



Anatomical variability of the arcuate fasciculus: a systematical review

Florian Bernard^{1,2} · Ilyess Zemmoura^{3,4} · Aram Ter Minassian^{5,6} · Jean-Michel Lemée^{1,7} · Philippe Menei^{1,7}

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Abstract

Purpose The arcuate fasciculus (AF) is a white matter fibers tract that links the lateral temporal with the frontal cortex. The AF can be divided into three components: two superficial indirect short tracts (anterior and posterior) and one deep direct long tract. Both DTI and white matter dissections studies find differences regarding the anatomy of the AF, especially its cortical connections. This paper aims at providing a comprehensive anatomical classification of the AF, using the *terminologia anatomica*.

Methods Articles ($n=478$) were obtained from a systematical PRISMA review. Studies which focused on primates, unhealthy subjects, as well as studies without cortical termination description and review articles were excluded from the analysis. One hundred and ten articles were retained for full-text examination, of which 19 finally fulfilled our criteria to be included in this review.

Results We classified main descriptions and variations of each segment of the AF according to fiber orientation and cortical connections. Three types of connections were depicted for each segment of the AF. Concerning the anterior segment, most of the frontal fibers (59.35%) ran from the ventral portion of the precentral gyrus and the posterior part of the pars opercularis, to the supramarginal gyrus (85.0%). Main fibers of the posterior segment of the AF ran from the posterior portion of the middle temporal gyrus (100%) to the angular gyrus (92.0%). In main descriptions of the long segment of the AF, fibers ran from both the ventral portion of the precentral gyrus and posterior part of the pars opercularis (63.9%) to the middle and inferior temporal gyrus (60.3%). Minor subtypes were described in detail in the article.

Conclusion We provide a comprehensive classification of the anatomy of the AF, regarding the orientation and cortical connections of its fibers. Although fiber orientation is very consistent, cortical endings of the AF may be different from one study to another, or from one individual to another which is a key element to understand the anatomical basis of current models of language or to guide intraoperative stimulation during awake surgery.

Keywords Arcuate fasciculus · Fiber dissection · Diffusion tensor imaging · Fiber tracts · Anatomy · Review

✉ Florian Bernard
bernardflorian.bf@gmail.com

- ¹ Department of Neurosurgery, Teaching Hospital, 49100 Angers, France
- ² Laboratory of Anatomy, Medical Faculty, 28 rue Roger Amsler, 49100 Angers, France
- ³ Department of Neurosurgery, CHRU de Tours, Tours, France
- ⁴ UMR1253, iBrain, Université de Tours, Inserm, Tours, France
- ⁵ Department of Reanimation, Teaching Hospital, 49100 Angers, France
- ⁶ INSERM, 1066 Department and EA7315 Team, Angers, France
- ⁷ CRCINA, UMR 1232 INSERM/CNRS and EA7315 Team, Angers, France

Introduction

Language is a complex faculty that allows us to encode, elaborate and communicate thoughts and experiences through the mediation of arbitrary symbols known as words. The coherent function of the language network and its interactions with other neurocognitive networks depend on an orderly set of interconnections, of which the arcuate fasciculus (AF) appears to be one of the most important anatomical support. From a historical perspective, definition of the AF evolved. Reil [1] was the first to identify a group of fibers running deeply into the white matter of the temporal, parietal and frontal regions located around the Sylvian fissure of each hemisphere [2]. In 1822, Burdach described in detail this system of perisylvian fibers and

named it the *Fasciculus Arcuatus*, due to the arching shape of its longest fibers [3]. Dejerine believed that the AF was mainly composed of short associative fibers connecting neighbouring gyri of the perisylvian cortical areas. It was Constantin Von Monakow who first identified the arcuate fasciculus as the tract connecting Broca's and Wernicke's areas [4, 5].

In recent decades, the anatomy of the AF has been studied using both fiber dissections and diffusion tensor imaging (DTI). The AF is a white matter fibers tract that links the lateral temporal with the frontal cortex via a projection that arches around the Sylvian fissure [6–8]. The AF can be divided into three different segments: two superficial indirect short tracts (anterior and posterior) and one deep direct long tract (Fig. 1). Examining the literature, we note that there are discrepancies between anatomical descriptions of the AF in DTI and white matter dissections studies. Indeed, the precise course and cortical connections of the AF are variably described [9–12]. Moreover, several models of AF connectivity exist in the contemporary literature. Because of the lack of consensus in anatomical nomenclature, understanding AF descriptions in anatomical and functional MRI studies may be difficult. In this systematical review, we replace the old fashioned terms with more precise anatomical definitions, using the standardized *terminologia anatomica* nomenclature. The aim of this systematical PRISMA (Preferred Reporting Items for Systematic Reviews

and Meta-Analyses) review was to standardize the AF anatomical description, so as to better understand its variations.

Methods

Data were compiled and categorized based on the PRISMA study design [13]. A total of 478 articles were obtained from a systematic search of English-language literature using MEDLINE (1946–December 2017) and EMBASE Classic (1947–December 2017), the cited references of the selected articles, and the “search cited” feature of PubMed. A focus was placed on anatomical and laboratory papers that assessed AF fiber orientation and cortical origin/terminations using both fiber dissection and DTI study. The search was limited to tractography and fiber dissection studies involving only humans. Studies which focused on primates, unhealthy subjects as well as studies without cortical termination description, and review articles were excluded from the analysis.

After examination of the abstracts, based on the inclusion and exclusion criteria, 110 articles were retained for full-text examination, of which 19 finally fulfilled our criteria to be included in this review. Articles of interest must have reported the precise description of orientation, origin/termination of AF. Figure 2 is a PRISMA flow diagram, which illustrates the number of articles at each data acquisition

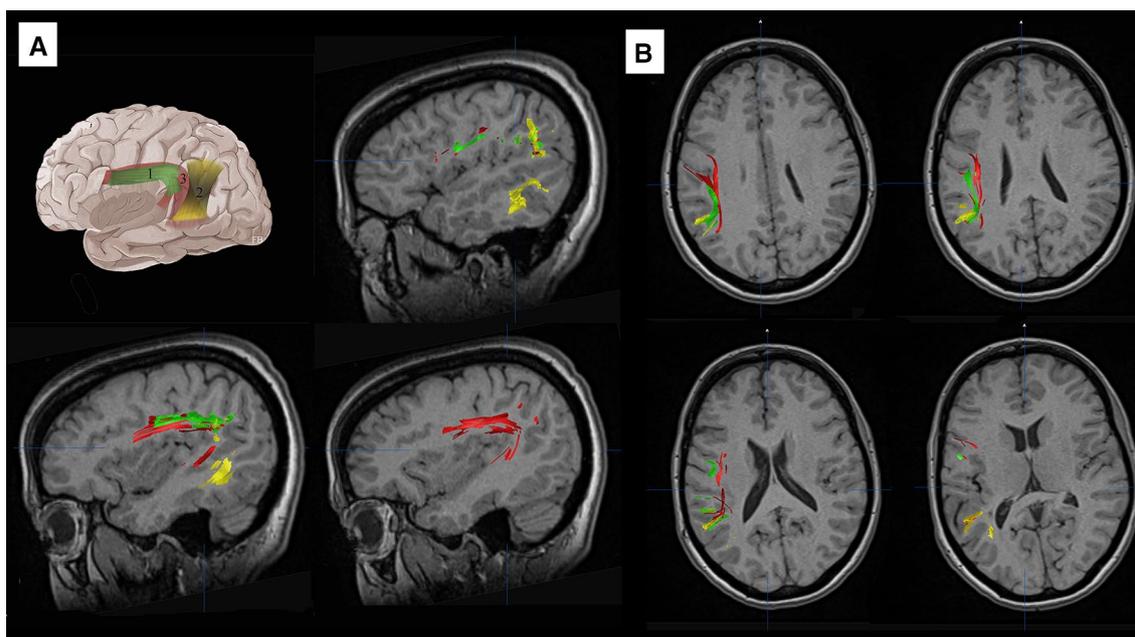


Fig. 1 Arcuate fasciculus segmentation (**a** sagittal slices; **b** horizontal slices). The arcuate fasciculus is divided in two superficial parts and one deep part. The anterior indirect segment (green) runs from the ventral portion of the precentral gyrus and the posterior part of the pars opercularis, to the supramarginal gyrus. The posterior indirect

segment of the AF (yellow) runs from the middle temporal gyrus to the angular gyrus. The long segment of the AF (red), fibers run from both the ventral portion of the precentral gyrus and posterior part of the pars opercularis to the middle and inferior temporal gyrus, deeper than superficial indirect segment (color figure online)

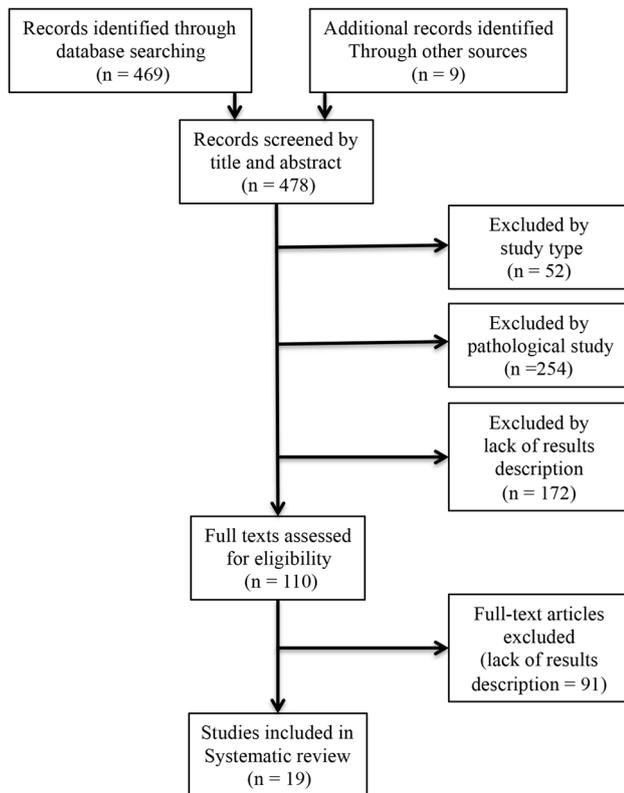


Fig. 2 A PRISMA flow diagram showing the flow of information through the different phases of the systematic review

level, the number of excluded articles, and the reasons for exclusion. Cortical connections were assessed using the study of Destrieux et al. according to the *terminologia anatomica* [14].

Results

The AF could be divided into three segments: two superficial indirect short tracts (anterior and posterior) and one deep direct long tract (Fig. 1, Table 1). We classified main descriptions of each segment regarding fiber orientation and cortical connections (origin/terminations) as *type (1)* and variations as *types (2) and (3)* (Fig. 3).

Anterior indirect segment of the AF (Figs. 1, 3a, Tables 1, 2, 3)

Main description (*type (1)*)

The fibers of this portion of the AF have a horizontal orientation. Many of the frontal fibers (*anterior termination*, 59.35%) course from the ventral portion of the precentral gyrus, and the posterior part of the pars opercularis, to

Table 1 Major variations of the arcuate fasciculus (AF) in the literature review

Classical description	AF anterior indirect segment		AF posterior indirect segment		AF direct segment	
	Anterior termination	Posterior termination	Ventral termination	Dorsal termination	Anterior termination	Posterior termination
type 1	The ventral portion of the precentral gyrus and the posterior part of the pars opercularis (59.35%)	Supramarginal gyrus (85.0%)	Posterior middle temporal gyrus (100%)	Angular gyrus (92.0%)	The ventral portion of the precentral gyrus and the posterior part of the pars opercularis (63.9%)	Middle and inferior temporal gyrus (60.3%)
Variation type 2	Ventral portion of the precentral gyrus (32.45%)	Supramarginal gyrus and posterior part of the superior temporal gyrus (15.0%)	–	Angular gyrus and the middle occipital gyrus (7.8%)	Posterior middle frontal gyrus (21.4%)	Middle temporal gyrus (38.5%)
Variation type 3	Pars opercularis (8.2%)	–	–	Angular gyrus, the supramarginal gyrus and the inferior portion of the superior parietal lobe (0.2%)	Pars triangularis (14.7%)	Inferior temporal gyrus (1.2%)

Percentages refer to the cortical distributions based on the literature review

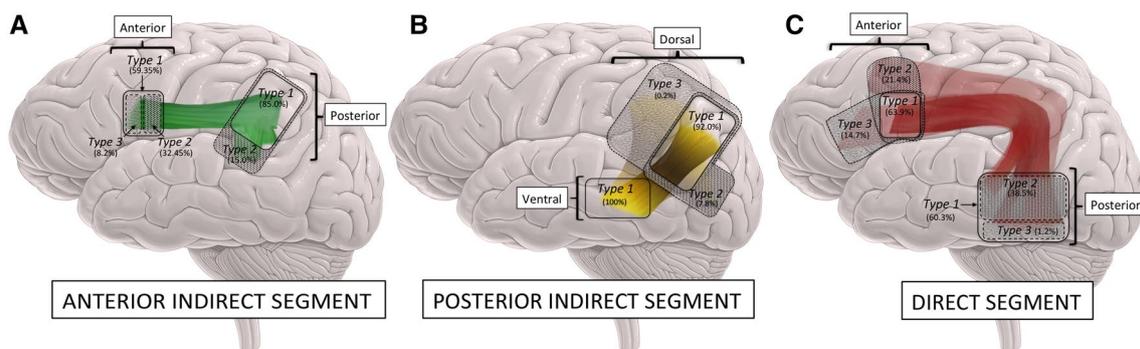


Fig. 3 Schematic representation of main cortical distributions of each AF segment according to our classification. **A** Anterior indirect segment of the AF, **B** posterior indirect segment of the AF, **C** direct long

segment of the AF. *Type 1*: main description; *type 2*: most frequent variation described; *type 3*: rarest variation described

Table 2 Literature review of the cortical distributions of the anterior indirect segment of AF-anterior termination

Anterior indirect segment of AF-anterior termination	PCG (Vent.)	PCG (Vent.), IFG (Pars op.)	IFG (pars op.)	NA	Number of hemispheres studied
Ture et al. [8]			40		40
Nucifora et al. [54]				54	54
Catani et al. [28]		11			11
Makris et al. [47]		10			10
Powell et al. [30]	20				20
Catani et al. [33]		100			100
Vernooij et al. [31]	40				40
Glasser et al. [41]				16	16
Catani et al. [2]		24			24
Fernández-Miranda et al. [6]		30			30
Kaplan et al. [55]				16	16
Thiebaut de Schotten et al. [50]				80	80
Martino et al. [40]	10	2		7	19
De Benedictis et al. [56]	8				8
Fernandez Miranda et al. [37]		72			72
Kamali et al. [57]	10				10
Wang et al. [58]				24	24
Yamurglu et al. [11]	70				70
Gungör et al. [59]			40		40
Total	158 (32.45%)	289 (59.35%)	40 (8.2%)	197	684

PCG (Vent.): precentral gyrus in its ventral part. IFG (Pars op.): pars opercularis of the inferior frontal gyrus

NA not assessed

the supramarginal gyrus (*posterior termination*, 85.0%). Variations: regarding the variations in *anterior cortical connections* of this tract (Fig. 3a, Tables 1, 2), there are two types of description. First, an exclusive connection with the ventral portion of the precentral gyrus, which was mostly described in recent DTI tractography studies (*type* (2), 32.45%); Second, an exclusive connection with the

posterior portion of the pars opercularis (*type* (3), 8.2%). Regarding the *posterior cortical connections* of this tract (Fig. 3a, Tables 1 and 3) two types are described: exclusive connection to the supramarginal gyrus (*type* (1), 85.0%) and to both the supramarginal gyrus and posterior part of the superior temporal gyrus (in the region just posterior to the Heschl’s gyrus) (*type* (2), 15.0%).

Table 3 Literature review of the cortical distributions of the anterior indirect segment of AF-posterior termination

Anterior indirect segment of AF-posterior termination	SMG	SMG, STG (Post)	IPL	NA	Number of hemispheres studied
Ture et al. [8]			40		40
Nucifora et al. [54]				54	54
Catani et al. [28]			11		11
Makris et al. [47]	10				10
Powell et al. [30]		20			20
Catani et al. [33]			100		100
Vernooij et al. [31]		40			40
Glasser et al. [41]			24		24
Catani et al. [2]				16	16
Fernández-Miranda et al. [6]			30		30
Kaplan et al. [55]				16	16
Thiebaut de Schotten et al. [50]				80	80
Martino et al. [40]	4	14		1	19
De Benedictis et al. [56]	10				10
Fernandez Miranda et al. [37]			72		72
Kamali et al. [57]			8		8
Wang et al. [58]				24	24
Yamurglu et al. [11]	70				70
Gungör et al. [59]	40				40
Total	134 (27.2%)	74 (15.0%)	285 (57.8%)	191	684

IPL inferior parietal lobule, NA not assessed, SMG supramarginal gyrus. STG (Post): superior temporal gyrus in its posterior part

Posterior indirect segment of the AF (Figs. 1, 3b, Tables 1, 4 and 5)

Main description (type 1))

The fibers of this portion of the AF have a vertical orientation that run laterally to the AF direct long segment, from the posterior part of the middle temporal gyrus (*ventral cortical connection*, 100%) to the angular gyrus (*dorsal cortical connection*, 92.0%). Variations: The *ventral cortical connection* of this bundle (Tables 1, 4, Fig. 3b) is in all cases the posterior portion of the middle temporal gyrus (100%). There was no variation described in the literature. Regarding the *dorsal cortical connection* of this tract (Tables 1, 5, Fig. 3b), (*type 2*) is a connection with both the angular gyrus and the middle occipital gyrus (7.8%), and (*type 3*) corresponds to a projection to the angular gyrus, the supramarginal gyrus and the inferior portion of the superior parietal lobe (0.2%).

Long/deep/direct segment of the AF (Figs. 1, 3c, Tables 1, 6 and 7).

Main description (type 1))

The long segment is a long white matter tract located at the deep aspect of the anterior and posterior indirect segments

of the AF. During fiber dissections, after lifting these two superficial indirect connections, the lateral surface of the long segment of the AF is completely exposed. The posterior portion of the long segment fibers of the AF has a vertical orientation within the temporal lobe. Here, AF fibers run laterally and perpendicularly to the fibers of the sagittal stratum (i.e. the densely packed fibers located on the lateral surface of the ventricular atrium and composed of the optic radiations, inferior fronto-occipital fasciculus and tapetum), which have a horizontal orientation. The AF fibers curve around the caudal limit of the insula to take a horizontal direction. The fibers then run within the white matter of the parietal and frontal operculum.

The long segment of the AF has *anterior cortical connections* to the ventral portion of the precentral gyrus and to the posterior portion of the inferior frontal gyrus (pars opercularis) (63.9%), and *posterior cortical connections* to both the middle and inferior temporal gyrus (60.3%).

Variations: The *anterior terminations* of this bundle can connect to the posterior middle frontal gyrus (*type 2*), 21.4%) or to the pars triangularis (*type 3*), 14.7%), while the *posterior terminations* can connect exclusively to the middle temporal gyrus (*type 2*), 38.5%) or exclusively to the inferior temporal gyrus (*type 3*), 1.2%). In our review, connections of the long segment of the AF to the superior temporal gyrus were not identified either in major fiber dissection or

Table 4 Literature review of the cortical distributions of the posterior indirect segment of AF-ventral termination

Posterior indirect segment of AF-ventral termination	MTG (Post)	NA	Number of hemispheres studied
Ture et al. [8]	40		40
Nucifora et al. [54]		54	54
Catani et al. [28]	11		11
Makris et al. [47]	10		10
Powell et al. [30]		20	20
Catani et al. [33]	100		100
Vernooij et al. [31]		40	40
Glasser et al. [41]		16	16
Catani et al. [2]	24		24
Juan C. Fernández-Miranda et al. [6]	30		30
Kaplan et al. [55]		16	16
Thiebaut de Schotten et al. [50]		80	80
Martino et al. [40]	13	6	19
De Benedictis et al. [56]	8		8
Fernandez Miranda et al. [37]	72		72
Kamali et al. [57]	10		10
Wang et al. [58]		24	24
Yamurglu et al. [11]	70		70
Gungör et al. [59]		40	40
Total	388 (100%)	296	684

MTG middle temporal gyrus, NA not assessed

in DTI tractography. As previously shown, in some studies the fibers from the superior temporal gyrus converged into the anterior-horizontal segment of the AF.

Discussion

In this systematical PRISMA review, we provide a comprehensive classification of the AF segments regarding the orientation and cortical connections of their fibers. Although fiber orientation is not subject to variation, cortical endings of the AF may be different from one study to another, or from one individual to another.

Nomenclature

From a historical perspective, anatomical nomenclature of the AF evolved. The SLF/AF pathway has dominated the study of the white matter connectivity of language for two centuries. Until the later part of the twentieth century, the AF and superior longitudinal fasciculus (SLF) were considered to be part of the same fasciculus—with non-dissociable fibers called SLF/AF—connecting the posterior superior

temporal gyrus (Wernicke’s area) to the inferior frontal gyrus (Broca’s area) [15].

Indeed, the early understanding of the SLF/AF originates from Burdach [16], and appears prominently in the major anatomical works of the nineteenth century (Mayo [17]; Meynert [18]; Wernicke [19]; Barker [20]), especially the two volumes by Déjèrine [21, 22]). Like those before him, Déjèrine [21] does not dissociate the superior longitudinal fasciculus and arcuate fasciculus fibers, calling the “faisceau longitudinal supérieur ou fasciculus arcuatus de Burdach”. Similarly, Meynert [18] makes mention of the arcuate fasciculus, but no mention of the superior longitudinal fasciculus, and Wernicke [19] treats the superior longitudinal fasciculus and arcuate fasciculus as the same pathway (the “superior longitudinal bundle, or arcuate bundle”). In the same way, Paturet and Bellocq [23], described as synonymous “the superior longitudinal fasciculus or fasciculus arcuatus”; This author described the SLF/AF as composed of two kinds of fibers; (1) superficial, short, rectilinear fronto-occipital fibers; (2) And the longer, arcuate deep fronto-temporal fibers. In his 1970 publication, Geschwind depicted the arcuate fasciculus connecting Broca’s area (i.e. the posterior part of the inferior frontal gyrus) with Wernicke’s area (in the posterior superior temporal cortex). The course of the SLF/AF pathway has remained relatively unchallenged since Geschwind reasserted its prominence for language. Geschwind also attached prominence to the arcuate fasciculus terminology with less emphasis on the superior longitudinal fasciculus terminology.

Since Geschwind, a number of divergent and sometimes conflicting descriptions of the SLF/AF fibre pathway have emerged. It is only recently that there have been some attempts to dissociate parts of the SLF/AF, and generally these promote the notion that the arcuate fasciculus represents a partition of a broader superior longitudinal fasciculus. Studies in non-human primates have divided the SLF/AF into four separate components: SLF I, SLF II, SLF III, and AF [7, 24]. SLF and AF are considered currently as completely different tracts: the SLF (I, II, III) is a frontoparietal tract while the AF is a perisylvian tract that connects frontal-parietal-temporal areas [11, 15, 24]. Anatomically, only the macaque’s SLF III and the “human” anterior indirect segment of the AF may have a correspondence [7, 24].

Inter-individual variations

According to our results, investigation of the structural connectivity of the AF revealed numerous cortical connections. Inter-individual variations in patterns of structural connectivity probably contributed to the inconsistencies in the cortical terminations reported in the literature. Although variability in the position of white matter fascicles can be explained by gross anatomical variability in

Table 5 Literature review of the cortical distributions of the posterior indirect segment of AF-dorsal termination

Posterior indirect segment of AF-dorsal termination	AG	AG, MOG	AG, SMG, SPL	NA	Number of hemispheres studied
Ture et al. [8]	40				40
Nucifora et al. [54]				54	54
Catani et al. [28]	11				11
Makris et al. [47]	10				10
Powell et al. [30]				20	20
Catani et al. [33]	100				100
Vernooij et al. [31]				40	40
Glasser et al. [41]				16	16
Catani et al. [2]	16	8			24
Fernández-Miranda et al. [6]	30				30
Kaplan et al. [55]				16	16
Thiebaut de Schotten et al. [50]				80	80
Martino et al. [40]	12		1	6	19
De Benedictis et al. [56]	8				8
Fernandez Miranda et al. [37]	72				72
Kamali et al. [57]	10				10
Wang et al. [58]		24			24
Yamurglu et al. [11]	70				70
Gungör et al. [59]				40	40
Total	379 (92.0%)	32 (7.8%)	1 (0.2%)	272	684

AG angular gyrus, MOG middle occipital gyrus, NA not assessed, SMG supramarginal gyrus, SPL superior parietal lobule

Table 6 Literature review of the cortical distributions of the direct segment of AF- anterior connection

Direct segment of AF-anterior connection	PCG (Vent), IFG (Pars op.)	PCG (Vent), IFG (Pars op.), MFG (Post)	PCG (Vent), IFG (Pars op.), IFG (Pars tri.)	NA	Number of hemispheres
Ture et al. [8]	40				40
Nucifora et al. [54]				54	54
Catani et al. [28]	11				11
Makris et al. [47]	10				10
Powell et al. [30]	20				20
Catani et al. [33]	68			32	100
Vernooij et al. [31]	40				40
Glasser et al. [41]	16				16
Catani et al. [2]	24				24
Fernández-Miranda et al. [6]	30				30
Kaplan et al. [55]	13		2	1	16
Thiebaut de Schotten et al. [50]				80	80
Martino et al. [40]	3		9	7	19
De Benedictis et al. [56]		8			8
Fernandez Miranda et al. [37]		43	29		72
Kamali et al. [57]	10				10
Wang et al. [58]	9		15		24
Yamurglu et al. [11]	32	18	20		70
Gungör et al. [59]		40			40
Total	326 (63.9%)	109 (21.4%)	75 (14.7%)	174	684

IFG (Pars op.) pars opercularis of the inferior frontal gyrus, IFG (Pars tri.) pars triangularis of the inferior frontal gyrus, MFG (POST) posterior part of the middle frontal gyrus, NA not assessed, PCG (Vent.) precentral gyrus in its ventral part

Table 7 Literature review of the cortical distributions of the direct segment of AF-posterior connection

Direct segment of AF-posterior connection	MTG (MID), ITG (Post)	MTG (Post)	ITG (Post)	NA	Number of hemispheres studied
Ture et al. [8]	40				40
Nucifora et al. [54]				54	54
Catani et al. [28]		11			11
Makris et al. 2005 [47]		10			10
Powell et al. [30]	20				20
Catani et al. [33]		68		32	100
Vernooij et al. [31]	40				40
Glasser et al. [41]		16			16
Catani et al. [2]		24			24
Fernández-Miranda et al. [6]		30			30
Kaplan et al. [55]				16	16
Thiebaut de Schotten et al. [50]				80	80
Martino et al. [40]	12		6	1	19
De Benedictis et al. [56]	8				8
Fernandez Miranda et al. [37]	72				72
Kamali et al. [57]		10			10
Wang et al. [58]		24			24
Yamurglu et al. [11]	70				70
Gungör et al. [59]	40				40
Total	302 (60.3%)	193 (38.5%)	6 (1.2%)	183	684

ITG (POST) posterior part of the inferior temporal gyrus, *MTG (MID)* middle part of the middle temporal gyrus, *NA* not assessed

brain size and shape [25], heterogeneity in connectivity patterns may represent something more organizational. Some individual variations may be related to inheritance while others may be the result, for instance, of gender, normal aging, experiential learning or development of new skills [25]. From a clinical point of view, knowledge of the anatomical variability of white matter fascicles in the normal population is of prime importance for neurosurgical planning. It is also fundamental to determine the clinical correlates of a lesion, and this could help gain a deeper understanding of the mechanisms underpinning brain plasticity and recovery of functions [26]. However, no imaging method makes it possible to know perfectly the fibers anatomy and to correlate it, at the individual level, with the language functions. Moreover no imaging method predict the recovery capacities of a patient in case of partial lesion of the arcuate fasciculus [27]. It is for this reason that individual brain mapping by direct electric stimulation during awake craniotomy remains essential in the hope to preserve language. Nevertheless, a better understanding of anatomical bases allows neurosurgeons to better appreciate the functional anatomy of the perisylvian region and its application to tumor surgery that is a prerequisite to perform an awake brain surgery.

Asymmetry of the AF

Over the last decade, DTI studies have revealed a significant leftward asymmetry of the long direct segment of the AF providing new insights into the connectivity of the AF and its assumed major functional role in language processing [28–31]. However, in the right hemisphere, the cortical areas and white matter fascicles involved in visuo-spatial and social cognition are almost symmetrical to those involved in language with a perisylvian network [32]. The occurrence of the AF in the right hemisphere is still a matter of debate. Some authors reported its presence in only 40% of their subjects [33], and others reported it in all (for instance, all 12 right-handed subjects in Gharabaghi's study) [34]. However, most postmortem fiber dissection studies do not report a significant difference between the left and right AF, neither in terms of cortical connections [11], nor of fascicles volumes [11, 35, 36]. Hence, anatomically, the white matter structure could be considered mostly symmetrical.

Implication to DTI-based models of language

Referring to the cortical origin/termination using the *terminologia anatomica* facilitates the understanding of current

models of language. Indeed, there is currently no consensus on the anatomical definition of the extent and precise location of language areas and networks. Moreover, many labels are used to describe the same regions of activation in functional MRI (e.g. ventral frontal cortex, premotor ventral cortex, pars opercularis, inferior frontal gyrus). In a bid to explain language faculty, authors have provided different DTI-based models exploring its functional connectivity.

Direct and indirects AF segmentation

Catani et al. [28]. proposed a DTI-based classification for the AF, separating the fascicle into two superficial indirect and one deep long segments. The indirect segment of the AF has been divided into an anterior one (frontoparietal) and a posterior one (temporoparietal) regarding the distinct orientation and cortical connections of their fibers, as shown in our review (Fig. 3). Some cadaveric studies have replicated this AF compartmentalization of the superficial fibers (AF indirect segments) into anterior and posterior segments of the AF [6, 27, 37–40].

Superior and middle temporal pathway

Glasser and Rilling charted the superior and middle temporal gyrus pathways using DTI and functional neuro-imaging [41]. The superior temporal pathway, presumably the anterior indirect AF, connects the inferior frontal gyrus (*anterior termination type 1–3*) to the superior temporal gyrus and goes within the supramarginal gyrus (*posterior termination type 1 and 2*) (Fig. 3). The middle temporal pathway, presumably the AF direct segment, connects the middle and inferior frontal gyri (*anterior termination type 1–3*) to the middle temporal gyrus (*posterior termination type 1 and 2*) and passes through the angular gyrus. A similar segmentation was suggested by Fernandez-Miranda et al. [37], wherein the ventral or inner pathway connects the pars opercularis to the superior temporal and rostral middle temporal gyri, and the dorsal or outer pathway connects the ventral premotor cortex and caudal middle frontal gyrus to the inferior temporal and caudal middle temporal gyri.

Dorsal and ventral pathway

Built on an analogy between the visual and auditory systems, the following dual stream model for language processing was suggested: a dorsal stream is involved in mapping sound to articulation, and a ventral stream in mapping sound to meaning [42]. The dorsal pathway connects the premotor cortices in the frontal lobe (*anterior termination type 1–3*) and the superior temporal lobe (*posterior termination type 2*) via the AF anterior indirect segment. The ventral pathway connects the ventrolateral prefrontal cortex (*anterior*

termination type 1 and 3) and the middle temporal lobe (*posterior termination type 1 and 2*) through the direct AF segment. The function of the dorsal route, traditionally considered to be the major language pathway, is mainly restricted to sensory-motor mapping of sound to articulation, whereas linguistic processing of sound to meaning requires temporo-frontal interaction transmitted via the ventral route.

Other pathways

DTI and blunt fiber dissection works conducted over the last few years have offered several alternative models of dorsal stream connectivity via the AF. According to Makris et al., the SLF III is involved in articulatory aspect of language while the AF is involved in lexical and semantical processing. Finally, Friederici et al. [43–45], suggest a model wherein two dorsal pathways connect the posterior temporal cortex to either the ventral premotor cortex or the posterior part of the inferior frontal gyrus, respectively involved in sensorimotor and syntactic processing.

Implication in intra-operative stimulation

It has been shown that stimulation of the indirect anterior AF results in anarthria or dysarthria, while stimulation of the AF direct segment results in phonological (repetition) disorder [27, 39, 40, 46, 47]. The deep loop supporting phonological disorder corresponds anatomically to the direct segment of the AF in its main description (*type 1 origin and termination*) while the superficial frontoparietal loop, which interconnects the supramarginal gyrus and the pars opercularis, corresponds anatomically to the anterior indirect segment of the AF in its main description (*type 1 anterior and posterior termination*) [7, 28, 40, 47]. In recent fiber dissections and DTI analysis, the AF indirect anterior and AF direct segments were clearly separated along the frontoparietal operculum, the AF indirect segment being located lateral to the AF direct segment [11].

Problematics—study limitations

Both gross fiber dissection and diffusion-tensor imaging techniques present limitations that can affect the AF study of cortical connections. Very sparse and delicate groups of fibers may be difficult to dissect and partially destroyed when the neighboring white matter is removed. Imaging techniques are not limited by this destruction problem; however, they are susceptible to noise, lack of resolution, contamination from adjacent bundles, and abrupt changes in fiber direction. Moreover, there is a wide age difference between subjects studied with fiber dissection (older) and those studied with DTI tractography (usually young healthy volunteers). This may have affected the data, as white matter

connectivity may change with age. Nevertheless, the major observations were consistent across the majority of subjects studied with DTI tractography and fiber dissection.

Fiber dissection has a limited value when studying white matter connectivity in areas of crossing fibers. At the level of the frontal operculum, the fibers of the AF strongly intersect with the terminal branches of other long association fascicles (especially with the inferior fronto-occipital fasciculus (IFOF), and frontal aslant tract) and with the cortico-spinal tract. On the other hand, dissection enables the isolation of fibers up to 2 mm in diameter. Consequently, with this technique it is not possible to follow smaller branches of the AF. Moreover, in fiber dissection, extensive removal of gray matter leads to the loss of important cortical landmarks making it difficult to analyze the precise cortical terminations of a specific fiber tract. For example in Fernandez-Miranda's study [6], the cortex and superficial white matter were removed to reveal the anterior portion of the AF. Consequently, their dissection figures reveal horizontally oriented fibers located in the frontal and parietal operculum, but not the fibers projecting into the cortex [6]. This could be an explanation as to why cortex-sparing fiber dissection studies depict different cortical projections than Klingler's usual methods [48].

Even though DTI tractography has been extensively used to study white matter connectivity, it has three inherent shortcomings: (1) the first, as with fiber dissection, is the inaccuracy of this technique to map the fiber architecture in areas where the trajectories of different fibers intersect. Several diffusion imaging techniques have been developed to reduce the fiber intersecting problem. Some of these MR-based approaches “beyond the diffusion tensor” are called diffusion spectrum imaging, q-ball imaging and spherical deconvolution [49, 50] but do not completely solve the problem. (2) Secondly, there are the difficulties in distinguishing the different fascicles in areas where tracts run in parallel (e.g., the optic radiations and the fibers of the IFOF). (3) Thirdly, there is the inability to follow the terminal branches of the white matter bundles: it is only possible to infer their final cortical destinations from the location and orientation of the average tract end points. According to Zemmoura and al. [51], novel approaches to solve this problem have been suggested, such as tract reconstruction based on their anatomical termination near the gray–white matter boundary and other postmortem neuroimaging techniques such as 3D polarized light imaging [52].

Some authors may argue that direct and indirect segmentation used in this systematic review could be confusing [53]. Hence the advent of virtual dissection by diffusion MRI tractography led several authors to integrate short-distance frontoparietal and parieto-temporal connections under the arcuate terminology. Indeed, a largely cited tractographic study introduced in 2005 the terms “direct” and “indirect” pathways to

described the temporo-parietal hub between temporo-parietal (posterior indirect segment) and parieto-frontal (anterior indirect segment) fibers [28]. As in the study of Mandonnet and al [53], the anterior indirect segment of our review corresponds to the SLF III, and the posterior indirect tract corresponds to the vertical temporo-parietal fasciculus. Whatever the taxonomy used, this review aims at collecting and harmonizing the description regarding each part of the arcuate fasciculus provided in the literature. This systematic review may help younger neuroscientist to better understand cortical terminations variations, whatever the taxonomy plebiscite in the future.

Conclusion

‘In all domains, physiology has its firmest foundations in anatomy’ (Brodman 1908).

Fiber dissection of postmortem human brains and DTI in vivo tractography has enabled the isolation of the three components of the AF. The following portions and cortical connections were identified: (1) the anterior indirect segment, connecting the supramarginal and superior temporal gyri with the precentral gyrus; (2) the posterior indirect segment, connecting the posterior portion of the middle temporal gyrus with the angular gyrus; and (3) the direct AF segment that connects the middle and inferior temporal gyri with the precentral and posterior portion of the inferior and middle frontal gyri. Understanding relationships between the AF and other tracts remains a challenge to better understand the complex organization of the functional processing of language in the human brain. Further study is needed to assess neuropsychological deficit using this classification, to know if inter-individual variability is correlated with subcomponents of the AF.

Author contributions FB: project development; data collection and management; data analysis; manuscript writing/editing; reviewed final version of the manuscript and approval for submission. IZ: data analysis; manuscript writing; critical revision of the article; reviewed final version of the manuscript and approval for submission. ATM: analysis and interpretation of data; critical revision of the article; reviewed final version of the manuscript and approval for submission. JML: reviewed final version of the manuscript and approval for submission. PM: project development; analysis and interpretation of data; critical revision of the article; reviewed final version of the manuscript and approval for submission.

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Compliance with ethical standards

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