Ventral Pathway, which interconnects roughly the same regions, but travels ventrally around the Sylvian fissure [78]. In contrast to the AF, the Ventral Pathway matures more rapidly in development and was also described to be phylogenetically more ancient [79,110]. It is assumed that the late maturation of the AF is due to the frontal portion, which is connected to Broca's area and not fully myelinated until the age of seven [110,111]. In fact, controversy persists whether this portion is also already present at birth [109,112–115].

Regarding lateralisation, the human AF was found larger in the left hemisphere for a number of macroscopic and microscopic measurements like the number of streamlines, volume of the tract, fibre density, and mean fractional anisotropy in 60% of normal adult humans. The remaining 40% of the adult population shows either a reduced lateralisation to the left (20%) or no lateralisation at all (20%) [18,116–120]. In early development, the leftward AF is the most asymmetrical region of the developing white matter ([113,121], but see also [122]). Interestingly, the early leftward asymmetry in newborns was correlated with later language capacities in children [123–125]. Catani et al. [18] argued that the AF's asymmetry represents a better structural marker for functional language specialisation than PT asymmetry [18]. This structure–function relationship is, however, debated [15,126–129]. For example, Verhelst et al. [129] demonstrated in a fixel based analysis that structural AF asymmetry did not differ between subjects with either right or left functional language hemispheric dominance.

Axon tracing in monkey brains and diffusion MRI in chimpanzee and monkey brains have highlighted the existence of the Arcuate Fasciculus across primates that interconnects frontal and temporal areas [130–139]. It is debated to what extent the AF's strength, lateralization, and frontal and temporal termination sites differ between primate species. In fact, recent findings speak for a rather conserved organisation across primates (for a review, see [9]). Therefore, latest functional results suggest that language abilities allowing humans to name, conceptualise, and thus better remember sound would be shared across primates [139]. In order to highlight anatomical differences across primates, which could explain the human uniqueness for language, several authors conclude that the left AF lateralisation is the crux of the human-specific distinction [136,138,139]. In fact, Rilling et al. [133] did not find any AF asymmetry in three macaque and four chimpanzee subjects. However, by adding more chimpanzee subjects, the authors were able to report a left lateralised AF, which was still weaker than in humans [134]. This result remained unique regarding AF lateralisation in nonhuman primates [136,138,139]. In fact, this inconsistency across the literature about the presence or not of population-level leftward AF bias might be explained by the small sample size (i.e., only few subjects) usually included in those AF studies in apes, which makes it difficult to infer any bias at the population-level. Only studies including an increased sample size would help elucidate this debate.

5. Insula

The Insula cortex lies in the depth of the Sylvian fissure, which separates the temporal lobe from the parietal and frontal lobes. The anterior part of the Insula is implicated for different language processing functions (General: [43,140,141]; auditory processing: [142]; motor aspects: [143]; syntax: [144,145]; sign language: [108]). Interestingly, the Insula seems to be particularly involved in motor planning of speech as seen in pathologies [140,143]. Further, Lœvenbrueck et al. [146,147] highlighted in adults that prosodic pointing gesture activates Broca's area as well the left anterior Insula [146,147].

Moreover, at the structural level, the volume asymmetry of this region may be associated with hemispheric dominance for language. In fact, Keller et al. [13] found that the size of the Insula could predict functional lateralisation for language in the same hemisphere in the majority of individuals. Therefore, the Insula was proposed as a more reliable marker for functional language specialisation than the Planum Temporale [13,148]. Although little is known about the functional implication of the Insula during language development in newborns and infants, several studies highlighted an early lateralisation of the Insula towards the left hemisphere [56]. Thanks to all the aforementioned data, the (anterior) Insula was established as a region of interest for studying linguistic (motor) processing. Additionally, the anterior Insula comprises Von Economo (VEN) and Fork neurons [149] that were for a long time thought to be uniquely human and implicated in social awareness. Therefore, the insula VEN and Fork neurons are often used for theories about the social origins of language [150].

While larger in humans, the insular cortex also exists in apes and monkeys, where the anterior portion especially, expanded during primate brain evolution [151]. Von Economo neurons, which were thought to be exclusive to apes [152], are also present in the anterior insular cortex of monkeys [150]. The authors argue that two distinct insular regions could be implicated in monkey communication [150]. First, a specific sensory-motor organisation for body parts in one part of the anterior Insula (the Idfa region) was found. Electric stimulation of this region elicited vocal cord movements in macaques. This region happens to be juxtaposed to a dorsal region, which receives inputs from area 44 (Part of Broca's Area). Together, the two regions could be homologous to the human anterior insula, implicated in several language processing functions (see above). Second, Von Economo and Fork neurons in another part of the anterior insula [the Ial region] project into a region of the thalamus (PAG) that is involved in vocalisations [150]. However, the structural lateralisation of this region was poorly investigated in nonhuman primates. One rare study comparing the Insula structure between a handful of different primate species subjects demonstrated that the anterior portion of the Insula, in which Von Economo neurons were found, displayed a human unique left asymmetry [151]. Further studies with a larger sample size are needed to investigate whether the Insula and particularly its anterior portion is structurally lateralised in nonhuman primates in relation to planification of communication, especially gesture.

6. Cingulate Cortex/Sulcus

The Cingulate Sulcus is in the medial part of the cerebral cortex delimitated ventrally by the Cingulate cortex and dorsally by the paracentral lobe and the superior frontal cortex. Its anterior part is considered a hub for domain-general cognitive processing, such as counterfactual thinking, mentalizing, and language, including cognitive control on signals production [153–156]. Pioneering studies regarding language processes have shown that for the Anterior and Midcingulate cortex, (1) stimulations evoke orofacial and tongue movements [157] and (2) lesioned patients experience akinetic mutism, associated with an absent motivation to speak [158]. Little is known about the Cingulate cortex concerning direct language development. Rare results come from Lœvenbruck et al. [147] highlighting, in adults, the functional neuroanatomical activation of the left anterior Cingulate cortex, besides Broca's area and the Insula in communicative pointing gestures [147]. However, the anterior Cingulate cortex was prominently shown to be important for joint attention in both adults and infants [159]. Joint attention is considered a prerequisite of the theory of mind as well as a prelinguistic communication act [159,160]. Interestingly, the hand, mouth, and tongue motor representations are grouped together around the caudal end of each vertical sulci departing from the Cingulate Sulcus [161], suggesting its key implication for a multimodal language system. In addition, 50% of human subjects present a Paracingulate Sulcus, located more rostrally above the anterior and Midcingulate Sulcus [162].

The presence of the Paracingulate Sulcus is lateralised in the human brain with nearly 70% located in the left hemisphere [14,162]. This lateralisation is influenced by genetic factors and the in-womb environment [163]. At the functional level, this human asymmetry has been shown to be correlated with the involvement of the left Cingulate cortex in language tasks in right-handed subjects [153,164].

Some authors have suggested that the anterior and Midcingulate cortices might have also played a role in language evolution. Loh et al. [155] hypothesised the existence of an evolutionary conserved ventrolateral frontal (around Broca's region) and dorsomedial frontal (roughly the Midcingulate cortex) network, which enables cognitive control of vocalisations. In fact, it is known that innate reflexive vocalisations such as 'screams' and 'shrieks', are associated with the 'cingulate vocalization pathway' [165]. In fact, the 'cingulate vocalisation area' in the anterior and Midcingulate cortex are connected (1) to the periaque–ductal gray, which directly projects to premotor nuclei in the brainstem and controls laryngeal motoneurons, which elicits vocalisations; and (2) to the facial motor nuclei to also produce affective facial movements [155]. In addition, in nonhuman primates, innate calls can be evoked by anterior and Midcingulate cortex stimulations [166] and

lesions impair the production of calls [167] similar as in humans. Additionally, as in the Insula cortex (see above), large spindle shaped Von Economo neurons are present in the anterior Cingulate cortex in humans, apes, and other mammals [152,168,169]. Together with the presence of Von Economo neurons in the anterior Insula, it has been proposed that Von Economo neurons may be implicated in primate communication [150]. In contrast to the Insula cortex, no Von Economo neurons have been found in the monkey's Cingulate cortex yet. According to a recent comparative study including macaques, baboons, chimpanzees, and humans, the Cingulate Sulcus shows a highly conserved morphological antero-posterior organisation of vertical sulci or their precursor 'dimples' [14].

While, surprisingly, no structural asymmetries data on the Cingulate Sulcus are available so far in humans, significant population-level leftward asymmetries were found in the anterior portion of the Cingulate Sulcus in chimpanzee, whereas significant rightward biases were found in its posterior portion [170]. In contrast to humans, no population-level lateralisation for the presence of the Paracingulate Sulcus was found in chimpanzees [14]. Nevertheless, interindividual variation of the presence or absence of a Paracingulate Sulcus and variability of the intralimbic sulcus was associated with the production of attention-getting sounds and right handedness for gestural communication in chimpanzees [170]. It is, therefore, not to be excluded that the Cingulate Sulcus could be linked to precursors of human language such as communicative gesture and vocalisations.

7. Superior Temporal Sulcus (STS)

The Superior Temporal sulcus [STS] is a long fold separating the superior from the middle temporal lobe. It is important for a variety of social cognition tasks important for communication [171,172] containing both specialised regions for a particular task and regions that respond to several tasks simultaneously [171]. In fact, specialised areas of the STS have been shown to be implicated in the perception of voices in the right hemisphere [172], faces [173], biological motion [174], audiovisual integration [175], and in the theory of the mind [176,177]. Regarding speech perception in particular, three temporal voice areas are dispatched symmetrically in both hemispheres along an anterio-posterior gradient [178]. Distinct areas of the STS have also been implicated in language processing in hearing and deaf participants, especially in the left hemisphere [2,47,179]. In children, responses to voices in the STS and STG are strongly right-lateralised, an asymmetry which decreased with age [114,180]. This finding suggested that newborns rely for speech processing more on prosodic information, known to be processes in the right hemisphere, than for phonological information, processed in the left hemisphere (see also [181] for a right hemispheric STG temporal primacy in children in contrast to adults). Interestingly, together with Broca's area, the posterior STS is proposed to constitute the neural network supporting syntactic processes [79], which, until the age of 10, does not process syntax and semantics independently [182].

Regarding structural asymmetries, the left STS has been shown to be longer than the right, but matures later, as seen in preterm newborn infants [55,56,58,183,184]. In addition, the right STS was found to be deeper than the left STS in a portion ventral to Heschl's gyrus, called the STAP (Superior Temporal Asymmetrical Pit, [53,178,183]). This robust asymmetry is irrespective of age, handedness, and language lateralisation, suggesting a strong genetic influence [53,180,183]. Functional correspondence was found between its deepest point and location of the voice sensitive peak [178]. Several sulcus interruptions 'plis de passage' are more present in the left STS, probably resulting from stronger white matter fibres passing underneath the STS [185]. The aforementioned results highlight the STS' implication in communication through the direct link of language perception and the indirect link with diverse social cognition tasks, which are crucial for complex language processing. This makes the STS and its asymmetric structure a promising key area in comparative studies in order to search for language prerequisites shared between primate relatives.

The STS was intensively studied in macaque monkeys and shown to be one main hub in the social interaction processing network, where it was mapped onto a fine-grain pattern of object, body, and face selectivity [186]. Indeed, its implication in a variety of social cognition tasks was demonstrated. This includes gaze following and joint attention [187] as well as facial movements in the upper STS [188]. In addition, the mid-STS in macaques was recently hypothesised to be equivalent of the human TPJ area, important for the theory of mind, because it was active for predicting social situations [189] and because macaques living in larger groups demonstrate an increased grey matter of this area [190]. Especially regarding communication, similar to humans, voice and face patches were also found in the monkey's STS [178,191–194]. In fact, recently it was demonstrated that audiovisual integration occurred in a distinct region in the anterior fundus [195]. The Superior Temporal Asymmetrical Pit 'STAP' was not robustly shown to be present in chimpanzees, suggesting a human specific landmark of perisylvian organisation, which was related to human specific social cognition and communication [183]. According to results presented at conferences, structural rightward STS depth asymmetries were also found present in adult and juvenile baboons, within a portion that may overlap with the STAP in humans. Interestingly, preliminary results in baboons suggest that the strength of this rightward STS asymmetry varies according to social cognition proxies such as social group size and gestural communication's right-handedness [196,197].

8. Inferior Parietal Lobe

The Inferior Parietal Lobe or Geschwind's territory comprising the angular and the supramarginal gyrus was demonstrated as essential in language processing, connecting indirectly to primary language areas (such as the Planum Temporale or Broca's area). For example, it was shown to be involved in episodic memory retrieval of words [198] or verbal working memory [199], but also in tool-use [200,201]. The Inferior Parietal Lobe is one of the latest to myelinate in development [202] and was related to the emergence of language in evolution [203] and in development [204]. The Inferior Parietal Lobe includes the Planum Parietale, which lies in the supramarginal gyrus, in the ascending portion of the Sylvian fissure, next to the Planum Temporale [62]. The Planum Parietale is implicated in dyslexia and communication disorders [69] and processing voice spectral information [205]. Adaptation during primate evolution of this area and its connectivity may provide the capacity of enhanced visual analysis of moving images that is important for tool handling and control [206–208]. However, due to its anatomical position, this region is a zone of convergence and integration of sensory and motor information via the fronto-parietal network [209]. In fact, the connection between Broca's area and the Inferior Parietal Lobe is right-lateralised, in contrast to the left lateralisation of the Arcuate Fasciculus (see above). In addition, the Inferior Parietal Lobe inhabits mirror neurons that fire not only during motor execution, but also when observing actions performed by others, and might therefore lead to action understanding and language evolution [210,211].

Due to the aforementioned data, the Inferior Parietal Lobe is a key-region for investigating the lateralised links between actions, tool-use, and language evolution. A structural asymmetry of this area was found in the Planum Parietale. It showed a rightward asymmetry in both right-handed males and left-handed females, which was not correlated with the Planum Temporale asymmetry, indicating functional independence [62]. Another structural asymmetry was found for the parietal operculum, which constitutes the gyrus directly above the Planum Temporale as part of the supramarginal gyrus [212]. It shows a leftward asymmetry, especially for right-handers [213]. Regarding connectivity, tool-making skills elicited plastic remodeling of fronto-parietal white matter projections from the right Inferior Parietal Lobe into the right Broca's area [201].

Because of the potential overlapping of brain circuits for tool-use and language, nonhuman primate brain studies have focussed on the Inferior Parietal Lobe. A potential interaction might lie in the semantic knowledge important for both language and tools to acquire the skill necessary to perform these actions [200,214,215]. In this view, modifications

of circuits that subserve gestures and imitations may have paved the evolutionary way for language and tool-use in humans [215], with the Inferior Parietal Lobe in its heart. Recently, Cheng et al. [216] found that leftward rostral- and rightward caudal inferior parietal structural asymmetries connecting to several areas related to tool-use in humans [215] were similar in chimpanzees and humans but not present in macaques. This finding could be related to human-like leftward asymmetries of the parietal operculum, which were also reported in chimpanzees and related to tool-use but not non-tool-use motor actions [76]. To learn to use tools, humans need a certain level of body awareness to match variations in kinematic details with the desired outcome during practice. Similar awareness is required for other animals on the Mirror Self-Recognition test [217], which also some chimpanzee subjects pass. In fact, chimpanzee subjects that passed the test (to recognize themself in a mirror) also possessed a more right lateralised fronto-parietal connection, exactly as in humans during tool-making learning [82,201,218,219]. This rightward asymmetry of connectivity could be related to a human-like rightward asymmetry initially found for the Planum Parietale in apes [220], a finding which was replicated in chimpanzees, particularly in females in relation to handedness [221]. Future studies in nonhuman primates should continue investigating potential links in lateralisation of the Inferior Parietal Lobe and behaviour. It would help clarifying whether left or right lateralised brain circuits for tool-use paved the way for language brain circuits.

9. The Central Sulcus (CS)

The Central Sulcus (CS) is a major landmark in the brain, dividing the parietal from the frontal lobe and is one of the primary sulci developed in the brain [57]. It also divides the primary motor cortex from the primary somatosensory cortex, where topographic sensory and motor representations of human body parts are organised [222]. Within this topographic organisation, a morphological landmark of hand and finger representations has been documented across the dorsal-ventral plane of the CS, known as KNOB or motor hand area, which has an omega-like shape [223].

Regardless of the hand, the direction of handedness was found associated with contralateral asymmetries of the motor hand area (humans: [92,224–226]. In fact, the portion of the CS that delimits the motor hand area was found deeper in the hemisphere contralateral to the preferred hand of the subjects [92]. This feature seems, however, not to be related with language lateralisation. In fact, it has recently been demonstrated that the neural substrates of typical handedness measures and language brain organisation might be not related, but rather independent from each other [27,29,227].

Within an evolutionary framework, hemispheric specialisation and handedness have been historically considered unique to human language evolution [228,229]. However, many primates, such as baboons or chimpanzees, also present right-handed dominance for manipulative actions (wild subjects: [230]), and even stronger right-handed dominance for communicative gestures (captive subjects: [30]). Just as in humans, the nonhuman primates' direction of handedness for object manipulation was found associated with contralateral asymmetries of the motor hand area within the Central Sulcus (Chimpanzees: [231,232]; Baboons: [233]; Capuchin monkeys: [234]; Squirrel monkeys: [235]). It is notable that the contralateral hand area effect in the CS was found exclusively for manipulative actions [233] but not for communicative gesture handedness. As mentioned in the previous section, handedness for gestural communication was exclusively found related to Broca's homologue [106], suggesting a potential independent neural substrate of handedness and language organisation in evolution. Preliminary results in juvenile baboons reported a similar neuroanatomical manifestation of early handedness, highlighting that structural asymmetries in the Central Sulcus appear early in development with the emergence of handedness behaviour [236]. Interestingly, the motor hand area of the Central Sulcus was also shown to be related to more complex hierarchical organisation of behaviours as it was related to tool-use handedness in chimpanzees [97].

10. Conclusions

Within an evolutionary framework across primates, we compared data on inter-hemispheric structural asymmetries in most of the key brain structures that are known to be associated with hemispheric specialisation for language processing in humans.

The results of this comparative neuroanatomical approach conducted between humans and mostly chimpanzees, and to a lesser extent baboons, are quite straightforward and challenge the historical view that hemispheric specialisation is a human specific feature of language evolution [228,229]. It becomes clear that we share the structural lateralised patterns for most language-related regions with other primate species, and even new-born monkeys, especially for perisylvian regions, including the Planum Temporale and Broca's area [24,69,71,73,74,95]. Although less documented in comparison to those two historical lateralised perisylvian regions, there is some evidence that other important regions of interest within the large human language network might share the same hemispheric structural lateralisation across primate species. According to rare recent comparative results, mostly conducted in chimpanzees and to a lesser extend in baboons, those shared features includes the leftward lateralised white matter connectivity tract between Broca's area and the Planum Temporale-the Arcuate Fasciculus [134], leftward lateralised parietal operculum, rightward lateralised Planum Parietale and fronto-parietal projection [76,220,221], the rightward posterior section of the STS [196,197], as well as the presence of paracingulate sulcus in the left hemisphere [170]. These collective findings suggest an important shared biological ancestral encoding between Old World monkeys, great apes, and humans, that were initially considered as neuroanatomical landmarks of brain lateralisation for language. Their presence in non-linguistic primate species clearly states that these landmarks are not human- or language- specific.

Nevertheless, it remains unclear for which shared 'domain-general' cognitive function between human and nonhuman primate species, that is also at the heart of language processing in modern humans, these structural hemispheric asymmetry patterns are related to and have evolved. While reviewing the nonhuman primate literature that reported clear links between anatomical asymmetries for language area homologues and hand preferences for tool-use or for gestural communication [71,75,106], some functional roads become plausible. For instance, it is thus not excluded that both 'syntactic' hierarchical sequential processing (such as the one involved in tool making and use in great apes), and the intentional communication properties (shared with the communicative gestural system in primates) might thus constitute a functional candidate to have paved the way for such brain asymmetric organisation within the evolutionary framework of human language. We demonstrate, therefore, that nonhuman primates such as chimpanzees, and even more phylogenetic distant species such as baboons among the Old World monkeys, offer compelling comparative models for the evolution of human brains and behaviours. In particular, a sulci and region-of-interest approach seems fruitful for comparing brain structures. In the same vein, handedness measurements for different behaviours seem fruitful for linking the lateralised brain anatomy to lateralised behaviours. Interesting future work could now be in transferring this handedness knowledge to humans, to clarify, for example, whether communicative gesture handedness might be a marker for language lateralisation.

To interpret brain asymmetry and its evolution, we highlighted the importance of investigating the lateralisation of behaviours such as gestural communication, tool use, and bimanual coordination within a comparative approach [38]. Indeed, a blending of the two is necessary in order to gain a holistic view on how language lateralisation has evolved, which ultimately also provides an initial platform for its emergence.

Regarding specifically language evolution, we hypothesise that asymmetries for language areas may not have initially evolved for language, if language is seen as a cognitive module. Rather, each asymmetry could have evolved independently for independent cognitive functions to adapt to unknown environmental pressures. This could explain the unclear relationship between structural and functional asymmetries related to language

areas. The structural asymmetry would here be a more ancient fossil of other cognitive specialisations on which the functional language asymmetry got piggybacked. The functional and structural specialisation of these structures may next have been important nests for developing intentional communicative behaviour in nonhuman primates, which later evolved to language processing in our species. In other words, 'perisylvian language asymmetries' are not specific to language but could rather be exaptations of pre-existing specialisations for other cognitive functions, which together make up what we call 'language'. Therefore, 'domain-general' language-related brain architecture associated with intentional communicative or syntactic behaviours might rather be shared between humans, apes, and at least baboons of the Old World monkey family. Such an asymmetric brain organisation might have, thus, emerged from their common ancestor around 25 million years ago and later increased during hominin evolution.

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