

A review of the anatomy and function of the white matter tracts in language
production and comprehension

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Abstract

Much is known about the role of various cortical areas in language production and comprehension. The shift towards network approaches in recent years has highlighted the importance of uncovering the role of the white matter in connecting these areas. However, despite a relatively large body of research, the function of many of these tracts is still underdefined. In this paper, we present a comprehensive review of the empirical evidence on the role of eight major tracts that are hypothesized to be involved in language processing (inferior longitudinal fasciculus, inferior fronto-occipital fasciculus, uncinate fasciculus, the extreme capsule, middle longitudinal fasciculus, superior longitudinal fasciculus, arcuate fasciculus and frontal aslant tract). For each tract, we hypothesize the tract's role based on the function of the cortical regions it connects. We then evaluate these hypotheses in light of data from three sources: studies in neurotypical individuals, neuropsychological data, and intraoperative stimulation studies. Finally, we summarize the conclusions supported by the data and highlight the areas in need of further investigation.

Keywords: white matter; connectivity; language production; language comprehension; inferior longitudinal fasciculus, inferior fronto-occipital fasciculus, uncinate fasciculus, the extreme capsule, middle longitudinal fasciculus, superior longitudinal fasciculus, arcuate fasciculus; frontal aslant tract

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Detailed reviews exist of the role of cortical regions in language production and comprehension (e.g., Kemmerer, 2019; Nozari, 2021; Price, 2012). In recent years, however, interest has extended from uncovering the role of gray matter to how the interactions between different cortical regions give rise to language processing. A significant methodological development in this vein has been the study of white matter tracts, i.e., the pathways that connect various bodies of gray matter. The ultimate white matter map, the human connectome, represents a complex network of connections that forms the neurobiological basis of human cognition, including language processing. Compared to the study of gray matter, the study of white matter tracts in language processing is still in its infancy. New tracts are discovered, better anatomical descriptions of known tracts are offered, and new and more nuanced functions for each tract are frequently proposed in recent publications. The purpose of the current article is to present an up-to-date review of the white matter tracts involved in language production and comprehension. We first present an overview of the computational architecture of comprehension and production, followed by a brief review of the role of the cortical regions in carrying out those computations. Next, we focus on each individual tract, its anatomical connections and its hypothesized role(s) based on the cortical regions it connects. We then review the empirical evidence for and against such hypotheses, summarize the conclusions, and point out areas in need of further research.

1. The computational architecture of language production and comprehension

Years of research and a large body of empirical evidence have been dedicated to uncovering the nature and levels of representations in language production and comprehension and the principles that govern these systems, leading to the proposal of sophisticated computational

models (e.g., Dell, 1986; Levelt et al., 1999; McClelland & Elman, 1986). The gist is that the two systems have much in common (Fig. 1). Production starts with formulating a message through the activation of semantic knowledge, and continues by activating lexical items, ordering them into a syntactic sequence, mapping each word onto its phonemes, activating the articulatory phonetic representations corresponding to the phonological plans, and ultimately executing speech motor commands. The system has a number of key properties: (1) spreading activation not only activates the target (e.g., cat), but also related representations (e.g., “dog”; Levelt et al., 1999; see Nozari & Pinet, 2020, for a review). (2) Activation is cascaded, meaning that activated non-target representations (e.g., “dog”) also activate their segments (e.g., /d/; Dell, 1986). (3) The system has some degree of feedback from later to earlier layers, i.e., phonemes /æ/ and /t/ in “cat” feed back to other words that share them (e.g., “mat”) and activate them (Dell, 1986; Rapp & Goldrick, 2000). These general properties are observed not only in spoken production, but also in other production modalities such as handwriting and typing (e.g., Pinet & Nozari, 2018; Rapp & Fischer-Baum, 2014).

In many ways, comprehension can be viewed as an inverted version of production (see Fig. 1). Here, the acoustic signal first activates the phonetic features. These features then activate phonemes, words, and ultimately semantic knowledge, translating sound into a meaningful message. While the nature of lower-level representations (articulatory-phonetic features vs. acoustic features) obviously differ between production and comprehension, most researchers agree that higher-level representations, e.g., words, semantic features, and syntactic structures are shared between the two (e.g., Nozari, 2020; Warker et al., 2009). Moreover, similar to production, comprehension also involves the co-activation of related non-target representations, cascading and feedback (McClelland & Elman, 1986). These properties have several consequences for the studies

of neurobiology of language. (a) Isolating various components (e.g., word representations) in cascaded systems is not easy. This is because activation can rapidly spread through the later layers of the system (e.g., Costa et al., 2009) while still converging on specific representations in earlier layers. The feedback from later to earlier layers further complicates the interpretation of events using a linear timeline. This, in turn, leads to difficulty in separating operations such as semantic-lexical activation and lexical selection (Riès et al., 2017). The good news is that despite the characteristics of cascading and interactivity, the evidence points to some degree of modularity in the language system (Dell, 1986; Rapp & Goldrick, 2000; see Dell, Nozari, & Oppenheim, 2014, for a review). This global modularity, despite local interactivity, has been a key factor in the success of neural studies in pinpointing individual operations to specific neural regions, but it is important to keep in mind that a clean demarcation between operations such as lexical activation and lexical selection and the neural regions responsible for the two is unlikely to be possible (Riès et al., 2017).

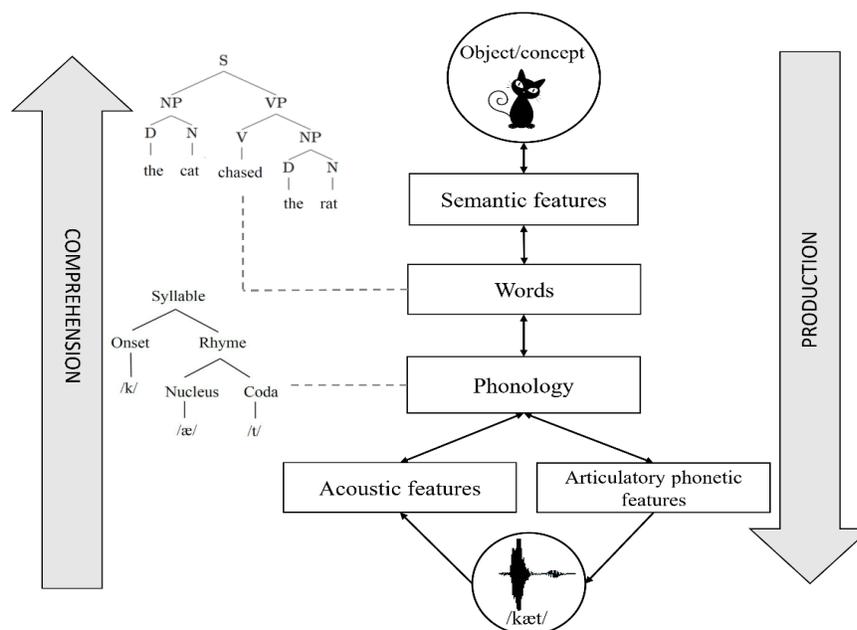


Figure 1. A schematic of the cognitive architecture of language production and comprehension.

2. Neural underpinnings of language production and comprehension

Early studies of the neurobiology of language were mostly focused on defining the specific role of various cortical regions in language production and comprehension. This research has been largely successful in reconstructing the *language network*. The most widely accepted version of this network is Hickok and Poeppel's (2007) dual-stream network. In this model, a largely bilaterally organized ventral stream is responsible for mapping sound to meaning. A predominantly left-lateralized dorsal stream, on the other hand, maps the acoustic signal to articulatory motor commands. The two streams, thus, roughly carry out the operations related to comprehension and production, although equating the dorsal stream with production emphasizes production tasks that start with an available phonological sequence (e.g., auditory repetition). Production attempts that start from meaning (as most real-life conversations do) are likely to also involve a large portion of the ventral stream which carries out semantic-lexical processing. Relatedly, comprehension may entail production components, e.g., in the form of subvocal articulation (e.g., Price, 2010), making the contributions of the two streams to comprehension and production less modular. With that in mind, we briefly review the role proposed for different cortical regions in these two streams for language production and comprehension. In later sections, we will use this information to generate predictions about the role of white matter tracts connecting these cortical regions.

Semantic-lexical processing. Semantic processing is common to both comprehension and production, and as mentioned earlier, is unlikely to contain duplicate representations for these two systems. Detailed reviews of the semantic network exist elsewhere (e.g., Binder, 2007), but the gist is that there is an extensive network of distributed features (many of which are in the sensory-motor cortex) with potential "hubs" or convergent zones which represent unified concepts (Patterson & Ralph, 2016). There is disagreement about the degree to which such hubs contain

lexical information vs. pure conceptual knowledge (e.g., Kemmerer, 2019), but computationally speaking, such hubs represent a graded translation of a massive, distributed network of semantic features into a much smaller space of phonological forms. Anterior and middle parts of the lateral temporal cortex (and less often the inferior temporal gyrus; ITG) have been the prime candidates for containing these semantic-lexical representations. Of the two, the anterior temporal lobe (ATL) has been more strongly linked to semantic and the middle temporal gyrus (MTG) to lexical processing. In addition to the temporal cortex, parietal regions, especially the angular gyrus (AG), have been implicated in semantic processing. However, unlike the temporal regions that largely represent individual objects and concepts, the parietal regions appear to be involved in integrative semantic processing, such as event representation (e.g., Binder & Desai, 2011; Ramanan et al., 2018). Finally, frontal regions are often activated during tasks that require semantic-lexical processing. This activation has been taken as representing a top-down boost, either for strengthening associations or for resolving conflict between competing alternatives (e.g., Thompson-Schill et al., 1997; 1998; Wagner et al., 2001). Both point to the concept of “semantic control” (as opposed to the simple activation of semantic knowledge) and mark the critical importance of the connections between temporo-parietal and frontal regions for semantic-lexical processing.

Processing of the acoustic signal. This function is primarily related to comprehension, although it also plays a role in regulating production through monitoring (e.g., Guenther, 2016). The regions usually implicated in the processing of the acoustic signal are the superior temporal gyrus (STG), Heschel’s gyrus and the superior temporal sulcus (STS; e.g., Hickok, 2012). However, tasks that entail auditory discrimination such as changes to the phonetic category may also tap into other regions, such as the left dorsal pars opercularis in the IFG (e.g., Blumstein et

al., 2005), indicating the importance of connections between the temporal auditory cortex and other regions.

Phonological processing. This function is hypothesized to be common to both production and comprehension, although not as uncontroversially as semantic-lexical processing. For example, while some researchers posit the existence of phonemes as distinct representations in perception (e.g., Hickok, 2012), others have questioned this assumption (e.g., Samuel, 2020). When assumed to be independent representations, the neural correlates of phonological processing have often been pinpointed to the posterior STG (pSTG), supramarginal gyrus (SMG), and sometimes posterior MTG (pMTG; e.g., Binder, 2015; Schwartz et al., 2012). It is noteworthy that phonological processing is often confounded with operations underlying phonological working memory (PWM), because keeping a phonological sequence active, say to output in production, relies on PWM. The latter is often localized to the inferior parietal cortex, especially SMG (e.g., Yue et al., 2019), and sometimes extending to the planum temporale (e.g., Buchsbaum & D'Esposito, 2009), although a frontal component has also been identified, which is hypothesized to mark the verbal rehearsal strategy related to keeping phonological forms active in working memory (e.g., Baldo & Dronkers, 2006).

Articulatory processing. This process is primarily related to speech production, although it is sometimes seen during comprehension as well (Price, 2010). The goal of this operation is to translate the phonological representations into motor commands. The neural regions proposed for this operation are the lateral and medial surfaces of the frontal cortex. GODIVA (see Guenther, 2016, for a history and complete review) is the most complete model of motor speech production and divides the process into a planning loop and a motor loop. The planning loop consists of the pre-supplementary motor area (preSMA) and left posterior inferior frontal sulcus (pIFS), and

temporarily buffers the utterance before articulation. The motor loop consists of the supplementary motor area (SMA) and the ventral premotor cortex (vPMC) and executes the articulatory motor commands. A combined signal from SMA and vPMC activates motor gestures in the ventral motor cortex (vMC), which drives the articulators (Guenther, 2016; Nozari, 2021).

Syntactic processing. The operations reviewed above are all involved in single-word processing, but speech often consists of phrases, sentences, and paragraphs. Although the body of literature probing the neural correlates of syntactic production is not small, pinpointing the neural substrates of syntax has been far from easy. For years, the inferior frontal gyrus (IFG), especially pars triangularis, was considered the main region involved in syntactic processing (Friederici, 2017; Grodzinsky & Santi, 2008; Hagoort, 2014; Matchin & Rogalsky, 2017), primarily based on the neuropsychological evidence of patients with Broca's aphasia suffering from agrammatism (Caramazza & Zurif, 1976; Goodglass, 1993; 1968). In line with this proposal, several high-powered lesion-symptom mapping studies linked IFG lesions to syntactic parsing deficits in comprehension (Fridriksson et al., 2018; Magnúsdóttir et al., 2013; Mesulam et al., 2015; Wilson et al., 2010; 2011). These were complemented with neuroimaging studies linking syntactic comprehension to IFG (Friederici, 2011; 2017; Hagoort, 2014). At the same time, more and more studies pointed out an even more prominent link between syntactic processing deficits and regions in the posterior temporal cortex (Baldo & Dronkers, 2007; Dronkers et al., 2004; Peelle et al., 2008; Pillay et al., 2017; Rogalsky et al., 2018; Wilson, Eriksson, et al., 2018; Wilson & Saygin, 2004; Wilson, Yen, et al., 2018). In reviewing the neuroimaging data linking IFG to syntactic comprehension, Matchin et al. (2017) point out that the activation of IFG is almost always observed along with that of the posterior temporal lobe. The distinction is further complicated by the proposed involvement of IFG in working memory and executive control processes that

syntactic processing, in most cases, taps into (e.g., Nozari & Thompson-Schill, 2016; Rogalsky & Hickok, 2011). For this reason, some have proposed the posterior temporal cortex as a more critical region in syntactic processing than the IFG (Bornkessel-Schlesewsky et al., 2015; Pillay et al., 2017). A more nuanced proposal has been recently put forth by Matchin and Hickok (2020). The proposal emphasizes the different computational demands of syntactic processing in comprehension and production, which give rise to differential predictions regarding the role of certain regions in syntactic processing depending on the task. Specifically, Matchin and Hickok (2020) propose that in comprehension, auditory sequences in pSTG are decoded into hierarchical structures in pMTG, and are further connected to two semantic hubs, the ATL and the AG, representing the knowledge of objects and events, respectively (Binder & Desai, 2011). In production, the unstructured semantic information is turned into hierarchical propositions by pMTG and passed on to IFG's pars triangularis for conversion into morphological chunks.

3. White matter tracts involved in language processing

As implied by their names, ventral and dorsal “streams” are more than just a collection of disconnected cortical regions. Rather, they mark connected pathways involved in semantic-lexical and phonological-motor processing, respectively. This rough division is a useful guide for identifying the white matter tracts potentially involved in language processing, although researchers sometimes differ in their assignment of tracts to streams, especially for multi-branch tracts that may encompass both streams. The ventral stream is often thought to include the inferior longitudinal fasciculus (ILF), the inferior fronto-occipital fasciculus (IFOF), the uncinate fasciculus (UF), the extreme capsule (EmC), a branch of the middle longitudinal fasciculus (MdLF), and possibly a short segment of the superior longitudinal fasciculus (SLF; Dick & Tremblay, 2012; Saur et al., 2008; Weiller et al., 2021; Wong et al., 2011; Yang et al., 2017). The

dorsal stream contains the bulk of SLF, consisting of SLF-I, SLF-II, SLF-III, and SLF-tp, a part of the SLF that connects temporal and parietal lobes. Some researchers also consider the arcuate fasciculus (AF) to be another branch of the SLF. Finally, a more recently discovered tract, the frontal aslant tract (FAT; Enatsu et al., 2016; Ookawa et al., 2017), lies in the anteriormost part of the dorsal tract. In addition to these, there are a few other small tracts that are not frequently included in studies of white matter for language, such as the operculo-premotor fascicle (OpPMF) connecting the pars opercularis to the premotor region and trianguloorbitalis system (TrOrS) connecting the pars triangularis to the pars orbitalis. Although some have suggested a role of these tracts in language processing based on their anatomical connections (Lemaire, Golby, Wells III, et al., 2013; 2013), functional data on these tracts are currently sparse. Therefore, we do not include them in this paper.

In what follows, we discuss the above-mentioned tracts individually (or sometimes in pairs for comparison). We first review the anatomy of the tract and the cortical regions it connects, based on which predictions about its function can be generated. We then review the empirical evidence regarding the role of the tract, with a heavier focus on its involvement in language processing, and discuss the extent to which the current evidence supports the predictions. Empirical evidence for studying white matter connectivity comes from several different sources. A precise method for studying the anatomy of white matter, used by early anatomists, is post-mortem fiber dissection. This technique entails the peeling of the white matter tracts from the brain and displaying their 3-dimensional structure. The complex and cumbersome procedures required for the preparation of the brain tissue for fiber dissection, together with the emergence of non-invasive methods, have decreased the popularity of this approach, although its precision for studying the subcomponents of white matter tracts has led to renewed interest in its revival in recent years (Komaitis et al.,

2019; Martino et al., 2013). Another precise method is autoradiography, an imaging technique using radioactive tracers, which allows for clear tracing of the origins and termination points of neural pathways (Cowan et al., 1972). Due to toxicity, in-vivo autoradiography is not an option in humans, but has been a widely used technique for the identification of white matter pathways in primates, such as Rhesus monkeys (Schmahmann & Pandya, 2006; Schmahmann et al., 2007).

Although precise, neither of the two methods described above is practical for studying white matter structures in living humans. A much more popular and widely used technique is diffusion-weighted magnetic resonance imaging (DW-MRI, or DWI for short) (Craddock et al., 2013; Mori & Zhang, 2006; Mukherjee et al., 2008). This technique relies on the systematic diffusion patterns of water molecules in the tissue, which can help delineate the tissue architecture (Alexander et al., 2007; Le Bihan et al., 2001). A special kind of DWI, diffusion tensor imaging (DTI), sometimes combined with resting-state fMRI, is especially popular for delineating the white matter tracts in the brain (i.e., tractography) (Greicius et al., 2009; Skudlarski et al., 2008). DTI is informative for uncovering the white matter structure in both neurotypical individuals and clinical populations. It uses a number of metrics, the most common of which are fractional anisotropy (FA), mean diffusivity (MD), radial diffusivity (RD), and axial diffusivity (AD). FA varies between 0 and 1 and measures the degree of diffusion anisotropy. When diffusion is unrestricted (or equally restricted in all direction), FA is 0. When, on the other hand, diffusion is fully restricted along one axis, FA is 1. Therefore, in gray matter which the motion of molecules is in all direction, FA is low. In the white matter, molecules are organized in one direction and FA is generally higher (Alexander et al., 2007; Le Bihan et al., 2001). Damage to, or the loss of, white matter is associated with lower FA values. Mean diffusivity (MD) measures the overall diffusivity in the tissue. Similar to FA, it is sensitive to the barriers of diffusivity but, unlike FA, it is insensitive to the direction of

the diffusion, i.e., it measures the rotationally invariant magnitude of water diffusion in the tissue (Alexander et al., 2007; Le Bihan et al., 2001). In case of lesions to the white matter, MD increases (Madden et al., 2012). AD and RD reflects the main direction of diffusivity. AD describes the magnitude of diffusion parallel to axons, whereas RD describes the diffusivity perpendicular to axonal fibers (Alexander et al., 2007; Le Bihan et al., 2001). Some of these measures are more sensitive than others for detecting white matter abnormalities. For example, relatively pure myelin deficits that are undetectable with FA, often lead to a modest increase in RD (De Erausquin & Alba-Ferrara, 2013). It is important to note that DTI is a correlational technique, meaning that although an association can be established between certain structural properties of the white matter tracts and behavior, it may not translate into a causal role of the tract in generating a certain behavior.

Another popular technique for studying white matter is voxel-based lesion-symptom mapping (VLSM) or its related technique voxel-based morphometry (VBM; Bates et al., 2003; Mechelli et al., 2005). These techniques are heavily employed in neuropsychological work and define a statistical relationship between lesion (measured in voxels) and behavioral impairment (Faulkner & Wilshire, 2020; Gleichgerrcht et al., 2017; Harvey & Schnur, 2015). The rationale is that if damage to a tract leads to an impairment in a behavior, the tract is likely to play a critical role in carrying out that behavior. Although the results are less prone to interpretation as an epiphenomenon compared to associative measures, it is still difficult to pinpoint a function to a single tract. The reason is that impaired behavior as a function of a lesioned tract may reflect the disruption of a network, another part of which may play an even more critical role in the behavior than the lesioned tract itself.

Unlike DTI and VLSM/VBM, direct stimulation of white matter (DES; Duffau, 2015; 2014; Mandonnet et al., 2010) is an invasive methodology that allows for real-time direct functional mapping of white matter tracts intraoperatively. It involves applying localized electrical stimulation to cortical and/or subcortical areas via either a monopolar or bipolar electrode to produce a transient inhibition or excitation in function. The technique may be employed in both an asleep and awake patient. In an asleep patient, where eliciting an overt behavioral response is not possible, electrophysiological measures such as electromyograms or visual evoked potentials are sometimes obtained. In awake patients, changes to performance on a behavioral task is often measured as a function of stimulation. Since the technique involves a direct manipulation of the tissue, a change in behavior can be more readily translated into a causal role for the tissue in generating that behavior.

The techniques named above have identified three main types of white matter pathway: *projection*, *commissural* and *association fibers* (Gottlieb & Cowan, 1973; Schmammann et al., 2007; Wedeen et al., 2008; Zhang et al., 2010). Projection fibers are ascending and descending fibers which connect the cortex with the brainstem, cerebellum, and spinal cord. The most well-known projection fiber in the brain is the internal capsule. The commissural fibers are axons that connect the two hemispheres (Catani et al., 2002). The main commissural fibers are the corpus callosum, the anterior commissure and the posterior commissure. Association fibers are axons which connect cortical areas within the same hemisphere. Long and short association fibers connect distant and adjacent areas, respectively (Guevara et al., 2020). Here, we focus on the role of association fibers in language processing.

4. ILF and IFOF

ILF and IFOF are the two major fiber tracts connecting the occipital lobe to the anterior regions (temporal and frontal lobes; Fig. 2a, 2b). After initial controversies about the nature of these pathways, DTI, electrostimulation and non-human primate studies have now established that ILF and IFOF are long association —and not projection— fibers (Catani et al., 2002; 2003; Hua et al., 2009; Mandonnet et al., 2007; Mettler, 1935; Oishi et al., 2011; Schmahmann & Pandya, 2006; Seltzer & Pandya, 1984; Wakana et al., 2004). There has also been much debate on whether ILF and IFOF are indeed two separate tracts or whether IFOF is the continuation of ILF into the MdLF, EmC, and UF (Schmahmann & Pandya, 2006). This debate is important, in part because of the different endpoints of these tracts: ILF ends in the temporal pole, whereas IFOF ends in the frontal cortex. Therefore, the existence of IFOF as an independent tract would point to direct connections between the occipital and frontal lobes. The evidence for the unity or separation of ILF and IFOF is mixed: autoradiography studies in non-human primates point to the ILF connecting occipital and temporal cortices, but not to a separate IFOF connecting occipital to frontal lobes directly (Mettler, 1935; Schmahmann & Pandya, 2006; Yeterian et al., 2012). In contrast, DTI studies in humans consistently support the separation of these two tracts (Catani et al., 2002; 2003; Caverzasi et al., 2014; Holl et al., 2011; Hua et al., 2009; Oishi et al., 2010; Thiebaut De Schotten et al., 2011; Turken & Dronkers, 2011; Wakana et al., 2007). Given our focus on the role of these tracts in human cognition, we will follow the DTI findings and assume that they are separate tracts, but discuss them together to compare and contrast when possible.

ILF (Fig. 2a) is a large multilayer fiber tract connecting the occipital cortex with the anterior temporal lobe (Catani et al., 2002; 2003; Panesar et al., 2018; Sali et al., 2018; Zemmoura et al., 2021). Its dorsal component originates from the cuneus and projects to the superior and middle temporal gyri. Its ventral component originates from the lingual and fusiform gyri, and

projects to the superior, middle, and inferior temporal gyri (Latini et al., 2017; Panesar et al., 2018; Sali et al., 2018; Zemmoura et al., 2021). IFOF (Fig. 2b) is also a large multilayered tract originating from the occipital and occipitotemporal, and parietal regions. It runs through the extreme and external capsules and terminates in anterior frontal areas, including the IFG and the dorsolateral prefrontal cortex or DLPFC (Conner, Briggs, Sali, et al., 2018; Duffau, 2015). IFOF has two components: (i) a superficial dorsal component, which connects the pars triangularis and orbitalis with the superior parietal lobe and the posterior portion of the superior and middle occipital gyri, and (ii) a deep ventral component, which connects the posterior portion of the inferior occipital gyrus and the posterior basal temporal region with three different areas in the middle frontal gyrus (MFG), the DLPFC and the orbitofrontal cortex (Martino et al., 2010; Sarubbo et al., 2013).

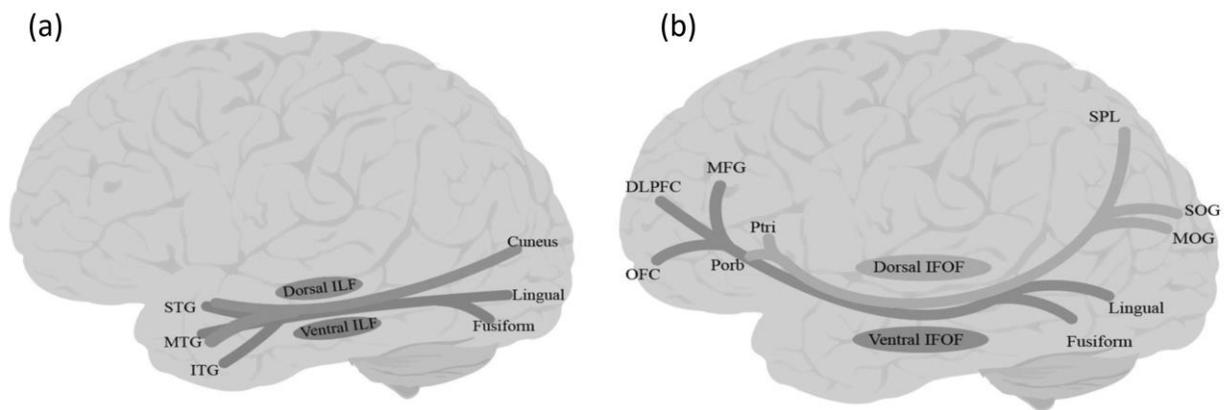


Figure 2. Anatomy of ILF (a) and IFOF (b). DLPFC = dorsolateral prefrontal cortex; ITG = inferior temporal gyrus; MFG = middle frontal gyrus; MTG = middle temporal gyrus; MOG = middle occipital gyrus; OFC = orbitofrontal cortex; Ptri = pars triangularis; Porb = pars orbitalis; SOG = superior occipital gyrus; SPL = superior parietal lobe; STG = superior temporal gyrus.

Given the occipital origin of both tracts and the links they provide to temporal, parietal and frontal regions, it is hardly surprising that they have both been implicated in operations that depend on visual perception, such as object and face recognition and spatial attention. In keeping with these predictions, DTI studies have shown a role for ILF in object recognition (e.g., Mandonnet et al., 2009; Ortibus et al., 2012), scene recognition (e.g., Tavor et al., 2014), and face recognition (e.g., Hodgetts et al., 2015; Tavor et al., 2014). Complementing these, are reports of prosopagnosia after the disruption of right ILF (e.g., Grossi et al., 2014; Thomas et al., 2009; Valdés-Sosa et al., 2011), and the induction of visual hemiagnosia after the stimulation of the right ILF (Coello et al., 2013), further pointing to a critical role of the ILF in face and object recognition.

Evidence for the role of IFOF in face perception is mixed. Some have linked the integrity of IFOF to face perception in prosopagnosia and neurotypical adults (e.g., Thomas et al., 2008; Valdés-Sosa et al., 2011) but others have explicitly shown that such a relationship is limited to the right ILF (e.g., Scherf et al., 2014). In contrast, and perhaps due to its stronger connections with the parietal regions, IFOF is more heavily implicated in spatial attention. For example, a decreased FA in the right IFOF in stroke survivors is associated with visual neglect (Toba et al., 2018; Urbanski et al., 2011). Similarly, Herbet, Yordanova, et al. (2017) showed that subcortical stimulation of right IFOF in glioma patients can cause spatial neglect. Both ILF and IFOF have also been linked to the processing of facial emotions (Baggio et al., 2012; Multani et al., 2017).

Aside from a general role in visually guided behavior, connections to a specific part of the temporal cortex, the visual word form area (VWFA), suggest a potential role of these tracts in a specific language task, i.e., reading and perhaps writing. ILF has been identified as one of the three major tracts associated with the VWFA, with SLF and the vertical occipital fasciculus (vOF) as

the other two (Chen et al., 2019). vOF is a fiber bundle connecting dorsolateral and ventrolateral visual cortices, but is rarely mentioned in studies of the matter tracts, most likely because of its overlap with the dorsal parts of ILF and IFOF (Yeatman et al., 2014). It is thus important to keep in mind that some of the functions attributed to ILF and IFOF in reading may actually be carried out by vOF. Various studies have linked reading or reading deficits to ILF, IFOF, or both (Arrington et al., 2017; Broce et al., 2019; Grotheer et al., 2021; Horowitz-Kraus et al., 2014; Kumar & Padakannaya, 2019; Sarubbo et al., 2015; Vandermosten et al., 2015; Zhao et al., 2016). For example, Broce et al. (2019) showed that the properties of ILF and IFOF were predictive of early literacy skills in 5-8-year-old children, after controlling for a number of factors, including age, gender, IQ, the overall development of the white matter and phonological skills. In a study comparing typically developing children with children with dyslexia, Zhao et al. (2016) showed that IFOF was significantly less left-lateralized in the dyslexic group, and the degree of lateralization was correlated with reading abilities (see also Carter et al., 2009; Steinbrink et al., 2008; Su, Zhao, et al., 2018; Vanderauwera et al., 2018; Vandermosten et al., 2015; Yeatman et al., 2012 see Vandermosten et al. 2012 for a review).

Left ILF's critical role in orthographic processing was demonstrated in a study of 67 individuals with brain damage, in whom a PCA-derived orthographic index (after regressing out non-orthographic tasks) correlated significantly with left ILF's integrity, even after controlling for other confounding factors (Wang et al., 2020 see also Farah et al., 2020; Su et al., 2018). Reports from awake craniotomy studies also confirm the link between these tracts and reading/writing abilities. In a study of glioma patients undergoing awake surgery, Sarubbo et al. (2015) found a close correspondence between the spatial distribution of alexia and that of the ILF (see also Enatsu et al., 2017; Epelbaum et al., 2008; Gil-Robles et al., 2013, for demonstrations of ILF stimulation

disturbing reading). Similarly, in a patient undergoing surgery for left inferior parietal glioma, Motomura et al. (2014) applied subcortical stimulation to IFOF and induced transient alexia and agraphia, suggesting a critical role of IFOF in these operations.

The literature above clearly links ILF and IFOF to language processing through reading. There is, however, evidence that these tracts contribute to language processing in more fundamental ways, namely through their involvement in semantic-lexical processing. General evidence for this claim comes from studies linking comprehension abilities to ILF, IFOF, or both (e.g., Del Tufo et al., 2019), or demonstrating their abnormalities in impaired semantic processing in neuropsychological disorders (e.g., Botha et al., 2015; D'Anna et al., 2016; Ivanova et al., 2016; Surbeck et al., 2020; Whitwell et al., 2010). There have also been attempts at pinpointing the function(s) of these tracts more precisely. Anatomically, there are two reasons to expect a contribution of these tracts to lexical semantic processing: (a) traversing through the length of the temporal lobe, they connect areas that are clearly implicated in storing conceptual, lexical, and auditory representations, and might thus point to a role in semantic and lexical *retrieval*. (b) Connections between the temporal lobe (especially MTG) and frontal (and some parietal) regions point to a potential role in semantic and lexical *control*. The main difference between the two is that the former includes any situations that require activation of semantic-lexical concepts, while the latter selectively involves situations that include either high competition or weak association (Martin & Cheng, 2006; Nozari, Mirman, & Thompson-Schill, 2016). We will return to this point at the end of this section.

The standard test of pure semantic processing is usually a test such as the Pyramids and Palm Trees Test which assesses semantic relations without the need to appeal to lexical labels. There are indeed reports of a correlation between scores on such tests and IFOF in particular (de

Zubicaray et al., 2011; Herbet, Moritz-Gasser, et al., 2017; Mirman et al., 2015; Moritz-Gasser et al., 2013). But the task is heavily influenced by visual processing abilities that are also linked to ILF and IFOF. To ensure pure contribution of these tracts to semantic processing independently of visual processing, it is important to use other modalities (e.g., the auditory modality). This often means that some of the tasks entail lexical items, which makes the extraction of pure semantics difficult. Fortunately, based on the earlier discussion of the stages of production, such a clear-cut distinction is perhaps neither necessary nor extremely useful in understanding the neurobiology of language: lexical-semantic representations are representations necessary for the mapping of distributed semantic features onto phonological representations, and likely include multiple layers of representations that gradually move from unifying semantic features to representing the more formal aspects of concepts. We will thus focus on studies providing converging evidence from multiple tasks on the involvement of ILF/IFOF in lexical-semantic processing.

Faulkner and Wilshire (2020) used VLSM in 63 postoperative tumor patients and found a correlation between lesions in the territory of left ILF and semantic-lexical mapping, which they computed as a function of semantic and omission errors in picture naming, as well as performance on a category probe task after regressing out phonological fluency scores (note that the use of probabilistic maps in that study makes disentangling from close tracts such as left IFOF very difficult). In a study of 55 right-handed older adults, de Zubicaray et al. (2011), used PCA to extract what they referred to as a “semantic memory” component, based on six cognitive tests (Pyramids and Palm Trees, Boston naming, PALPA sentence–picture matching, Category fluency, WAIS-III information and WAIS-III similarities). They then demonstrated a correlation between this measure and FA values in left IFOF and UF. In a VLSM study of 43 individuals with chronic left-hemisphere stroke, Griffis et al. (2017) showed that lesions in ILF and IFOF (as well as AF) were

associated with poorer performance in picture naming. This may be interpreted as a problem in extracting the visual semantic information, but these lesions were also predictive of poor verbal fluency and auditory semantic decisions, two tasks that do not require visual processing, but instead, semantic-lexical processing. In another large-scale VLSM study of 99 individuals with chronic stroke, Mirman et al. (2015) used a large battery of cognitive tests, and used factor analysis to extract three main factors: semantic recognition (encompassing both verbal and non-verbal comprehension), speech recognition (auditory processing of verbal materials), and speech production (phonological and articulatory phonetic encoding). Of the three, semantic recognition was associated with lesions in IFOF (as well as UF and anterior thalamic radiation or ATR). In another large-scale study of 76 individual with brain damage, Han et al. (2013) used visual and auditory variants of naming and semantic judgement tasks and found impaired performance to correlate with the FA value of IFOF, as well as left ATR and UF, after controlling for lesion volume and refuting the influence of gray matter, non-semantic operations (e.g., oral repetition) and numerical cognition.

Together, these studies demonstrate that these tracts play a role in semantic-lexical processing, distinct from other aspects of language processing, such as processing phonological information. The involvement of ILF and IFOF in semantic-lexical processing naturally predicts a role for them in language production from meaning. In line with this prediction, Grossman et al. (2013) studied 15 individuals with nonfluent aphasia, and reported a correspondence between the integrity of the fronto-occipital white matter (most likely IFOF), as well as UF, and the mean length and well-formedness of utterances. Several studies have more sharply focused on the relationship between these tracts and speech errors in picture naming. If these tracts play a critical role in mapping semantics to lexical items during word production, their disruption should lead to

an increase in certain error types but not others. Specifically, we would expect an increase in lexical errors (including semantically related and unrelated words) and possibly omissions (due to the inability to retrieve the correct semantic concept or lexical item). The empirical data are aligned with this prediction: in a study of 32 participants with chronic post-stroke aphasia, McKinnon et al. (2018) found a close correspondence between the number of semantic paraphasias and axonal loss in the ILF. Similarly, in a combined navigated transcranial magnetic stimulation (nTMS) and DTI of 10 patients with brain tumors, Raffa et al. (2016) found a link between semantic errors in picture naming and ILF and IFOF (see Sarubbo et al., 2013 for a similar link between semantic paraphasias and IFOF). Finally, Stark et al. (2019) studied speech errors of 120 individuals with chronic left-hemisphere stroke in a picture naming task, and also administered a test of connected speech using picture description. In both picture naming and connected speech, unrelated errors were linked to ILF and IFOF, and in connected speech, semantic paraphasias were also linked to these two tracts (it is noteworthy that SLF was implicated in all of these cases as well).

Complementing these, are studies of intraoperative stimulation of ILF/IFOF. The majority of such studies have found IFOF stimulation to cause semantic paraphasias (Almairac et al., 2015; Duffau, 2015; 2003; 2008; 2009; Fernández et al., 2020; Gil-Robles et al., 2013; Mandonnet et al., 2007; Moritz-Gasser et al., 2013; Motomura et al., 2018; 2014). ILF's role is more contested; some have found ILF stimulation to cause omission errors (Herbet et al., 2019) and some have found no adverse effect on language production when stimulating this tract (e.g., Gil-Robles et al., 2013; Mandonnet et al., 2007; Moritz-Gasser et al., 2013). Collectively, the body of literature reviewed above supports the involvement of these tracts in semantic-lexical processing, with a suggestion that the ILF may be more strongly involved in lexical-to-semantic mapping (i.e., comprehension) and IFOF in semantic-to-lexical mapping (i.e., production). This distinction was supported in a

study by Harvey and Schnur (2015). There are, however, other studies that have attributed comprehension vs. production functions to different parts of each tract. For example, some studies have claimed that middle and posterior parts of the ILF and IFOF are related to comprehension (Ivanova et al., 2016; Zhang et al., 2018), whereas anterior portions of these tracts are important for speech production (Ivanova et al., 2016; Tuncer et al., 2021). Focusing on disentangling comprehension/production contribution of ILF and IFOF is a fruitful area for future research.

More recent studies have started to tap more closely into the functions of ILF and IFOF in terms of semantic-lexical *control*. Control has been discussed in two senses in the language literature: conflict and weak associations (e.g., Thompson-Schill & Botvinick, 2006; Martin & Cheng, 2006; see Nozari, Mirman, & Thompson-Schill, 2016, for a unifying view). For example, words belonging to the same semantic category but with opposite valences can make semantic judgment harder by inducing conflict. Similarly, words with distant relationships are harder to judge as related, because of the weak association between them. Dávolos et al. (2020) presented participants with visual cue words, followed by three words, from which to choose the most related word to the cue word. Congruency and strength of association were manipulated between the cue and target words and were shown to be correlated with FA in the left ILF, suggesting a role of this tract in lexical-semantic control. FA in the right IFOF, on the other hand, was related to processing under low demands (i.e., no conflict, strong association). In another study, Harvey & Schnur (2015) compared semantic interference in production (using the blocked cyclic naming task) and comprehension (using a word-to-picture matching task) in 18 participants with left hemisphere stroke. They reported an association between ILF and semantic interference in word comprehension, whereas IFOF was critical for resolving semantic interference in production. Finally, Nugiel et al. (2016) used a verb generation task in which verbs were elicited from

neurotypical individuals either by nouns that strongly elicit a certain verb (e.g., scissors → cut) or by nouns that are loosely associated with multiple verbs (e.g., ball → throw, roll, play, etc.), with the latter requiring greater semantic-lexical control. They found both ILF and IFOF's structure to be predictive of semantic control in this study. This brief review shows that there is growing evidence for the critical contribution of these two tracts not just to semantic retrieval, but specifically to semantic control, although it remains debated whether the tracts contribute differently to semantic control in comprehension vs. production.

Lastly, we must also mention verbal fluency, as a test commonly used in assessing the contribution of white matter to language production. Verbal fluency tasks come in two varieties: semantic or category fluency refers to a test in which participants are prompted to produce as many words as possible from a certain semantic category (e.g., animals). Phonemic or letter fluency tasks, on the other hand, require participants to produce as many words beginning with a certain sound or letter, irrespective of their semantic category. The idea is that the two variants index semantic-lexical and lexical-segmental processing, respectively. One issue with verbal fluency tasks is that they confound primary production functions (i.e., the ability to activate, retrieve, and produce a word) with cognitive control functions that are often inherent to these tasks. For example, scoring high on the category fluency task when the target group is "animals" often entails a strategy of focusing on a sub-category (e.g., farm animals), exhausting that and then successfully switching to a new sub-category (e.g., sea animals; Hirshorn & Thompson-Schill, 2006). This ability requires cognitive control. Without detailed analyses to extract the processes involved in this task, it is unclear whether a correlation between performance and white matter measurements is reflecting a primary production operation or, instead, the implementation of control in language production. This caveat makes the interpretation of findings from these tasks difficult, as will be

seen in several of the following sections in which we review the results of correlating performance in verbal fluency tasks with the properties of different tracts. For example, several studies have found a correlation between ILF, IFOF or both in category fluency tasks (e.g., Almairac et al., 2015; Gonzalez et al., 2021; Griffis et al., 2017), but there are also reports of an association of the same tracts with phonemic fluency performance (e.g., Sanvito et al., 2020). Rather than pointing to the involvement of ILF and IFOF in both semantic and phonological processing, these findings most likely show the underspecified nature of the verbal fluency tasks for pinpointing cognitive functions.

Summary. In addition to visually guided tasks, including reading, the evidence suggests that ILF and IFOF play a clear role in semantic-lexical processing in language. The evidence seems to point to a more prominent role of ILF in comprehension and IFOF in production, although alternative accounts, e.g., a posterior-anterior division of labor in each tract, have not been conclusively ruled out. Finally, there is clear evidence linking IFOF and ILF to semantic-lexical control, although more studies will be useful to examine whether a division along comprehension/production lines also exists in the control functions of these tracts.

5. Uncinate fasciculus (UF)

UF (Fig. 3) is a short, hook-shaped bidirectional fiber bundle around the Sylvian fissure, running through the extreme and external capsule, and connecting the temporal pole with the orbitofrontal cortex (OFC; Briggs, Rahimi, et al., 2018; Kier et al., 2004; Papinutto et al., 2016; Von Der Heide et al., 2013). The temporal segment originates from the uncus, entorhinal, and perirhinal cortices, and temporal pole/anterior temporal lobe (Ebeling & Cramon, 1992; Von Der Heide et al., 2013). The frontal termination of the UF has two branches: a larger ventrolateral

branch and a smaller medial branch. The ventral branch terminates in the lateral orbitofrontal cortex while the medial branch terminates in the frontal pole (BA 10; Von Der Heide et al., 2013).

Given the essential role of the orbitofrontal cortex and the limbic system in social cognition (e.g., Rushworth et al., 2007) and the extensive connections between UF and these regions, it is not surprising that abnormalities of UF have been frequently observed in autism spectrum disorder (ASD; Ameis et al., 2011; Lo et al., 2011; Poustka et al., 2012; Pugliese et al., 2009; Travers et al., 2012), conduct disorder (CD; Passamonti et al., 2012; Sarkar et al., 2013; Zhang et al., 2014), social anxiety disorder (Baur et al., 2012; Phan et al., 2009; Tröstl et al., 2011), and schizophrenia (Burns et al., 2003; Jung et al., 2020; Kitis et al., 2012; Kubicki et al., 2005). Also, several studies have demonstrated a correlation between UF and emotional processing, including the interpretation of emotions and the expression of empathy (Coad et al., 2020; Granger et al., 2021; Nakajima et al., 2018; Oishi et al., 2015; Zuurbier et al., 2013). The connection established between the anterior temporal lobe and orbito-frontal cortex and the bidirectional flow of information in UF have also led researchers to propose that the tract is heavily involved in modulating mnemonic representations in the temporal lobe through a temporo-frontal reward-punishment loop, i.e., a learning reinforcement loop for forming episodic memory and learning (see Von Der Heide et al., 2013, for a review). Compatible with such a position, UF has been implicated in learning abilities in both verbal and non-verbal tasks (Alm et al., 2016; Rossi et al., 2017; Thomas et al., 2015), and performance in memory tasks, especially, but not exclusively, verbal memory (Christidi et al., 2014; Diehl et al., 2008; Fujie et al., 2008; Schaeffer et al., 2014; Serra et al., 2012).

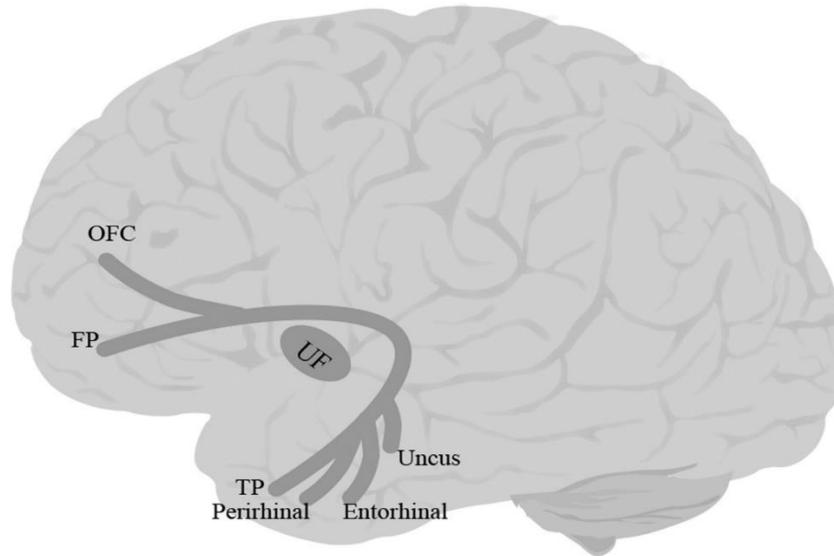


Figure 3. Anatomy of UF. FP = frontal pole; OFC = orbitofrontal cortex; TP = temporal pole.

This tract's connection to the ATL also brings up the possibility of involvement in semantic processing. Generally aligned with a role in semantic processing, UF deficits are often observed in dementia, including the semantic variant of PPA (Agosta et al., 2013; Bouchard et al., 2019; Briggs, Rahimi, et al., 2018; Iaccarino et al., 2015; Powers et al., 2013; Tu et al., 2016), with some studies claiming decreased FA of the UF to be the main predictor of semantic dementia (Agosta et al., 2012; Bouchard et al., 2019), and others showing a correlation between cognitive decline and the integrity of UF (Hiyoshi-Taniguchi et al., 2015; Morikawa et al., 2010). Moreover, UF has been implicated, along with IFOF, in several studies that have used a battery to tap into semantic processing (de Zubicaray et al., 2011; Mirman et al., 2015; see also semantic processing deficits in schizophrenia; Surbeck et al., 2020).

If UF is involved in semantic selection, one could naturally expect it to be important for a variety of language functions that involve semantic processing. In keeping with this, UF is also often implicated in language and language disorders. For example, in stroke patients, some studies

have reported UF's FA values to correlate positively with various measures of language processing, including auditory comprehension, naming, and spontaneous speech (Fridriksson et al., 2013; Zhang et al., 2021; cf., Ivanova et al., 2016).

In PPA too, UF's integrity has been linked to naming and category fluency performance (Catani et al., 2013; Powers et al., 2013). Similarly, the microstructure of UF is predictive of core language scores in children (Dodson et al., 2018). Finally, several studies have implicated UF in reading abilities, including phonemic decoding efficiency (Arrington et al., 2017; Bakhtiari et al., 2014; Cummine et al., 2015; Welcome & Joanisse, 2014). Evidence directly linking UF to picture naming is mixed. Some studies have reported that intraoperative stimulation of UF causes lexical and semantic paraphasia, hesitations and omission errors in picture naming (Raffa et al., 2016). Others have reported that simple language production tasks like picture naming and counting were not disturbed by UF stimulation (Duffau et al., 2009).

One possibility is that of a more nuanced picture. Recall that UF connects ATL to the prefrontal cortex. It is thus possible that its role is not simple semantic retrieval, but semantic control (which is achieved through the interaction between temporal and frontal cortices; e.g., Thompson-Schill et al., 1997). If this is true, one would expect a critical contribution of UF to tasks with greater control demands on the semantic-lexical system. Specific tests of the role of UF in semantic-lexical control in tightly controlled studies are rare in the literature, and the current evidence is mixed. Harvey et al. (2013) tested 10 stroke survivors on two tasks that require semantic/semantic-lexical control, Pyramids and Palm Trees (PPTT), and an auditory word-to-picture matching task with semantic, phonological and unrelated lures. After controlling for total lesion volume, the integrity of UF was a significant predictor of performance both on PPTT and on the word-to-picture matching task with semantic lures, suggesting a role of UF in

semantic/lexical control. Interestingly, this study found no relationship between semantic control and either ILF or IFOF (cf. Harvey & Schnur, 2015). In contrast, Nugiel et al. (2016) found no relationship between performance in the verb generation task, which as explained in the previous section indexes semantic-lexical control when multiple competitors are equally activated, and the microstructural measures of UF, whereas both ILF and IFOF were implicated in that study.

UF is also frequently linked to performance in semantic fluency tasks in various populations, including individuals with Parkinson and Alzheimer's Disease (Di Tella et al., 2020; Lauro et al., 2010; Papagno et al., 2016; 2011; Rodríguez-Aranda et al., 2016), but as explained in the previous section, it is hard to disentangle semantic retrieval from semantic control in the category fluency tasks. Moreover, several studies have suggested UF's involvement in phonemic/letter fluency tasks (Kljajevic et al., 2016; Papagno et al., 2011; Serra et al., 2012), even though some have reported greater contribution to semantic over letter fluency performance (Li et al., 2017). If phonemic/letter fluency truly indexes segmental processing abilities, this finding, together with the role of UF in phonemic decoding proposed in reading, may attribute a dorsal-stream function to a ventral tract, a conclusion that does not fit well with the rest of this tract's function, or with the null effects regarding its influence on segmental processing (e.g., no phonological errors or disruption in phonological processing during its stimulation; Duffau et al., 2009; Nomura et al., 2013; Raffa et al., 2016). A more plausible explanation is that the phonemic/letter fluency tasks also tap into other abilities, e.g., controlled lexical selection, that are more aligned with the functions of UF. This can be tested by ruling out UF's function in tasks that require phoneme/letter processing without strong demands on semantic-lexical selection.

One last finding that is relevant here is the selective impairment of naming pictures of famous people and objects when UF is removed: in a study of 44 glioma patients before and after

the surgical removal of UF, Papagno et al. (2011) reported changes to word production in picture naming, naming of famous faces, as well as impaired performance on verbal fluency tasks. However, a later study that followed up on 17 glioma patients up to nine months after their surgery, showed that performance on picture naming and verbal fluency tasks had been restored to normal, but patients still had a significant impairment in the famous-face naming task (Papagno et al., 2016). It is possible that this selective impairment is linked to emotional processing (Papagno et al. (2016) or to semantic control and selection, both of which are more marked for famous faces and places than for generic objects.

Summary. UF's connections to the orbito-frontal cortex implies a clear role for this region in processing reward and punishment, which is connected to both social/emotional processing and reward-based learning. These functions can affect various aspects of language processing, especially those with a social component. The question is whether beyond these, the linking of ATL to the prefrontal cortex implies a role for UF in semantic-lexical selection in situations with high selection demands. Current results sometimes implicate UF, sometimes ILF and/or IFOF, and sometimes a combination of these tracts. One interpretation of these diverging results is that UF plays a complementary role to ILF and IFOF in semantic processing (Cocquyt et al., 2020). More empirical data will be helpful in testing this hypothesis.

6. Extreme Capsule (EmC)

EmC (Fig. 4) is often mentioned in studies of white matter. However, researchers vary greatly in their definition of what EmC is. Some view it simply as a topographical region between the insula and claustrum (Axer et al., 2013). Others have described it as part of IFOF or UF or the MdLF/ILF pathway (Northam et al., 2012; Patterson et al., 2014; Saur et al., 2008; Verly et al., 2019). Yet others have described it as a more substantial fiber complex or system, e.g., the

“extreme capsule fiber complex” (Mars et al., 2016) or the “extreme capsule fascicle” (Martinez Oeckel et al., 2021), and have included large sections of the ventral pathway in this bundle. Finally, in a careful study focused specifically in delineating the trajectory of EmC, Makris and Pandya (2009) were able to clearly distinguish between the tract and the adjacent MdLF, UF, AF, and SLF-II and SLF-III. They defined EmC as a long association fiber coursing between the inferior frontal cortex and the STG, extending into the inferior parietal lobule. This description, obviously, implicates several regions that are important for language processing, thus suggesting a possible role for EmC in language production and comprehension. Studying 25 individuals with aphasia and 24 healthy controls, Kourtidou et al. (2021) found that radial diffusivity of the right temporo-frontal extreme capsule fasciculus was predictive of a number of language functions, including oral and reading comprehension, word and sentence repetition and number of words/minute produced in story telling tasks, such as the Cookie Theft Picture Test (see also Martinez Oeckel et al., 2021). Others have proposed EmC’s involvement in various language functions including speech rate in stroke survivors (Efthymiopoulou et al., 2017), semantic paraphasia in glioma patients in intra-operative stimulation (Duffau et al., 2005), comprehension (Kümmerer et al., 2013), and vocabulary development in children with developmental language disorders (Verly et al., 2019), while others have reported no relationship between EmC’s lesion size and language production abilities such as naming and rate and informativeness of speech (e.g., Marchina et al., 2011). Finally, impaired syntactic processing has also been linked to EmC deficits in some studies (e.g., Griffiths et al., 2013; Papoutsi et al., 2011; Rolheiser et al., 2011), but not in others (Teichmann et al., 2015; Wilson et al., 2011).

Given the temporal origin of the tract which is close to Heschel’s gyrus, auditory processing has been one of the proposed functions of this tract (Frey et al., 2008). More nuanced

hypotheses have been formed around the connection that this tract provides between STG and IFG, in terms of mediating verbal working memory. For example, Lopez-Barroso et al. (2011) showed that performance under articulatory suppression (asking participants to repeatedly produce the syllable “bla” while listening to the language stream) was significantly correlated with FA in left EmC and the external capsule. Naturally, a role in verbal working memory links EmC to language learning. In line with this hypothesis, Wong et al. (2011) trained participants on a sound-to-word learning paradigm, where they had to use foreign phonetic contrasts to access meaning. They found the FA of a left temporo-parietal region to be correlated with learning in this paradigm, and reported EmC, along with ILF, to mediate auditory comprehension.

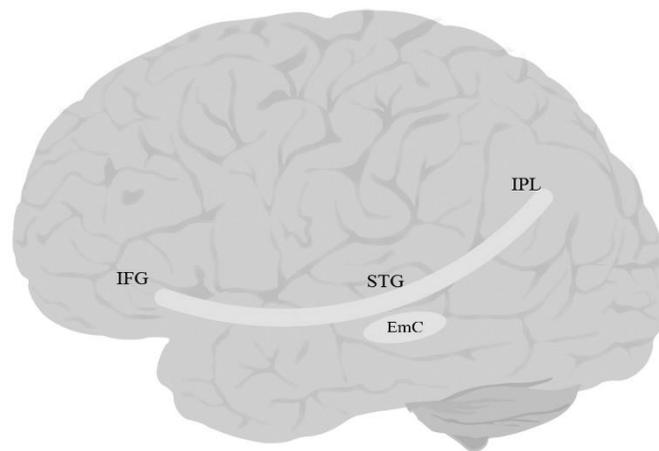


Figure 4. Anatomy of EmC. EmC = extreme capsule; IFG = inferior frontal gyrus; IPL = inferior parietal lobe; STG = superior temporal gyrus.

Summary. To summarize, EmC’s function is little understood partly due to the lack of consensus about its anatomical definition, but there is more and more evidence that the tract represents a pathway distinct from its neighboring white matter, and may be involved in some

aspect of language processing. So far, detailed studies of the linguistic function of EmC have been relatively sparse, but the connection between STG and frontal cortex, and its implication for sound processing and verbal working memory, appears to be a promising venue for more theoretical approaches to the possible function of this tract in language acquisition, comprehension and production.

7. Middle longitudinal fasciculus (MdLF)

MdLF (Fig. 5) is a long association fiber that connects temporal regions with parietal and occipital lobes (Burks et al., 2017; Conner, Briggs, Rahimi, et al., 2018). First reported by Seltzer and Pandya (1984) using autoradiographic histological tract-tracing and later confirmed using more recent non-human tract-tracing studies (Schmahmann et al., 2007), the pathway had been historically absent from human anatomical reports (Burdach, 1826; Dejerine, 1901; 1895; Foville, 1844; Meynert, 1885) and even some recent anatomical atlases (e.g., Oishi et al., 2010) and studies of white matter tracts (Bürgel et al., 2006; Catani et al., 2005; Catani & Thiebaut De Schotten, 2008; Holl et al., 2011; Hua et al., 2009; M. T. Thiebaut De Schotten et al., 2011; Wakana et al., 2007). More recent studies in humans, however, have begun to identify MdLF as a distinct pathway. Some, such as Saur et al. (2008) discuss MdLF as two composite fiber bundles, one in the dorsal pathway together with AF/SLF and one in the ventral pathway together with ILF. Others have identified MdLF as an independent tract extending from the AG to the anterior superior temporal cortex, running dorsal and medial to the AF/SLF (Frey et al., 2008; Makris & Pandya, 2009; Turken & Dronkers, 2011; Wong et al., 2011). Today, researchers agree that the tract is heavily involved in connecting STG to other parts of the cortex, although there is not always consensus among studies on what these other parts are. Candidates include other regions in the temporal cortex, such as MTG (Turken & Dronkers, 2011), parietal regions such as the superior

parietal lobule/precuneus and AG (Makris et al., 2013; Turken & Dronkers, 2011; Wang et al., 2013), and possibly some of the occipital regions such as the cuneus, and lateral occipital lobe (Makris et al., 2017). In one of the most recent attempts to define the anatomical branches of MdLF, Kalyvas et al. (2020) performed a combined study of cadaveric dissections together with DTI in neurotypical adult participants and identified three branches of MdLF (Fig. 5): the first, MdLF-I, connects TP and STG to the SPL through Heschel's gyrus. The second, MdLF-II, connects TP and STG to the parieto-occipital regions. The third, MdLF-III connects the most anterior part of TP to the posterior part of the occipital lobe through the AG.

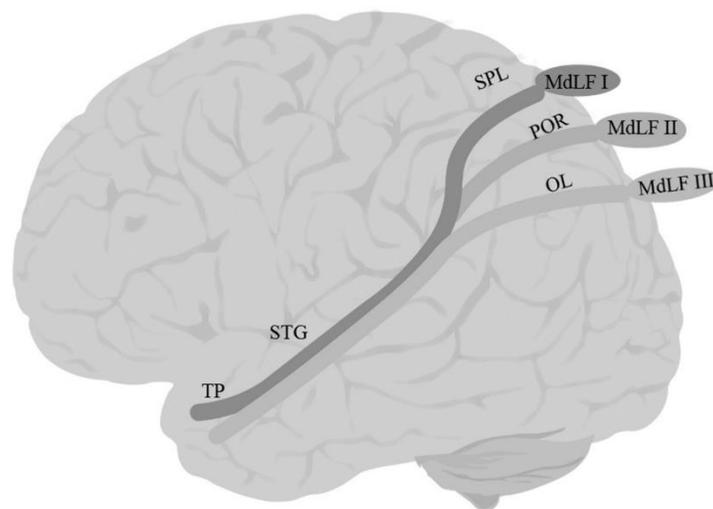


Figure 5. Anatomy of MdLF. OL = occipital lobe; POR = parieto-occipital regions; TP = temporal pole.

Based on its clear connections to the temporal lobe and AG, there have been attempts to link MdLF to language processing. For example, bundling AF/SLF with one branch of MdLF and ILF with another branch of MdLF, Saur et al. (2008) proposed the former's role in sublexical repetition, and the latter's role in comprehension in 33 neurotypical adults. However, because of bundling with other fibers in the dorsal and lateral pathways, respectively, it is difficult to isolate

the role of MdLF in such tasks. MdLF has not been a frequent target of aphasia studies, but the little evidence that exists is mixed. In a study of 20 individuals with PPA, Luo et al. (2020) reported significant correlations between word comprehension and naming and the white matter changes to the MdLF in the dominant hemisphere. In contrast, Blom-Smink et al. (2020) found no clear link between the integrity of MdLF and naming performance in 10 individuals with sub-acute post-stroke aphasia. Finally, in one of the few intraoperative electrostimulation studies investigating the role of MdLF in language, De Witt Hamer et al. (2011) tested counting and picture naming of eight glioma patients after the stimulation of MdLF and found no changes to either task. Moreover, the resection of the left MdLF did not result in impaired naming. It must be noted, however, that resection was not complete in all patients, and only included the part of the MdLF anterior to Heschel's gyrus, therefore, these results must be interpreted with caution.

The brief review above highlights the sparsity of research on the role of MdLF in language processing, but the few existing results do not seem to provide strong support for an essential role of this tract at least in language production, including the semantic-lexical mapping required for picture naming. Two findings in the anatomical study of Kalyvas et al. (2020) provides theoretical support for the non-critical role of MdLF in language processing: (1) there is no clear termination of the fibers from any of the MdLF branches in the AG, and (2) no clear leftward symmetry of the tract. In contrast, the centrality of STG and the auditory cortex in at least two branches of this tract motivates a role in auditory processing (Dick & Tremblay, 2012; Saur et al., 2010). Evidence in support of this view is more convincing, although there is much room for additional evidence and careful studies. For example, MdLF was one of the ventral pathways implicated in the study of Wong et al. (2011) where they measured participants' ability to learn new phonetic contrasts for

discriminating words in a foreign language. But perhaps the most detailed study of the role of MdLF in auditory processing is the study of Tremblay et al. (2019), in which the authors used high angular resolution diffusion imaging (HARDI) with advanced anatomically constrained particle filtering tractography algorithms that are robust against problems such as crossing fibers and partial volume effects, to disentangle the role of AF and MdLF in auditory processing. Younger and older adults participated in a syllable discrimination task with broadband masking noise. After controlling for differences in individuals' hearing sensitivity, an age-independent effect linked both tracts to performance in the task, but in relatively distinct ways: while AF was predictive of sensitivity (d-prime in the signal detection framework), MdLF was linked to response bias (criterion in the signal detection framework). These results suggest a distinct role for MdLF in higher-level auditory processing, such as decision making.

Summary. MdLF is a relatively understudied tract. But recent evidence suggests that it is a distinct tract in humans, and that it has possibly up to three separate branches. Of the roles proposed so far for this tract, an involvement in auditory processing is the most plausible and well-supported role. The nature of such involvement, however, remains underspecified. Future studies should clarify the extent to which the processing is speech-specific (or not), and whether the tract's role is more pronounced in cognitive aspects of auditory processing, such as implicit or explicit decision making. Finally, the links to the occipital cortex remain intriguing, and potentially related to processes mediating audiovisual integration (Wang et al., 2013), although an empirical investigation of this hypothesis has, to our knowledge, not yet been carried out.

8. Superior longitudinal fasciculus (SLF)

When we think about the classic language pathway, we often think about Geschwind's iconic illustration of a pathway connecting Broca's and Wernicke's areas. For years, variations of this pathway connecting the inferior frontal cortex with temporal and parietal lobes comprised a non-dissociable SLF/AF bundle, which has been called by various names, including the Burdach fasciculus, the superior longitudinal bundle or the arcuate bundle (e.g., Burdach, 1826; Dejerine et al., 1895; Wernicke et al., 1897). More recently, the two tracts have been deemed distinct, although AF is still widely considered as one of the branches of SLF.

SLF is a bundle of association fibers that connects the superior and inferior parietal cortices to the frontal cortex (Petrides & Pandya, 1984; Yeterian et al., 2012). SLF is usually divided into three distinct branches, SLF-I, SLF-II, and SLF-III (Barbeau et al., 2020; Caverzasi et al., 2016; Petrides & Pandya, 1984, 2002, 2006; Yeterian et al., 2012), although some disagreement remains about the exact origin and destination of each branch. SLF-I is the dorsal-most branch, and connects the superior parietal lobule and precuneus to the superior frontal cortex, the dorsal premotor area, the SMA, and possibly the anterior cingulate cortex (Petrides & Pandya, 1984; Schmahmann & Pandya, 2006; Schmahmann et al., 2007; Thiebaut de Schotten et al., 2012; Yeterian et al., 2012). SLF-II originates in the caudal inferior parietal lobule, the intraparietal sulcus and the angular gyrus and terminates in the DLPFC, including the dorsal premotor area (Petrides & Pandya, 1984, 2002, 2006; Yeterian et al., 2012). SLF-III is the ventral-most branch and connects the rostral part of the inferior parietal lobule, i.e., the supramarginal gyrus, and the anterior parts of the intraparietal sulcus to the ventral premotor cortex and the caudal banks of the arcuate and principal sulci (Petrides & Pandya, 1984, 2002, 2006; Yeterian et al., 2012). Recently, Barbeau et al. (2020) proposed a division of SLF-III into two branches, the ventral branch terminating in BA 6 (pre-SMA and SMA) and BA 44 (pars opercularis of IFG), and the dorsal

branch terminating in BA 9 and BA 46 (DLPFC). Finally, some studies describe a temporoparietal component of SLF, which traverses from the posterior part of the STG to the inferior and superior parietal lobules, and is often labeled SLF-tp (e.g., Caverzasi et al., 2016), and is sometimes further divided into SLF-tp-IPL (inferior parietal lobule) and tp-SPL (superior parietal lobule; Bullock et al., 2019; Kamali et al., 2014). It is worth mentioning that AF, which courses in parallel to SLF-III and connects the temporoparietal junction to the frontal cortex, has sometimes been considered a part of the larger SLF bundle. In this paper, we will discuss AF separately in the next section.

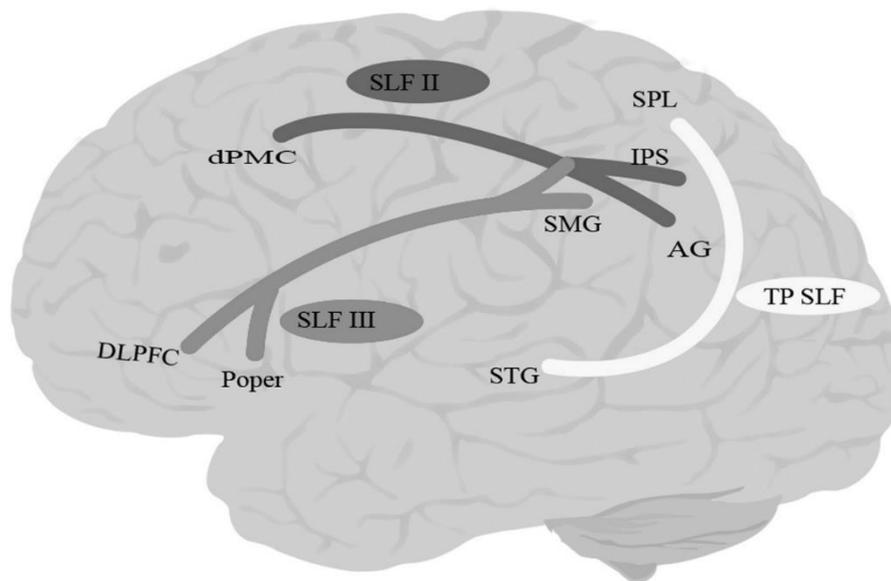


Figure 6. Anatomy of SLF (SLF-I is not shown). DLPFC = dorsolateral prefrontal cortex; dPMC = dorsal premotor cortex; IPS = intraparietal sulcus; Poper = Parsopercularis; SPL = superior parietal lobule; TP = temporoparietal.

Empirical studies do not always separate the three branches of the SLF, but in those which do, it is often SLF-III and sometimes SLF-II that are related to language processing. Due to its anatomical location and connections, SLF-I is usually not considered a language-related tract. Its

main connectivity is to the superior parietal cortex, which encodes body part locations in relation to space and eye-hand coordination for reaching. Consequently, damage to the caudal part of the superior parietal lobule can cause optic ataxia, i.e., difficulty in visually guided reach (Ferraina et al., 2009; Granek et al., 2012; Naito et al., 2008). By connecting this region to the premotor cortex, SLF-I is thought to play a role in regulating fine motor behavior, especially in tasks that require selection among competing motor plans (Hyde et al., 2021). SLF-tp is not always mentioned, but together with AF, there are reports of its connection to language (Caverzasi et al., 2016). Galantucci et al. (2011) claimed to have separated SLF-tp from the temporoparietal AF, and showed that only damage to the former was observed in the logopenic variant of PPA. They also reported SLF-tp's damage in the nonfluent variant of PPA.

The investigation of the linguistic functions of the SLF have ranged from broad to specific aspects of language processing. For example, in a study of 20 children between 8 and 10 years of age, Asaridou et al. (2017) showed that children's vocabulary growth was uniquely predicted by the cortical thickness of the left SMG, and concluded that the direct link between this region and the IFG provided by SLF-III makes the tract a critical pathway for the development of the lexicon. Likewise, in a comparison between children on the autism spectrum with and without language impairment, Nagae et al. (2012) linked elevated mean diffusivity values of SLF to language impairments. More recently, Gao et al. (2020) showed increased FA in the right SLF in bilingual compared to monolingual speakers. The link is stronger for production than comprehension. For example, in a study of 49 typically developing children and adolescents ranging from 5 to 17 years of age, Urger et al. (2015) reported that only production but not comprehension was associated with the FA of left SLF. Likewise, Hillis et al. (2018) reported a link between naming recovery in post-stroke aphasia and the integrity of SLF/AF.

More detailed hypotheses usually concern the role of SLF-III: by the virtue of connecting the SMG, which is frequently implicated in phonological processing and phonological deficits (e.g., Schwartz et al., 2012), to the frontal cortex, this branch of SLF is a prime candidate for language processing, especially phonological production. The more recent division into ventral and dorsal branches terminating in premotor and DLPFC, respectively (Barbeau et al., 2020), has further motivated finer-grained distinctions in the function of this tract into mapping phonological codes onto abstract motor plans (Bohland et al., 2010; Miller & Guenther, 2021) vs. maintaining phonological information in working memory. In keeping with this hypothesized role, several lines of research have linked phonological processing abilities to SLF (and in some cases, specifically to SLF-III). First, measures of phonological awareness are often correlated with the properties of SLF. The tests used to measure phonological awareness vary, but often include tasks such as sound matching, elision, and word blending. In sound matching tasks, participants hear two or more stimuli and must make a perceptual judgment about whether they match or not. Elision tasks measure the ability to remove phonemes from spoken words to form other words, and blending words tasks measure the ability to synthesize phonemes to form words. In a comparison of two groups of children born pre-term and full-term, tested when 6 years old, Dodson et al. (2018) showed a significant association between the FA of the left SLF (and AF) and phonological awareness measures (see also Travis et al., 2017).

A second phenomenon linking SLF to phonological abilities in production is the Tip of the Tongue (TOT) state. This is a state in which the speaker almost remembers a word but cannot fully produce it. TOT states usually benefit from phonological cues more than semantic cues, which has led to the localization of the problem to the mapping of lexical items to phonemes (Meyer & Bock, 1992). Stamatakis et al. (2011) tested 24 neurotypical adults between 19 and 82 years of age on

the Boston Naming Task and showed that even though accuracy was associated with several tracts, including SLF, the TOT state was uniquely related to the most posterior part of the left SLF and a homologous area in the right hemisphere (cf., Kljajevic & Erramuzpe, 2019). A third line of research linking SLF to phonological abilities is the neuropsychological data on word production. McKinnon et al. (2018) tested 32 participants with chronic post-stroke aphasia and showed that the probability of making semantic and phonological errors was strongly linked to ILF and SLF axonal loss, respectively (see also Han et al., 2016; Kyeong et al., 2019; Stark et al., 2019). Similarly, in a study of 24 participants with PPA, Powers et al. (2013) showed that participants' naming performance in the logopenic—but not the semantic—variant was associated with the integrity of the left SLF. Moreover, auditory repetition performance, which has a stronger emphasis on phonological encoding than lexical retrieval (Dell et al., 2013; Nozari & Dell, 2013; Nozari et al., 2010), has also been linked to the SLF (Breier et al., 2008). Adding to this evidence are data from individuals who stutter. Chang et al. (2015) studied 77 children who stuttered and reported that these children, compared to controls, showed decreased FA of the left SLF and the gray matter regions connected by this tract, including IFG, premotor, motor, STG, MTG, and inferior parietal regions. Likewise, intraoperative stimulation of SLF has led to dysarthria and anarthria (Maldonado et al., 2011), although distinguishing problems of articulation from phonological encoding is difficult, especially during surgery with limited time.

Finally, the last line of research connecting SLF to phonological processing is the close link posited between the tract's properties and reading abilities (e.g., Bakhtiari et al., 2014; Borchers et al., 2019; Bruckert et al., 2019; Travis et al., 2017). SLF is one of the three major pathways related to the VWFA, providing critical connections between this region, STG, IFG, and DLPFC (Chen et al., 2019). Borchers et al. (2019) showed that the FA values for the left and right

SLF and left AF at 6 years of age were predictive of the oral reading index at age 8. These findings are mirrored in studies of dyslexia: Zhao et al. (2016) showed that, as a group, children with dyslexia demonstrated greater right-lateralization of SLF-II (together with less left-lateralization of IFOF) than non-dyslexic readers. The lateralization index was also predictive of reading performance in the dyslexic group (see also Hoeft et al., 2011). Even though reading requires more than just phonological processing abilities, such abilities do play an important role, especially in sublexical reading. Therefore, although not a sufficient piece of evidence by itself, the link between SLF and reading abilities adds to the other bodies of evidence connecting this tract to phonological processing abilities.

There are also many studies investigating the correlation between SLF properties and verbal fluency tasks. As noted in earlier sections, although verbal fluency is one of the most popular language tests in studies of the neurobiology of language, it is not nearly as pure of a measure for semantic and phonological abilities as it has often been assumed. Unsurprisingly, even though SLF has been implicated in both semantic and phonemic fluency tasks, these reports are not consistent across studies and populations (e.g., Gonzalez et al., 2021; Madhavan et al., 2014; Powers et al., 2013; Pustina et al., 2014; Sanvito et al., 2020; Urger et al., 2015), and in most cases do not differentially implicate SLF's involvement in one task vs. the other. Rather than taking such evidence as suggesting a role for SLF in both semantic and phonological processing, it is plausible to consider the tract's relevance to some general task demand shared by both phonemic and semantic verbal fluency tasks. For example, it has been suggested that the association between SLF and verbal fluency in studies of aging is in fact mediated by verbal working memory, which has been linked to the FA of the bilateral SLF (Peters et al., 2012).

The studies reviewed above clearly link SLF to phonological processing. More sporadic have been attempts to link SLF to syntactic processing. In a study of 17 neurotypical children, Mills et al. (2013) found that those with a more complex narrative had higher diffusion coefficients in their left SLF (and AF; see also Friederici et al., 2006 for implicating SLF in parsing sentences with complex hierarchical structures). A few neuropsychological studies have also provided support for the link between SLF and syntactic processing. Wilson et al. (2011) studied 27 participants with PPA and found reduced FA in the left SLF/AF to be correlated with syntactic deficits in both comprehension and production. In another PPA study, Marcotte et al. (2017) linked the deficits in the non-fluent variant (nfv) vs. the semantic variant (sv) to increased radial diffusivity in the left SLF vs. in the bilateral UF and ILF, respectively (see also Tetzloff et al., 2018; Whitwell et al., 2010). There is also a report of inducing grammatical gender errors produced in response to noun probe in nine French speaking glioma patients undergoing surgery, as a result of what appears to be the stimulation of a part of SLF (Vidorreta et al., 2011).

Although not as clear as the motivation for linking SLF to phonological processing, it is possible that parts of the tract traversing from the parietal to frontal cortex may connect pMTG and IFG and thus carry out the syntactic operations proposed by Matchin and Hickok (2020) in production. More difficult is explaining the role of the tract in syntactic comprehension, unless one notes the generally high demands on working memory and control processes often required in sentences with complex hierarchical structures that have often been used in experiments tapping into syntactic comprehension. In such cases, it is conceivable that the DLPFC and IFG's connection to the temporoparietal regions may be essential for maintaining information actively in working memory and resolving competition between different interpretations. This is particularly important, as SLF, and especially SLF-II and SLF-III, have been independently

implicated in working memory (Peters et al., 2012; Rizio & Diaz, 2016) as well as executive control (Linortner et al., 2020; Ramsey et al., 2017; Unger et al., 2015). Finally, unless carefully controlled in the experimental materials, syntactic complexity is often confounded with length, which itself imposes higher demands on phonological working memory, providing yet another alternative interpretation for the role of SLF in syntactic processing.

Summary. A rather large and converging body of evidence points to a clear role of the SLF (especially SLF-III, and possibly SLF-II) in phonological processing, especially in language production. SLF-tp is a promising but understudied candidate. Further studies can focus on disentangling the functions of the components of SLF, such as the maintenance of phonological information in working memory vs. mapping such information onto motor plans. There is also some evidence for the involvement of this tract in syntactic processing, but potential confounds such as higher demands on verbal working memory and executive control processes must be ruled out before the tract can be claimed to have a pure ‘syntactic’ function. This is another great avenue for future research.

9. Arcuate Fasciculus (AF)

The arcuate fasciculus (Fig. 7) is a dorsal tract that connects the posterior superior temporal cortex (pSTC) to the IFG and ventral premotor cortex (vPMC). Its anatomy is still under debate, although there is agreement that the tract has multiple branches (Dick et al., 2014; Dick & Tremblay, 2012). One common classification divides the tract into direct and indirect segments (Catani et al., 2005). The direct segment connects pSTC to IFG, MFG, and vPMC, while the indirect segment itself further divides into two components, a posterior component connecting STC to the inferior parts of the parietal lobe, and an anterior component connecting the inferior

parietal areas to IFG, MFG and vPMC (Catani et al., 2005; Catani & Thiebaut de Schotten, 2012; Thiebaut De Schotten et al., 2011; Tremblay et al., 2019; Weiner et al., 2017). A different model, the dual pathway architecture (Berwick et al., 2013; Brauer et al., 2013), also exists and is of potential functional importance. The key difference between the two branches in this model is not their origin (which is presumed to be pSTC in both cases), but rather their termination points, i.e., vPMC vs. IFG. It is hypothesized that the branch connecting pSTC and vPMC is involved in sensory-motor mapping and phonological processing, whereas the branch connecting pSTC to IFG is involved in higher-level processing, possibly syntactic processing.

Although a tract similar to AF is found in non-human primates, axonal studies in monkeys have demonstrated that it is more closely connected to the dorsal regions of the temporo-parietal cortex (Petrides & Pandya, 1984; Schmahmann et al., 2007), while in humans, the tract has strong ties to the auditory regions in the temporal lobe (Catani et al., 2005; Thiebaut de Schotten et al., 2012). Another difference between the AF in non-human primates and humans is that the tract is not strongly lateralized in monkeys (Eichert et al., 2019), but the evidence points to a prominent left-lateralization in humans (Allendorfer et al., 2016; Bruckert et al., 2019; Eichert et al., 2019; Lebel & Beaulieu, 2009; Silva & Citterio, 2017; Sreedharan et al., 2015; Travis et al., 2017; Vernooij et al., 2007; cf., Yeatman et al., 2011). These anatomical differences are strong indicators of a role of this tract in language processing, and specifically, in auditory-motor mapping.

In line with this, the empirical evidence has often linked the left AF to language processing. For example, in a study of 106 neurotypical adults, Teubner-Rhodes et al. (2016) reported a positive correlation between vocabulary knowledge and microstructural properties of the left AF in the segment of the tract behind the posterior part of the Sylvian fissure. Similarly, AF lesions have been linked to language deficits in aphasia (e.g., Tak & Jang, 2014; cf., Forkel et al., 2020),

as well as language recovery (Primaßin et al., 2015). The critical role of AF, irrespective of damage to the gray matter, has been recently demonstrated in a study of 134 stroke survivors whose lesions were relatively limited to the left frontal cortex. Gajardo-Vidal et al. (2021) showed that production impairment lasting beyond 3 months after the stroke was selectively related to the damage of the anterior part of the AF directly above the insula, regardless of damage to Broca's area (see also Hillis et al., 2018). Interestingly, production scores were lower in the case of AF damage with an intact Broca's area compared to Broca's damage with an intact AF, ruling out a central role for Broca's damage in the impairment.

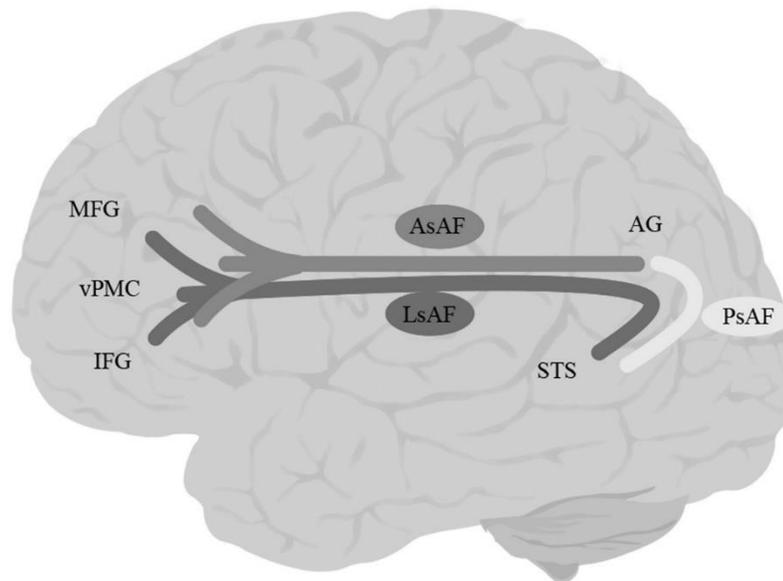


Figure 7. Anatomy of AF. AG = angular gyrus; AsAF = anterior segment of the arcuate fasciculus; IFG = inferior frontal gyrus; LsAF = long segment of the arcuate fasciculus; MFG = middle frontal gyrus; PsAF = Posterior segment of the arcuate fasciculus; STS = superior temporal sulcus; vPMC = ventral Premotor Cortex.

Some have claimed the involvement of AF in both language production and comprehension (Turken & Dronkers, 2011). For example, Broce et al. (2015) showed that microstructural

properties of this tract were predictive of both expressive and receptive language in children of 5-8 years of age. More recent studies have begun to localize these functions to different segments of the AF. For example, in a study of 33 individuals with aphasia, Ivanova et al. (2021) showed that AF's anterior segment was predictive of fluency and naming, and its posterior segment of comprehension abilities. On the perception side, the role of AF has been most extensively studied in auditory processing. Several studies have compared musicians and non-musicians in their ability to process fine-grained details of sound and have linked the superior performance in the former to different properties of AF in that group (Li et al., 2021; Moore et al., 2017; Oechslin et al., 2010; cf. Perron et al., 2021). Interestingly, the volume and microstructural complexity of the tract also differ between vocal and instrumental musicians, compatible with the idea that the tract plays a special role in vocal-motor processing (Halwani et al., 2011). In non-musicians too, basic auditory processes have been linked to the microstructural properties of AF (e.g., Vaquero et al., 2021). In a more detailed study, Tremblay et al. (2019) showed that sensitivity in a syllable discrimination task was related to the properties of the AF, while response bias was related to MdLF, putting AF in the center of the operations involved in fine-grained speech sound processing.

But the bulk of evidence, so far, is in favor of a role in production. In a study of 30 post-stroke individuals in the chronic phase, Marchina et al. (2011) showed that lesions to AF uniquely predicted naming ability, as well as the rate and informativeness of speech (see also Halai et al., 2017). Several other studies in individuals with brain damage have also linked AF lesions to the fluency of spoken production (Basilakos et al., 2014; Chenausky et al., 2020; Fridriksson et al., 2013; Ivanova et al., 2021). Note that by “fluency” here, we mean fluency in the context of connected speech, as opposed to tests of “verbal fluency”. As alluded to in several of the earlier sections, results of those tests are difficult to interpret. The issue is also evident in the AF literature:

while some studies have reported a correlation between verbal fluency scores and the properties of AF (e.g., Blecher et al., 2019; Gonzalez et al., 2021; Sanvito et al., 2020), others have not (Contentin et al., 2019; Phillips et al., 2011). Moreover, the findings are not consistent across studies that do report a correlation, with some only finding a correlation with letter fluency (e.g., Blecher et al., 2019), while others reporting a correlation with category fluency or both (e.g., Gonzalez et al., 2021; Sanvito et al., 2020). As for fluency in connected speech, there are many contributing factors (Nozari & Faroqi-Shah, 2017).

More evidence for the role of AF in lower-level processing in production comes from its involvement in auditory repetition (Breier et al., 2008; Kim & Jang, 2013; Shinoura et al., 2013), especially sublexical repetition which indexes mapping input phonology to output phonology (Saur et al., 2008; Sierpowska et al., 2017). Similarly, damage to AF has been shown to be specifically associated with phonological errors (Schwartz et al., 2012) as opposed to semantic errors, which arise at higher levels of processing in the production system (Dell et al., 2014; Nozari et al., 2011). This finding has been corroborated by the intraoperative stimulation of AF or AF termination sites, which has often led to speech errors (Giampiccolo et al., 2020), anomia (Duffau et al., 2002), and most pointedly, phonological errors (Mandonnet et al., 2007). Disentangling phonemic errors from dysarthric errors is not easy and has not been a focus in many of the studies reviewed above. It is thus possible that some of the problems reported in such studies are due to articulatory issues. In line with this idea, Liégeois et al. (2013) compared 32 individuals with a history of childhood TBI, and showed that those with persistent dysarthria had reduced FA in the left AF and reduced volume of the left AF and corpus callosum compared to those without dysarthria.

The critical role of AF in phonological processing has also been tested with an array of phonological awareness tests. Different studies use different measures, and sometimes a mix of perception and production, but common tests include sound matching, elision and word blending, (see task definitions under the SLF section). The reports link AF (often along with SLF, and often on the left side) to phonological awareness (Dodson et al., 2018; Gullick & Booth, 2014, 2015; Saygin et al., 2013; Vandermosten et al., 2015; Yeatman et al., 2011). Some researchers have also suggested that the auditory-motor mapping role of AF entails storing phonological information in working memory, essential for learning complex phonological sequences (Schulze et al., 2012). In keeping with this idea, López-Barroso et al. (2013) demonstrated a negative correlation between word learning and radial diffusivity of the long segment of the left AF in a group of adult participants learning an artificial language. Similar evidence followed in a longitudinal study of vocabulary development in children; Su and colleagues followed the developmental trajectory of 79 children from age 4 to 14 years and reported a correlation between vocabulary development in the direct and posterior segments of AF in the left hemisphere (Su, Thiebaut de Schotten, et al., 2018).

AF has also been strongly linked to reading, at least in part due to its role in phonological processing. Thiebaut de Schotten et al. (2014) showed that increased FA and decreased perpendicular diffusivity of the temporoparietal portion of the left AF accompanied literacy. Furthermore, the microstructure of the AF was correlated with the response of VWFA to letter strings. In a longitudinal study of 30 children between the ages of 8 and 14 years, Gullick & Booth (2014) found a correlation between reading development and the FA of the direct segment of AF for both younger and older halves of their sample (see also Gullick & Booth, 2015). The correlation between AF and reading abilities have also been reported in children with dyslexia. In a

longitudinal study of 75 children from ages 5-6 to 7-8 years, Vanderauwera et al. (2017) showed that only the left AF was exclusively related to the development of dyslexia (see also Hoeft et al., 2011). Also, a comparison of children with a family risk of dyslexia with a control sample showed that at-risk children had lower FA in the posterior AF (as well as the left IFOF; Vandermosten et al., 2015).

A special connection has also been suggested between AF, as the tract connecting auditory to motor regions, and conduction aphasia, a deficit of mapping sensory to motor speech (Benson et al., 1973). For instance, individuals with conduction aphasia often show good semantic processing, but make phonological errors in naming. Importantly, their auditory repetition performance is markedly impaired compared to their naming performance. One suggestion has been that conduction aphasia may result from damage to the AF. There has been some empirical support for this idea, with lesions severely damaging AF and the surrounding tissue causing phonemic paraphasia and notable repetition deficits (e.g., Tanabe et al., 1987; Yamada et al., 2007). However, lesions to the AF do not necessarily cause conduction aphasia (e.g., Epstein-Peterson et al., 2012; Selnes et al., 2002; Shuren et al., 1995), suggesting that AF damage is not sufficient to produce this disorder.

Finally, some have attributed higher-level processing functions, such as syntactic processing, to AF. In one study, Mills et al. (2013) found a trend linking the syntactic complexity of the sentences produced by children to the diffusivity measures of the left AF. In another study, Papoutsis et al. (2011) found AF lesions to be predictive of syntactic processing impairment. But it is important to note, as alluded to in the SLF section, that increasing syntactic complexity is often accompanied by increasing phonological complexity, i.e., longer phrases, more embeddings, etc.

Therefore, unless specifically controlled for phonological processing load, drawing conclusions about the AF's direct involvement in syntactic processing would be difficult.

Summary. The evidence reviewed above shows a clear role for AF in processing auditory details, mapping sound to motor actions, and more generally, phonological processing especially in production. A possible role has also been proposed for syntactic processing, but so far, the evidence supporting this proposal has been limited. Moreover, careful controls for other factors that may increase processing load have not always been implemented in studies assessing syntactic functions of AF. Disentangling phonological load from syntactic load would be a fruitful avenue for future studies on AF. Another fruitful avenue for future research would be to separate phonological and articulatory phonetic functions of AF (and SLF).

10. Frontal aslant tract (FAT)

FAT (Fig. 8) is a short monosynaptic association fiber connecting the lateral IFG to SMA and pre-SMA in the superior frontal gyrus (Enatsu et al., 2016; Ookawa et al., 2017). Although a tract with these characteristics had been discussed before (e.g., Aron et al., 2007; Lawes et al., 2008; Oishi et al., 2008), the term “Aslant tract” was first coined by Catani et al. (2012; see also Thiebaut de Schotten et al., 2012), who described it specifically as a pathway connecting IFG's pars opercularis to pre-SMA (see also Bozkurt et al., 2016). Today, the existence of this tract and its role in connecting IFG and the superior frontal gyrus is well established in both primates and humans (Briggs et al., 2018; Martino & De Lucas, 2014; Petrides & Pandya, 2002).

Based on its connectivity, several functions have been proposed for the role of FAT in cognition. Due to its clear connection to IFG, the debates that have impacted the role of IFG have directly impacted the ideas about the role of FAT. On the one hand, the classic view of Broca's

area as a key language region has generated the hypothesis that FAT's connection to this region makes it a key language tract (e.g., Tremblay & Dick, 2016). The tract's connection to pre-SMA and SMA and the link between language production and these regions has further supported FAT's role in language processing (Tremblay & Gracco, 2009). The alternative, domain-general view of IFG (e.g., Nozari & Thompson-Schill, 2016; cf. Nozari & Novick, 2017), on the other hand, has led some researchers to implicate FAT in conflict resolution functions, in both linguistic and non-linguistic domains, that have been attributed to this region (Dick et al., 2019). This view is further reinforced by the fact that pre-SMA and SMA have often been implicated in complex motor tasks, especially those that involve high competition (Derrfuss et al., 2004; Mars et al., 2007), such as the Flanker task (Ullsperger & Von Cramon, 2001). Consequently, FAT's links to these regions have been taken as a possible involvement of the tract in motor selection, conflict monitoring and resolution and the execution of motor plans regardless of specific domains (e.g., Tremblay & Small, 2011). Dick et al. (2019) present a thorough review of the linguistic and non-linguistic functions of FAT, with an eye towards the tract's laterality. Below, we briefly review the evidence and the conclusions.

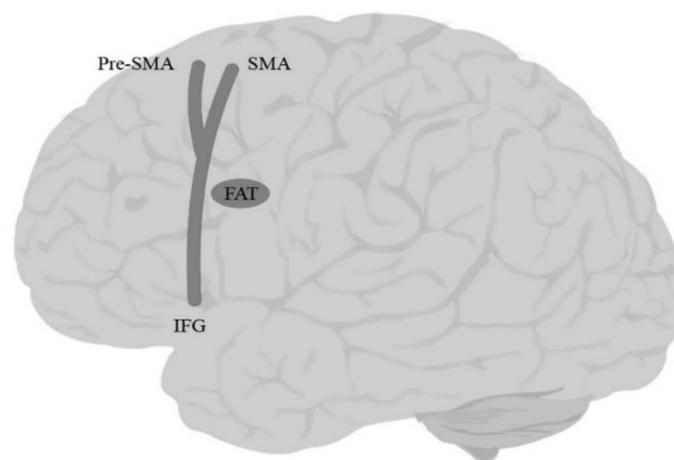


Figure 8. Anatomy of FAT. IFG = inferior frontal gyrus; SMA = supplementary motor area.

The evidence linking FAT to language processing and language disorders is ample. For example, a large-scale study of 834 participants from the Human Connectome Project found a significant correlation between the bilateral FAT volume and language performance (Varriano et al., 2018). In another study, Broce et al. (2015) found that the length of the left FAT was predictive of language comprehension abilities in young children. Moreover, in stroke survivors, the extent of damage to FAT is predictive of improvement of language skills (Sihvonen et al., 2021; c.f., Tuncer et al., 2021). Direct evidence for the importance of FAT in speech production comes from intraoperative stimulation of the tract, which often causes speech arrest (Fujii et al., 2015; Kinoshita et al., 2015; Vassal et al., 2014) or stuttering (Kemerdere et al., 2016). Post-operative damage to FAT can cause a transient problem of initiating spontaneous speech, although this problem often resolves itself rapidly and almost completely (Fujii et al., 2015; Kinoshita et al., 2015; Vassal et al., 2014; Young et al., 2020).

More specifically, a link has been established between fluency in speech production and FAT using different techniques and populations. In a study of 35 individuals with PPA, Catani et al. (2013) did not find a general correlation between FAT measures and overall language impairment, grammatical impairment, repetition or word comprehension, but they reported that FAT abnormalities are particularly correlated with agrammatic PPA. Moreover, FA of FAT was positively correlated with fluency, measured as words per minute, and mean length of utterance, while radial diffusivity showed an inverse correlation with the same two measures (see also Mandelli et al., 2014). Similarly, in a study of 46 chronic post-stroke individuals, Alyahya et al. (2020) found that the properties of FAT and the anterior parts of AF were predictive of both the quantity and quality of the connected speech (see also Basilakos et al., 2014; Halai et al., 2017; Ille et al., 2018). In yet another population, Chenausky et al. (2017) tested 10 minimally verbal

children with Autism Spectrum Disorder (ASD), and found a correlation between FA in AF and FAT in the percentage of correct syllable-initial consonants and percentage of syllable-insertion errors, respectively.

FAT abnormalities have also been linked to stuttering (Kronfeld-Duenias et al., 2016). The nature of the findings has been different though. While Kornfeld-Duenias and colleagues found different diffusivity rates in the left FAT to be predictive of stuttering, Neef et al. (2018) found stronger connectivity of the right FAT to be predictive of more severe stuttering. Consequently, the interpretations were different: the former highlighted the critical importance of left FAT for linguistic sequencing, while the latter took their findings to imply an amplification of the function of the right IFG, namely enforcing global inhibition. While a contribution is clear, more work is needed to understand the role of the left vs. right FAT in stuttering. More recently, FAT has been linked to articulatory-motor planning (Faulkner & Wilshire, 2020; although the use of a probabilistic map in that study makes tract localization less reliable). As noted in the earlier sections, disentangling phonological and post-phonological processes in language production can be tricky, but at least one study that has specifically tested the contribution of FAT to speech apraxia in 52 stroke survivors found apraxia to be associated with lesions to the pre- and post-central gyri and the left dorsal AF but not with FAT (Chenausky et al., 2020).

It is worth mentioning that FAT is often implicated in verbal fluency tasks along with other tracts, especially IFOF, although the evidence is, as in the other cases, far from convergent. Some studies have reported a correlation with both category and letter fluency scores (Blecher et al., 2019; Costentin et al., 2019; Li et al., 2017; Sanvito et al., 2020), some only with letter/phoneme fluency (Cipolotti et al., 2016; Keser et al., 2020), some with morpheme-based fluency (Yablonski et al., 2021) and some with none of these (Tseng et al., 2019; Vallesi & Babcock, 2020). Costentin

et al. (2019) found a correlation between verbal fluency scores and lesions to FAT and a number of other tracts in 48 individuals with Parkinson's Disease. However, the decline in performance in these tasks after surgery was not correlated with the proportion of the fibers or the number of tracts disconnected. In short, the same heterogeneity observed in the correspondence between verbal fluency scores and some of the other white matter tracts is evident here as well.

Moreover, and similar to SLF and AF, a syntactic function has also been proposed for FAT, mainly due to its connection to IFG, which has, by some, been proposed as a critical region for syntactic production (e.g., Friederici et al., 2003). The evidence for this link, however, is not watertight. For example, the evidence linking agrammatic aphasia to FAT abnormalities (e.g., Catani et al., 2013) is often confounded with other problems, e.g., phonological planning for longer utterances and higher demands on working memory. Incidentally, some researchers have linked bilateral FAT to working memory in older adults (Rizio & Diaz, 2016). A study that is often taken as clear evidence in favor of a syntactic role for FAT is the study of Sierpowska et al. (2015). These authors reported a case of intraoperative stimulation of the left FAT, where the patient showed a selective deficit for generating verbs by adding morphemes to nouns (e.g., book → booked) instead of producing the verb usually associated with the noun (book → read). This was taken as a marker of a deficit specific to morphological processing. However, the task has a strong cognitive control demand (rejecting a high-frequency, strongly associated verb in favor of a lower-frequency, weakly associated alternative), typical for left IFG recruitment (e.g., Thompson-Schill et al., 1997). It is thus possible that FAT's role is related to conflict resolution.

In line with this hypothesis are two other reports of intraoperative stimulations, by Chernoff et al. (2018) and Dragoy et al. (2020). In the former study, the authors reported a patient with surgical damage to the connectivity of the left FAT, who showed a selective post-surgical

impairment of fluency in the form of difficulty with voluntary speech and more complex sequences, while remaining unimpaired in production tasks such as picture naming and auditory repetition. In the latter, Dragoy and colleagues reported that cortical stimulation of the termination points of the left FAT (superiorly in SMA and pre-SMA and inferiorly in the pars triangularis and opercularis of IFG) caused selective impairment in a sentence completion task with low close probability (e.g., sentence prompts such as “A piggy is chewing...” which can be completed with a number of different words). Past research has shown a similar involvement of IFG (and potentially ACC, SMA and pre-SMA) in high-conflict tasks and those with under-determined responses, such as spontaneous speech or completing sentences with many possible endings (e.g., Robinson et al., 2010).

These results bring up the question of whether FAT is truly involved in “syntactic” processing or rather in conflict resolution operations that are often required for the processing of syntactically complex structures. Chernoff et al. (2019) proposed an alternative syntactic function for the tract, namely, sequencing complex actions with a hierarchical structure. In a case study of a patient undergoing awake craniotomy for removing a left frontal tumor, the authors showed that electrical stimulation of the left FAT affected pauses at the beginning of grammatical phrases without influencing either word durations or the durations of noun phrases. This is a neat and informative finding, but it does not necessarily mean involvement in any complex syntactic function. In section 2, under *Articulatory processing*, we reviewed the role of the planning loop, consisting of pre-SMA and left pIFS, which buffers utterances before it is time to send them to SMA, vPMC and ultimately vMC for articulation. It is reasonable to assume that buffering happens at the level of short grammatical phrases, and to the extent that FAT is involved in the transmission of these buffered chunks, it is expected that the stimulation effects should manifest at phrasal

boundaries. But note that this is a lower-level sequencing operation for motor execution, rather than a higher-level syntactic operation, as in generating a hierarchical syntactic structure per se.

A closer look at the right FAT may help adjudicate some of these competing representations. Right IFG (rIFG) has long been proposed as a critical pathway in “stopping” behavior (Aron, 2007; 2003; 2004). Through the direct pathway, rIFG activates the subthalamic nucleus to enforce stopping (Aron & Poldrack, 2006; Cai & Leung, 2009; Favre et al., 2013; Jahanshahi, 2013; Obeso et al., 2014; Van Wouwe et al., 2017; Wiecki & Frank, 2013). There is now evidence that pre-SMA may be a part of this pathway (Aron et al., 2016; Nachev et al., 2008). The right pre-SMA is usually more activated during successful than unsuccessful stops (Aron, 2007; Aron & Poldrack, 2006; Boehler et al., 2010). Its lesions cause a deficit in the execution of complex motor movements, especially in the presence of competing action plans (Nachev et al., 2007), and its direct stimulation stops ongoing movement (Lüders et al., 1988; Mikuni et al., 2006). Whether specialized for “stopping” or rather, context monitoring (Chatham et al., 2012; Erika-Florence et al., 2014; Hampshire, 2015; 2010), the evidence strongly points to the involvement of these regions, and their connecting fiber right FAT, in inhibitory control of behavior. Given this evidence, and the symmetry of the cortico-basal ganglia-thalamic-cerebellar circuits in the two hemispheres, Dick et al. (2019) proposed that FAT is involved in the same function, namely selecting the appropriate plan for motor actions among competing alternatives, in both hemispheres. On the left side, this function is primarily—but not exclusively (Budisavljevic et al., 2017)—applied to language. On the right side, the function applies more broadly to the action domain, especially in visuo-motor tasks. Such a gating function is highly appealing from the perspective of domain-general computations applied to domain-specific representations (e.g.,

Hepner & Nozari, 2019; Middleton & Strick, 2000), and is a promising framework for future studies of FAT.

Summary. Due to its links to IFG, pre-SMA, and SMA, FAT is a good candidate for implementing domain-general functions that also apply to language processing. Although both motor and syntactic functions have been proposed, a broader consideration of the role of the regions connected by this tract implicates it in monitoring and control processes that, especially on the left side, regulate the chunking and outputting of articulatory segments. Future work can further test the scope and limits of these functions in FAT.

11. Summary and recommendations for future directions

Table 1 provides a summary of the language-related functions attributed to the eight major tracts reviewed above. Generally speaking, the operations linked to the tracts reviewed in the earlier sections of this paper are compatible with the architecture of the dual-stream model. The ventral tracts are involved primarily in mapping the auditory input to lexical and ultimately semantic representations in comprehension, as well as mapping semantic concepts onto lexical representations in production. On the other hand, the dorsal tracts are primarily involved in more distal operations in the production pathway, i.e., mapping phonological representations to articulatory plans, buffering of those plans, and mapping them on to their corresponding articulatory motor outputs. These tracts also carry out the mapping between auditory representations and the production chain mentioned above, and are thus critical in auditory repetition tasks. Past this rough characterization, however, there are several as-of-yet unknown details. Below, we discuss some of the outstanding issues (Box 1), and some recommendations for addressing them in future research.

Table 1. Summary of the language-related functions attributed to the eight major tracts reviewed in this paper.

Function	Tract	References
Generally implicated in comprehension	ILF	Del Tufo et al., 2019; Griffis et al., 2017; Ivanova et al., 2016; Turken & Dronkers, 2011; Zhang et al., 2018
	IFOF	Griffis et al., 2017; Turken & Dronkers, 2011; Zhang et al., 2018
	UF	Catani et al., 2013; Dodson et al., 2018; Fridriksson et al., 2013
	EmC	Kourtidou et al., 2021; Kümmerer et al., 2013; Rolheiser et al., 2011; Verly et al., 2019; Wong et al., 2011
	MdLF	Luo et al., 2020; Saur et al., 2008
	AF	Ivanova et al., 2021; Turken & Dronkers, 2011
	FAT	Broce et al., 2015
Generally implicated in production	ILF	Ivanova et al., 2016; Tuncer et al., 2021
	IFOF	Dávolos et al., 2020; Grossman et al., 2013; Ivanova et al., 2016; Tuncer et al., 2021
	UF	Dodson et al., 2018
	SLF	Asaridou et al., 2017; Kyeong et al., 2019; Maldonado et al., 2011; Urger et al., 2015
	AF	Gajardo-Vidal et al., 2021; Liégeois et al., 2013
	FAT	Faulkner & Wilshire, 2020; Fujii et al., 2015; Kinoshita et al., 2015; Vassal et al., 2014; Young et al., 2020
Semantic processing	ILF	Harvey & Schnur, 2015
	IFOF	de Zubicaray et al., 2011; Han et al., 2013; Herbet, Moritz-Gasser, et al., 2017; Mirman et al., 2015; Moritz-Gasser et al., 2013; Sierpowska et al., 2019; Surbeck et al., 2020
	UF	de Zubicaray et al., 2011; Mirman et al., 2015; Surbeck et al., 2020
Lexical-semantic retrieval in comprehension	ILF	Griffis et al., 2017; Harvey & Schnur, 2015
	IFOF	Griffis et al., 2017; Han et al., 2013; Mirman et al., 2015; Sierpowska et al., 2019
	UF	Han et al., 2013; Mirman et al., 2015; Zhang et al., 2018) (Catani et al., 2013; Fridriksson et al., 2013
	EmC	Rolheiser et al., 2011
	MdLF AF	Luo et al., 2020 Ivanova et al., 2021; Tanabe et al., 1987
Semantic-lexical retrieval in production	ILF	Fridriksson et al., 2013; Griffis et al., 2017; Herbet et al., 2019; McKinnon et al., 2018; Moritz-Gasser et al., 2013;

	IFOF	Powers et al., 2013; Raffa et al., 2016; Sierpowska et al., 2019; Stark et al., 2019
	UF	Duffau et al., 2009; 2008; Faulkner & Wilshire, 2020; Fernández et al., 2020; Gil-Robles et al., 2013; Griffis et al., 2017; Han et al., 2013; Harvey & Schnur, 2015; Leclercq et al., 2010; Mandonnet et al., 2007; Moritz-Gasser et al., 2013; Motomura et al., 2018; 2014; Raffa et al., 2016; Sierpowska et al., 2019; Stark et al., 2019
	EmC	Duffau et al., 2005; Rolheiser et al., 2011
	MdLF	Luo et al., 2020
	SLF	Hillis et al., 2018; Kyeong et al., 2019; McKinnon et al., 2018; Powers et al., 2013; Stamatakis et al., 2011
	AF	Duffau et al., 2002; Ivanova et al., 2021; Marchina et al., 2011; Tanabe et al., 1987
Proper noun naming	UF	Lauro et al., 2010; Papagno et al., 2016; Papagno et al., 2010
Lexical-semantic control	ILF	Dávolos et al., 2020; Harvey & Schnur, 2015; Nugiel et al., 2016
	IFOF	Harvey & Schnur, 2015; Nugiel et al., 2016
	UF	Di Tella et al., 2020; Harvey et al., 2013
Phonological processing	SLF	Dodson et al., 2018; Han et al., 2016; Kyeong et al., 2019; McKinnon et al., 2018; Travis et al., 2017
	AF	Giampiccolo et al., 2020; Mandonnet et al., 2007; Schwartz et al., 2012; Tanabe et al., 1987; Yamada et al., 2007
Auditory repetition	EmC	Kourtidou et al., 2021
	MdLF	Saur et al., 2008
	SLF	Breier et al., 2008; Kyeong et al., 2019
	AF	Breier et al., 2008; Forkel et al., 2020; Kim & Jang, 2013; Saur et al., 2008; Shinoura et al., 2013; Sierpowska et al., 2017; Tanabe et al., 1987; Yamada et al., 2007
Auditory processing	MdLF	Tremblay et al., 2019; Wong et al., 2011
	AF	Li et al., 2021; Oechslin et al., 2010; Tremblay et al., 2019; Vaquero et al., 2021
Reading	ILF	Arrington et al., 2017; Broce et al., 2019; Carter et al., 2009; Enatsu et al., 2017; Epelbaum et al., 2008; Farah et al., 2020; Gil-Robles et al., 2013; Grotheer et al., 2021; Horowitz-Kraus et al., 2014; Sarubbo et al., 2015; Steinbrink et al., 2008; Mengmeng Su et al., 2018; Vanderauwera et al., 2017; Wang et al., 2020
	IFOF	Arrington et al., 2017; Broce et al., 2019; Grotheer et al., 2021; Kumar & Padakannaya, 2019; Steinbrink et al., 2008;

		Vanderauwera et al., 2018; 2017; Vandermosten et al., 2015; Zhao et al., 2016
	UF	Arrington et al., 2017; Bakhtiari et al., 2014; Cummine et al., 2015; Welcome & Joannis, 2014
	SLF	Bakhtiari et al., 2014; Borchers et al., 2019; Bruckert et al., 2019; Travis et al., 2017.
	AF	Dodson et al., 2018; Gullick & Booth, 2014, 2015; Hoeft et al., 2011; Saygin et al., 2013; Thiebaut de Schotten et al., 2012; Vanderauwera et al., 2017; 2015; Yeatman et al., 2011
Syntactic processing	EmC	Griffiths et al., 2012; Papoutsi et al., 2011; Rolheiser et al., 2011
	SLF	Mills et al., 2013; Vidorreta et al., 2011; Wilson et al., 2011
	AF	Mills et al., 2013; Papoutsi et al., 2011
	FAT	Catani et al., 2013; Chernoff et al., 2019; 2018; Dragoy et al., 2020; Mandelli et al., 2014; Yablonski et al., 2021
Language-related working memory	EmC	Lopez-Barroso et al., 2011
	SLF	Peters et al., 2012
	FAT	Rizio & Diaz, 2016; Varriano et al., 2018, 2020
	AF	Teubner-Rhodes et al., 2016
Speech fluency	EmC	Efthymiopoulou et al., 2017; Kourtidou et al., 2021
	AF	Basilakos et al., 2014; Chenausky et al., 2020; Fridriksson et al., 2013; Halai et al., 2017; Ivanova et al., 2021; López-Barroso et al., 2013; Marchina et al., 2011
	FAT	Basilakos et al., 2014; Catani et al., 2013; Chenausky et al., 2017; 2020; Halai et al., 2017; Ille et al., 2018; Kemerdere et al., 2016; Kronfeld-Duenias et al., 2016; Mandelli et al., 2014; Neef et al., 2017
Semantic fluency	ILF	Griffis et al., 2017
	IFOF	Almairac et al., 2015; Gonzalez et al., 2021; Griffis et al., 2017
	UF	Di Tella et al., 2020; Lauro et al., 2010; Li et al., 2017; Papagno et al., 2016; 2010; Powers et al., 2013; Rodríguez-Aranda et al., 2016
	SLF	Gonzalez et al., 2021; Powers et al., 2013; Pustina et al., 2014
	AF	Gonzalez et al., 2021; Sanvito et al., 2020
	FAT	Blecher et al., 2019; Costentin et al., 2019; Li et al., 2017; Sanvito et al., 2020
Phoneme/letter fluency	UF	Kljajevic et al., 2016; Li et al., 2017; Papagno et al., 2010; Serra et al., 2012
	SLF	Gonzalez et al., 2021; Madhavan et al., 2014; Pustina et al., 2014
	AF	Blecher et al., 2019

Ventral stream. Two outstanding questions are (1) Are some tracts specialized for comprehension vs. production? And (2) Are some tracts specialized for semantic control as opposed to semantic activation? Currently, the empirical data are not conclusive on these two points. Although there is some evidence that IFOF and ILF may be more involved in production and perception, respectively, this distinction is not uncontested. The evidence linking individual tracts to semantic-lexical control is even less consistent, with ILF, IFOF, and UF each implicated in some, but not in other, studies. Thus, future research on ventral tracts can benefit from cognitive tasks that (a) compare production vs. comprehension using a similar set of materials, e.g., picture naming vs. picture-word matching in individuals with brain damage, and (b) compare production/perception in conditions with low control demands to those with high control demands. An example in production is picture naming in the context of other semantically related vs. unrelated pictures (e.g., Costa et al., 2006; Nozari, Freund, et al., 2016; Schnur et al., 2009). The comprehension equivalent is picture-word matching with semantically related vs. unrelated distractors (e.g., Nozari, 2019). Although some of these tasks have been used in some studies, there is a clear need for more studies with larger sample sizes, larger sets and better-controlled materials to reconcile some of the discrepancies in the existing findings.

Dorsal stream. Two outstanding questions here are (1) Which tracts are involved in pure mapping of phonological representations to more peripheral representations, and which tracts are critical in the working memory (i.e., buffering) operations involving phonological representations. This distinction can be behaviorally tested by comparing the production of shorter vs. longer word (which require greater buffering; e.g., Goldrick & Rapp, 2007), or other tests of phonological working memory, although preferably those that do not pose additional demands on conflict

resolution, such as discriminating between close phonological alternatives in working memory. Some researchers have proposed that the same regions storing phonological representations are also involved in buffering them (Acheson et al., 2010), while others have suggested separate neural regions specialized for phonological buffering (Yue et al., 2019). The identification of the white matter tracts selectively involved in phonological working memory may shed some light on this debate. (2) The role of FAT is also a central issue among the dorsal tracts, with the proposal of a domain-general conflict-resolution and selection function, with some degree of domain-specificity for language in the left hemisphere, as the most promising theoretical framework for designing empirical studies.

Ventral and dorsal streams. Two sets of operations have been frequently suggested for tracts in both streams, reading and syntactic production. It is not surprising that reading has its signature over both tracts, as it can encompass a wide range of operations including the retrieval of phonological, lexical, and semantic representations, conflict resolution for visually, phonologically, or semantically similar items, and in some cases even activating motor commands. Most studies that link reading to different tracts have not disentangled different aspects of reading. Similarly, syntax encompasses a wide range of operations, some but not all of which require maintaining long-distance dependencies and reconciling competition between alternative representations, which may reflect more domain-general abilities rather than syntactic processes per se (e.g., Nozari & Omaki, 2022). Most studies of syntactic processing have not attempted to carefully disentangle these facets of processing.

In short, two questions are outstanding here: (1) Which tracts are involved in which aspect(s) of reading? More data from studies that differentiate the contribution of lexical and sublexical reading inspired by cognitive theories (e.g., Coltheart et al., 2001) would shed light on

this question. (2) Which tracts are involved in which aspect(s) of syntactic processing? A more systematic study of syntactic processing by carving it at its joints is likely to yield more informative results. One proposed dimension is Matchin and Hickok's (2020) separation of syntactic operations in comprehension vs. production. But there are many other possible divisions (or subdivisions within the comprehension/production framework) that can further shed light on the role of different neural regions in various aspects of syntactic processing. For example, one could test whether morphological processing can be disentangled from working memory processes which mediate the relationship between two parts of a sentence with dependencies.

Box 1. Outstanding questions for future research.

Ventral tracts

- 1) Are some tracts specialized for comprehension vs. production?
- 2) Are some tracts specialized for semantic control?

Dorsal tracts

- 1) Which tracts are specialized for phonological buffering in working memory?
- 2) What is the role of FAT?

Ventral and dorsal tracts

- 1) Which tracts are involved in which aspects of reading?
- 2) Which tracts are involved in which aspects of syntactic processing?

12. Conclusion

Much has already been learned about the network involved in processing language production and comprehension, including the white matter pathways that connect various cortical regions. The field has moved beyond the general question of whether a tract is or is not involved

in language processing and has reached a state of probing the nuanced nature of such involvement. This is an excellent time for combining theoretically inspired approaches with neural investigations. Specifically, the review above shows the need for moving away from paradigms that confound multiple operations, e.g., verbal fluency tasks, and towards those that can better tease apart cognitive components such as semantic activation vs. semantic control, phonological activation vs. phonological buffering, and pure syntactic operations vs. domain-general processes that support such operations.

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Figure captions

Figure 2. A schematic of the cognitive architecture of language production and comprehension.

Figure 2. Anatomy of ILF (a) and IFOF (b). DLPFC = dorsolateral prefrontal cortex; ITG = inferior temporal gyrus; MFG = middle frontal gyrus; MTG = middle temporal gyrus; MOG = middle occipital gyrus; OFC = orbitofrontal cortex; Ptri = pars triangularis; Porb = pars orbitalis; SOG = superior occipital gyrus; SPL = superior parietal lobe; STG = superior temporal gyrus.

Figure 3. Anatomy of UF. FP = frontal pole; OFC = orbitofrontal cortex; TP = temporal pole.

Figure 4. Anatomy of EmC. EmC = extreme capsule; IFG = inferior frontal gyrus; IPL = inferior parietal lobe; STG = superior temporal gyrus.

Figure 5. Anatomy of MdLF. OL = occipital lobe; POR = parieto-occipital regions; TP = temporal pole.

Figure 6. Anatomy of SLF (SLF-I is not shown). DLPFC = dorsolateral prefrontal cortex; dPMC = dorsal premotor cortex; IPS = intraparietal sulcus; Poper = Parsopercularis; SPL = superior parietal lobule; TP = temporoparietal.

Figure 7. Anatomy of AF. AG = angular gyrus; AsAF = anterior segment of the arcuate fasciculus; IFG = inferior frontal gyrus; LsAF = long segment of the arcuate fasciculus; MFG = middle frontal gyrus; PsAF = Posterior segment of the arcuate fasciculus; STS = superior temporal sulcus; vPMC = ventral Premotor Cortex.

Figure 8. Anatomy of FAT. IFG = inferior frontal gyrus; SMA = supplementary motor area.