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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 of humans and nonhuman primates are the result of a continuous or convergent evolution can be investigated by comparing their respective underlying structure: the brain. 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 also 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 these key-markers of functional language lateralisation. The question arises, then, 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.

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 (e.g., Berwick and Chomsky, 2016). However, in recent years the conception of one holistic language faculty has been contrasted with an alternative view that language may be the results of an assembly of cognitive properties that are domain general and not specific to language (e.g., Fedorenko, 2014). 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 (e.g., Fitch, 2010, Liebal et al., 2014, Fagot et al., 2019). Whether these shared cognitive properties between humans and nonhuman primates are the results of a continuous (homologies)- or convergent evolution (analogies) can be investigated by comparing their respective underlying structure: the brain. 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 (Geschwind, 1970; Toga and Thompson, 2003a; Bidula & Kroliczak, 2015; Becker et al., 2021a). However, in recent years, data are expanding to more distributed models, taking into account several different fibre tracts and regions crucial for language processing as demonstrated by clinical cases (e.g., Catani and Mesulam, 2008) and questioning a localisationist viewpoint of language specialisation (e.g., Duffau et al., 2018). 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 (Catani & Dawson, 2017), as well as the anterior Insula cortex and the anterior and mid-Cingulate Sulcus. Most of these structures share one fundamental feature: They are functionally and also structurally specialised towards one hemisphere, mostly the left (Toga and Thompson, 2003; Keller et al., 2011; Amiez et al., 2019). Specifically, “functionally 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 unclear and questioned (e.g.,

Gerrits et al., 2021; Tzourio-Mazoyer et al., 2018), 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 (Dehaene-Lambertz et al., 2002; Catani et al., 2007; Keller et al., 2011).

Thus, the fundamental question of “how language lateralisation has evolved” is more topical 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 fact, “evolution” implies that language has developed progressively (e.g., as exaptations from preexisting cognitive functions) and intermediate steps may be found across common ancestors from primate lineage. However, because brain tissue hardly fossilises, one fruitful way of trying to find such intermediate steps is the comparison of brains between primate species including humans to infer potential features inherited from their shared common ancestors. 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 anaesthetised subjects, allowing no limitation in terms of sample sizes and species diversity (Poirier et al., 2021). As a result, primate brain research has benefited in the recent years from considerable increase of available MRI databases on large cohorts in many primate species, including macaques: Prime-De, (Milham et al., 2020) and chimpanzees: www.chimpanzeebrain.org (e.g., Hopkins et al., 2008). Just as in human brain research, research on primate brain anatomy allows morphological quantification of regions in each hemisphere and determine 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-markers of functional language lateralisation (e.g., Hopkins et al., 2015; Marie et al., 2018).

Thus, the question arises for which function these asymmetries in non-linguistic primates have developed, if not for language per se? In humans, handedness for manual actions was for a long time considered as such a behavioural reflection of a language related brain lateralisation (e.g., Knecht et al., 2000). However, more recent studies indicate that direction of handedness for manual actions poorly predicts language lateralisation, especially in left-handed humans. Indeed, 96% of right-handers and also 70% of left-handers have their left

hemisphere functionally specialised for most language functions (e.g., Knecht et al., 2000). In fact, handedness for manual actions was shown associated to the contralateral lateralisation of the motor hand area within the Central Sulcus, rather than key language areas (Amunts et al., 2000). Altogether, it is now acknowledged that direction of handedness might be independent from direction of language lateralisation (Groen et al, 2013; Mazoyer et al, 2014; Ocklenburg et al, 2014). 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 manual lateralisation of gestural communication in nonhuman primates - and not handedness for manipulative actions - might constitute a more fruitful approach (e.g. Meguerditchian et al., 2013; Hopkins et al., 2012). In fact, following the evolutionary framework about the gestural origins of language (e.g., Hewes, 1973), gestural communication system in nonhuman primates were found to share key features of domain general processes, important for language, such as intentionality, referentiality and learning flexibility (e.g., Tomasello, 2008; Meguerditchian & Vauclair, 2014; Molesti et al., 2020). 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 different from those found for communicative gestures at both the populational but also the individual level (Meguerditchian et al., 2013). 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 than handedness for manipulative actions (Meguerditchian et al., 2014). Therefore, there is a necessity of taking stock of what the work on neuroanatomical correlates of gestural communication in nonhuman primates has provided, in order to test its supposed continuity with language lateralisation.

In the present paper, we aimed to review the literature comparing structural brain asymmetries across primates for areas related to language in humans. We will 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 will consider the Central Sulcus (CS), which delimitates the primary motor from primary somatosensory 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 will first

review their structural and functional lateralisation in humans including infants to discuss whether structural markers can predict the functional lateralisation of language. In a next step we will compare these findings with non-human primates and discuss whether this asymmetric organisation is shared between species. Finally, we addressed 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 give 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 behavioral link with brain asymmetries for language in our common ancestor.

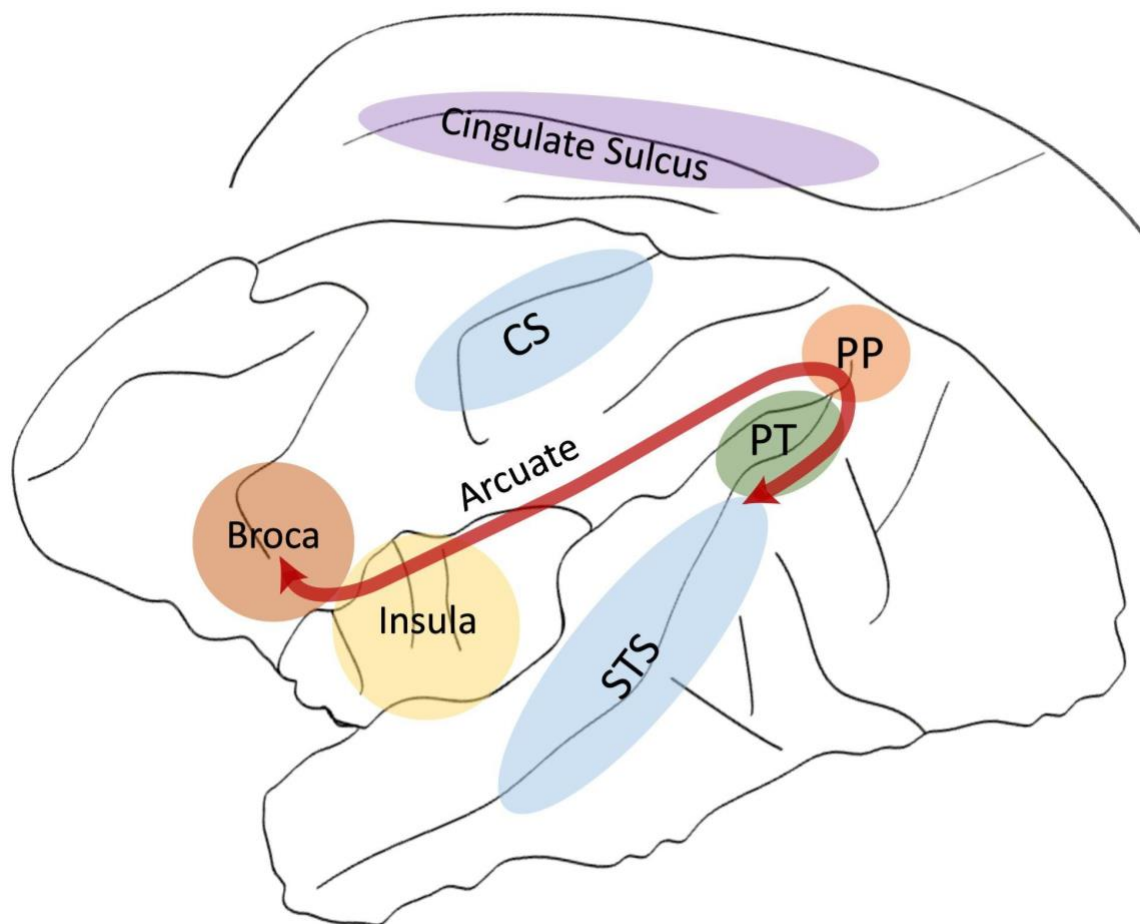


Figure 1. Illustration of the reviewed key structures in a monkey brain. In brown: Broca's area, in yellow: the Insula, in red: the Arcuate Fasciculus, in blue: the Central Sulcus, in green: the Planum Temporale, in light red: the Planum Parietale, in grey: the Superior Temporal Sulcus, in purple: the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

Arcuate: Arcuate Fasciculus, CS: Central Sulcus, PT: Planum Temporale, PP: Planum Parietale, STS: Superior Temporal Sulcus.

Planum Temporale

The most emblematic marker of the lateralised language organisation is the Planum Temporale (*PT*) which is located within the Sylvian fissure and which is part of the auditory association cortex (Galaburda et al., 1978) and Wernicke's area (Mesulam et al., 1998).

In adults, left hemispheric lesion of this region resulted in severe language comprehension and production deficits (Wernicke, 1874; Dronkers et al., 2004; Borovsky et al., 2007). Therefore, many studies have shown the particular functional significance of the *PT* in the left hemisphere in a variety of auditory language processing (Shapleske et al., 1999), including the main perception component of the audio-motor loop for phonological processing (Vigneau et al., 2006). Interestingly, also in preverbal new-borns the functional implication of the left *PT* was highlighted from birth on (Dehaene Lambertz et al., 2002; 2010; Mahmoudzadeh et al., 2013). In the pioneering work of Geschwind and Levitsky (1968) 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 (Shapleske et al., 1999) and also highlighted in early development (Post-mortem Infants: Wada, 1975; Witelson, S.F., Pallie, W., 1973. In-vivo MRI infants: Glasel et al., 2011; Hill et al., 2010; Dubois et al., 2008a; 2010a; fetuses: Chi et al., 1977a;b). These asymmetries are later increasing during development, which was associated with language development (Wada 1975; Dehaene-Lambertz et al., 2002; 2010; Mahmoudzadeh et al., 2013). The *PT* asymmetry is therefore seen a marker for the human unique innate readiness to acquire language (eg. Dehaene-Lambertz et al., 2002).

Indeed, in adults a direct relationship was shown between the left *PT*'s size and functional asymmetry of language tasks (Josse et al., 2003; 2006). In addition, an absence or reversed *PT* asymmetry has been linked to several language related pathologies like dyslexia (Gauger et al., 1997; Altarelli et al., 2014). This function-structure relationship is however debated (Jäncke & Steinmetz 1993; Dorsaint-Pierre et al. 2006; Eckert et al. 2006; Keller et al. 2011; Greve et al. 2013; Kolinsky et al. 2014; Tzourio-Mazoyer & Mazower, 2017; Tzourio-Mazoyer, Crivello & Mazoyer 2018; Ocklenburg et al., 2018; Gerrits et al., 2021). For example, Greve et al. (2013) showed that regardless of the functional hemispheric dominance for language, the structural *PT* volume asymmetry is left biased. In contrast, Ocklenburg et al. (2018) 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. (2018) 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 (Gannon et al., 1998), in-vivo MRI scans (Hopkins et al., 1998; Hopkins & Nir, 2010) as well as voxel-based morphology on MRI scans (Hopkins et al., 2008), showed larger left *PTs* in chimpanzees and in apes in general (Cantalupo et al., 2003). 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 (Marie et al., 2018; Becker et al., 2021c;d). Interestingly, the asymmetry strength increased with age in this longitudinal study (Becker et al., 2021c). The 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., (2012) 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 (Gilissen and Hopkins, 2013).

Broca's area

Broca area and its left hemispheric specialisation was historically considered as the centre of speech production (Broca, 1861) This modular view of language neural bases was progressively questioned by the view that language involves a plastic and large distributed network (Hickok & Poeppel, 2007; Duffeau et al., 2018) and even implicates the two hemispheres. However, it is still well acknowledged that Broca area in the left hemisphere remains a key knot for language specialisation within its neural distributed network (eg. Friederici, 2017). Interestingly, complementary work thereby highlighted Broca's area as lateralised interface between speech and multimodal motor integration including gesture and mouth movements (eg. Gentilucci & Volta, 2008). Broca is also known for its involvement in motor planning, sequential and hierarchical organisation of behaviours, including syntax (Koechlin & Jubault, 2006), tool-use (Stout and Hecht, 2017) and sign language production

including thus manual and oro-facial gestures (Emmorey et al., 2004; Campbell, MacSweeney, & Waters, 2008). In infants, speech perception activates Broca's area from very early development on as highlighted in MEG or functional MRI studies (e.g., Imada et al., 2006; Dehaene-Lambertz et al., 2006; 2010). This activation before the babbling stage suggested that activity of this area is not due to motor learning but might drive learning of complex sequences (Dehaene-Lambertz et al., 2006).

In contrast to the *PT* (see section above), a clear structural leftward asymmetry has not been reproducibly demonstrated (Keller et al., 2009; Sprung-Much et al., 2021), which may be due to natural variability between subjects in sulcal contours defining this area (Keller et al., 2007; 2009). Cytoarchitectonic analyses however reported a leftward asymmetry of some parts of area 44 and/or area 45, which together form Broca's area (Scheibel, 1984; Amunts et al., 1999; 2003). 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 (Kurth et al., 2020). In development, an early structural primacy of right-sided dendrite systems shortly after birth and a progressive shift to left-sided primacy during years 3 to 6 was highlighted and related to critical periods for language acquisition (Simonds and Scheibel, 1989). A second study found leftward asymmetries on the cellular level very early from 1-year old infants on (Amunts et al., 2003), 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 (Amunts et al., 2003). 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 (Friederici, 2017).

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 (eg. Cantalupo & Hopkins, 2001; Keller et al., 2011; Hopkins, 2017). 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 (Schenker et al., 2010). Leftward lateralisation was found at a macrostructural level (Cantalupo & Hopkins, 2001) but not at a cytoarchitectonic level in a relative smaller sample-size (Schenker et al., 2010; but see also Graic et al., 2020). 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* (Petrides, 2005a;b; Belmalih et al., 2009). 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 (Petrides, 2005b nature). 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 (Hage and Nieder, 2013). Moreover, the use of positron emission tomography (PET) in 3 captive chimpanzees has revealed that begging food from a human by using either gestures, atypical attention-getting sounds, or both of them simultaneously, activated a homologous region of Broca's area (IFG) predominantly in the left hemisphere (Tagliabattola et al., 2008). Some functions associated to 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 (Hopkins et al., 2017). Such a link might be attributed to the typical Broca's function described in humans, namely hierarchical organisation of behaviours involved in tool use (e.g., Koehlin & Jubault, 2006; Stout and Hecht, 2017). Regarding gestural communication, Meguerditchian et al., (2012) 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 of hand preference for communicative gesture - but not for non-communicative manipulative actions - is related with 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 (Becker et al, 2021b).

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 (e.g., Catani and Thiebaut de Schotten, 2012). It was highlighted that the connectivity between language areas, due 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 (e.g., Duffau, 2016). 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 causing conduction aphasia (eg. Catani and Mesulam, 2008), also in deaf signers (Metellus et al., 2017). The AF is already present at birth (Dubois et al., 2016) but matures slowly until late childhood Brauer et al., 2013, Dubois et al., 2016). 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 (Hickok and Poeppel, 2004?). In contrast to the AF the “Ventral Pathway“ matures more rapidly in development and was also described to be phylogenetically more ancient (e.g., Brauer et al., 2013; Friederici, 2017). The late maturing of the AF is proposed to be due to the frontal portion, which connects to Broca’s area and is only fully myelinated by the age of 7 (Brauer et al., 2011; Brauer et al., 2013). In fact, controversy persists whether this portion is also already present at birth (Dubois et al., 2006; 2009; 2016; Perani et al., 2011; Friederici 2012 *frontiers*).

Regarding lateralisation, the human AF was shown 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 not lateralisation at all (20%) (Büchel et al., 2004, Nucifora et al., 2005, Powell et al., 2006; Catani et al., 2007; Thiebaut de Schotten et al., 2011; Takaya et al., 2015). In early development, the leftward AF is the most asymmetrical region of the developing white matter (Dubois et al. 2009; Liu et al., 2010, but see also Song et al., 2015). Interestingly, the early leftward asymmetry in newborns was correlated with later language capacities in children (Lebel and Beaulieu, 2009; Lopez-Barroso et al., 2013; Salvan et al., 2017). Catani et al., (2007) argued that the AF’s asymmetry represents a better structural marker for functional language specialisation than the Planum Temporale asymmetry (Catani et al., 2007). This structure-function relationship is however debated (Propper et al., 2010; Zhu et al., 2014; Silva & Citterio, 2017 ; Gerrits et al., 2021; Verhelst et al., 2021). For example, Verhelst et al. (2021) demonstrated in a fixel based analysis, that the 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 (Schmahmann and Pandya, 2006; Petrides and Pandya, 2009;

Petrides, 2014; Rilling et al., 2008, Rilling et al., 2011; Frey et al., 2014; Eichert et al., 2019; Barrett et al., 2020; Balezeau et al., 2020; Rocchi et al., 2021). It is to date debated however, to what extent frontal and temporal connections, its strength as well as lateralisation of this pathway differ between primate species. In fact, recent findings speak for a rather conserved organisation across primates (for a review: Becker et al., 2021a). Therefore, latest functional results suggest that language abilities allowing humans to name, conceptualize and thus better remember sound (Schulze et al., 2012) would be shared across primates (Rocchi et al., 2021). 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 (Eichert et al., 2019; Balezeau et al., 2020; Rocchi et al., 2021). In fact, Rilling et al. (2008) 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 (Rilling et al., 2012). This result remained unique regarding AF lateralisation in nonhuman primates (Eichert et al. 2019, Balezeau et al., 2020; Rocchi et al., 2021). 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 difficult to infer any bias at population-level. Only studies including much more substantial sample size of subjects would help elucidate this debate.

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 hereby implicated for different language processing functions (General: Wernicke, 1874; Dronkers et al., 1996, Oh et al., 2014; Auditory processing: Bamiou et al., 2003; Motor aspects: Ackermann and Rieker, 2004; Syntax: Friederici et al., 2018; Merge: Zaccarella et al., 2015; sign language: Metellus et al., 2017). Interestingly, the Insula seems to be particularly involved in motor planification of speech as seen in pathologies (Dronkers et al., 1996; Ackermann and Rieker, 2004). Further, Loevenbrueck et al., (2005; 2008) highlighted in adults that prosodic pointing gesture activates Broca's area as well the left anterior Insula (Loevenbrueck et al. 2005; 2008).

Moreover, at the structural level, the volume asymmetry of this region may be associated to hemispheric dominance for language. In fact, Keller et al., (Keller et al., 2011)

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 (Keller et al., 2011; Chiarello et al., 2013). Although little is known about the functional implication of the Insula during language development in new-borns and infants, several studies highlighted an early lateralisation of the Insula towards the left hemisphere (Dubois et al., 2010). Thanks to all the aforementioned data, the (anterior) Insula got established as region of interest for studying linguistic (motor) processing. Additionally, the anterior Insula comprises Von Economo and Fork neurons (Von Economo, 1926) that were 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 (Evrard et al., 2018).

While larger in humans, the insular cortex also exists in apes and monkeys, where especially the anterior portion expanded during primate brain evolution (Bauernfeind et al., 2013). Von Economo neurons, which were thought to be exclusive to apes (Nimchinsky 1999), are also present in the anterior insular cortex of monkeys (Evrard et al., 2012; 2018). The authors argue that two distinct insular regions could be implicated in monkey communication (Evrard et al., 2018). 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) are projecting into a region of the thalamus (PAG), that is involved in vocalisations (Evrard et al., 2018). 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 (Bauernfeind et al., 2013). Further studies with larger sample size are needed to investigate whether the Insula and particularly its anterior portion is structurally lateralised in non-human primates in relation to planification of communication, especially gesture.

Cingulate Cortex/Sulcus

The Cingulate Sulcus lays in the medial part of the cerebral cortex delimited ventrally by the Cingulate cortex and dorsally by the paracentral lobe and the superior frontal cortex. Its anterior part is considered as a hub for domain general cognitive processing like counterfactual thinking, mentalising and language including cognitive control on signals production (Toga and Thompson, 2003b. Amodio and Frith, 2006; Loh et al., 2017; 2020). Pioneer studies regarding language processes have shown that for the anterior and midcingulate cortex, 1) stimulations are evoking orofacial and tongue movements (Tailerach et al., 1973) and 2) lesioned patients experience akinetic mutism, associated with an absent motivation to speak (Ackermann and Ziegler, 1995). Little is known about the Cingulate cortex concerning direct language development. Rare results come from Loevenbruck et al. (2008) highlighting, as in adults, the functional neuroanatomical activation of the left anterior Cingulate cortex, besides Broca's area and the Insula in communicative pointing gestures (Loevenbruck et al., 2008). However, the anterior Cingulate cortex was prominently shown to be important for joint attention in both adults and infants. Joint attention is considered a prerequisite of the theory of mind as well as a prelinguistic communication act (Mundy et al., 2018; Benga et al., 2005). Interestingly, the hand, mouth and tongue motor representations are grouped together around the caudal end of every vertical sulci departing from the Cingulate Sulcus (Amiez & Petrides, 2014), suggesting its key implication for the multimodal language system. In addition, 50% of human subjects present a Paracingulate Sulcus, located more rostrally above the anterior and Midcingulate Sulcus (Ide et al., 1999).

The presence of the Paracingulate Sulcus is lateralized in the human brain with nearly 70 percent located in the left hemisphere (Aboitiz et al., 1999; Amiez et al., 2019). This lateralisation is influenced by genetic factors and by the in-womb environment (Amiez 2018 scientific reports). At the functional level, this human asymmetry was shown to be correlated with the involvement of the left Cingulate cortex in language tasks in right-handed subjects (Paus et al. 1996; Toga and Thompson, 2003b).

Some authors suggested that the anterior and Midcingulate cortex might have also played a role in language evolution. Loh et al. (2017) 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 vocalizations like screams' and 'shrieks', are associated with the "cingulate vocalization pathway" (Jürgens and Pratt, 1979). In fact, the "cingulate vocalisation area" in the anterior and Midcingulate cortex are connected 1) to the periaqueductal 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 (Loh et al., 2017). In addition, in nonhuman primates' innate calls can be evoked by anterior and Midcingulate cortex stimulations (Jürgens and Ploog, 1970) and lesions impair the production of calls (Aitken et al., 1981) 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 (Allman et al., 2010; Nimchinsky et al., 1999; Hakeem et al., 2009). Together with the presence of Von Economo neurons in the anterior Insula, it was proposed that Von Economo neurons may be implicated in primate communication (Evrard, 2018). In contrast to the Insula cortex, no Von Economo neurons were 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" (Amiez et al., 2019).

Whereas, 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 (Hopkins et al., 2021). In contrast to humans, no population-level lateralisation for the presence of the Paracingulate Sulcus was found in chimpanzees (Amiez et al., 2019). 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 (Hopkins et al., 2021). 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.

Superior Temporal Sulcus (STS)

The Superior Temporal sulcus (STS) is a long fold separating the superior from the middle temporal lobe. It was shown important for a variety of social cognition tasks important for communication (e.g., Deen et al., 2015; Belin et al., 2000), containing both specialised regions for a particular task and regions that respond to several tasks simultaneously (Deen et al., 2015). In fact, specialised areas of the STS have been shown implicated in the perception of voices in the right hemisphere (Belin et al. 2000), faces (Pitcher et al., 2011), biological

motion (Pelphrey et al. 2005), audiovisual integration (Taylor et al., 2006) and in the theory of mind (Ciaramidaro et al., 2007; Vander Wyk et al., 2009). Regarding speech perception in particular, three temporal voice areas are dispatched symmetrically in both hemispheres along an antero-posterior gradient (Bodin et al., 2018). Distinct areas of the STS have also been implicated in language processing in hearing and deaf subjects especially in the left hemisphere (e.g., Vigneau et al. 2006; Fedorenko et al. 2012; Moreno et al., 2018). In children, responses to voices in the STS and STG are strongly right-lateralised, an asymmetry which decreased with age (Perani et al., 2011; Bonte et al., 2013). 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 Brauer et al. (2008) for a right hemispheric STG temporal primacy in children in contrast to adults). Interestingly, together with Broca's area, the posterior Superior Temporal Sulcus is proposed to constitute the neural network supporting syntactic processes (Friederici, 2017), which, until the age of 10, does not process syntax and semantics independently (Skeide et al., 2014).

Regarding structural asymmetries, the left STS was shown longer than the right, but matures more lately, as seen in preterm newborn infants (Chi et al., 1977a; Dubois et al., 2008; 2010; Leroy et al., 2011; Leroy et al., 2015). 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, Leroy et al. 2015; Glasel et al. 2011; Bodin et al., 2018). This robust asymmetry is irrespective of age, handedness and language lateralisation, suggesting a strong genetic influence (Glasel et al., 2011; Bonte et al., 2013; Leroy et al. 2015). Functional correspondence was found between its deepest point and location of the voice sensitive peak (Bodin et al, 2018). Several sulcus interruptions "plis de passage", are more present in the left STS, probably resulting from stronger white matter fibers passing underneath the STS (Le Guen et al., 2018). The aforementioned results highlight the STS's 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 mapped onto a fine-grain pattern of object, body and face selectivity (Sliwa and Freiwald, 2017). Indeed, its implication in a variety of social cognition tasks was demonstrated. This includes gaze following and joint attention

(e.g. Marciniak et al. 2014) as well as facial movements in the upper STS (e.g. Fisher and Freiwald, 2015). In addition, the mid-STS in macaques was recently hypothesized to be equivalent of the human TPJ area, important for the theory of mind, because it was active for predicting social situations (Roumazeilles et al., 2020) and because macaques living in larger groups demonstrate an increased grey matter of this area (Sallet et al., 2011). Regarding especially communication, similar to humans, voice and face patches were also found in the monkey's STS (Ghazanfar et al., 2008; Petkov et al., 2008; Beli et al., 2018; Bodin et al., 2020; 2021). In fact, recently it was demonstrated that audiovisual integration happened in a distinct region in the anterior fundus (Khandhadia et al., 2021). 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 (Leroy et al. 2015). 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 (Meguerditchian et al., 2016; 2021).

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 (Vilberg and Rugg, 2008), or verbal working memory (Jacquemot and Scott, 2006), but also in tool-use (e.g., Stout and Chaminade, 2012; Hecht et al., 2015). The Inferior Parietal Lobe is one of the latest to myelinate in development (Flechsigs, 1901) and was related to the emergence of language in evolution (e.g., Geschwind, 1965) and in development (e.g., Catani and Bambini, 2014). 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 (Jäncke et al., 1994). The Planum Parietale is implicated in dyslexia and communication disorders (Gannon et al., 2005) and processing voice spectral information (Lattner et al., 2005). 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 (Vanduffel et al., 2002; Grefkes and Fink 2005; Orban et al., 2006). But also, due to its anatomical position, this region is a zone of convergence and integration of sensory and motor information, via the fronto-parietal network (Budisavljevic et al., 2021). 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 (e.g., Arbib, 2005; Rizzolatti and Sinigaglia, 2010).

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 (Jäncke et al., 1994). Another structural asymmetry was found for the parietal operculum, which constitutes the gyrus directly above the Planum Temporale as part the supramarginal gyrus (Eickhoff et al., 2006). It shows a leftward asymmetry, especially for right handers (Habib et al., 1995). 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 (Hecht et al., 2015).

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 lay in the semantic knowledge important for both language and tools to acquire the skill necessary to perform these actions (Johnson-Frey, 2004; Lewis, 2006; Stout and Chaminade, 2012). In this view, modifications of circuits that subserves gestures and imitations may have paved the evolutionary way for language and tool use in humans (Lewis, 2006), with the Inferior Parietal Lobe in its heart. Recently, Cheng et al. (2021) found that leftward rostral- and rightward caudal inferior parietal structural asymmetries connecting to several areas related to tool-use in humans (Lewis, 2006), 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 nontool-use motor actions (Gilissen and Hopkins, 2003). To fulfill tool-use learning, humans require a degree of bodily awareness to match during practice variation in kinematic detail with the desired outcome. Similar awareness is required for other animals on

the Mirror Self-Recognition test (Anderson and Gallup, 2015), which also some chimpanzee subjects pass. In fact, chimpanzee subjects that passed the test (to recognize themselves in a mirror), also possessed a more right lateralised fronto-parietal projection, exactly as in humans during tool-making learning (Hecht et al., 2015; 2017; Stout et al., 2015; Stout and Hecht, 2017). This rightward asymmetry of connectivity could be related to a human-like rightward asymmetry initially found for the Planum Parietale in apes (Gannon et al., 2005), a finding which was replicated in chimpanzees particularly in females in relation to handedness (Tagliabue et al., 2007). Future studies in nonhuman primates should continue investigating potential links in lateralisation of the Inferior Parietal Lobe and the behaviour. It would help clarifying whether left or right lateralised brain circuits for tool-use paved the way for language brain circuits.

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 (Chi et al., 1977). It also divides the primary motor cortex from the primary somatosensory cortex, where topographic sensory and motor representations of human body parts are organized (Penfield and Boldrey, 1937). 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 (Yousry et al., 1997).

Regardless of the hand, the direction of handedness was found associated with contralateral asymmetries of the motor hand area (e.g., humans: Amunts et al., 1996; 2000; Cykowski et al., 2008, Sun et al., 2012). 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 (eg. Amunts, 2000). 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 (Groen et al., 2013; Ocklenburg et al., 2014; Häberling et al., 2016).

Within an evolutionary framework, hemispheric specialisation and handedness have been historically considered unique to human language evolution (Crow, 2004; Warren, 1980). However, many primates, such as baboons or chimpanzees, also present right-handed dominance for manipulative actions, and even stronger right-handed dominance for communicative gestures (Meguerditchian et al., 2013). Just as in humans, the nonhuman

primates', direction of handedness for object manipulation was found associated to contralateral asymmetries of the motor hand area within the Central Sulcus (Chimpanzees: Hopkins and Cantalupo, 2004; Dadda et al., 2008; Baboons: Margiotoudi et al., 2019; Capuchin monkeys: Phillips and Sherwood, 2005; Squirrel monkeys: Nudo et al., 1992). It is notable that the contralateral hand area effect in the CS was found for manipulative actions exclusively (Margiotoudi et al., 2019) but not for communicative gesture handedness. As mentioned in the previous section, handedness for gestural communication was exclusively found related to Broca's homologue (Becker et al., 2021b), 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 (Bouziane et al., 2021). 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 (Hopkins et al., 2017).

Conclusion

In this review, within an evolutionary framework across primates, we compared data about the structural inter-hemispheric asymmetries of most key brain structures that are well 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 (Crow, 2004; Warren, 1980). 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 (Gannon et al., 1998; Cantalupo & Hopkins, 2001; Hopkins & Nir, 2010; Marie et al., 2018; Becker et al., 2021c,d). 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 extent in baboons, those shared features includes the leftward lateralised white matter connectivity tract between Broca's area and the Planum

Temporale - the Arcuate fasciculus (Rilling et al., 2012), leftward parietal operculum, rightward Planum Parietale and fronto-parietal projection (Gilissen and Hopkins, 2003; Gannon et al., 2005; Tagliabue et al., 2007), the rightward posterior section of the STS (Meguerditchian et al., 2016, 2021) as well as the presence of paracingulate sulcus in the left hemisphere (Hopkins et al., 2021). These collective findings suggest an important shared biological ancestral encoding between Old world monkeys, great apes and humans of what have initially been 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 (e.g., Hopkins and Nir, 2010; Meguerditchian et al., 2012; Hopkins et al., 2019; Becker et al. 2021b), 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 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 seems fruitful for linking the lateralised brain anatomy to lateralised behaviours. Interesting future work could now lay in transposing this handedness knowledge to humans, to clarify for example, whether communicative gesture handedness might be a marker for language lateralisation.

Regarding specifically language evolution, we hypothesise that asymmetries for language areas may not have initially evolved for language, if language is seen as one 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 specialisation 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.

Author Contribution

Conceptualization, Y.B. and A.M.; writing—original draft preparation, Y.B.; writing—review and editing, Y.B. and A.M.; supervision, A.M.; project administration, A.M.; funding acquisition, A.M. All authors have read and agreed to the published version of the manuscript.

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Conflict of Interest

The authors declare no conflict of interest.

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