HAL
open science

The Arcuate Fasciculus disentangled: Different conceptions are depicting different evolutionary trajectories

Yannick Becker, Olivier Coulon, Adrien Meguerditchian

To cite this version:

Yannick Becker, Olivier Coulon, Adrien Meguerditchian. The Arcuate Fasciculus disentangled: Different conceptions are depicting different evolutionary trajectories. 2021. hal-03255234v1

HAL Id: hal-03255234

https://amu.hal.science/hal-03255234v1

Preprint submitted on 9 Jun 2021 (v1), last revised 30 Nov 2021 (v3)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

The Arcuate Fasciculus disentangled:
Different conceptions are depicting different evolutionary trajectories

Yannick Becker[1,2], Olivier Coulon[2], Adrien Meguerditchian[1,3]

[1]*Laboratoire de Psychologie Cognitive, CNRS UMR 7290, Marseille, France*
[2]*Institut de Neurosciences de la Timone, Aix-Marseille Univ, CNRS UMR 7289, Marseille, France*
[3]*Station de Primatologie CNRS, Rousset, France*

Keywords: language network, language evolution, frontal terminations, temporal terminations, discontinuity, continuity, lateralization, nomenclature, terminology, hemispheric specialization, Comparative anatomy, White matter, Tractography

Of all brain connections, the Arcuate Fasciculus is of considerable interdisciplinary interest, because of its major implication in language processing. The more peculiar is that its exact course and terminations remain inaccurately defined in the literature. Additionally, its appellation has been confused with the Superior Longitudinal Fasciculus and the Dorsal pathway. This morphological inconsistency led to diverging evolutionary accounts, which becomes visible in the recent renewed interest for the Arcuate Fasciculus across primate species. Historical knowledge about the Arcuate Fasciculus originated from human blunt dissections and later from tract tracing studies in the monkey brain. Contemporary diffusion weighted MRI studies reinvestigate the fasciculus' morphology but remain heavily bound to unclear anatomical priors and methodological limitations.
While reviewing the three epistemological steps chronologically, we try to disentangle the major fibre bundle for language processing and highlight how each conception influenced current views about the evolution of language.

Abbreviations: AF (Arcuate Fasciculus), SLF (Superior Longitudinal Fasciculus), MdLF (Middle Longitudinal Fasciculus), dMRI (diffusion magnetic resonance imaging), NHP (Non-human primate)

Highlights:

- *We disentangled the AF from the SLF and the dorsal pathway in primates*
- *Divergent studies on AF travelling and terminations affect language evolution theories*
- *Evidence for continuity for both inferior frontal and anterior temporal terminations*
- *Discontinuity in lateralisation may be due to small sample sizes*
- *Language and the AF may have co-evolved progressively in primate evolution*

Introduction

Language is in the heart of what is generally accepted to make us special as a species. The "How did it evolve?" persists hereby as one of the most debated questions in science. Prominent theories do not follow an evolutionary and progressive logic but are of saltatory and discrete nature, dividing into lingual versus non-lingual and using language as an argument to divide human versus animal (eg. Berwick and Chomsky, 2016; Richerson et al., 2021). Many authors have stated that the difference between humans and non-human primates (NHP) might lay in a different neural architecture between primate species (eg. Boe et al., 2017, Friederici, 2017) including one of its key features: its connectivity.

In the human brain, the classic language pathway model describes a fibre pathway – the Arcuate Fasciculus (AF) - arching around the Sylvian fissure, linking superior temporal language regions (roughly Wernicke's area) to ventrolateral frontal regions (roughly Broca's area). Posterior Broca's area is engaged in phonological tasks and anterior Broca's area is specialised in syntactic and semantic functions. On the temporal end, superior Wernicke's area is engaged in phonological - and the posterior area for semantic tasks (Catani and Thiebaut de Schotten, 2012).

Modern forms of the language pathway model highlight the connexion of the AF with other cortical areas critical for language processing such as the inferior parietal lobe and the insula (Catani and Thiebaut de Schotten, 2012). Even if their exact respective role is still unknown, some hypotheses have been discussed in the literature. For instance, the inferior parietal lobe might be involved in processing concrete concepts, episodic memory retrieval of words and verbal working memory as well as sensory and motor integration (Catani and Thiebaut de Schotten, 2012). In addition, as it was already suggested during the 19th century, the insula was recently shown to have a crucial role in articulatory planning, language repetition ability, and phonological recognition (Ardila et al., 2014).

Not surprisingly, it was observed that interrupting lesions of the AF lead to clinical symptoms. Traditionally, AF lesions are associated with conduction aphasia, characterised by the inability to repeat words while speaking. However, modern investigations depict very global and complex roles for every sub-branch of the AF, with its lesions implicated in language disorders like dyslexia, apraxia, alexia and several types of aphasia (Catani and Thiebaut de Schotten, 2012).

This major language brain fasciculus matures during childhood into a dominant and left-hemisphere lateralised pathway (Catani et al., 2007; Dubois et al., 2009; Perani et al., 2011). While the architecture for language brains regions is highly conserved between primate species, main morphological changes happened in the AF, potentially explaining our uniqueness to process language (Rilling et al., 2008). Some authors extend this hypothesis to propose that the AF with parts of Broca's area represents the biological manifestation of Chomsky's controversial "Universal Grammar" (Friederici et al., 2017; Zaccharella and Friederici, 2017).

In other words, the AF is at the heart of the debate about what makes us human.

In this review, we briefly present the historical findings and techniques that advanced knowledge about primate neuroanatomy and the Arcuate Fasciculus. We also present the different terminology used in this domain and highlight how conclusions about AF evolution depend on nomenclature. In a second time, we review studies concerning the continuity or discontinuity between human and non-human primates. The debate is centred around three main controversies:

1. Inferior Frontal Terminations: An evolutionary continuity between primate species stipulates its locations in the monkeys' Broca's homologue, whereas a discontinuity stipulates its locations rather in the monkeys' superior frontal areas but not in Broca's homologue.

2. Extended temporal lobe terminations: An evolutionary continuity between primate species stipulates its locations in the monkey's anterior temporal lobe whereas a discontinuity stipulates more posterior terminations in the monkeys' parieto-temporal junction.

3. Lateralisation: An evolutionary continuity between primate species stipulates the left lateralisation of the monkeys' AF whereas a discontinuity stipulates an absence or inverse lateralisation.

BOX 1

Methodological approaches:

Different methods and techniques advanced the understanding of the Arcuate Fasciculus in human and non-human primates.

Dissection: The historically first techniques to identify the AF were *post-mortem* dissections of the human brain in the 19th century. This technique includes in particular blunt dissections, in which the surgeon separates tissue layers by means of an instrument without a cutting edge. This method of dissection has not changed significantly in centuries, is time consuming and requires considerable skills. Especially the Klingler technique, by freezing already formalin-fixed brains before dissection, is widely used today because of the possibility of direct correlation with dMRI techniques (eg. Agrawel et al., 2011).

Tract tracing: In order to shed light into more detailed AF anatomy, tract tracing is a powerful *post-mortem* method. A fibre or axon connects via a synapse with a second axon. Only tract tracing methods can unveil a monosynaptic connection between cortical area *ex-vivo*. It consists in injecting tracers, such as radiating amino acids in the cortex, which follow the trajectory of the fibre and labels its axons as well as its terminations ("autoradiographic technique"). Histological observations can then locate the traced axons. This technique has been used in macaques and facilitated a better understanding of the AF's and SLF's origins, course and terminations (eg. Petrides and Pandya, 1988; Schmahmann and Pandya 2006).

Diffusion MRI: The only technique available, to study fibre pathways *in-vivo* and in a large sample sizes, is diffusion MRI (dMRI). It consists in a form of magnetic resonance imaging (MRI) based on the measurement of random water molecule motion within a voxel of tissue. The diffusion of water molecules is constrained by the borders of axon membranes and thus brain connections can be reconstructed thanks to the direction of the water's diffusion vector.
Diffusion MRI reconstructs bundles of numerous fibres and does not have the resolution of a single fibre. Because of such uncertainty, the extracted pathways are referred to as streamlines or tracts rather than fibres. In addition, dMRI does not unveil monosynaptic connections.

Challenges of dMRI: As in the real brain, virtual dissection of the white matter is possible (Catani et al., 2005) using several masks for seeding, inclusion, exclusion and for termination of streamlines. Anatomical priors based on atlases are however indispensable to resolve crossing fibres **(**Girard et al. 2020**)**, false streamlines (Maier-Heine et al., 2017), and difficulties to tract inside the grey matter (Reveley et al., 2015), which are limiting this technique. Regarding especially the issue of crossing fibres, "bottleneck" configurations, where several fasciculi are entangled (eg. the AF and the SLF), are known to generate false positive streamlines in dMRI (Girard et al., 2020) and morphology can therefore differ across studies.
Therefore, several methods are proposed in the literature to overcome inherent diffusion MRI problems:
-To increase resolution and sample size of *in-vivo* studies, some authors also include *ex-vivo* brains, which requires no health monitoring and adds the possibility to scan during several hours and increases spatial resolution (ex. Barrett et al., 2020).
-To overcome the difficulty of tracking into grey matter, some studies focus exclusively on the body of the tract because of its most reliable aspect for tractography reconstruction (eg. Bryant et al., 2020; Warrington et al., 2020). Thus, frontal and temporal terminations can't be directly described, which makes an overall structural comparison between the monkey and human AF challenging. To solve this issue, surface-based methods can provide vertex-wise connectivity matrices (St-Onge et al., 2018) from which the terminations of the AF and the dorsal pathways can be identified. The resulting connectivity fingerprint technique can be used for interspecies comparisons (Mars, et al., 2021).
In recent years, diffusion MRI has been favoured for comparative approaches across primate species, in order to investigate the origin of the human language pathways. Therefore, the number of diffusion MRI studies in nonhuman primates has significantly increased (Milham et al., 2020).

History of terminology and delineation:

The first description of what would be known as the Arcuate Fasciculus (AF) dates back to the beginning 19th century by Reil, describing a fibre bundle "… curving around the posterior wall of the [Sylvian] Fissure in an arc-like fashion …" from the frontal to the temporal lobes (Reil, 1809, pp. 202-203). A well-known description by Burdach, who acknowledged this observation by naming it "Bogenbündel" (i.e. "Arcuate Fasciculus") was published some years later (Burdach, 1822, p.371). Burdach's appellation persisted until Wernicke's detailed atlas description, who was the first to refer to the bundle as the "superior longitudinal bundle", or "arcuate bundle" (Wernicke, 1887 Tafel XII).

From there on, the terms of either "Superior Longitudinal Fasciculus" (SLF) or "Arcuate Fasciculus" (AF) are used as synonyms in the literature.

In fact, as detailed dissection descriptions of the human brain were not updated, the aforementioned historical descriptions were used until the modern time. Clinical investigators like Geschwind (1965) relied on these historical descriptions of the AF to conceive models of language brain networks and their involvement in pathologies like conduction aphasia.

AF versus SLF:

Nevertheless, the overlapping labels (SLF versus AF) keep causing confusions until today, given that the SLF and the AF might actually be distinct from each other in terms of terminations according to recent advances (see below). Such confusions might be related to the difficulties to determine the exact origin and termination of fibres, especially with *post-mortem* dissections.

The AF delimitations have further been investigated in the 1980s by the use of tract tracing techniques in an animal model, the rhesus macaque. Two major discoveries were made: First, three relatively distinct parietal to frontal lobe fibres were observed and labelled as SLF I – II - III, regarding their dorsal to ventral gradient (Petrides and Pandya 1984, see also Schmahmann and Pandya 2006, Petrides, 2014). Second, the AF was proposed to be distinct from the SLF in terms of terminations, namely the caudal part of the superior temporal gyrus for the AF and the parietal regions for the SLFs (Petrides and Pandya, 1988). These two discoveries are still the ground for contemporary debates and investigations.

The SLF is subdivided in three different branches depending on its dorsal to ventral gradient and its terminations. SLF I is the most dorsal sub-branch linking the superior parietal lobule with the caudal dorsolateral and dorsomedial frontal cortex. SLF II is located more ventrally, linking the caudal part of the inferior parietal lobule (the angular gyrus in the human brain) with area 45 of the ventrolateral frontal cortex. SLF III is coursing as ventral as the AF and linking the rostral part of the inferior parietal lobule (the supramarginal gyrus in the human brain) with area 6VR and area 44 (for monkeys see Petrides, 2014; for Chimpanzee see Hecht et al., 2015).
In some studies, the AF is considered as the "persylvian-SLF" or "SLF IV" (Catani and Thiebaut de Schotten, 2008; Ocklenburg et al., 2016; Honnedevasthana Arun et al., 2021), or as the temporal part of the "SLF complex" (eg. Sugrue and Yang, 2019) or "SLF system" (eg. Vavassori et al., 2021).

Dorsal and/ Ventral Pathway:

For methodological reasons, one of the limitations of dMRI is that it can hardly disentangle association pathways like the AF or the SLF (Girard et al. 2020). Most studies therefore refer to it as "the dorsal language pathway or stream". The term "dorsal pathway" is also used as a synonym of any of those pathways connecting frontal to parieto-temporal regions. It is opposed to the "ventral language pathway, running ventrally from the Sylvian fissure and emulating the well-known visual pathway division.
While the ventral pathway was considered differentiated into the inferior fronto-occipital fascicle (IFOF), the uncinate fascicle (UF) and the temporo-frontal extreme capsule fascicle (ECF), very recent

views consider all these parts as one and the same pathway, passing through the extreme capsule (Weiller et al., 2021).
Functionally, the dorsal pathway is involved in mapping sound to articulation, while the ventral pathway is involved in mapping sound to meaning (Hickok and Poeppel, 2004; Saur et al., 2008). However recent advances are challenging this dichotomic view and are also highlighting the importance of the dorsal pathway in semantics (Hula et al. 2020).

Anterior/posterior indirect segment and long direct segment:
Using diffusion MRI, Catani and colleagues (2005; 2014) have dealt with the issue of axons that enter the human AF in the temporal lobe, but terminate in the inferior parietal lobe, without being directed to the ventrolateral frontal region. They distinguish between a direct and two indirect segments of the AF (Catani et al., 2005). One of these indirect segments, "the posterior segment" is connecting the lateral temporal region with the inferior parietal region and could be the equivalent to the posterior segment of the monkey's middle longitudinal fasciculus (MdLF), resulting in the AF's prominent "arch" in the temporal lobe.

The other indirect branch "the anterior segment" may be homologous of the SLF III (Petrides and Pandya, 1984 in the monkey and Frey et al. 2008 with dMRI in humans), connecting rostral inferior parietal regions with the ventrolateral frontal regions. The direct segment would hereby be the AF as defined by monosynaptic connections, connecting temporal regions with inferior frontal regions (Frey et al., 2014; Petrides, 2014).

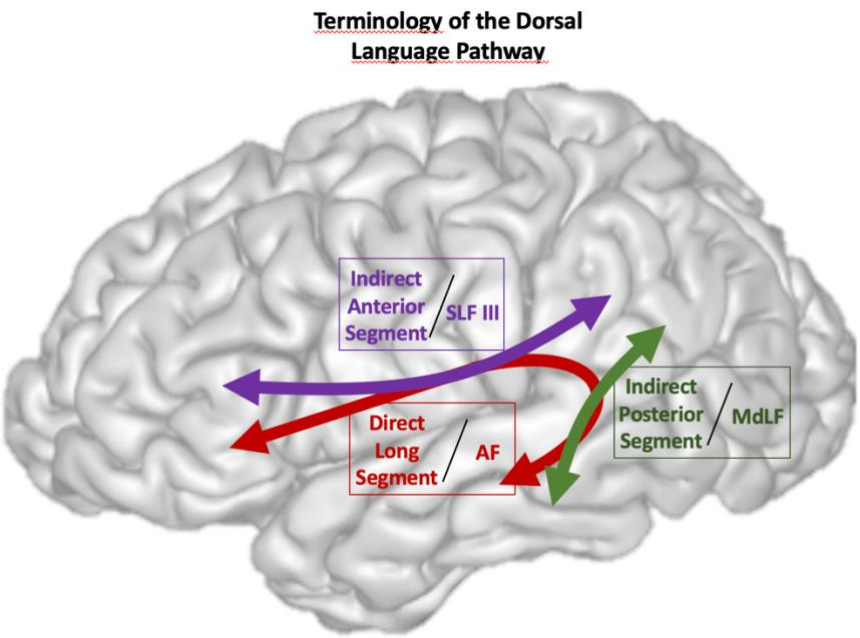

Figure 1: Schematic illustration of the dorsal language pathway terminology in the human brain. SLF III: Third branch of the Superior Longitudinal Fasciculus, AF: Arcuate Fasciculus, MdLF: posterior segment of the Middle Longitudinal Fasciculus

Role of terminology

Discrepancies of terminology in the literature might not only be confusing for the field but have also theoretical implications.

For instance, based on the aforementioned differences in terminology, the "dorsal pathway" consists of different components (either/or of the SLF I+II+III, AF, posterior MdLF) (Aboitiz, 2018). However, these components have different properties, in terms of termination sites and lateralisation. Trying to compare the dorsal pathway between human and non-human primate could be imprecise and source of confusion, because as we have reviewed above, the dorsal pathway consists of different tracts that have different properties.

We might compare things between species that are not equivalent. For example, the SLF, which is rightward lateralised (Thiebaut de Schotten et al., 2011; Amemiya et al., 2021), has typically less terminations within the inferior frontal gyrus (IFG) and no anterior temporal terminations (Budisavljevic et al., 2015). Therefore, the SLF is to a lesser degree implicated in language processing and its phylogenetic precursors. Moreover, the SLF is proposed to be related to spatial information processing and to the visual motor domain (Hecht et al., 2017).

Differences in terminology matters, because a same result could have different theoretical implications depending on its labelling and therefore its functional connotation.

In a similar example in the literature, it was documented that a strengthening of fibres could be observed during primate evolution, linking the superior temporal lobe (Wernicke's region in the human) with the inferior parietal lobe (Geschwind's region) (Aboitiz and García, 1997; Catani and Bambini, 2014). Different interpretations can be made depending on terminology. Implications for the AF evolution would be equivalent if these fibres are a component of the AF or a less related bundle (eg. posterior segment of the MdLF).

Although the termination sites of each of the tracts are still debated throughout the literature, some convergences seem to emerge in the terminology:

- the AF is linking the frontal lobe with temporal regions;
- the SLF is linking frontal with parietal regions;
- the posterior segment of the MdLF is linking parietal with temporal regions

Wherefore we used such a terminology in the rest of the present paper.

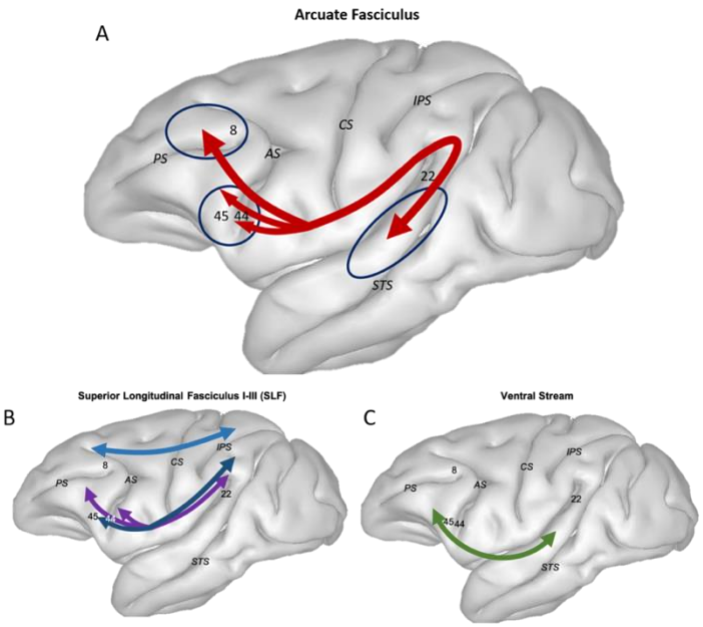

Figure 2: Schematic illustration of the homologues main language pathways in monkeys.
A: Illustration of the course and terminations (arrowheads) of the Arcuate Fasciculus (AF) in red. Blue circles are indicating the possible terminations as discussed in the literature.
B: Illustration of the course and terminations (arrowheads) of the three branches of the Superior Longitudinal Fasciculus (SLF) after Petrides, 2014. Purple: branch III, dark blue: branch II, light blue: branch I.
Note that the AF and the SLF are often named "dorsal pathway" in the literature.
C: Illustration of the ventral pathway course and terminations (arrowheads) in green.
PS: Principalis Sulcus, AS: Arcuate Sulcus, CS: Central Sulcus, IPS: Inferior Parietal Sulcus, STS: Superior Temporal Sulcus, Area 45 and 44, parts of Broca's area, Area 22 part of Wernicke's area.

Evolution of AF frontal projections

By definition the AF connects to frontal language areas for distributing linguistic information from the temporal lobe in the human brain. Influential views in macaques trace terminations into dorsal area 8 integrating head and eye mouvements with sound localisation (Schmahmann and Pandya, 2006, Thiebaut de Schotten et al., 2012). Other views propose terminations into homologous Broca's area in the inferior frontal gyrus (IFG), which functionally links directly to precursors of language processes (Petrides et al., 2005b; Frey et al., 2014; Petrides et al., 2014). Theoretical accounts about the uniqueness of human language neuroanatomy rely heavily on the absence of monkey's AF termination into the inferior frontal areas (Fitch, 2010, Friederici, 2017; Zaccarella and Friederici 2017). Indeed, the putative absence of supra-regular grammar in monkeys (but see Jiang, 2018; Malassis et al., 2020) and young children were explained with an anatomical absence of the AF in the IFG (Friederici et al., 2012, 2016, 2017; Zaccarella and Friederici, 2017).

1) **Absence of IFG terminations in monkeys:**

a. <u>Tract tracing</u>

In humans the AF terminates in the Inferior Frontal Gyrus referred to as Broca's area (including area 44 and area 45). Within comparative approaches, the evolutionary question about AF frontal terminations in nonhuman primates debuted with tract tracing studies in monkeys. In the original experiment, Petrides and Pandya (1988) localised the frontal terminations not in area 44 but into the dorsal part of area 8, of area 46 and of area 6. In addition, the tract showed a dorsal travelling course with a slight bench towards the insula (Petrides and Pandya, 1988). The lack of Broca's terminations was confirmed by later studies in the 2000s, leading to the influential atlas of Schmahmann and Pandya (2006), which constitutes an anatomical reference and source of priors for many studies. This AF connexion between the Planum Temporale/tpt area (which overlaps with the monkey's homologue of Wernicke area) and area 8 elicited theories about the role of the AF in monkeys, which might thus be coordinating the respective functions of each regions, namely sound localization (Clarke and Thiran,

2004) with the involvement of head and eye movement (Barbas and Mesulam 1981). Following this view, the AF in monkeys would be an equivalent in the audio-spatial domain to the SLF II specialized in the visual spatial domain. Such low-level processes in monkeys (i.e. sounds spatial localisation) combined with the lack of Broca's homologue's terminations were seen as an evolutionary gap with the high-level language functions attributed to the humans' AF (eg. Petrides and Pandya, 1988; Schmahmann and Pandya, 2006).

b. Diffusion MRI

However, very recently, Barbeau and colleagues (2020) documented with diffusion MRI a similar tract in humans connecting area 8 (referred to as middle frontal gyrus in the paper) with area tpt (referred to as posterior/dorsal temporal regions in the paper). Humans thus seem to share with monkeys this distinct sub-branch of the AF, which was assumed to be the main AF branch specific to monkeys.

The difficulty to describe frontal terminations of the AF is well known in human data, due to dMRI methodological issues. A similar case is observed in human infants where the AF is not completely mature (i.e. myelinated) until the age of seven (Perani et al., 2011). Some authors propose the physiological existence of frontal terminations into Broca's area, even though these are not completely visible on diffusion images (Dubois et al., 2006; 2009). Other authors argue against the sheer existence of these terminations, relying on behavioural observations that children won't accomplished higher order grammar until the exact age of seven, when the AF fully matures, implying a functionally responsibility of the AF in syntax processes (Perani et al., 2011; Friederici; 2017).

2) Towards a continuity of frontal termination between primates:

a. Tract Tracing

An alternative description of the AF trajectory in macaques reported terminations in Broca's homologue (Petrides, 2014). Interestingly, such findings contradict the previous initial works of the team (Petrides and Pandya, 1988). In fact, during the first studies in the 1980s, no cytoarchitectural equivalence was known for homologous Broca's area in the macaque brain. The author explains that no terminations to ventrolateral frontal areas (ie. Broca's homologue) were found, because the initial injection site was not placed ventrally enough within the temporal lobe.

This level of knowledge increased in the 1990s and 2000s with the documentation of cytoarchitectural and electrophysiological homologies of area 44 and area 45 (Broca's homologue) in and around the most ventral part of the inferior arcuate sulcus (Petrides and Pandya, 2002; Petrides et al. 2005a; b). When tackling specifically the connectivity of Area 44 and 45 in retrograde and anterograde tract tracing studies, Petrides (2014) was able to show three distinct branches of the AF. While all branches travel more ventrally benched around the insula than in the 1988 study, the first branch terminates in the same areas of dorsal 8 and 6 like in the 1988 study (Petrides and Pandya, 1988; Petrides, 2014). The second branch terminates in area 44 and the third in area 45 (Petrides and Pandya, 2009; Frey et al. 2014).

Additionally, functionally, neurons in the ventro-lateral-prefrontal cortex neurons of macaques respond to vocalization sounds (Romanski and Goldman-Rakic, 2002).

These Broca's terminations have major alternative theoretical implication and speak clearly for a conserved machinery in primate evolution, close to Geschwind's theory (1965) in humans, connecting superior-ventral temporal language region (roughly Wernicke's area) with ventrolateral frontal region (roughly Broca's area). Challenging older descriptions (ie. Schmahmann and Pandya 2006; Petrides and Pandya, 1988).

b. Diffusion MRI

Rilling and colleagues (Rilling et al. 2008; 2012) compared the AF across primate species, using a multi-fibre Diffusion Tensor model. Anterior terminations were found in the frontal operculum, insular cortex, dorsal frontal lobe and ventral lateral frontal lobe (Area 44 and area 45).
Very recent studies reproduced these findings. In *ex-vivo* but not in lesser resolution *in-vivo* macaque brains Barrett et al. (2020) described an AF running from the temporo-parietal junction into the inferior frontal areas towards Broca's homologue. Even though not discussed, Balezeau et al. (2020) found projections into the inferior frontal areas in *in-vivo* macaques.
In addition, (Barrett et al., 2020) results also highlighted that the human brain exhibits a greater proportion of frontal lobe connections compared to other primates when normalized to total brain matter.
Further (Rocchi et al., 2021) confirmed these findings at the functional level, with functional MRI and electric brain stimulations in two macaques and human patients. Both species showed evoked potentials in Broca's area (referred to as ventro-lateral-premotor cortex) when stimulating the auditory cortex.

These diffusion MRI results concerning frontal terminations resemble the AF description of Petrides, 2014. and are implying an evolutionary continuity of the AF development, while contrasting others (eg. Schmahmann and Pandya 2006; Friederici, 2017).

Evolution of AF temporal projections

By definition, the AF "arches" around the Sylvian fissure. In humans, the AF exceeds the tpt/Planum Temporale area into the ventral temporal lobe. Its projection to ventral temporal areas is therefore crucial in the NHP to investigate potential evolutionary continuities with humans.
Because the AF's temporal terminations is discussed (Schmahmann and Pandya, 2006; Rilling et al., 2008; 2011; Eichert et al., 2019, Barrett et al., 2020), Rilling (2008) hypothesised that the emergence of a dorsal pathway projection to the anterior temporal lobe in humans only, might have contributed to transfer lexical-semantic information and some elements of syntax into the dorsal pathway. Whether the monkey's homologue is rather involved in spatial processing of sounds (Rilling et al., 2008; Aboitiz, 2018).
Very recent discoveries are contrasting this view by highlighting anterior temporal termination in monkeys (Balezeau et al., 2020). The authors speculate that this auditory pathway is moreover involved in sound and vocal patterning in the time domain (Wilson et al., 2015; Balezeau et al., 2020; Zhang and Ghazanfar, 2020).
Note that the debated question about AF temporal terminations in monkeys is mainly based on diffusion MRI studies.

1) Absence of anterior temporal terminations in monkeys:

a. Diffusion MRI

In their pioneering work, Rilling and colleagues (Rilling et al. 2008; 2012) described major changes during primate evolution with an increased temporal lobe projection in the human brain and related this finding to language evolution. The resulting pathway of highest probability travelled deep to the insula, in the surroundings of the extreme capsule and with weaker pathways running both dorsal and lateral to the insula. Additionally, to the frontal terminations into Broca's area (as stated above), cortical terminations were found in the anterior inferior parietal cortex and in the temporal lobe, in the very caudal end of area 22 (also referred to as tpt or planum temporale and part of Wernicke's area).

Concerning species differences, Rilling et al. (2008) suggested that the human AF is unique in projecting to the anterior temporal cortex. The authors hypothesised the temporal extension of the AF in recent *Homo sapiens* evolution, invading new temporal territories, including the MTG. This finding

has become the basis of a number of models of human language processing (eg. Catani & Bambini, 2014; Friederici, 2017).

At the same time Van Essen and Dieker (2007) also proposed a theory of primate brain evolution, describing a cortical expansion across primates for key regions of interest. Based on an early attempt of computational methods for comparative research, Van Essen and colleagues describe that, if the macaque brain was inflated to the size of a human brain, areas like the inferior parietal lobule, the middle temporal cortex and the lateral frontal cortex had to be expanded disproportionally in size to match the actual human brain organisation. The authors concluded that these areas must have expended during human evolution.

The cortical expansion theory therefore suggests that AF's temporal terminations have simply expanded together with the cortical area expansion, but didn't invade new territories *per se*.

A series of studies from the Rogier Mars lab tackled this question whether the human AF's temporal tail was due to cortical expansion only, or to new temporal territories invasion, by examining the evolution of temporal association fibres across primate species (Eichert et al., 2019; Eichert et al., 2020; Roumazeilles et al., 2020; Bryant et al.; 2020; Warrington et al, 2020). Studies of this lab are sharing the Schmahmann and Pandya (2006) atlas for anatomical priors and focussing exclusively on the body of the tract (Bryant et al., 2020; Warrington et al., 2020).
Using representations based on connectivity fingerprints built from tractography and surface alignment techniques using myelin maps, Eichert et al. (2019; 2020) moreover highlight that several human temporal tract expansions can be explained by cortical expansion alone. In contrast, this was not the case for the AF expansion. The authors therefore conclude that the AF underwent additional changes in its course by invading new middle temporal areas. Thus, the authors propose that the temporal lobe and especially the middle temporal gyrus (MTG) expanded significantly in the great ape lineage. Next, in the evolution of the human lineage, the AF invaded new territories of the temporal cortex, which made cognitive computational advances possible (Roumazeilles et al., 2020).
Confirming these findings, Barrett et al. (2020) found no anterior temporal terminations in macaque *ex-vivo* data to connect with frontal areas as in humans. They state that the AF shows the most striking differences of association tracts between humans and monkeys with monkeys only sharing a small subcomponent of the AF with humans.

2) Towards a continuity of anterior temporal terminations in primates:

a. Tract tracing

Sparse but influential neuronal tracer studies combined with functional stimulation have established the notion of a dual stream in auditory processing, emulating the well-known visual pathway division into ventral and dorsal pathways (Romanski et al., 1999a; b; Kaas and Hackett, 1999).
Indeed, Romanski et al., 1999 combined anterograde tract tracing with microelectrode stimulation in the auditory belt. This way, the authors showed functional evidence for directional connectivity between auditory areas in the middle temporal lobe and Broca's area (Romanski et al., 1999 a; b ; Kaas and Hackett, 1999). Similar structural and functional organization was also described in humans and the notion of a ventral and dorsal pathway was quickly taken up to describe models of human language processing (Hickok and Poeppel, 2004; Saur et al., 2008).

b. Diffusion MRI

In one of the field's first studies, using diffusion spectrum imaging with four ex-vivo macaques, Schmahmann and Pandya (2007) were able to reproduce their atlas findings initially conducted with tract tracing (Schmahmann and Pandya, 2006). Differently than in the atlas, the AF travelled more ventrally into the temporal lobe.

In addition, the debated question about NHP AF projections into the anterior temporal lobe took very recently a new turn. Balezeau et al., 2020 compared three human subjects to three chimpanzee and three macaque subjects in *in-vivo* diffusion MRI. In macaques, tract seeding originated from functionally defined auditory cortex areas, which sits in the anterior temporal lobe. The authors demonstrated that AF projections were found in the grey matter of distinct auditory cortex areas more anterior in the temporal lobe as stated before (Rilling et al., 2008, 2011; Schmahmann and Pandya 2006, 2007; Eichert et al., 2019; Barrett et al., 2020) and despite the absence of a middle temporal gyrus (MTG) in the monkey. Balezeau et al. (2020) highlight further that the ventral pathway was more prominent in comparison to the dorsal-AF pathway.
In addition, Rocchi et al. (2021) confirmed the finding of an anterior temporal AF termination on a functional level, by functional MRI and electric brain stimulations in two macaques and human patients. The effective connectivity between Broca's area (referred to as ventro-lateral-premotor cortex) and the anterior temporal lobe was equal for the ventral and the dorsal pathway (in contrast to structural findings in Rilling et al., 2008; 2011; Friederici; 2017; Balezeau et al., 2020 and functional findings in Wilson et al., 2017).
These aforementioned findings depict an evolutionary continuity between primate species regarding anterior temporal terminations and an earlier phylogenetic origin of the functional importance of the AF.

Additionally, the specific human large arching into the most inferior anterior temporal lobe, is questioned by Petrides (2014). In fact, as demonstrated in the monkey brain, monosynaptic AF connections originate around area tpt/Planum Temporale. Fibres arching more ventrally in the temporal lobe (ie. temporo-parietal fibres like the posterior middle longitudinal fasciculus (MdLF)) are independent and build synapses with the AF (Seltzer & Pandya, 1984; Distler et al., 1993; Petrides 2014). This morphology may be similar in the human brain, with the human AF also originating in area tpt/Planum Temporale if defined monosynaptically. However, with diffusion MRI, one is unable to distinguish a monosynaptical AF originating in area tpt/Planum Temporale or a polysynaptical AF entanglement with the posterior MdLF. In other words, in this view, the AF is losing its predominant "arch" (which corresponds to the posterior indirect segment (Catani et al., 2005)), due to methodological issues.

Lateralisation

1. Inter-hemispheric asymmetries of the language brain:

Starting from early human development, inter-hemispheric cerebral asymmetry was documented for most language-related regions at both structural and functional level, language tasks eliciting more activation in the left than in the right hemisphere (eg. Dehaene-Lambertz et al., 2002). Structural cortical markers of such brain lateralisation for language were proposed such as the leftward surface lateralisation of the Planum Temporale, of Broca's area or of the Insula (eg. Geschwind and Levitsky, 1968; Keller et al., 2011).
However, some of these structural markers such as the Planum Temporale were also found to be leftward lateralised not only in apes (eg. Hopkins et al., 2015) but also in an Old World monkey, the baboon, in both adults and newborns (Marie et al., 2018; Becker et al., 2021a; 2021b).

In order to complete investigations about the evolution of the human language-ready brain, recent interest has increased about the lateralisation of the language-related connectivity, and of the AF particularly.

In humans, white matter volume of the SLF II and SLF III is larger in the right hemisphere (eg. Thiebaut de Schotten et al., 2011; Amemiya et al., 2021), which is a phylogenetically shared feature with chimpanzees (Hecht and colleagues, 2015). In contrast, the human AF was shown larger in the left hemisphere for a number of macroscopic and microscopic measurements like the number of streamline, volume of the tract, fibre density and mean fractional anisotropy in adults and infants (Nucifora et al.,

2005, Powell et al., 2006; Catani et al., 2007; Dubois et al., 2009; Thiebaut de Schotten et al., 2011; Takaya et al., 2015).
Therefore, the structural AF asymmetry, and specifically its temporal terminations, is indeed discussed as a marker for the functional lateralisation of the language network (eg., Powell et al., 2006; Takaya et al., 2015; but see also eg. Vernooiij et al., 2007). Moreover, this latter hypothesis was further supported by resting state MRI data showing functional lateralisation of the language network (Zhu et al., 2014). (But see also a recent report: Verhelst et al., 2021 demonstrated that the AF is left lateralised, regardless of left or rightwards language lateralisation.)
Because of the human's prominent AF lateralisation, theoretical accounts on language evolution rely heavily on the absence of monkey's AF asymmetry to explain the uniqueness of human language neuroanatomy (eg. Friederici, 2017; Zaccarella and Friederici 2017).

2. Absence of AF lateralisation in monkeys:

Initially, Rilling et al. (2008) did not find any AF asymmetry in three macaque and four chimpanzee subjects. A follow-up study in chimpanzees including a higher number of subjects (Rilling et al., 2012), showed a left lateralised AF for the 26 subjects. Nevertheless, Rilling et al. 2012 noticed some differences with humans: the strongest connections to Broca's area are found via the dorsal pathway in humans *versus* via the ventral pathway in chimpanzees, suggesting the AF/dorsal pathway particularly was significantly modified across human evolution. The effect was even stronger in the left hemisphere, indicating that the AF left lateralisation is stronger in humans than in chimpanzees. In contrast, the ventral pathway was not found lateralised in either humans or chimpanzees. This reversed pattern of dorsal- and ventral pathway connectivity strength between humans and NHP was influentially associated with human-specific language development.

10 years after Rilling's et al. (2008) classical study, recent diffusion MRI investigations retrieve the interest for quantifying AF lateralisation. Eichert et al. (2019) studied AF terminations in four *ex-vivo* macaque images with high resolution and one *in-vivo* macaque image, comparing the dorsal and the ventral language pathway to human data. The name AF was hereby used as a synonym for the dorsal language pathway, hence comprising several other major tracts (eg. The SLF branches), like in Rilling et al. (2008; 2012). Confirming Rilling et al. 2008 for monkeys, no left asymmetry was found for the AF/dorsal pathway. In addition, a strong left lateralisation was however reported in the ventral pathway, which was found slightly right lateralised in humans (Eichert et al. 2019).
Similarly, Balezeau et al. (2020) reported no lateralisation for the dorsal pathway in monkeys but also no lateralisation for the chimpanzee subjects.
This latter finding was confirmed on a functional level by Rocchi et al. (2021) for human and macaque subjects. Despite only treating two macaque subjects, differences in lateralisation were highlighted with human subjects being leftwards lateralised and monkeys showing no lateralisation. In addition, the dorsal- and the ventral pathway were found equally connecting inferior frontal with anterior temporal regions across primate species (contrary to Rilling et al., 2008, 2012). The authors conclude that therefore only the left AF lateralisation is the crux of the human-specific distinction (Eichert et al., 2019; Balezeau et al., 2020; Rocchi et al., 2021).

However, an absence of AF lateralisation, could be due to a small sample size and inhomogeneous groups in regard to handedness. It is common in neuroscience to use not more than two macaque individuals in a given study, which makes interpretation of a populational level lateralisation impossible. In addition, lateralisation of homologous perisylvian language areas were found present in several ape species (ie. Hopkins et al., 2015). However, these asymmetries were not detected in macaques (Lyn et al., 2011), which are commonly representing the family of Old World monkeys. In contrast, recent studies demonstrated that another Old World monkey, the baboon, possess homologous asymmetries (Marie et al., 2018; Becker et al., 2021a, Becker et al., 2021c). It remains unclear why cerebral asymmetries are commonly detected in baboons but not in macaques.

Conclusion

The apparent literature about the evolution of the AF is rapidly gaining in interest in very recent years and is used as bases for theories about language evolution. A consensus is hindered by the confusion of appellations and exact anatomical courses, which are resulting in diverging definitions of what exactly the AF is. This is also of importance since advances in humans and NHP are mutually beneficial.

Indeed, the appellation “Arcuate Fasciculus” comprises different terminations or courses, depending on the author’s definition and the studied primate species. Generally, the notion “dorsal pathway” is used more broadly, but uncertainty persists about its exact fibre composition, which depends again on the definition of the author.

Historically, the knowledge about the AF’s terminations depend strongly on invasive tract tracing studies in the monkey brain. Findings about different frontal termination in the macaque brain than in the human brain led to theories about the specific frontal development of the AF in the human species related to language process. However, new knowledge about human-like frontal termination in monkeys contrasts this view.

Similar applies to the temporal terminations. Initially found to be significantly less pronounced in the chimpanzee and the macaque brain, the AF is now supposed to arch into the anterior temporal lobe and the auditory cortex, very similar to the human AF. These advances are challenging the view of the human species’ evolutionary exclusiveness.

Regarding evolution in particular, recent discussions concern:
(1) The strong development of the dorsal pathway in relation to the ventral pathway for the human species, which got recently contrasted by results of an equal effective connectivity.
(2) The absence of AF lateralisation in monkeys, while its left lateralisation is to date debated in chimpanzees. However low sample sizes and an absent control for handedness are challenging accounts for lateralisation.

Overall, the extent and strength of language related tracts might have expanded during hominin evolution, also resulting in more pronounced lateralisation in the human species, probably related to cognitive functions implicated in language related processes.

In conclusion, recent works in humans and NHP therefore suggest that AF courses and terminations are more similar between species than described before. The remarkable human ability of language might therefore have evolved progressively in primate evolution, exactly as its underlying anatomic implementation in the brain. Or to put it in the words of Charles Darwin: "Nevertheless the difference in mind between man and the higher animals, great as it is, certainly is one of **degree** and not of **kind**." (page 105: Darwin, Charles 1896)

	Tract tracer studies		Diffusion MRI	
	Absent	*Present*	*Absent*	*Present*
IFG terminations (monkey)	Schmahmann and Pandya 2006 Thiebaut de Schotten et al., 2012 Petrides and Pandya 1988	Petrides and Pandya 2009 Frey et al., 2014 Petrides et al., 2014	Eichert et al., 2019 ; 2020 Bryant et al., 2020 Roumazeillez et al., 2020	Rilling et al., 2008 Barrett et al., 2020 Balezeau et al., 2020
Anterior temporal lobe terminations (monkey)	Schmahmann and Pandya 2006	Petrides et al., 2014	Eichert et al., 2019 ; 2020 Barrett et al., 2020 Roumazeillez et al., 2020 Rilling et al., 2008 ; 2012	Balezeau et al., 2020
Lateralisation (chimpanzee)	/	/	Balezeau et al., 2020	Rilling et al., 2008 ; 2012
Lateralisation (monkey)	/	/	Rilling et al., 2008 ; 2012 Eichert et al., 2019 Balezeau et al., 2020 Rocchi et al., 2021	/

Table 1.: Summary of the main work analysed in the present review, in regard to the contrasting descriptions of the Arcuate Fasciculus (AF) in tract tracer and diffusion MRI studies. Four features are highlighted as absent or present: Frontal terminations into the IFG, expanded terminations into the anterior temporal lobe, lateralisation in chimpanzee brains and lateralisation in monkey brains.

Acknowledgements:

The project has received funding from the European Research Council under the European Union's Horizon 2020 research and innovation program grant agreement No 716931 - GESTIMAGE - ERC-2016-STG (P.I. Adrien Meguerditchian) as well as from grants ANR-16-CONV-0002 (ILCB) and the Excellence Initiative of Aix-Marseille University (A*MIDEX). The Center IRM-INT (UMR 7289, AMU-CNRS) is a platform member of France Life Imaging network (grant ANR-11-INBS-0006).

Author contributions: Y.B, A.M and O.C prepared the paper.

Competing interests: Authors declare no competing interests.

References:

Aboitiz, F. (2018). A Brain for Speech. Evolutionary Continuity in Primate and Human Auditory-Vocal Processing. *Frontiers in Neuroscience*, *12*. https://doi.org/10.3389/fnins.2018.00174

Aboitiz, F., & García V., R. (1997). The evolutionary origin of the language areas in the human brain. A neuroanatomical perspective. *Brain Research Reviews*, *25*(3), 381–396. https://doi.org/10.1016/S0165-0173(97)00053-2

Agrawal, Abhishek, Josef P. Kapfhammer, Annetrudi Kress, Hermann Wichers, Aman Deep, William Feindel, Volker K. H. Sonntag, Robert F. Spetzler, and Mark C. Preul. (2011). 'Josef Klingler's Models of White Matter Tracts: Influences on Neuroanatomy, Neurosurgery, and Neuroimaging'. *Neurosurgery* 69(2):238–54. doi: 10.1227/NEU.0b013e318214ab79.

Amemiya K, Naito E, Takemura H (2021) Age dependency and lateralization in the three branches of the human superior longitudinal fasciculus. *Cortex* 139:116–133. https://doi.org/10.1016/j.cortex.2021.02.027

Ardila, A., Bernal, B., & Rosselli, M. (2014). Participation of the insula in language revisited: A meta-analytic connectivity study. *Journal of Neurolinguistics*, *29*, 31–41. https://doi.org/10.1016/j.jneuroling.2014.02.001

Balezeau, F., Wilson, B., Gallardo, G., Dick, F., Hopkins, W., Anwander, A., Friederici, A. D., Griffiths, T. D., & Petkov, C. I. (2020). Primate auditory prototype in the evolution of the arcuate fasciculus. *Nature Neuroscience*. https://doi.org/10.1038/s41593-020-0623-9

Barbas, H., & Mesulam, M.-M. (1981). Organization of afferent input to subdivisions of area 8 in the rhesus monkey. *Journal of Comparative Neurology*, *200*(3), 407–431. https://doi.org/10.1002/cne.902000309

Barbeau, E. B., Descoteaux, M., & Petrides, M. (2020). Dissociating the white matter tracts connecting the temporo-parietal cortical region with frontal cortex using diffusion tractography. *Scientific Reports*, *10*(1), 8186. https://doi.org/10.1038/s41598-020-64124-y

Barrett, R. L. C., Dawson, M., Dyrby, T. B., Krug, K., Ptito, M., D'Arceuil, H., Croxson, P. L., Johnson, P. J., Howells, H., Forkel, S. J., Dell'Acqua, F., & Catani, M. (2020). Differences in

Frontal Network Anatomy Across Primate Species. *Journal of Neuroscience*, *40*(10), 2094–2107. https://doi.org/10.1523/JNEUROSCI.1650-18.2019

Becker, Y., Sein, J., Velly, L., Giacomino, L., Renaud, L., Lacoste, R., Anton, J.-L., Nazarian, B., Berne, C., & Meguerditchian, A. (2021a). Early Left-Planum Temporale Asymmetry in Newborn Monkeys (*Papio anubis*): A longitudinal structural MRI study at two stages of development. NeuroImage, 117575. https://doi.org/10.1016/j.neuroimage.2020.117575

Becker, Yannick, Romane Phelipon, Julien Sein, Lionel Velly, Luc Renaud, and Adrien Meguerditchian. (2021b). 'Planum Temporale Grey Matter Volume Asymmetries in Newborn Monkeys (Papio Anubis)'. *Brain Structure and Function*. doi: 10.1007/s00429-021-02278-9.

Becker, Yannick, Konstantina Margiotoudi, Damien Marie, Muriel Roth, Bruno Nazarian, Romain Lacoste, Jean-Luc Anton, Olivier Coulon, Nicolas Claidiere, and Adrien Meguerditchian. 2021. 'On the Gestural Origin of Language Lateralisation: Manual Communication Reflects Broca's Asymmetry in Monkeys'. *BioRxiv* (2021c).02.09.430276. doi: 10.1101/2021.02.09.430276.

Berwick, R. C., & Chomsky, N. (2016). *Why only us: Language and evolution*. MIT Press.

Boë, L.-J., Berthommier, F., Legou, T., Captier, G., Kemp, C., Sawallis, T. R., Becker, Y., Rey, A., & Fagot, J. (2017). Evidence of a Vocalic Proto-System in the Baboon (Papio papio) Suggests Pre-Hominin Speech Precursors. *PLOS ONE*, *12*(1), e0169321. https://doi.org/10.1371/journal.pone.0169321

Bryant, K. L., Li, L., & Mars, R. B. (2020). *A comprehensive atlas of white matter tracts in the chimpanzee* [Preprint]. Neuroscience. https://doi.org/10.1101/2020.01.24.918516

Budisavljevic, S., Dell'Acqua, F., Rijsdijk, F. V., Kane, F., Picchioni, M., McGuire, P., Toulopoulou, T., Georgiades, A., Kalidindi, S., Kravariti, E., Murray, R. M., Murphy, D. G., Craig, M. C., & Catani, M. (2015). Age-Related Differences and Heritability of the Perisylvian Language Networks. *Journal of Neuroscience*, *35*(37), 12625–12634. https://doi.org/10.1523/JNEUROSCI.1255-14.2015

Burdach, K. F. (1826). *Vom Baue und Leben des Gehirns*. Dyk.

Catani, M., Jones, D. K., & ffytche, D. H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology*, *57*(1), 8–16. https://doi.org/10.1002/ana.20319

Catani, M., Allin, M. P. G., Husain, M., Pugliese, L., Mesulam, M. M., Murray, R. M., & Jones, D. K. (2007). Symmetries in human brain language pathways correlate with verbal recall. *Proceedings of the National Academy of Sciences*, *104*(43), 17163–17168. https://doi.org/10.1073/pnas.0702116104

Catani, M., & de Schotten, M. T. (2012). *Atlas of human brain connections*. Oxford University Press.

Catani, M., & Bambini, V. (2014). A model for Social Communication And Language Evolution and Development (SCALED). *Current Opinion in Neurobiology*, *28*, 165–171. https://doi.org/10.1016/j.conb.2014.07.018

Chance, S. A., & Crow, T. J. (n.d.). *Distinctively human: Cerebral lateralisation and language in Homo sapiens*. 19.

Clarke, S., & Thiran, A. B. (2004). Auditory Neglect: What and Where in Auditory Space. *Cortex*, *40*(2), 291–300. https://doi.org/10.1016/S0010-9452(08)70124-2

Crow, T. J. (2004). *The Speciation of Modern Homo Sapiens*. OUP/British Academy.

Darwin, C. (1981). *The descent of man and selection in relation to sex* (Vol. 1). Princeton unviersity press.

Distler, C., Boussaoud, D., Desimone, R., & Ungerleider, L. G. (1993). Cortical connections of inferior temporal area TEO in macaque monkeys. *Journal of Comparative Neurology*, *334*(1), 125–150. https://doi.org/10.1002/cne.903340111

Dubois, J., Hertz-Pannier, L., Dehaene-Lambertz, G., Cointepas, Y., & Le Bihan, D. (2006). Assessment of the early organization and maturation of infants' cerebral white matter fiber bundles: A feasibility study using quantitative diffusion tensor imaging and tractography. *NeuroImage*, *30*(4), 1121–1132. https://doi.org/10.1016/j.neuroimage.2005.11.022

Dubois, J., Hertz-Pannier, L., Cachia, A., Mangin, J. F., Le Bihan, D., & Dehaene-Lambertz, G. (2009). Structural Asymmetries in the Infant Language and Sensori-Motor Networks. *Cerebral Cortex*, *19*(2), 414–423. https://doi.org/10.1093/cercor/bhn097

Eichert, N., Verhagen, L., Folloni, D., Jbabdi, S., Khrapitchev, A. A., Sibson, N. R., Mantini, D., Sallet, J., & Mars, R. B. (2019). What is special about the human arcuate fasciculus?

Lateralization, projections, and expansion. *Cortex*, *118*, 107–115. https://doi.org/10.1016/j.cortex.2018.05.005

Eichert, N., Robinson, E. C., Bryant, K. L., Jbabdi, S., Jenkinson, M., Li, L., Krug, K., Watkins, K. E., & Mars, R. B. (2020). Cross-species cortical alignment identifies different types of anatomical reorganization in the primate temporal lobe. *ELife*, *9*, e53232. https://doi.org/10.7554/eLife.53232

Fitch, W. T. (2010). *The Evolution of Language*. Cambridge University Press.

Frey, S., Mackey, S., & Petrides, M. (2014). Cortico-cortical connections of areas 44 and 45B in the macaque monkey. *Brain and Language*, *131*, 36–55. https://doi.org/10.1016/j.bandl.2013.05.005

Friederici, Angela Dorkas. (2012). Language Development and the Ontogeny of the Dorsal Pathway. *Frontiers in Evolutionary Neuroscience*, *4*. https://doi.org/10.3389/fnevo.2012.00003

Friederici, Angela D. (2016). The Neuroanatomical Pathway Model of Language. In *Neurobiology of Language* (pp. 349–356). Elsevier. https://doi.org/10.1016/B978-0-12-407794-2.00029-8

Friederici, Angela D., Noam Chomsky, Robert C. Berwick, Andrea Moro, and Johan J. Bolhuis. 2017. 'Language, Mind and Brain'. *Nature Human Behaviour* 1(10):713–22. doi: 10.1038/s41562-017-0184-4.

Friederici, Angela D. (2017). *Language in our brain: The origins of a uniquely human capacity*. The MIT Press.

Geschwind, N. (1965). Disconnexion Syndromes in animals and Man *Brain*, *88*(2), 237–237. https://doi.org/10.1093/brain/88.2.237

Girard, G., Caminiti, R., Battaglia-Mayer, A., St-Onge, E., Ambrosen, K. S., Eskildsen, S. F., Krug, K., Dyrby, T. B., Descoteaux, M., Thiran, J.-P., & Innocenti, G. M. (2020). On the cortical connectivity in the macaque brain: A comparison of diffusion tractography and histological tracing data. *NeuroImage*, *221*, 117201. https://doi.org/10.1016/j.neuroimage.2020.117201

Goucha, T., Zaccarella, E., & Friederici, A. D. (2017). A revival of Homo loquens as a builder of labeled structures: Neurocognitive considerations. *Neuroscience & Biobehavioral Reviews*, *81*, 213–224. https://doi.org/10.1016/j.neubiorev.2017.01.036

Hecht, E. E., Gutman, D. A., Bradley, B. A., Preuss, T. M., & Stout, D. (2015). Virtual dissection and comparative connectivity of the superior longitudinal fasciculus in chimpanzees and humans. *NeuroImage*, *108*, 124–137. https://doi.org/10.1016/j.neuroimage.2014.12.039

Hecht, E. E., Mahovetz, L. M., Preuss, T. M., & Hopkins, W. D. (2017). A neuroanatomical predictor of mirror self-recognition in chimpanzees. *Social Cognitive and Affective Neuroscience*, *12*(1), 37–48. https://doi.org/10.1093/scan/nsw159

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, *92*(1), 67–99. https://doi.org/10.1016/j.cognition.2003.10.011

Honnedevasthana Arun, Arush, Alan Connelly, Robert E. Smith, and Fernando Calamante. 2021. 'Characterisation of White Matter Asymmetries in the Healthy Human Brain Using Diffusion MRI Fixel-Based Analysis'. *NeuroImage* 225:117505. doi: 10.1016/j.neuroimage.2020.117505.

Hopkins, W. D., Misiura, M., Pope, S. M., & Latash, E. M. (2015). Behavioral and brain asymmetries in primates: A preliminary evaluation of two evolutionary hypotheses: Evolution of asymmetries. *Annals of the New York Academy of Sciences*, *1359*(1), 65–83. https://doi.org/10.1111/nyas.12936

Hula, W. D., Panesar, S., Gravier, M. L., Yeh, F.-C., Dresang, H. C., Dickey, M. W., & Fernandez-Miranda, J. C. (2020). Structural white matter connectometry of word production in aphasia: An observational study. *Brain*, *143*(8), 2532–2544. https://doi.org/10.1093/brain/awaa193

Jiang, X., Long, T., Cao, W., Li, J., Dehaene, S., & Wang, L. (2018). Production of Supra-regular Spatial Sequences by Macaque Monkeys. *Current Biology*, *28*(12), 1851-1859.e4. https://doi.org/10.1016/j.cub.2018.04.047

Kaas, Jon H., and Troy A. Hackett. 1999. '"What" and "Where" Processing in Auditory Cortex'. *Nature Neuroscience* 2(12):1045–47. doi: 10.1038/15967.

Lyn, H., Pierre, P., Bennett, A. J., Fears, S., Woods, R., & Hopkins, W. D. (2011). Planum temporale grey matter asymmetries in chimpanzees (Pan troglodytes), vervet (Chlorocebus aethiops sabaeus), rhesus (Macaca mulatta) and bonnet (Macaca radiata) monkeys. *Neuropsychologia*, *49*(7), 2004–2012. https://doi.org/10.1016/j.neuropsychologia.2011.03.030

Maier-Hein, K. H., Neher, P. F., Houde, J.-C., Côté, M.-A., Garyfallidis, E., Zhong, J., Chamberland, M., Yeh, F.-C., Lin, Y.-C., Ji, Q., Reddick, W. E., Glass, J. O., Chen, D. Q., Feng, Y., Gao, C., Wu, Y., Ma, J., He, R., Li, Q., … Descoteaux, M. (2017). The challenge of mapping the human connectome based on diffusion tractography. *Nature Communications*, *8*(1), 1349. https://doi.org/10.1038/s41467-017-01285-x

Mandonnet, E., Sarubbo, S., & Petit, L. (2018). The Nomenclature of Human White Matter Association Pathways: Proposal for a Systematic Taxonomic Anatomical Classification. *Frontiers in Neuroanatomy*, *12*. https://doi.org/10.3389/fnana.2018.00094

Malassis, R., Dehaene, S., & Fagot, J. (2020). Baboons (Papio papio) Process a Context-Free but Not a Context-Sensitive Grammar. *Scientific Reports*, *10*(1), 1–12. https://doi.org/10.1038/s41598-020-64244-5

Marie, D., Roth, M., Lacoste, R., Nazarian, B., Bertello, A., Anton, J.-L., Hopkins, W. D., Margiotoudi, K., Love, S. A., & Meguerditchian, A. (2018). Left Brain Asymmetry of the Planum Temporale in a Nonhominid Primate: Redefining the Origin of Brain Specialization for Language. *Cerebral Cortex*, *28*(5), 1808–1815. https://doi.org/10.1093/cercor/bhx096

Mars, R. B., Sotiropoulos, S. N., Passingham, R. E., Sallet, J., Verhagen, L., Khrapitchev, A. A., Sibson, N., & Jbabdi, S. (2018). Whole brain comparative anatomy using connectivity blueprints. *ELife*, *7*, e35237. https://doi.org/10.7554/eLife.35237

Meguerditchian, A., Gardner, M. J., Schapiro, S. J., & Hopkins, W. D. (2012). The sound of one-hand clapping: Handedness and perisylvian neural correlates of a communicative gesture in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1735), 1959–1966. https://doi.org/10.1098/rspb.2011.2485

Meguerditchian, A., & Vauclair, J. (2014). Communicative Signaling, Lateralization and Brain Substrate in Nonhuman Primates: Toward a Gestural or a Multimodal Origin of Language? *HUMANA.MENTE Journal of Philosophical Studies*, *7*(27), 135–160.

Milham, M., Petkov, C. I., Margulies, D. S., Schroeder, C. E., Basso, M. A., Belin, P., Fair, D. A., Fox, A., Kastner, S., Mars, R. B., Messinger, A., Poirier, C., Vanduffel, W., Van Essen, D. C., Alvand, A., Becker, Y., Ben Hamed, S., Benn, A., Bodin, C., … Zhou, Y. (2020). Accelerating the Evolution of Nonhuman Primate Neuroimaging. *Neuron*, *105*(4), 600–603. https://doi.org/10.1016/j.neuron.2019.12.023

Ocklenburg, S., Friedrich, P., Güntürkün, O., & Genç, E. (2016). Intrahemispheric white matter asymmetries: The missing link between brain structure and functional lateralization? *Reviews in the Neurosciences*, 27(5), 465–480. https://doi.org/10.1515/revneuro-2015-0052

Perani, D., Saccuman, M. C., Scifo, P., Anwander, A., Spada, D., Baldoli, C., Poloniato, A., Lohmann, G., & Friederici, A. D. (2011). Neural language networks at birth. *Proceedings of the National Academy of Sciences*, *108*(38), 16056–16061. https://doi.org/10.1073/pnas.1102991108

Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *Journal of Comparative Neurology*, *228*(1), 105–116. https://doi.org/10.1002/cne.902280110

Petrides, M., & Pandya, D. N. (1988). Association fiber pathways to the frontal cortex from the superior temporal region in the rhesus monkey. *The Journal of Comparative Neurology*, *273*(1), 52–66. https://doi.org/10.1002/cne.902730106

Petrides, M., & Pandya, D. N. (2002). Comparative cytoarchitectonic analysis of the human and the macaque ventrolateral prefrontal cortex and corticocortical connection patterns in the monkey. *European Journal of Neuroscience*, *16*(2), 291–310. https://doi.org/10.1046/j.1460-9568.2001.02090.x

Petrides, M., & Pandya, D. N. (2009). Distinct Parietal and Temporal Pathways to the Homologues of Broca's Area in the Monkey. *PLOS Biology*, *7*(8), e1000170. https://doi.org/10.1371/journal.pbio.1000170

Petrides Michael. (2005a). Lateral prefrontal cortex: Architectonic and functional organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1456), 781–795. https://doi.org/10.1098/rstb.2005.1631

Petrides, M., Cadoret, G., & Mackey, S. (2005b). Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, *435*(7046), 1235–1238. https://doi.org/10.1038/nature03628

Petrides, Michael. (2014). *Neuroanatomy of language regions of the human brain* (First edition). Elsevier/AP, Academic Press is an imprint of Elsevier.

Powell, H. W. Robert, Geoff J. M. Parker, Daniel C. Alexander, Mark R. Symms, Philip A. Boulby, Claudia A. M. Wheeler-Kingshott, Gareth J. Barker, Uta Noppeney, Matthias J. Koepp, and John S. Duncan. (2006). 'Hemispheric Asymmetries in Language-Related Pathways: A Combined Functional MRI and Tractography Study'. *NeuroImage* 32(1):388–99. doi: 10.1016/j.neuroimage.2006.03.011.

Reil J (1809) Die Sylvische Grube oder das Thal, das gestreifte grobe hirnganglium, dessen kapsel und die seitentheile des grobn gehirns. Archiv für die Physiologie 9:195–208.

Reveley, C., Seth, A. K., Pierpaoli, C., Silva, A. C., Yu, D., Saunders, R. C., Leopold, D. A., & Ye, F. Q. (2015). Superficial white matter fiber systems impede detection of long-range cortical connections in diffusion MR tractography. *Proceedings of the National Academy of Sciences*, *112*(21), E2820–E2828. https://doi.org/10.1073/pnas.1418198112

Richerson, Peter J., Sergey Gavrilets, and Frans B. M. de Waal. (2021). 'Modern Theories of Human Evolution Foreshadowed by Darwin's Descent of Man'. *Science* 372(6544). doi: 10.1126/science.aba3776.

Rilling, J. K., Glasser, M. F., Preuss, T. M., Ma, X., Zhao, T., Hu, X., & Behrens, T. E. J. (2008). The evolution of the arcuate fasciculus revealed with comparative DTI. *Nature Neuroscience*, *11*(4), 426–428. https://doi.org/10.1038/nn2072

Rilling, J., Glasser, M. F., Jbabdi, S., Andersson, J., & Preuss, T. M. (2012). Continuity, Divergence, and the Evolution of Brain Language Pathways. *Frontiers in Evolutionary Neuroscience*, *3*. https://doi.org/10.3389/fnevo.2011.00011

Rocchi, Francesca, Hiroyuki Oya, Fabien Balezeau, Alexander J. Billig, Zsuzsanna Kocsis, Rick L. Jenison, Kirill V. Nourski, Christopher K. Kovach, Mitchell Steinschneider, Yukiko Kikuchi, Ariane E. Rhone, Brian J. Dlouhy, Hiroto Kawasaki, Ralph Adolphs, Jeremy D. W. Greenlee, Timothy D. Griffiths, Matthew A. Howard, and Christopher I. Petkov. 2021. 'Common Fronto-Temporal Effective Connectivity in Humans and Monkeys'. *Neuron*. doi: 10.1016/j.neuron.2020.12.026.

Romanski, L. M., B. Tian, J. Fritz, M. Mishkin, P. S. Goldman-Rakic, and J. P. Rauschecker. 1999. 'Dual Streams of Auditory Afferents Target Multiple Domains in the Primate Prefrontal Cortex'. Nature Neuroscience 2(12):1131–36. doi: 10.1038/16056.

Romanski, L. M., J. F. Bates, and P. S. Goldman-Rakic. 1999. 'Auditory Belt and Parabelt Projections to the Prefrontal Cortex in the Rhesus Monkey'. *Journal of Comparative Neurology 403(2):141–57*. doi: https://doi.org/10.1002/(SICI)1096-9861(19990111)403:2<141::AID-CNE1>3.0.CO;2-V.

Romanski, Lizabeth M., and Patricia S. Goldman-Rakic. 2002. 'An Auditory Domain in Primate Prefrontal Cortex'. *Nature Neuroscience* 5(1):15–16. doi: 10.1038/nn781.

Roumazeilles, L., Eichert, N., Bryant, K. L., Folloni, D., Sallet, J., Vijayakumar, S., Foxley, S., Tendler, B. C., Jbabdi, S., Reveley, C., Verhagen, L., Dershowitz, L. B., Guthrie, M., Flach, E., Miller, K. L., & Mars, R. B. (2020). Longitudinal connections and the organization of the temporal cortex in macaques, great apes, and humans. *PLOS Biology*, *18*(7), e3000810. https://doi.org/10.1371/journal.pbio.3000810

Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M.-S., Umarova, R., Musso, M., Glauche, V., Abel, S., Huber, W., Rijntjes, M., Hennig, J., & Weiller, C. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences*, *105*(46), 18035–18040. https://doi.org/10.1073/pnas.0805234105

Schmahmann, J. D., & Pandya, D. N. (2006). *Fiber pathways of the brain*. Oxford University Press.

Schmahmann, J. D., & Pandya, D. N. (2007). The Complex History of the Fronto-Occipital Fasciculus. *Journal of the History of the Neurosciences*, *16*(4), 362–377. https://doi.org/10.1080/09647040600620468

Seltzer, B., & Pandya, D. N. (1984). Further observations on parieto-temporal connections in the rhesus monkey. *Experimental Brain Research*, *55*(2), 301–312. https://doi.org/10.1007/BF00237280

St-Onge, E., Daducci, A., Girard, G., & Descoteaux, M. (2018). Surface-enhanced tractography (SET). NeuroImage, 169, 524–539. https://doi.org/10.1016/j.neuroimage.2017.12.036

Sughrue, Michael E., and Isaac Yang, eds. New Techniques for Management of 'Inoperable'Gliomas. Academic Press, 2019.

Takaya, S., Kuperberg, G. R., Liu, H., Greve, D. N., Makris, N., & Stufflebeam, S. M. (2015). Asymmetric projections of the arcuate fasciculus to the temporal cortex underlie lateralized language function in the human brain. *Frontiers in Neuroanatomy*, *9*, 119. https://doi.org/10.3389/fnana.2015.00119

Thiebaut de Schotten, M., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, *14*(10), 1245–1246. https://doi.org/10.1038/nn.2905

Thiebaut de Schotten, M., Dell'Acqua, F., Valabregue, R., & Catani, M. (2012). Monkey to human comparative anatomy of the frontal lobe association tracts. *Cortex*, *48*(1), 82–96. https://doi.org/10.1016/j.cortex.2011.10.001

Van Essen, D. C., & Dierker, D. L. (2007). Surface-Based and Probabilistic Atlases of Primate Cerebral Cortex. *Neuron*, *56*(2), 209–225. https://doi.org/10.1016/j.neuron.2007.10.015

Vavassori, Laura, Silvio Sarubbo, and Laurent Petit. (2021). 'Hodology of the Superior Longitudinal System of the Human Brain: A Historical Perspective, the Current Controversies, and a Proposal'. *Brain Structure and Function*. doi: 10.1007/s00429-021-02265-0.

Vernooij, M. W., M. Smits, P. A. Wielopolski, G. C. Houston, G. P. Krestin, and A. van der Lugt. 2007. 'Fiber Density Asymmetry of the Arcuate Fasciculus in Relation to Functional Hemispheric Language Lateralization in Both Right- and Left-Handed Healthy Subjects: A Combined FMRI and DTI Study'. *NeuroImage* 35(3):1064–76. doi: 10.1016/j.neuroimage.2006.12.041.

Warrington, S., Bryant, K. L., Khrapitchev, A. A., Sallet, J., Charquero-Ballester, M., Douaud, G., Jbabdi, S., Mars, R. B., & Sotiropoulos, S. N. (2020). XTRACT - Standardised protocols for automated tractography in the human and macaque brain. *NeuroImage*, *217*, 116923. https://doi.org/10.1016/j.neuroimage.2020.116923

Weiller, Cornelius, Marco Reisert, Ivo Peto, Jürgen Hennig, Nikos Makris, Michael Petrides, Michel Rijntjes, and Karl Egger. (2021). 'The Ventral Pathway of the Human Brain: A Continuous Association Tract System'. *NeuroImage* 234:117977. doi: 10.1016/j.neuroimage.2021.117977.

Wernicke C (1903): *Photographischer Atlas de Gehirns*. Schnitte durch das menschliche Gehirn in photographischen Originalen. Abteilung I – 32 Frontalschnitte durch eine Grosshirnhemisphäre. Schletter'schen Buchhandlung (Franck & Weigert). Breslau, 1897. Abteilung II – 20 Horizontal- schnitte durch eine Grosshirnhemisphäre. Verlag der psychiatrischen Klinik. Breslau, 1900. Abteilung III – 21 Sagittalschnitte durch eine Grosshirnhemisphäre. Verlag der psychiatrischen Klinik. Breslau.

Wilson, Benjamin, Yukiko Kikuchi, Li Sun, David Hunter, Frederic Dick, Kenny Smith, Alexander Thiele, Timothy D. Griffiths, William D. Marslen-Wilson, and Christopher I. Petkov. 2015. 'Auditory Sequence Processing Reveals Evolutionarily Conserved Regions of Frontal Cortex in Macaques and Humans'. *Nature Communications* 6(1):8901. doi: 10.1038/ncomms9901.

Zaccarella, E., & Friederici, A. D. (2017). The neurobiological nature of syntactic hierarchies. *Neuroscience and Biobehavioral Reviews*, *81*(Pt B), 205–212. https://doi.org/10.1016/j.neubiorev.2016.07.038

Zhang, Yisi S., and Asif A. Ghazanfar. 2020. 'A Hierarchy of Autonomous Systems for Vocal Production'. *Trends in Neurosciences* 43(2):115–26. doi: 10.1016/j.tins.2019.12.006.

Zhu, Linlin, Yang Fan, Qihong Zou, Jue Wang, Jia-Hong Gao, and Zhendong Niu. 2014. 'Temporal Reliability and Lateralization of the Resting-State Language Network'. *PLOS ONE* 9(1):e85880. doi: 10.1371/journal.pone.0085880.