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1 **The Arcuate Fasciculus and language origins:**
2 *Disentangling existing conceptions that influence evolutionary accounts*

3
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10
11
12 **Abstract**

13
14 *The Arcuate Fasciculus (AF) is of considerable interdisciplinary interest, because of its major*
15 *implication in language processing. Theories about language brain evolution are based on*
16 *anatomical differences in the AF across primates. However, changing methodologies and*
17 *nomenclatures have resulted in conflicting findings regarding interspecies AF differences.*
18 *Historical knowledge about the AF originated from human blunt dissections and later from*
19 *monkey tract-tracing studies. Contemporary tractography studies reinvestigate the fasciculus'*
20 *morphology but remain heavily bound to unclear anatomical priors and methodological*
21 *limitations. First, we aim to disentangle the influences of these three epistemological steps on*
22 *existing AF conceptions, and to propose a contemporary model to guide future work. Second,*
23 *considering the influence of various AF conceptions, we discuss four key evolutionary*
24 *changes that propagated current views about language evolution: 1) frontal terminations, 2)*
25 *temporal terminations, 3) greater Dorsal- versus Ventral Pathway expansion, 4) lateralisation.*
26 *We conclude that new data point towards a more shared AF anatomy across primates than*
27 *previously described. Language evolution theories should incorporate this continuous AF*
28 *evolution across primates.*

29
30
31 **Keywords:** language network, language evolution, frontal terminations, temporal terminations,
32 discontinuity, continuity, lateralization, nomenclature, terminology, hemispheric specialization,
33 comparative anatomy, white matter, tractography, evolutionary neuroscience, monkey,
34 nonhuman primate

35
36 **Abbreviations:** AF (Arcuate Fasciculus), SLF (Superior Longitudinal Fasciculus), MdLF
37 (Middle Longitudinal Fasciculus), dMRI (diffusion magnetic resonance imaging), NHP
38 (Nonhuman primate)

39 **Highlights:**

- 40 1) Existing conceptions of the AF are disentangled to derive a current model
41 2) Data indicates a continuity in AF's frontal and temporal terminations across primates
42 3) Data indicates a continuity in the AF's strength relative to the Ventral pathway
43 4) More data is needed to conclude about the (dis)continuity of AF's lateralisation
44 5) Language evolution theories should incorporate this continuous AF evolution

Introduction

The Arcuate Fasciculus (AF), or the *arched/curved bundle* in latin, is traditionally regarded as one of the major language pathways in the human brain: It arches around the Sylvian or lateral fissure to connect the key speech production region (Broca's area) in the frontal lobe, with the speech comprehension region (Wernicke's area) in the posterior temporal lobe (Geschwind 1970). Congruent with Geschwind's influential model, decades of subsequent research have generally converged on the AF's critical involvement in language and speech functions (e.g., Catani and Mesulam, 2008; Catani and Schotten, 2012; Dick and Tremblay, 2012). Interestingly, the anatomical homologue of this critical white matter pathway for human language exists in the nonhuman primates, where language is absent (e.g., Eichert et al. 2019; Frey et al. 2014; Rilling et al. 2008, 2012). This crucial phylogenetic link provides a valuable avenue to probe the evolutionary origins of human language i.e., by comparing how the AF differs across human and nonhuman primates. Indeed, in the past decade, the emergent field of nonhuman primate or comparative magnetic resonance imaging (MRI) neuroimaging (Friedrich et al. 2021; Milham et al. 2020) have enabled detailed anatomical and functional comparisons of the AF across humans and various nonhuman primate species, such as the macaque monkey and the chimpanzee (e.g., Balezeau et al. 2020; Mars et al., 2021; Rilling et al. 2008, 2012; Rocchi et al. 2021; Wilson et al. 2015). The overarching aim of this review is to synthesize this exciting new body of work that compares the anatomy and function of the AF in humans versus nonhuman primates, to understand *how the Arcuate Fasciculus might, or might not, have changed across primate evolution to support the emergence of language in humans.*

In the first part of this review, we tackle a major challenge that confronts present-day researchers seeking to investigate the AF: *There is currently poor consensus about the anatomical definition of the AF* (e.g., where it terminates in the frontal and temporal lobes), *and its nomenclature* (e.g., whether it is considered part of, or distinct from the Superior Longitudinal Fasciculus (SLF) or Middle Longitudinal Fasciculus (MdLF)). This is primarily driven by the fact that, since its discovery, the methodologies used to study and delineate the AF (e.g., blunt dissections, diffusion MRI tractography, neural tract-tracing) have been constantly evolving, resulting in different descriptions and naming of the AF (e.g., Oliveira et al., 2021; Vavassori et al., 2021). As such, we start the current review with an overview of how the definition and nomenclature of the AF have evolved along with the emergence of different methodologies in the field. This overview, in disentangling the various existing conceptions of the AF, aims to provide a contemporary definition of the fibre bundle that will guide our subsequent review of existing comparative studies of the primate AF.

The second part of this review will discuss four key findings from recent comparative research that shed light on the question about how the AF has changed in humans relative to nonhuman primates: 1) *An expansion of the AF's frontal terminations into the inferior frontal cortex* (e.g., Schmahmann and Pandya 2006); 2) *An expansion of the AF's temporal terminations exceeding the middle temporal cortex* (e.g., Eichert et al. 2019); 3) *Greater expansion of the Dorsal Language Pathway (which includes the AF), relative to the Ventral Language Pathway* (e.g., Rilling et al., 2008); and 4) *An absence of lateralisation in the monkey's AF* (e.g., Balezeau et al., 2020). For each finding, we will discuss how the different conceptions of the AF have led to the different views on these questions, and subsequently influenced theorisations about the evolution of language. We will conclude that the collective data point towards a continuity in AF anatomy across primates. Last but not least, this review will open a discussion regarding the existing questions and future directions in the field.

Part I: Disentangling existing conceptions of the Arcuate Fasciculus

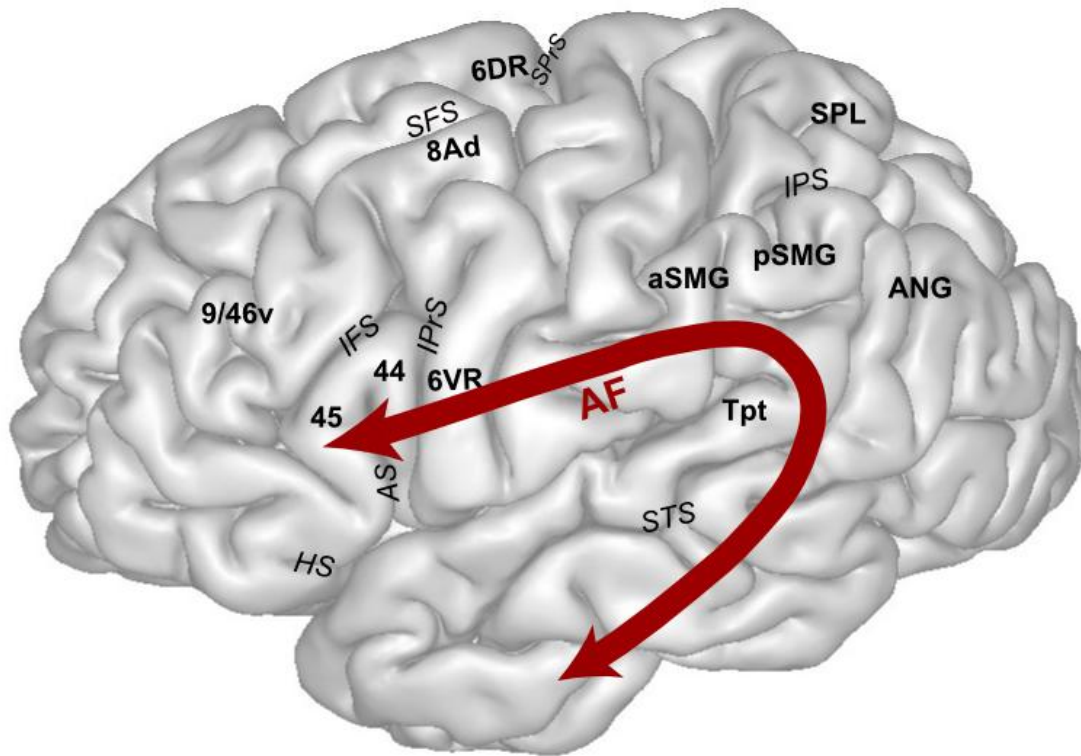
Differing anatomical descriptions and nomenclatures of the Arcuate Fasciculus (AF) fibre bundle have surfaced since its initial discovery by Reil in 1809 (see Dick and Tremblay 2012; cf. Oliveira et al., 2021; Vavassori et al., 2021 for historical reviews of the AF). To a large extent, the various conceptions result from the various emerging methodologies used to investigate the AF, including post-mortem brain dissections, neural tract-tracing, and more recently, diffusion magnetic resonance imaging (dMRI) tractography. Here, we briefly trace the emergence of various conceptions of the AF, relating them to the methods employed to investigate the tract, to finally arrive at a contemporary definition of the AF to guide our subsequent review of the comparative AF literature.

Early 19th to late 20th century: Post-mortem blunt dissections and the synonymity between Arcuate Fasciculus (AF) and Superior Longitudinal Fasciculus (SLF)

Post-mortem blunt dissections was the first methodology adopted to investigate the Arcuate Fasciculus (AF). The method briefly involves first, the post-mortem extraction and fixation of the brain, followed by the use of a blunt dissection tool to meticulously peel away the grey and white matter progressively to reveal the extents of the various axon bundles. The blunt dissection method was the dominant method employed throughout the 19th century to study human neuroanatomy and had led to many seminal works and discoveries of that era (e.g., Burdach 1826; Dejerine, Dejerine, and Dejerine 1895; 1901; Gratiolet, 1839; Meynert 1885). While this technique enabled the identification of distinct white matter bundles and their individual courses in the brain, they were limited in 1) making distinctions between axon bundles that run in parallel, or that overlap or cross in their courses; and 2) determining the precise axonal origins and terminations of the bundles (Petrides 2014; Yaşargil et al. 2004).

Indeed, it was through blunt dissections that Johann Christen Reil, in 1809, first discovered the system of longitudinal white matter fibres that arched along the Sylvian (or lateral) fissure to interconnect the frontal, parietal and temporal cortices (Figure 1). Using the same method, Friedrich Burdach further characterised and first named these long arching fibres as the “Bogenbündel” in German, which translates to the “arched bundle” or *arcuate fasciculus* in Latin (Burdach, 1822). For most of the 19th century, two nomenclatures -- “Arcuate Fasciculus (AF)” and “Superior Longitudinal Fasciculus (SLF)” were synonymously used by the most prominent neuroanatomists to describe the longitudinal frontal-parieto-temporal fibre bundle (Dick and Tremblay, 2012). For instance, while Meynert (1885) used the term AF, Wernicke (1874) and Déjèrine (1895, 1901) used both AF and SLF to refer to the same longitudinal fibre bundle. The interest for the SLF/AF fibre bundle rose to prominence at the start of the 20th century as Wernicke (1908) identified it as one of two main associative fibre systems for language. Notably, in Geschwind's influential neurological model of language (1970), the term AF, and not the term SLF, was used to depict the fibre system linking the language production centre (inferior frontal cortex) to the language comprehension centre (posterior middle temporal cortex). Since then, the label AF had received an increased recognition and usage to refer to the classical language pathway (more than the term SLF), even though the terms AF and SLF are generally referred to the same tract bundle until the late 20th century (Figure 1).

1
 2 Figure 1: Classic dissection derived AF/SLF Model (Reil, 1809; Burdach, 1822; Déjèrine, 1895)



3
 4 *Figure 1: Classic dissection derived AF/SLF Model (e.g., Reil, 1809; Burdach, 1822; Déjèrine,*
 5 *1895, 1901) in the human brain. AF: Arcuate Fasciculus; SFS=Superior frontal sulcus;*
 6 *SPrS=Superior Precentral Sulcus; IPrS=Inferior Precentral Sulcus; IFS=Inferior frontal*
 7 *sulcus; AS=Ascending branch of SF; HS=Horizontal branch of SF; IPS=Intraparietal Sulcus;*
 8 *Tpt=Temporal-parietal area (BA22); aSMG=anterior supramarginal gyrus (BA40);*
 9 *pSMG=posterior supramarginal gyrus (BA40); ANG=angular gyrus (BA39); SPL=Superior*
 10 *Parietal Lobule (BA7).*

11
 12 From the turn of the 20th century until today, two other methodologies were adopted,
 13 alongside blunt dissections, to investigate the Arcuate Fasciculus bundle: *neural tract-tracing*
 14 and *diffusion MRI (dMRI) tractography*. These techniques have led to dissociate the classic
 15 AF/SLF longitudinal fibre bundle into different constituent bundles with distinct courses and
 16 terminations. However, due to the differences between the two methods, various models of the
 17 AF/SLF fibre system had emerged. Here, we briefly describe each method and its associated
 18 models and conceptions of the AF/SLF fibre system.

19
 20 **Late 20th Century: Neural tract-tracing reveals distinctions between the AF and SLF fibre**
 21 **systems**
 22

1 *Neural tract-tracing* is a precise, but also highly invasive method for studying brain
2 connections (see Lanciego and Wouterlood, 2020; Saleeba et al., 2019 for recent reviews about
3 the tract-tracing methodology). Briefly, it involves the injection of anatomical tracers into a
4 living brain, which would be transported from the injected region to other regions via
5 interconnecting axons, followed by histological analyses of the brain ex-vivo to visualise the
6 axons and their terminations that have been labelled by the injected tracers. Depending on
7 whether a *retrograde* or *anterograde* tracer was administered, the brain region that *sends*
8 *projections into* the injected region or the brain region that *receives projections from* the injected
9 region along with the interconnecting axons, will be labelled, respectively. Hence, using a
10 combination of retrograde and anterograde tracing, the origins and terminations of cortico-
11 cortical connections associated with a brain region of interest can be precisely determined. As
12 such, contrary to blunt dissection and dMRI tractography, tract-tracing possesses the resolution
13 to distinguish between fibre bundles that overlap or cross in their courses but have different
14 terminations and can therefore also define a monosynaptical connection. Thus, it is commonly
15 regarded as the gold-standard technique for studying brain connections. A key drawback,
16 however, is that tract-tracing is currently only performed in few nonhuman primate subjects due
17 to its invasive nature, which requires the euthanasia of the animal.

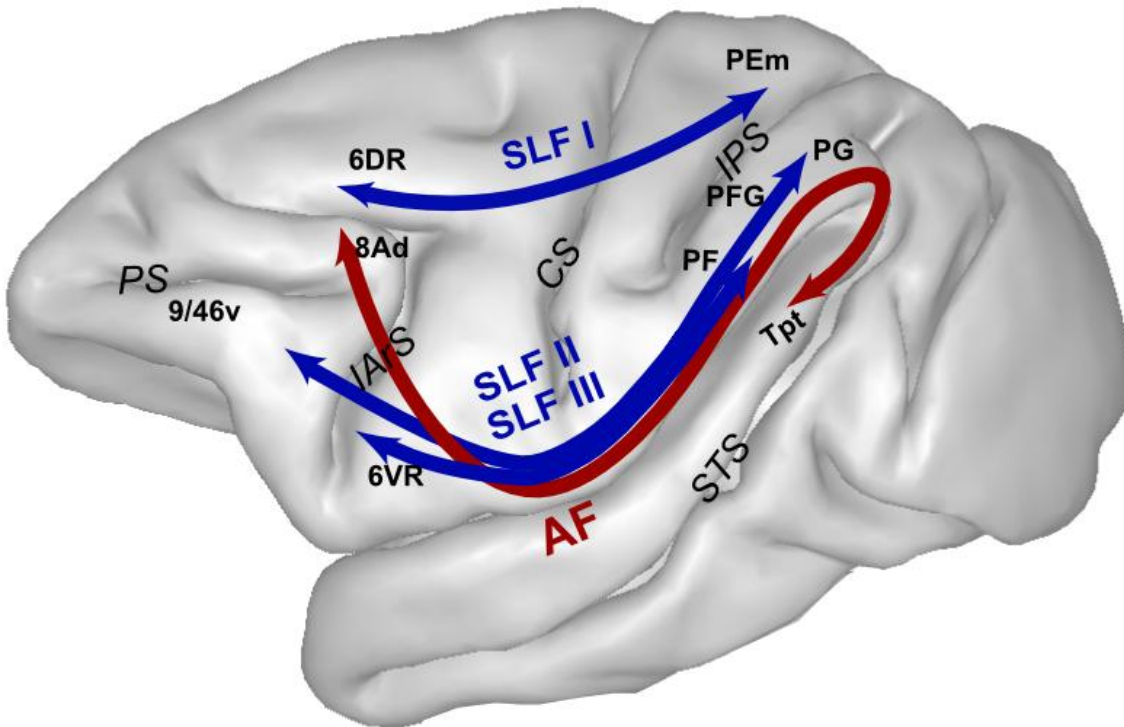
18
19 Tract-tracing was employed in a series of important studies that resulted in the
20 dissociation of the classical AF/SLF longitudinal fibre system into several distinct fibre bundles
21 based on their origins and terminations in the macaque brain (Frey et al., 2014; Petrides and
22 Pandya, 1984, 1988, 2006, 2009; Schmahmann et al., 2007; Schmahmann and Pandya, 2006;
23 Yeterian et al., 2012 etc.) (Figure 2). In these studies, anatomical tracers were injected into
24 various frontal, parietal and temporal regions in the macaque brain, which have known
25 homologies with the human brain, to study their interconnections. Notably, this body of work has
26 led to a new model of the AF/SLF longitudinal fibre system which consists of four distinct fibre
27 bundles including:

28 1) the AF, which comprise the fibres that arch dorsally around the Sylvian fissure and
29 connect the posterior temporal cortex with the frontal cortex (the exact frontal and temporal
30 terminations of the AF will be further discussed in Part 2, see also Figure 5); and

31 2) the SLF I, II and III, which comprise the three longitudinal fibre bundles that
32 interconnect distinct parts of the frontal and parietal cortex and are not arching around the
33 Sylvian fissure (Figure 2).

34 Since the advent of this approach, the term SLF is used to designate portions of the
35 AF/SLF complex, which are distinct from the AF and which are further distinguished in three
36 different branches I, II and III (Figure 5).

1 Figure 2: Initial Macaque AF and SLF Tract-tracing Model (Petrides and Pandya, 1988,
 2 Schmahmann and Pandya, 2006)



3 *Figure 2: Initial Tract-tracing Model that separated the AF from the SLF in the macaque brain.*
 4 *Adapted from Petrides and Pandya (1988), Schmahmann and Pandya (2006). SLF I, II, III:*
 5 *First, second and third branch of the Superior Longitudinal Fasciculus, AF: Arcuate Fasciculus;*
 6 *IARS=inferior arcuate sulcus, PS=Principal sulcus; CS central sulcus; IPS intraparietal sulcus;*
 7 *PF; PEm; PFG; PG are cytoarchitectonic labels for the parietal areas based on Von Economo*
 8 *and Koskinas (1925)*

9
 10
 11 **Towards a contemporary conception of the AF: diffusion MRI tractography**

12
 13 *Diffusion MRI (dMRI) tractography* is, at present, the only technique available to
 14 investigate white matter fibre pathways both in-vivo and ex-vivo, across a large sample of
 15 individuals. It involves a form of magnetic resonance imaging that measures the diffusivity of
 16 water molecules in the brain. Since water diffusion in the brain is highly constrained by axons
 17 (i.e., water tends to flow along the direction of the axons), by tracking the most probable
 18 directions of water diffusion voxel-by-voxel, one would be able to reconstruct the main fibre
 19 pathways that course between two specific areas in the brain. Alternatively, even the total
 20 pathways between all areas in the brain can be reconstructed, yielding a so-called *whole-brain*
 21 *tractogram*. Note that these reconstructed pathways are essentially “streamlines” that connect
 22 vectors of water diffusion computed in each brain voxel and might not necessarily depict true
 23 axonal connections. Therefore, tractograms notoriously contain a large number of false positive
 24 (Maier-Hein et al. 2017). This is especially so when there are multiple crossing fibres passing

1 within a single voxel, which makes it notoriously difficult to determine the actual orientation of
2 fibres (Girard et al. 2020). Additionally, dMRI tractography does not reveal whether a
3 connection is monosynaptic (single axon from origin to termination sites) or polysynaptic (more
4 than one axon interconnecting between origin and termination sites). Due to the limitation to
5 disentangle association pathways like the AF or the SLF (e.g., Girard et al., 2020), most dMRI
6 studies therefore refer to the “Dorsal language pathway or stream” for any pathway connecting
7 frontal to parieto-temporal regions (i.e., AF, SLF II, SLF III) (e.g., Saur et al., 2008). It is
8 opposed to the “Ventral language pathway or stream”, curving ventrally around the Sylvian
9 fissure by passing through the extreme capsule and connecting inferior frontal- with temporal
10 areas. This division emulates the well-known visual pathway division (Hickok and Poeppel,
11 2004). Functionally, the Dorsal pathway is involved in mapping sound to articulation, while the
12 Ventral pathway is involved in mapping sound to meaning (Hickok and Poeppel, 2004; Saur et
13 al., 2008). However recent advances are challenging this dichotomic view and are also
14 highlighting the importance of the dorsal pathway in semantics (Hula et al. 2020). Changes in the
15 AF evolution across primates, concerning the proportional strength between the Dorsal and
16 Ventral pathways, are further discussed in the following section (Question 4, Figure 5).

17 Here we discuss two contemporary and influential conceptions of the classical SLF/AF bundle
18 and how they were derived based on different theoretical underpinnings:

19 The first conception, which was proposed by Catani and colleagues using dMRI
20 tractography (Catani et al., 2005), is based on priors from classical dissection studies (Figure 3
21 left panel). This conception names the peri-sylvian longitudinal fibres (both arching and non-
22 arching) collectively as the AF, and divides it into three distinct segments: 1) a *long direct*
23 *segment* that connects the posterior part of the superior temporal gyrus (Wernicke’s area) to the
24 inferior frontal cortex (Broca’s area); 2) an *anterior indirect segment* that connects Broca’s area
25 and inferior parietal cortices; and 3) a posterior indirect segment that links the inferior parietal
26 cortices with the Wernicke’s area. This model was obtained via a two-regions-of-interest (ROI)
27 “virtual dissection” approach using diffusion tractography (Catani et al., 2002). First, one ROI
28 was defined that delineated the main body of the AF identified on the fractional anisotropy (FA)
29 image. Next, two other ROIs were defined in the inferior frontal cortex and posterior superior
30 temporal cortex respectively. Fibres were then tracked between each pair of ROIs which yielded
31 the three segments of the AF. Note that the placement of ROIs was strongly influenced by
32 Geschwind’s model of the language system (1970) that proposed a pathway, which was termed
33 the AF, linking the Broca’s and Wernicke’s speech areas in the brain. Indeed, this 3-segment AF
34 model was consistent with neurological models of aphasia and evidence from aphasic patients
35 (e.g., Damasio and Geschwind 1984, Lichtheim, 1885), where the *direct long pathway* (frontal-
36 temporal) is associated with *phonological-related language processes* (e.g., rapid word
37 repetitions that do not involve semantic retrieval processes); while the *indirect anterior* (frontal-
38 parietal) and *posterior* (parietal-temporal) pathways are associated with *semantic-related*
39 *language processes*, such as speech comprehension and the production of meaningful words or
40 speech, respectively (Catani et al., 2005). Subsequently, this 3-segment AF model was also
41 validated by other studies using human electrocorticography (Matsumoto et al. 2004), functional
42 connectivity (Holland et al., 2007) and post-mortem dissections (Fernández-Miranda et al., 2008;
43 Lawes et al., 2008).

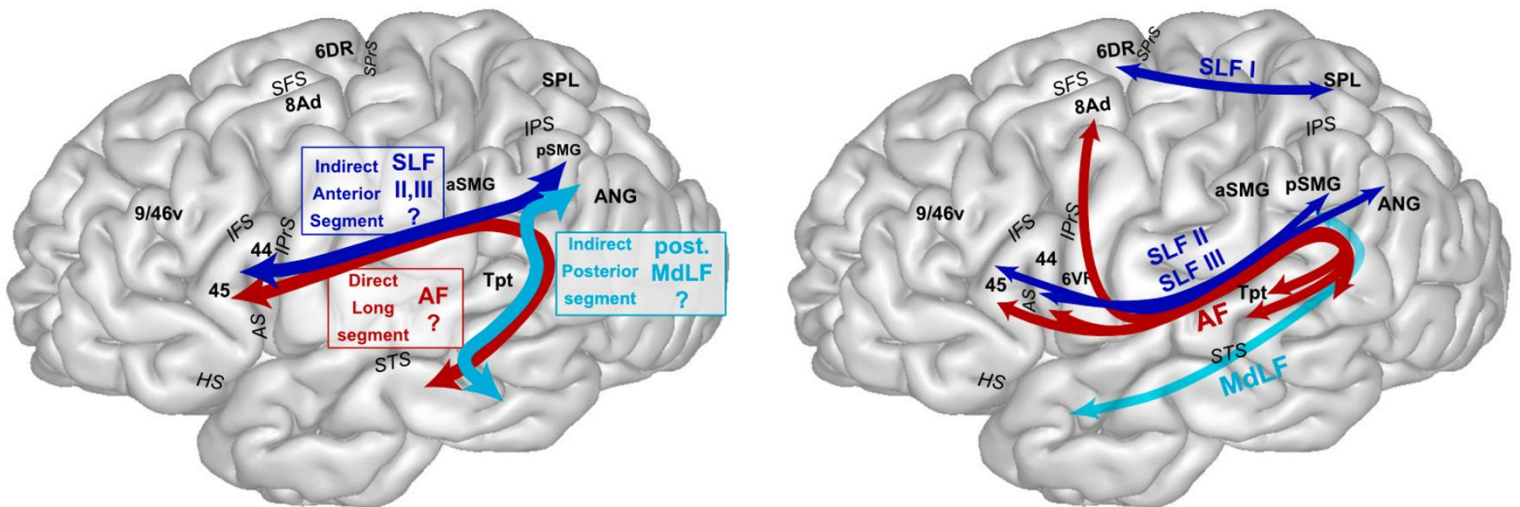
44
45 A second conception comes from researchers who have reconstructed the longitudinal
46 pathways with dMRI tractography based on anatomical priors from macaque tract-tracing

1 experiments (Figure 3 right panel) (e.g., Barbeau et al., 2020; Frey et al., 2008; Makris et al.,
 2 2005; Warrington et al., 2020). Considering that neural tract-tracing is the gold standard for
 3 determining the precise origins and terminations, and axonal courses of brain connections, the
 4 macaque model that separates the peri-sylvian longitudinal fibres into the AF, SLF I, II and III
 5 bundles (i.e., Frey et al., 2014) would constitute the most anatomically accurate model of the
 6 primate longitudinal fibre system at present (Figure 3 right panel). Critically, it remains
 7 questionable how generalizable this macaque model is to the human brain, since after all
 8 language (which is associated with the AF) is not present in the macaque. One strategy, adopted
 9 by Petrides and colleagues (e.g., Frey et al., 2014; Petrides and Pandya, 1988; 2009), was to
 10 perform tract-tracing from macaque cortical regions whose human counterparts are known, based
 11 on cytoarchitectonics, which facilitates the macaque-human transfer of the anatomical findings.
 12 Indeed, by performing in-vivo dMRI tractography in the human brain using carefully defined
 13 anatomical landmarks that are known to be homologous to the macaque, recent researchers have
 14 been able to replicate the macaque AF, SLF I, II, and III fibre tracts in the human brain (e.g.,
 15 Barbeau et al., 2020; Frey et al. 2008; Makris et al., 2005).

16 How then might we reconcile those two legitimate conceptions of the AF? A potential
 17 hypothesis is that “the long direct segment”, “the anterior indirect segment”, and “the posterior
 18 indirect segments” defined in the first conception might correspond to “the AF”, “the SLF II
 19 and/or III”, and “posterior part of the AF and the posterior part of the middle longitudinal
 20 fasciculus (MdLF; see e.g., Latini et al., 2021) as defined in the second conception respectively.
 21 This could be verified via a virtual dissection experiment using dMRI tractography to test
 22 whether it is possible to obtain the macaque-derived model of the AF from Catani’s model (i.e.,
 23 first conception) using additional region-of-interests, since currently, the latter has been derived
 24 using a two-ROI approach to detect each of the three segments (Catani et al., 2005).

25
 26
 27

Figure 3: Contemporary Models of the AF fibre pathways in humans.



28
 29 *Figure 3: Contemporary Models of the AF fibre pathways in humans. Left: Dissection based*
 30 *human tractography AF/SLF model. Figure adapted from Catani et al., (2005). Right: Tract-*

1 tracing based human AF/SLF model. Figure adapted from Petrides (2014). Potential
2 correspondences between figures are displayed.

3 SLF I, II, III: First, second and third branch of the Superior Longitudinal Fasciculus, AF:
4 Arcuate Fasciculus, MdLF: posterior segment of the Middle Longitudinal Fasciculus
5 Abbreviation for the human brain. SFS=Superior frontal sulcus; SPrS=Superior Precentral
6 Sulcus; IPrS=Inferior Precentral Sulcus; IFS=Inferior frontal sulcus; AS=Ascending branch of
7 SF; HS=Horizontal branch of SF; IPS=Intraparietal Sulcus; Tpt=Temporal-parietal area
8 (BA22); aSMG=anterior supramarginal gyrus (BA40); pSMG=posterior supramarginal gyrus
9 (BA40); ANG=angular gyrus (BA39); SPL=Superior Parietal Lobule (BA7)

11 Box 1: Overcoming diffusion MRI tractography limitations

13 To overcome diffusion MRI limitations, several methods have been adopted by
14 researchers using dMRI tractography:

15 (1) *Increasing the resolution and sample sizes of in-vivo dMRI studies, or to include ex-*
16 *vivo brains* that allow longer acquisition times and higher spatial resolutions (e.g., Barrett et al.,
17 2020). This will reduce the rates of false positives, and increase reproducibility during tract
18 reconstructions.

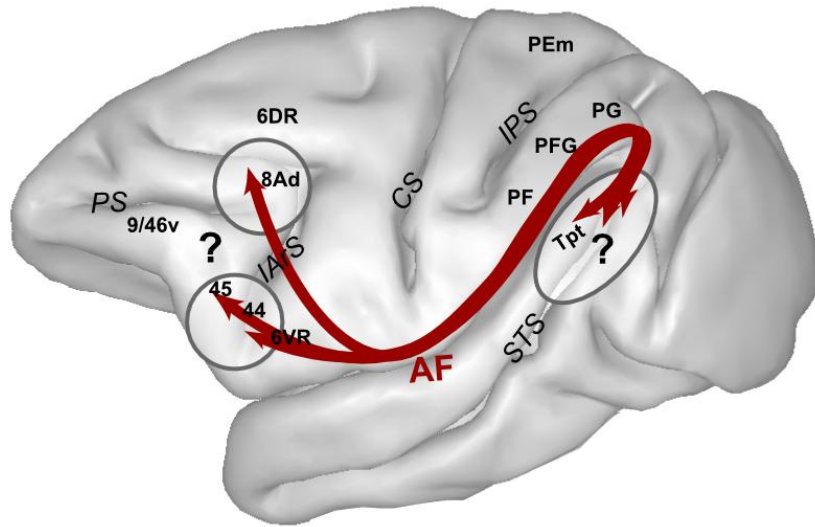
19 (2) *Focusing fibre reconstructions on the main bodies of the tracts (which are less*
20 *ambiguous to detect) rather than their cortical projections* (e.g., Bryant et al., 2020; Warrington
21 et al., 2020). This will enable a more stable and reproducible set of tracts to be reconstructed
22 across individuals, and even across species, for comparative studies (Mars et al. 2019); and, last
23 but not least,

24 (3) *Relying on precise anatomical priors when defining tracts for reconstruction* (e.g.,
25 Barbeau et al., 2020; Catani et al., 2005). Here, the tracking of the streamlines would be
26 constrained using prior anatomical knowledge inherited from ex-vivo techniques (i.e., defining
27 seeds, targets and exclusion masks based on knowledge about the origin, terminations and course
28 of a particular fibre tract), resulting in a more accurate “dissection” of specific fibre pathways
29 using diffusion tractography.

32 Part II: Four questions about the evolution of the Arcuate Fasciculus across 33 primates

34
35 Current comparative work has revealed four key findings about the unique evolution of the
36 human AF anatomy and compared these to macaques and chimpanzees. First, studies have
37 proposed that the frontal cortical terminations of the AF have changed in the human brain (e.g.,
38 Schmahmann and Pandya, 2006). Second, studies have proposed that the temporal cortical
39 terminations of the AF have expanded in the human brain (eg. Eichert et al., 2019). Third,
40 studies have proposed a greater Dorsal (which includes the AF) *versus* Ventral Pathway
41 expansion across primate evolution (e.g., Rilling et al., 2008). Fourth, studies have proposed an
42 absence of left-lateralisation in the monkeys AF, that is present in humans (e.g., Rocchi et al.,
43 2021). Here, we will re-examine the evidence for these findings with respect to their AF
44 conceptions and discuss their implications for language evolution theories.

1 Figure 4: Illustration of the possible AF's frontal (Question 1) and temporal (Question 2) cortical
 2 terminations in the macaque brain



19 *Figure 4: Schematic illustration of the homologue's main language pathways in the macaque monkey*
 20 *brain. Illustration of the course and terminations (arrowheads) of the Arcuate Fasciculus (AF) in red.*
 21 *Grey circles indicate the possible terminations as discussed in the literature (see table 1). Question marks*
 22 *highlight the research questions.*

25 **Question 1: Are AF terminations in the inferior frontal cortex (Broca's area) present in the**
 26 **human-, but not in the nonhuman primate brain?**

27
 28 Classically, the human AF connects to the classical Broca's area in the inferior frontal
 29 cortex (Brodmann's areas 44 and 45). These frontal regions are significant for language because
 30 they are involved in the high-level control of orofacial and vocal motor responses that are needed
 31 for language production (Loh et al. 2020). Direct AF connections to these frontal regions thus
 32 provide access to the key motor actions (e.g., articulation, facial expressions, gestures) needed
 33 for language expression in humans (Petrides and Pandya, 2009). Whether the same AF frontal
 34 projections exist in nonhuman primates (NHPs) is therefore a crucial question that would shed
 35 light on why language exists only in humans. Currently, there are several theoretical accounts
 36 based on how a lack of AF frontal terminations in the nonhuman primate brain could explain the
 37 uniqueness of human language (e.g., Aboitiz and García, 1997; Friederici 2017; Pulvermueller
 38 2018; Schmahmann and Pandya, 2006). However, the most recent data from tract-tracing
 39 experiments (e.g., Frey et al., 2014) appear to contradict these accounts as AF connections to
 40 macaque areas 44 and 45 were demonstrated. Here, we carefully review past and present tract-
 41 tracing studies of the macaque peri-sylvian longitudinal fibre system to resolve the question
 42 about whether AF inferior frontal terminations exist in the macaque brain.

43
 44 Based on the landmark tract-tracing investigation in the macaque brain, Petrides and
 45 Pandya (1988) had traced AF terminations into the dorsal part of the frontal cortex (dorsal areas
 46 6, 8A and prefrontal area 46), but not to the inferior frontal cortex, where Broca's area's
 47 homologue lies. Instead, the inferior frontal cortex only connected to the parietal cortex via SLF

1 II and III. This result remained important in the field over the next two decades: it was included
2 and reproduced in the highly influential atlas of fibre pathways of the macaque brain by
3 Schmahmann and Pandya (2006; see Fig 13-5 on pp 407 for a depiction of the AF) and served as
4 the anatomical reference for several dMRI studies (e.g., Thiebaut de Schotten et al. 2012) (Figure
5 5 Left panel). Critically, this discovery had led to several theoretical accounts suggesting that the
6 change in AF's frontal projections from dorsal part of the frontal cortex in nonhuman primates to
7 Broca's area in humans could explain the emergence of human language (e.g., Aboitiz and
8 García, 1997; Friederici 2017; Pulvermueller 2018; Schmahmann and Pandya 2006). For
9 instance, Schmahmann and Pandya (2006) proposed that the macaque AF might not be a
10 "language bundle" (pp 408) as it does not connect the homologues of Broca's (inferior frontal
11 cortex) and Wernicke's areas (posterior superior temporal gyrus), but instead the caudal temporal
12 area Tpt (which is associated with auditory-spatial processing) and the dorsal frontal areas (that
13 is associated with oculomotor and attentional control). Due to the lack of a direct dorsal
14 connection of Broca's homologue with the temporal lobe, but rather with the parietal lobe,
15 Aboitiz & García (1997) proposed the parietal lobe to play a fundamental element in language
16 evolution, linking indirectly the two key structures (Broca's and Wernicke's) by means of the
17 SLF II and III. In their view, it "permitted the development of an interphase between the auditory
18 processing device and a working memory circuit for complex vocalisations that includes
19 inferoparietal and ventral premotor regions". Other theoretical accounts suggested that the
20 absence or reduced degree of the AF's terminations in the inferior frontal cortex (area 44) in
21 NHPs led to the lack of syntax (Friederici, 2017) or action-perception representations
22 (Pulvermueller, 2018) that are necessary for language.

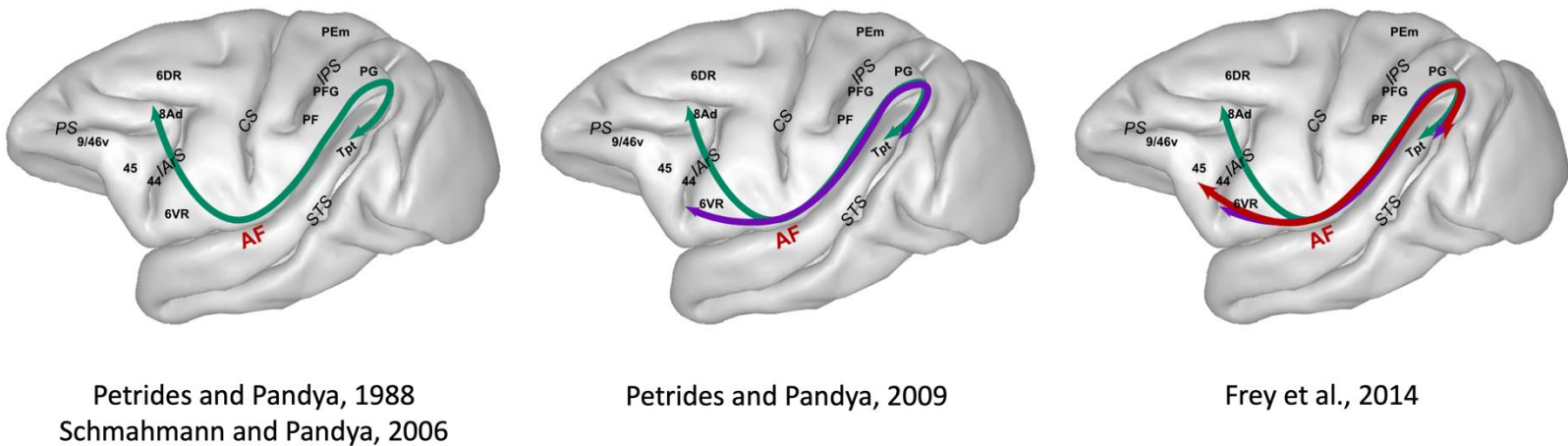
23
24 A conceptual change in the views of the AF's frontal terminations happened when a the
25 cytoarchitectonical equivalence of Broca's area was established in the macaque (Petrides et al.,
26 2005), which prompted a series of tract-tracing experiments to reinvestigate the frontal-parietal-
27 temporal pathways with new and more precise tracer injection sites (Petrides, 2014) (Figure 5).
28 Following a detailed comparative analysis of the cytoarchitecture of macaque and human frontal
29 cortex, Petrides and Pandya (Petrides et al. 2005a; b; Petrides and Pandya 1999; 2002)
30 established critical correspondences between the various frontal areas between the two species.
31 In particular, this work revealed for the first time the precise organisation of the homologues of
32 Broca's area 44 and 45 in the macaque brain. With these knowledge, the longitudinal fibre
33 connections between the frontal, parietal and temporal lobe were re-investigated, leading to the
34 major discovery of the existence of long arching fibres that directly connect macaque areas 44
35 and 45 to the caudal temporal cortex (Frey et al., 2014; Petrides and Pandya, 2009). Petrides
36 explains in his 2014 book, that no terminations to area 44 and 45 were previously found, because
37 the initial injection site was not placed ventrally enough within the temporal lobe (Petrides &
38 Pandya, 2009; Petrides, 2014) (see Figure 5 right panel that shows each different injection site
39 with an arrowhead and the resulting course with a different colour)

40 In fact, this work revealed three AF branches projecting to the frontal cortex (see Petrides
41 2014, pp 160, Fig 52): 1) A dorsal branch that connects from the dorsal part of the superior
42 temporal gyrus to dorsal frontal area 8Ad and area 6; 2) A second branch that connects from the
43 ventral part of the superior temporal gyrus, and the upper bank of the superior temporal sulcus to
44 area 44; and 3) A last branch that connects from the caudal superior temporal gyrus and the
45 adjacent bank of the superior temporal sulcus to area 45 (Figure 5). This result was recently
46 reproduced in comparative diffusion MRI studies, in-vivo and ex-vivo, in macaques and

1 chimpanzees (Balezeau et al. 2020; Barrett et al. 2020; Bryant et al. 2020; Eichert et al. 2019,
 2 2020; Rilling et al. 2008; Roumazeilles et al. 2020) and on a functional level using effective
 3 connectivity (Rocchi et al., 2021).

4
 5 As such, based on the above recent tract-tracing data, it is clear that AF connections to
 6 the inferior frontal cortex exist in the macaque brain, as in humans, suggesting that the so-called
 7 human language pathway between Broca's and Wernicke's areas might be more preserved in
 8 nonhuman primates than previously thought. Further supporting this conserved primate AF-
 9 inferior frontal cortical connectivity, recent studies have also reported common roles of macaque
 10 and human frontal areas 44 and 45 in cognitive vocal control (Loh et al., 2017; Loh et al., 2020).
 11 As such, contemporary theories that explain the uniqueness of human language based on the
 12 absence of inferior frontal projections of the AF must be revised accordingly. If AF frontal
 13 terminations are highly conserved, the question arises why language has evolved in humans
 14 alone? This important open question remains to be addressed by future research.

15
 16
 17 Figure 5: Knowledge progress about the macaque Arcuate Fasciculus from tract-tracing
 18 experiments.
 19



20 *Figure 5. Knowledge progress about the macaque Arcuate Fasciculus courses and terminations*
 21 *from in tract-tracing experiments. (Left) Injections into the macaque caudal superior temporal*
 22 *gyrus (area Tpt) reveal the dorsal branch of the AF (Petrides and Pandya, 1988; Schmahmann*
 23 *and Pandya, 2006). (Middle) Injections into the ventral part of Tpt, and the upper bank of the*
 24 *STS reveals a second branch of the AF to area 44 (Petrides and Pandya, 2009; Case 5). (Right)*
 25 *More ventral injections into the caudal superior temporal gyrus and STS reveals a third branch*
 26 *of the AF to area 45 (Frey et al., 2014). Abbreviations: IARS=inferior arcuate sulcus,*
 27 *PS=Principal sulcus; CS central sulcus; IPS intraparietal suclus; PF; PEm; PFG; PG are*
 28 *cytoarchitectonic labels for the parietal areas based on Von Economo and Koskinas (1925).*

29
 30 **Question 2: Do human AF terminations extend further into the temporal lobe than in**
 31 **nonhuman primates?**
 32

1 In the human brain, the AF arches around the Sylvian fissure and extends beyond the
2 posterior part of the temporal cortex, where the Planum Temporale and tpt lies, and beyond the
3 middle temporal gyrus (MTG) into the inferior and anterior temporal cortex (e.g., Catani et al.,
4 2005) (e.g., Figure 3 left panel). This part of the temporal cortex is associated with semantic
5 verbal (or multimodal) information (Binder et al., 2009), and as such, this implies that the human
6 AF provides the frontal speech areas access to semantic information in the MTG. The difference
7 in temporal terminations between human and NHP is therefore crucial, in order to investigate
8 potential evolutionary divergences, which, in turn, influence functional theories about language
9 evolution. It is widely agreed that the human AF is unique in extending into the middle part of
10 the temporal cortex (e.g., Rilling et al., 2008), even though recent investigations in monkeys also
11 highlight slightly more anterior temporal cortical terminations into the middle auditory cortex
12 (Balezeau et al., 2020). It is, however, not to be excluded that this human-unique feature could
13 be: 1) due to the expansion of the temporal lobe alone (Eichert et al. 2019; Van Essen and
14 Dierker 2007); or 2) due to methodological differences (Latini et al., 2021; Petrides, 2014)
15 (Figure 4).

16
17 In their diffusion MRI work, Rilling and colleagues (2008; 2012) described major
18 changes during primate evolution with an increased temporal lobe projection in the human brain
19 and related this finding to language evolution. While the human AF reaches the MTG, the
20 macaque AF terminates at the caudal end of temporal area 22, near the temporo-parietal junction.
21 As such, Rilling et al. (2008) suggested that the human AF is unique in its extended projections
22 into the middle part of the temporal cortex. This finding has become the basis of a number of
23 models of human language processing. For example, in their model for “Social Communication
24 And Language Evolution and Development” (SCALED), Catani and Bambini (2014) linked the
25 lack of the AF’s deep terminations into the middle anterior part of the temporal lobe (long
26 temporal tail) in NHPs to the absence of syntax processing and reduced semantics processing.

27 At the same time, Van Essen and Dieker (2007) also proposed a theory of primate brain
28 evolution that described a cortical expansion across primates using certain key regions of interest
29 as common landmarks. They proposed that if the macaque brain was inflated to the size of a
30 human brain, some areas would be too small in comparison to their human counterparts. Thus,
31 these areas, including the middle temporal cortex, must have expanded disproportionately in size
32 during evolution to match the actual human brain organisation. As such, this temporal cortical
33 surface expansion could explain the apparent expansion of AF terminations into the middle part
34 of the temporal lobe in the human brain, as a by-product of cortical expansion.

35 By examining the evolution of temporal association fibres across primate species, a series
36 of studies from Rogier Mars’ laboratory, using common space comparisons, tackled the question
37 of whether the observed extension of the AF’s termination into the human temporal lobe was due
38 to cortical expansion alone, or also to an actual extension of the tract into new cortical regions
39 (Bryant et al.; 2020; Eichert et al., 2019; 2020; Mars et al., 2021; Roumazeilles et al., 2020;
40 Warrington et al, 2020).

41 In a similar approach to Van Essen and Dieker (2007), Eichert et al., (2019) first
42 calculated a common space for macaques and humans, based on cortical areas. In a second step,
43 they extracted the main AF tract body (based on Schmahmann and Pandya (2006) atlas – which
44 did not depict the AF’s termination into the inferior frontal cortex) using common protocols
45 between species (Warrington et al, 2020) and computed surface projections from these tracts by
46 creating tract maps that show where the tract projected to on the surface. Finally, they tested

1 whether the cortical area comparison alone would explain the AF cortical projections. In other
2 words, if a predicted tract map is greater than the actual tract map, than cortical surface
3 expansion does not fully account for the observed expansion of the particular tract (see also
4 Eichert et al., (2020) for a similar method based on T1w/T2w maps alignments). This way, they
5 highlight that cortical expansion alone cannot account for the AF expansion (Eichert et al. 2019;
6 2020). The authors therefore conclude that the AF underwent additional changes in its course by
7 invading new middle and anterior temporal areas. Thus, the authors propose that the temporal
8 lobe and especially the middle temporal gyrus (MTG) expanded significantly in the great ape
9 lineage. Finally, in the evolution of the human lineage, the AF invaded new territories of the
10 temporal cortex, which made cognitive changes possible (Roumazeilles et al., 2020). Confirming
11 these findings, Barrett et al. (2020) found no middle temporal terminations to connect with
12 frontal areas in macaque *ex-vivo* dMRI data as in humans. They state that the AF shows the most
13 striking differences of association tracts between humans and monkeys, with monkeys only
14 sharing a small subcomponent of the AF (roughly the body of the tract) with humans.
15

16 Even though other diffusion MRI investigations on monkeys have found AF temporal
17 terminations more anterior in the temporal lobe (Schmahmann and Pandya, 2007; Balezeau et al.,
18 2020; Rocchi et al., 2021) than previously shown by tract tracing (e.g., Schmahmann and
19 Pandya, 2006), the monkey's AF's temporal tail is still incomparable with that of the human,
20 where it exceeds the middle part of the temporal lobe. However, very recent studies found for the
21 first-time connections between the functionally defined auditory cortex and Broca's homologue.
22 The auditory cortex areas, which sit in the middle and posterior temporal lobe showed
23 connections with Broca's homologue in the monkeys (Balezeau et al., 2020; Rocchi et al., 2021).
24 Because of this newly highlighted extension into the auditory cortex, the authors speculate "that
25 this dorsal auditory pathway is involved in not just spatial processing in the classical sense but
26 also sound and vocal patterning in the time domain", a function that had previously been
27 exclusively linked to the ventral pathway (see section: "Dorsal vs Ventral Pathway proportion").
28 Note that in this description, the human AF also terminates in the posterior temporal lobe and
29 does not exceed into the middle part of the temporal lobe.
30

31 In fact, it is to note that the very fact that the human AF arches into the middle, anterior
32 and inferior part of the temporal lobe, is questioned by some authors (Latini et al. 2021;
33 Maldonado et al. 2013; Petrides 2014; Wang et al. 2013). In fact, in the monkey brain it was
34 demonstrated that monosynaptic AF connections originate around area tpt/Planum Temporale.
35 Fibres arching more ventrally in the temporal lobe (ie. temporo-parietal fibres like the posterior
36 middle longitudinal fasciculus (MdLF)) are independent and build synapses with the AF (Distler
37 et al. 1993; Petrides 2014; Seltzer and Pandya 1984). This morphology may be similar in the
38 human brain, with the human AF also originating in area tpt/Planum Temporale if defined
39 monosynaptically. However, with diffusion MRI, one is unable to distinguish a monosynaptical
40 AF originating in area tpt/Planum Temporale or a polysynaptical AF entanglement with the
41 posterior MdLF. In other words, in this view, the AF is losing its predominant "arch" (which
42 corresponds to the posterior indirect segment (Catani et al., 2005)), due to methodological issues
43 (Figure 3). It is possible that this hypothesis influenced the most recent comparative investigations
44 (Balzeau et al., 2020; Rocchi et al., 2021). Indeed, in these studies the human AF is terminating
45 more posteriorly and less ventrally in the temporal lobe than in previous work (Barrett et al.,

1 2020; Eichert et al., 2019; Rilling et al., 2008; 2012), but terminating like their monkey
2 homologue in the posterior end of the auditory cortex (Balzeau et al., 2020; Rocchi et al., 2021).

3 In summary, current consensus lies in the divergence of AF temporal terminations. Monkeys
4 possess terminations in the most posterior part of the temporal lobe, even though recent advances
5 pushed these terminations more anterior into the auditory cortex. In humans, the AF extends into
6 the middle part of the temporal cortex, and for some authors more anterior-inferiorly into the
7 anterior temporal cortex. Even though the possibility has to be highlighted that this extension
8 might be due to polysynaptic connection with other fasciculi like the posterior part of the MdLF.
9 In the future, nearer investigations have to show whether this difference in temporal terminations
10 between human and NHP is genuinely crucial and accounts for the evolution of language in the
11 human lineage.

15 **Question 3: The Dorsal Language Pathway, relative to the Ventral Pathway, has expanded** 16 **significantly in humans than NHPs?**

17
18 In humans the AF together with the SLF II, III makes up the Dorsal language pathway in
19 opposition to the Ventral pathway (e.g., Saur et al., 2008) (Figure 6). Both pathways are
20 connecting inferior frontal with temporal language areas. The Ventral pathway passing through
21 the extreme capsule curves ventrally around the Sylvian fissure in opposition to the Dorsal
22 pathway which curves dorsally around the Sylvian fissure (e.g., Hickok and Poeppel, 2004).
23 Many diffusion MRI studies cannot account for a clear separation of AF and SLF II, III and have
24 therefore based their interpretations on a mix of these bundles rather than only the AF (e.g.,
25 Balezeau et al., 2020; Eichert et al., 2019; Rilling et al., 2008; 2012). Therefore, we also keep
26 here the appellation “Dorsal pathway” as in the original articles (e.g., Rilling et al., 2008; 2012)
27 knowing it includes broadly the AF and SLF II and SLF III. Traditionally, at the functional level,
28 the Dorsal pathway is involved in mapping sound to articulation, while the Ventral pathway is
29 involved in mapping sound to meaning (Hickok and Poeppel, 2004; Saur et al., 2008). While
30 both pathways connect similar areas, it is the Dorsal/AF pathway that is dominant in humans
31 (i.e., stronger structural connectivity than the Ventral pathway) (Rilling et al., 2008). Therefore, a
32 crucial question is whether the same organisation is shared with monkeys, or whether actually
33 the Ventral pathway is dominant over the Dorsal pathway in monkeys.

34 Currently, there are several theoretical accounts based on how a reduced or inversed Dorsal-
35 *versus* Ventral dominance in nonhuman primates could explain the uniqueness of human
36 language (e.g., Friederici, 2017; Pulvermueller, 2018; Rilling et al., 2008; 2012). However, with
37 differences in seeding and the addition of functional connectivity, recent investigations have
38 challenged this view and show increased connectivity on the structural side for the dorsal
39 pathway and an equal dominance of both pathways on the functional side in monkeys (Balezeau
40 et al., 2020; Rocchi et al., 2021). Here, we review tractography and effective connectivity studies
41 of the Dorsal and Ventral pathways to investigate whether or not a stronger ventral-than-dorsal
42 ratio exists in the nonhuman primate’s brain.

43 In their pioneering work, Rilling and colleagues (2008) compared the Dorsal and Ventral
44 pathway across primate species, using diffusion MRI and a probabilistic multi-fibre diffusion
45 model. They found a stronger (more streamlines) Dorsal-than Ventral Pathway in human, which
46 was not the case in macaques and chimpanzees. In fact, for macaques a very weak (i.e., low

1 number of streamlines) Dorsal pathway was described, where frontal terminations were found in
2 area 46 and delicately in area 44 (part of Broca's homologue). Temporal terminations were
3 described only in the most posterior end of the temporal lobe in the junction with the parietal
4 lobe. In contrast, a strong Ventral pathway was highlighted with terminations in area 44 and 45
5 (Broca's homologue) as well as in the frontal operculum and across the temporal lobe (see
6 Figure 4, left panel). In humans the authors described an opposite organisation with a Dorsal
7 pathway stronger than the Ventral one, connecting both similar areas (Rilling et al., 2008). In
8 addition, in comparisons to chimpanzees, they described qualitatively stronger connections to
9 Broca's area (area 44 and 45) via the Dorsal pathway, than via the Ventral pathway (Rilling et
10 al., 2012) in humans. The authors concluded that the Dorsal pathway changed significantly more
11 than the Ventral pathway in human evolution, due to the overall strengthening, greater strength
12 than the Ventral pathway, stronger area 44 and new area 45 terminations as well as extended
13 terminations into (and beyond) the middle part of the temporal lobe (replicated e.g., by Eichert et
14 al., 2019) (*Figure 6 left panel*). The authors further conclude that the proportional strengthening
15 of the Dorsal Pathway might have contributed to transfer lexical-semantic information and some
16 elements of syntax in the evolution of human language. In contrasts, its monkey's homologue
17 would be rather involved in low-level spatial processing of sounds (Aboitiz, 2018; Rilling et al.,
18 2008), similar to the view of Schmahmann & Pandya (2006) (Question 1 above). Also, the great
19 extent of temporal lobe information like auditory information would be exclusively conveyed via
20 the ventral pathway in monkeys (in agreement with functional and tract tracing results
21 (Romanski et al. 1999)). This finding and interpretation had a conceptual impact on several
22 theories trying to retrace the evolution of human language. Here we will focus on two of them
23 (Friederici, 2017; Pulvermueller, 2018).

24
25 A first prominent theory comes from Angela Friederici as highlighted in her 2017 book
26 "Language in the brain" (Friederici, 2017). She proposes that complex syntax and therefore
27 human language developed in human only, due to the strengthening of the Dorsal pathway with
28 extension of terminations into area 44 (part of Broca's area). The reasoning is the following:
29 The Dorsal pathway conveys complex syntax in the human brain due to the connection to area 44
30 (Friederici et al. 2006), whereas the Ventral pathway conveys semantic aspects of language and
31 simple syntax due to the connection to area 45 and the frontal operculum (Friederici, 2017).
32 Monkeys however show non or only weak dorsal connections to area 44 (Rilling et al., 2008),
33 but have ventral termination to this area. Therefore, they don't show complex syntax, but aspects
34 of semantics and simple syntax (Friederici, 2017). Indeed, behavioural data indicates that
35 monkeys fail to show the processing of complex syntax, but showed aspects of semantics
36 (Friederici, 2017). In addition, behavioural data in developmental studies highlight that infants
37 only acquire complex syntax by the age of seven, exactly when the most anterior portion of the
38 Dorsal pathway matures and connects to Broca's area (Brauer et al. 2013; Brauer et al. 2011;
39 Friederici 2017; Perani et al. 2011). In contrast, the Ventral pathway connection into this area is
40 already present at that age (Brauer et al. 2013; Brauer et al. 2011; Friederici 2017; Perani et al.
41 2011).

42 However, there are also some limitations to this theory:

43 First, several diffusion MRI studies interpret the developmental data differently (Dubois et al.
44 2009, 2016). In their view Broca's Dorsal pathway terminations are present before the age of 7,
45 but intractable in diffusion MRI due to their immature microstructure. Second, more recent
46 behavioural studies highlight that monkey can "break to the syntax barrier" (Ferrigno et al. 2020;

1 Jiang et al. 2018; Malassis et al., 2020; Fitch 2018).

2
3 A second recent and influential theory based on a weaker Dorsal pathway in NHP was proposed
4 by Pulvermueller (2018). He hypothesised that the overall strengthening, and the evolutionary
5 new and stronger area 44 termination of the Dorsal pathway enabled frontotemporal
6 sensorimotor shortcuts, connecting further than just next neighbouring areas. This way, humans
7 can better bind action and perception into circuits that support cognitive functions important for
8 language processing, like working memory, prediction, attention, and combination, including
9 abstract rule formation. In this work, action representations lie at the heart of language
10 processing.

11 Very recently however, changes in techniques and seeds for tracking have challenged the view of
12 a stronger-Ventral-than-Dorsal-pathway in monkeys. In a diffusion MRI studies across primate
13 species, Balezeau and colleagues (2020) used a functionally defined auditory cortex as the seed
14 for tractography. This way, they highlighted a Dorsal pathway connection into the auditory
15 cortex, which was until then reserved to the Ventral pathway (Rilling et al., 2008; Romanski et
16 al, 1999). The authors therefore suggest that the monkey AF is not solely involved in low-level
17 processes but instead important for sound and vocal patterning in the time domain (Balezeau et
18 al., 2020).

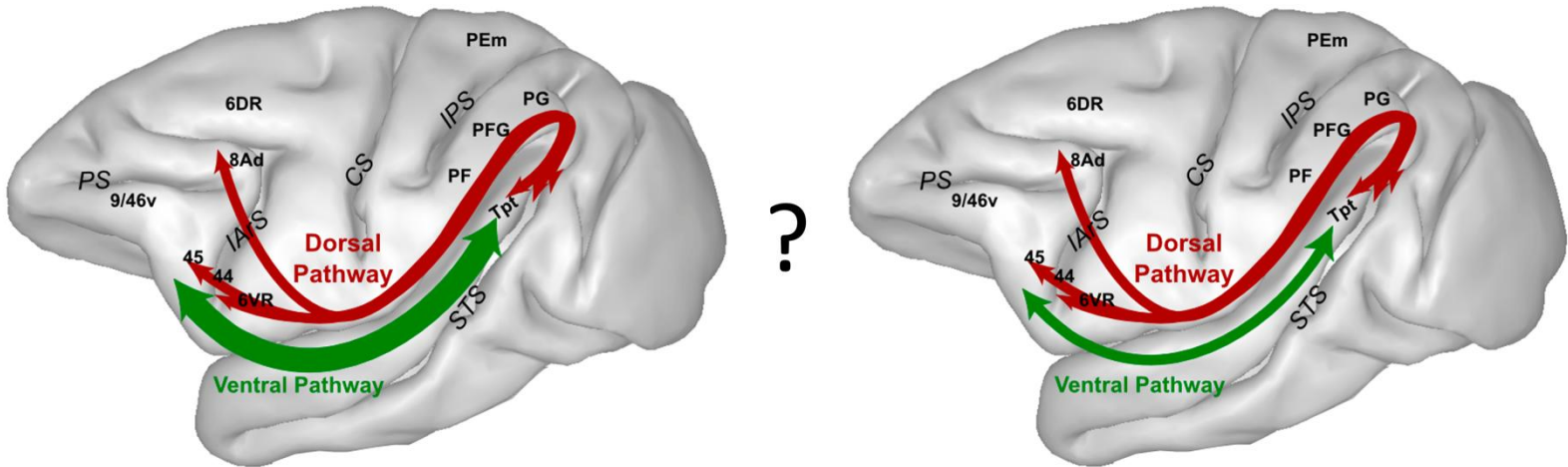
19 Furthermore, on the functional level, using effective connectivity while stimulating the same
20 auditory cortex, Rocchi and colleagues (2021) reported that Dorsal and Ventral pathways
21 connect to the same degree to Broca's homologue (area 44 and 45) and the frontal operculum. In
22 other words, even though the Ventral pathway was shown stronger on a structural level (Rilling
23 et al., 2008; 2012), functionally both pathways have the same strength. The authors suggest
24 therefore that language abilities allowing humans to name, conceptualize and thus better
25 remember sound (Schulze et al., 2012) would be shared across primates (Figure 6 right panel).

26 Based on the above recent data, the long-standing bulwark of an inversed pathway dominance
27 that could explain language evolution is challenged. As a result, contemporary theories that
28 explain the uniqueness of human language based on the inverted proportional strength of the
29 dorsal and ventral pathway, should be revised accordingly. While structural differences in
30 strength may persist between the human and the monkey Dorsal pathway, this is not the case
31 functionally. A question that exceeds the current review is to investigate whether structural
32 differences are therefore of importance on other functional levels as investigated by Rocchi et al.
33 (2021).

34

35

1 Figure 6: Dorsal- versus Ventral Pathway strength (question 3)



2 Figure 6: Dorsal- versus Ventral Pathway strength (question 3). (Left) A dominance in strength
3 (in structure and function) in the Ventral pathway (green) against the Dorsal pathway (red)
4 (e.g., Rilling et al., 2008; 2012). (Right) Equal strength (in structure and function) between both
5 pathways (e.g., Rocchi et al., 2021).

6

7 **Question 4: A continuous evolution of the AF across primates -- Could AF lateralisation be**
8 **the key to human language?**
9

10 In humans, the AF is strongly lateralised towards the left hemisphere (e.g., Thiebaut de Schotten
11 et al., 2011). This structural lateralisation is of interest, because the majority of the language
12 system is also functionally left-lateralised in the brain (e.g., Toga and Thompson 2003). Whether
13 such a same lateralisation exists, or not in nonhuman primates is therefore a crucial question that
14 would shed light on the origins of human language lateralisation. Especially, since the most
15 recent investigations about the AF's anatomy across primates agree on a highly evolutionarily
16 conserved anatomy (see sections above). Thus, the question about anatomical differences across
17 primates, that might explain the human uniqueness for language, persists. Authors of recent
18 investigations highlight that the left AF lateralisation is the crux of the human-specific
19 distinction (Balezeau et al., 2020; Eichert et al., 2019; Rocchi et al., 2021). While carefully
20 reviewing the recent comparative brain lateralisation data, we conclude that this compelling idea
21 lacks sufficient sample size.

22

23 From early human development on, inter-hemispheric asymmetry was documented for most
24 language-related regions at both structural and functional level. In fact, language tasks elicit
25 greater activation in the left- than in the right hemisphere, even in newborns (e.g., Dehaene-
26 Lambertz et al. 2002). Structural markers of such language brain lateralisation were proposed,
27 like the leftward lateralisation of the Planum Temporale, Broca's area or the Insula (e.g.,
28 Geschwind and Levitsky 1968; Keller et al. 2010).

29 However, the human uniqueness of such results was challenged by finding some of these

1 structural markers not only in apes (e.g., Hopkins et al. 2015) but also in an Old World monkey,
2 the baboon, in both adults and newborns (Becker et al. 2021a; b; c; Marie et al. 2018).

3 Regarding white matter in humans, volume of the SLF II and SLF III was shown larger in the
4 right hemisphere (e.g., Amemiya et al. 2021; Thiebaut de Schotten et al. 2011), which is a
5 phylogenetically shared feature with chimpanzees (Hecht et al. 2015). In contrast, the human AF
6 was shown larger in the left hemisphere for a number of macroscopic and microscopic
7 measurements like the number of streamlines, volume of the tract, fibre density and mean
8 fractional anisotropy in adults and infants (Catani et al. 2007; Dubois et al. 2009; Nucifora et al.
9 2005; Powell et al. 2006; Thiebaut de Schotten et al. 2011; Takaya et al. 2015; Thiebaut de
10 Schotten et al. 2011). Therefore, the structural AF asymmetry, and specifically its temporal
11 terminations, is indeed discussed as a marker for the functional lateralisation of the language
12 network (e.g., Catani et al., 2007; Powell et al., 2006; Takaya et al., 2015; but see also e.g., Silva
13 and Citterio 2017; Vernooij et al. 2007) and was further supported by resting state MRI data
14 showing functional lateralisation of the language network (Zhu et al. 2014). However, Verhelst
15 et al. (2021) recently reported that the AF is left-lateralised, regardless of left or rightwards
16 language lateralisation.

17 But what is known about the nonhuman primate's AF lateralisation?

18 Initially, Rilling et al. (2008) did not find any AF asymmetry in three macaque and four
19 chimpanzee subjects. A follow-up study in chimpanzees including a higher number of subjects
20 (Rilling et al., 2012), showed a left-lateralised AF for 26 subjects. However, this lateralisation in
21 chimpanzee was weaker than in humans. Eichert et al., (2019) confirmed an absence of left
22 asymmetry for the AF/Dorsal pathway in four *ex-vivo* macaque with high resolution and one *in-*
23 *vivo* macaque image. In contrast, a strong left lateralisation was reported for the Ventral
24 pathway, which was found slightly right lateralised in humans (Eichert et al., 2019). Similarly,
25 Balezeau et al., (2020) reported no lateralisation for the Dorsal pathway in three macaques but
26 also no lateralisation for the three chimpanzee subjects. This latter finding was confirmed on a
27 functional level by Rocchi et al. (2021) for human and macaque subjects. Despite only treating
28 two macaque subjects, a phylogenetical discontinuity in lateralisation was highlighted, with
29 humans being leftwards lateralised and monkeys showing no lateralisation.

30 As one can easily see, studies that investigated lateralisation produced inconsistent results and
31 are limited to small sample sizes. Indeed, it is common in neuroscience to use not more than two
32 macaque individuals in a given study, which makes interpretation of a populational level
33 lateralisation impossible. Tract tracing methods, for example, are not able to give a response to
34 the questions, while diffusion MRI tractography may do. A small sample-size also limits
35 homogeneous groups in regards to handedness, which was shown to be linked to brain
36 lateralisation (e.g., Hopkins et al., 2015; Meguerditchian et al., 2013), and which might influence
37 therefore influence a population -level lateralisation.

38 In addition, while lateralisation of homologous perisylvian language areas were found present in
39 several ape species (i.e., Hopkins et al., 2015), these asymmetries were not detected in macaques
40 (Lyn et al., 2011), which are commonly representing the family of Old world monkeys. In
41 contrast, recent studies demonstrated that another Old world monkey, the baboon, possesses
42 homologous asymmetries (Becker et al., 2021a; c; Marie et al., 2018). It remains unclear why
43 cerebral asymmetries are commonly detected in baboons but not in macaques.

44

1 Based on the above tractography data, the question about evolutionary continuities or
2 discontinuities in AF lateralisation will need further investigations with 1) ample sample sizes
3 also in regard to handedness and 2) the inclusion of the baboon as a representative of the Old
4 world monkey family. Therefore, we predict that future studies will focus on this crucial question
5 in language brain evolution.
6
7
8

9 **Part III: Discussion and Conclusion**

10
11 The apparent literature about the evolution of the AF has been rapidly gaining in interest in very
12 recent years and is used as a base for theories about language evolution. However, no clear
13 consensus was found, due to differences in appellations and divergent anatomical courses and
14 terminations, which are resulting in diverging definitions of what exactly the AF is.

15 For example, anatomically, AF and SLF are generally referred to the same tract. This is
16 important as the label “AF” implies “language pathway” more than the label SLF, MdLF or
17 Dorsal pathway. But note that all terms are used interchangeably throughout the literature.
18 However, differences in terminology matters, because a same result could have different
19 theoretical implications depending on its labelling and therefore its functional connotation.

20 To illustrate this point we can do a thought experiment: If, during primate evolution, an increase
21 of connectivity strength between the superior temporal lobe (Wernicke’s area) and the inferior
22 parietal lobe (Geschwind’s region) (as in e.g., Aboitiz and García, 1997; Catani and Bambini,
23 2014) was documented, different functional interpretations could be drawn from this, depending
24 on terminology. We could label this segment for example AF, SLF, MdLF or Dorsal pathway.
25 However, the functional implication would be the most associated with language evolution for
26 the label “AF”, even though the segment is the same.
27

28 In this review, we have therefore carefully highlighted the history of AF anatomy across primate
29 species and defined a clear current anatomical model. The AF/SLF complex can be divided into
30 four distinct fibre bundles including: 1) the AF, which comprise in itself three fibre branches that
31 arch dorsally around the Sylvian fissure and connect the posterior temporal cortex (area Tpt,
32 posterior auditory cortex) with the frontal cortex (area 44, 45, area 8Ad and 6) and 2) the SLF I,
33 II and III, which comprise the three longitudinal fibre bundles that interconnect distinct parts of
34 the frontal and parietal cortex and are not arching around the Sylvian fissure.
35

36 In addition, we focused on four discontinuous key changes in AF anatomy that are discussed to
37 differentiate the human from the nonhuman primate. These are grouped in research questions
38 concerning: frontal terminations (1), temporal terminations (2), the proportion of the Dorsal-
39 versus Ventral pathway strength (3) and lateralisation (4). These four key questions are of high
40 importance, because their results in (dis)continuity influence theories about language evolution.

41 Based on the latest results of these four key questions, we argue that the evolution of the AF
42 anatomy is more continuous across primate species than previously described.
43

44 When summarizing the four questions (see also Table 1), we can notice the importance of
45 methodological changes that are pivotal in the conceptualisation of the AF anatomy:

1 - Historically, knowledge about the AF's terminations (Question 1) relies strongly on invasive
2 tract tracing studies in the monkey brain. Findings about differences in frontal termination in the
3 macaque brain (no Broca's terminations) compared to the human brain (Broca's termination) led
4 to theories about the specific frontal development of the human AF, important for language
5 processing. However, human-like terminations into Broca's homologue in monkeys were found
6 when cytoarchitectonic equivalence was demonstrated and tract tracing injection sites changed.
7 Therefore, the frontal termination's organisation seems to be conserved during primate
8 evolution, even though terminations might have become overall stronger in humans.

9 - The same applies to the temporal terminations (Question 2), which were initially found to be
10 very extended in humans, exceeding the middle part of the temporal lobe into its anterior and
11 inferior parts. New data from methodological changes indicate however, that first, the monkey's
12 terminations are also slightly more extended (tracking from the functionally characterised
13 auditory cortex) and second, the human extension could be a technical artefact (possible
14 entanglement with MdLF fibres). Therefore, it is not excluded that the temporal termination's
15 organisation might also be conserved during primate evolution, even though the temporal
16 connections might have become overall stronger in humans.

17 - Finally, pivotal changes in the question of the proportion of the Ventral- versus the Dorsal
18 pathway's strength (Question 3), can also be illustrated by changes in techniques (effective
19 connectivity) and seed masks (tracking from the functionally characterised auditory cortex).
20 Initially found to be very weak and not terminating into the auditory cortex, the Dorsal pathway
21 in monkeys is now demonstrated to be functionally as strong as the Ventral pathway and also
22 connecting with the auditory cortex. Therefore, the Ventral-versus-Dorsal pathway strength
23 organisation seems to be conserved during primate evolution, even though the Dorsal pathway
24 might have become overall structurally stronger in humans.

25 - Using this method-based framework on the question of lateralisation (Question 4), we can say
26 that currently only the progress of tractography methods and dMRI acquisition techniques could
27 advance this question as tract-tracing methods are not adapted. In particular, a forthcoming
28 development of tractography applied to a large-scale cohort of non-human primate data could
29 further advance the question as it was already conducted in chimpanzees concerning the
30 lateralisation of other tracts like the SLF (Hecht et al., 2015), or structural grey matter
31 asymmetries (e.g., Hopkins et al., 2015). Therefore, the question of AF lateralisation across
32 primates needs a specific attention in the future. Given existing results about the left-
33 lateralisations of perisylvian regions in monkeys (Becker et al., 2021a; Marie et al., 2018), it is
34 not excluded that a human-like left lateralisation could also be demonstrated in monkeys in the
35 future, even though lateralisation might have become stronger in human evolution.

36
37 In addition, future studies must also focus on other tracts that might have undergone substantial
38 change during primate evolution and that are linked to language processing in humans. Possible
39 tracts of interest are the Ventral pathway (and its subcomponents), the middle longitudinal
40 fasciculus and the frontal aslant (for a review: La Corte et al., 2021).

41
42 In conclusion, recent works in humans and nonhuman primates suggest that the AF course and
43 terminations are more similar between species than described before. The remarkable human
44 ability of language might therefore have evolved progressively in primate evolution, exactly as
45 its underlying anatomic implementation in the brain. Or to put it in the words of Charles Darwin:
46 "Nevertheless the difference in mind between man and the higher animals, great as it is, certainly

1 is one of degree and not of kind." (page 105: Darwin, 1871/1981). Future theories about
 2 language brain evolution should account for this continuous, and not discrete AF evolution.

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	Tract tracer studies		Diffusion MRI	
	<i>Absent</i>	<i>Present</i>	<i>Absent</i>	<i>Present</i>
Broca's terminations (monkey)	Petrides & Pandya 1988 Schmahmann & Pandya 2006 Thiebaut de Schotten et al., 2012	Petrides & Pandya 2009 Frey et al., 2014 Petrides et al., 2014	/	Rilling et al., 2008 Eichert et al., 2019 ; 2020 Barrett et al., 2020 Balezeau et al., 2020 Bryant et al., 2020 Roumazeilles et al., 2020
Auditory cortex terminations (temporal lobe) (monkey)	Schmahmann & Pandya 2006 Petrides & Pandya 2009 Frey et al., 2014 Petrides et al., 2014	/	Eichert et al., 2019 ; 2020 Barrett et al., 2020 Roumazeilles et al., 2020 Rilling et al., 2008 ; 2012	Balezeau et al., 2020 Rocchi et al., 2021
Extended temporal lobe terminations (human)	/	/	Maldonado et al., 2013; Wang et al., 2013; Petrides, 2014; Balezeau et al., 2020 Barbeau et al. ; 2020 Latini et al., 2021	Catani et al., 2005 Rilling et al., 2008 Thiebaut de Schotten et al., 2012 Eichert et al., 2019
Ventral > Dorsal Pathway (monkey)	/	/	Rocchi et al., 2021	Rilling et al., 2008 ; 2012
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	/

6

7 Table 1.: Summary of the main work analysed in the present review, in regard to the contrasting
 8 descriptions of the Arcuate Fasciculus (AF) in tract-tracer and diffusion MRI studies. Six
 9 features are highlighted as absent or present: Broca's terminations in monkeys, temporal
 10 terminations into the monkeys' auditory cortex in the temporal lobe, expanded terminations into
 11 the human's inferior or anterior temporal lobe, dominance of the Ventral pathway over the
 12 Dorsal pathway in monkeys, lateralisation in chimpanzee brains and lateralisation in monkey
 13 brains. "/": No data available.

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