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Chapter 10

White-matter pathways for speech and language processing

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INTRODUCTION

The white-matter fiber bundles in the brain play a crucial role in the transmission of information between different regions. These fiber bundles are composed of millions of axons that are surrounded by myelin, which is essential for fast transmission of electrical impulses (Wake et al., 2011).

The relevance of white-matter fiber bundles for speech perception and speech production was first recognized in the late 19th century, when they were proposed to form possible connections between the different language centers (Wernicke, 1874). In his model, Wernicke (1874) proposed a speech production center (based on the work of Broca, 1861), a sensory language center, and a connection between the centers supporting their interaction. Broca's area in the inferior frontal cortex and Wernicke's area in the superior temporal cortex as the classical language areas are subparts of temporofrontal language network that also support higher-language function processes such as grammatical assignment and attribution of meaning (Vigneau et al., 2006; Hickok and Poeppel, 2007; Friederici, 2011).

The connections between the classic language regions that have been identified over the past decades are multifold. Initially, two broad processing streams connecting temporal and frontal areas were proposed: a ventral stream supporting sound-to-meaning mapping and a dorsal stream subserving sound-to-motor mapping (Hickok and Poeppel, 2000; Rauschecker and Scott, 2009).

In recent years, new imaging techniques, such as diffusion-weighted magnetic resonance imaging (dMRI), also called diffusion tensor imaging (DTI), allow white-matter fiber bundles to be tracked *in vivo* in the human brain (Mori and Zijl, 2002). DTI can provide information about the internal fibrous structure based on the measure of water diffusion. Since water will diffuse more rapidly in the direction aligned with the internal structure, the principal direction of the diffusion tensor can be used to infer white-matter connectivity in the brain. Often DTI is used to identify the different fiber tracts in the human brain (Behrens et al., 2003; Catani and Thiebaut de Schotten, 2008; Berthier et al., 2012). This approach is primarily structure-based and independent from function, but once identified, the role of those tracts that connect brain areas known to be involved in particular processes, e.g., language, are discussed (Catani et al., 2005; Makris and Pandya, 2009). This approach only allows very indirect conclusions about a particular fiber tract's function.

A second approach is called a function-based approach. It combines functional MRI (fMRI) and dMRI, and thereby allows specification of a given fiber tract's function, indirectly, in a two-step approach. In a first step, particular brain regions relevant for a specific language task are identified in a functional experiment by fMRI, and then in a second step these regions are used as seed regions from which a tractogram is calculated (Friederici et al., 2006; Saur et al., 2008). The resulting fiber tract is taken to transmit information relevant for the particular function investigated by the fMRI, although it is not always certain whether the tracing originates only from the seed region or also from adjacent parts. Within this function-based tractography approach, two methodologies can be applied: probabilistic and deterministic tracking. The probabilistic approach takes one seed point, which is neurofunctionally defined, as the starting point of tractography (Friederici et al., 2006). The deterministic approach takes two regions that are activated simultaneously as a function of a particular task and calculates the fiber tract between these (Saur et al., 2008).

The most direct test of a particular fiber tract's function, however, is to investigate language performance in

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patients with lesions in the white-matter fiber tracts (Galantucci et al., 2011; Papoutsi et al., 2011; Turken and Dronkers, 2011; Wilson et al., 2011), or to correlate language performance with the degree of myelination of particular fiber tracts in the developing brain (Brauer et al., 2011).

Based on these approaches different white-matter pathways that are relevant for auditory language processing have been identified. Most generally the long-range fiber bundles which connect the frontal cortex (including the classic language region of Broca's area and premotor cortex (PMC)) and the temporal cortex (including the classic language region of Wernicke's area and the auditory cortex) can be classified into two anatomic pathways, i.e., the dorsal and the ventral pathway. Each of the pathways consists of more than one fiber bundle. Below we will specify the different subparts of the dorsal and ventral pathways, both structurally and functionally. Note that, in addition to these long-range connections between the frontal and the temporal cortex, there are a number of short-range connections within the frontal cortex and the temporal cortex. Here we will only describe those that have been considered as relevant for speech and language.

THE LANGUAGE-RELEVANT BRAIN REGIONS

White-matter pathways that are relevant for speech and language can be defined neuroanatomically by their different target regions. Interestingly, these target regions often differ in their function (Friederici, 2002; Vigneau et al., 2006; Price, 2010), but moreover, with respect to their cytoarchitectonic structure (Brodmann, 1909; Amunts and Zilles, 2012) and their receptorarchitectonic structure (Zilles and Amunts, 2009; Amunts et al., 2010). Moreover, the different regions can be parcellated on the basis of their particular structural connectivity to other regions (Johansen-Berg et al., 2004; Anwander et al., 2007). Thus, target regions can be identified on the basis of different structural and functional aspects.

Left frontal cortex

The language-relevant areas in the frontal cortex have been cytoarchitectonically defined to span along a posterior-to-anterior gradient from the PMC and Brodmann's area 6 (BA 6) in the precentral gyrus to BA 44 (the pars opercularis) and BA 45 (the pars triangularis), which together constitute Broca's area in the inferior frontal gyrus (IFG), and then they continue to the more anterior located BA 47 (the pars orbitalis) (for a schematic view, see Fig. 10.1). Spanning more medial and ventrally to BA 44 and BA 45, there is the frontal operculum (FOP), which cytoarchitectonically subdivides into different subregions (op8 and op9; Amunts et al., 2010). Recent receptorarchitectonic analyses even suggest that area 44 can be further divided into a dorsal (44d) and a ventral (44v) portion, and area

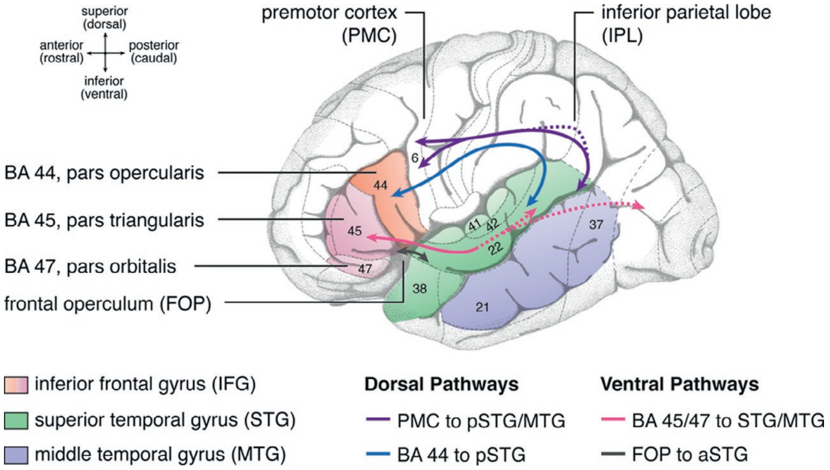

Fig. 10.1. Language-relevant brain regions and schematic fiber tracts (displayed in the left hemisphere). Numbers represent cytoarchitectonically defined Brodmann areas (BAs). BA 44 and BA 45 together constitute Broca's area. BA 22 constitutes Wernicke's area. Different pathways are color-coded according to the color legend in the figure. The connection from the prefrontal motor cortex (PMC) to the posterior superior temporal gyrus (pSTG)/middle temporal gyrus (MTG) involves the superior longitudinal fascicle (SLF). The connection from BA 44 to the pSTG involves the arcuate fascicle (AF). The connection from BA 45/47 to the superior temporal gyrus (STG)/MTG involves the extreme capsule fiber system (ECFS)/longitudinal inferior-fronto-occipital fascicle (IFOF). The connection from the frontal operculum to the anterior superior temporal gyrus (aSTG) involves the uncinate fascicle (UF). pMTG, posterior middle temporal gyrus. (Adapted from Friederici and Gierhan, 2013.)

45 can be separated into an anterior (45a) and a posterior (45p) portion (Amunts et al., 2010).

Functionally, these areas have been argued to support different aspects of language processing: BA 6 is involved in phonology and articulation; BA 44, together with area 45p, is involved in syntactic structure building; and area 45a, together with BA 47, supports semantic processes (Bookheimer, 2002; Friederici, 2002; Uddén and Bahlmann, 2012). Note that there is still some debate about the role of Broca's area in processing syntactic information (Musso et al., 2003; Hagoort, 2005; Novick et al., 2005; Grodzinsky and Amunts, 2006) and which part of Broca's area (BA 44/45) is involved: is it BA 44 proper or BA 45/BA 44 (Friederici, 2002; Hagoort, 2005; Grodzinsky and Santi, 2008; Tyler and Marslen-Wilson, 2008; Rogalsky and Hickok, 2011). This may be partly due to the fact that different fMRI studies have used different stimulus material: either natural sentences containing semantic and syntactic information, or so-called "jabberwocky" sentences that only contain syntactic information (function words) and no semantic information (pseudowords), or random word lists containing function words and pseudowords. Moreover, they have employed different presentation modes (written vs auditory) and different tasks (such as sentence comprehension, grammaticality judgement, plausibility judgement, or probe identification) (Caplan et al., 2008).

Left temporal cortex

The temporal cortex neuroanatomically subdivides into the inferior, middle, and superior temporal gyri (STGs). Cytoarchitectonically, the STG can be differentiated into BA 41/42, as the primary and secondary auditory cortex (roughly "core" and "belt" in animal research terminology), and BA 22 (very roughly, "parabelt"), which constitutes the large region of Wernicke's area (Brodmann, 1909; Morosan et al., 2005). Functional connectivity-based analyses suggest a subdivision of the STG into three parts: (1) the middle part of the STG (mSTG) located lateral to Heschl's gyrus (which contains BA 41/core auditory areas) and the primary auditory cortex; (2) a portion located anterior to the Heschl's gyrus (aSTG); and (3) a portion located posterior to Heschl's gyrus (pSTG) (Upadhyay et al., 2008) (Fig. 10.2).

This subdivision of the STG into subparts is generally in line with proposed functional differentiation of the STG and superior temporal sulcus (STS). An early functional imaging study already proposed a subdivision of the STS/STG into an anterior, middle, and posterior portion, with the middle portion being involved in sound and speech processing and both the anterior and posterior portions being involved only in speech (Giraud and Price, 2001). A recent meta-analysis over 115 studies claims a posterior-to-anterior gradient with increasing complexity of the auditory stimulus, going from phoneme processing (mSTG) to the processing of words and phrases (aSTG) (DeWitt and Rauschecker, 2012) (Fig. 10.3).

The middle temporal gyrus (MTG) is also considered to be language-relevant (Turken and Dronkers, 2011), subserving lexical-semantic and conceptual semantic aspects in particular (Patterson et al., 2007; Lau et al., 2008).

Left parietal cortex

In addition to the left frontal and temporal cortices, the left parietal cortex, in particular the inferior parietal lobe (IPL), is also seen to be involved in language processing whenever language tasks that require phonologic working memory have to be performed. Initially, the left inferior and posterior parietal cortices, in particular, were found to support aspects of phonologic working memory and storage (Jonides et al., 1998; Bushara et al., 1999; Gruber and von Cramon, 2001). Although this region is not considered as one of the classic language areas, it appears to come into play in language tasks that require certain memory capacities, such as in a verbal working memory task or a repetition task in which auditorily perceived words or sentences have to be recalled and/or actively reproduced (Jonides et al., 1998; Ravizza et al., 2011). Moreover, this region is activated during sentence comprehension tasks that require the binding of two distant elements across a number of intervening elements in a sentence (Grossman et al., 2002; Meyer et al., 2012). This was demonstrated in an fMRI sentence comprehension study varying systematically the working memory demands (long vs short distance of related elements) and the reordering demands of elements (subject-first structure vs object-first structure). The effect of reordering was found in BA 44 and the effect of storage in temporoparietal regions (Meyer et al., 2012) (Fig. 10.4). Note that temporoparietal regions have been previously claimed to be involved in the processing of working memory and language performance (Hickok et al., 2003; Buchsbaum and D'Esposito, 2008; Buchsbaum et al., 2011).

THE LANGUAGE PATHWAYS

Language regions in the frontal cortex and in the temporal cortex are neuroanatomically connected by both dorsally located and ventrally located long-range fiber tracts known as the dorsal and the ventral pathways.

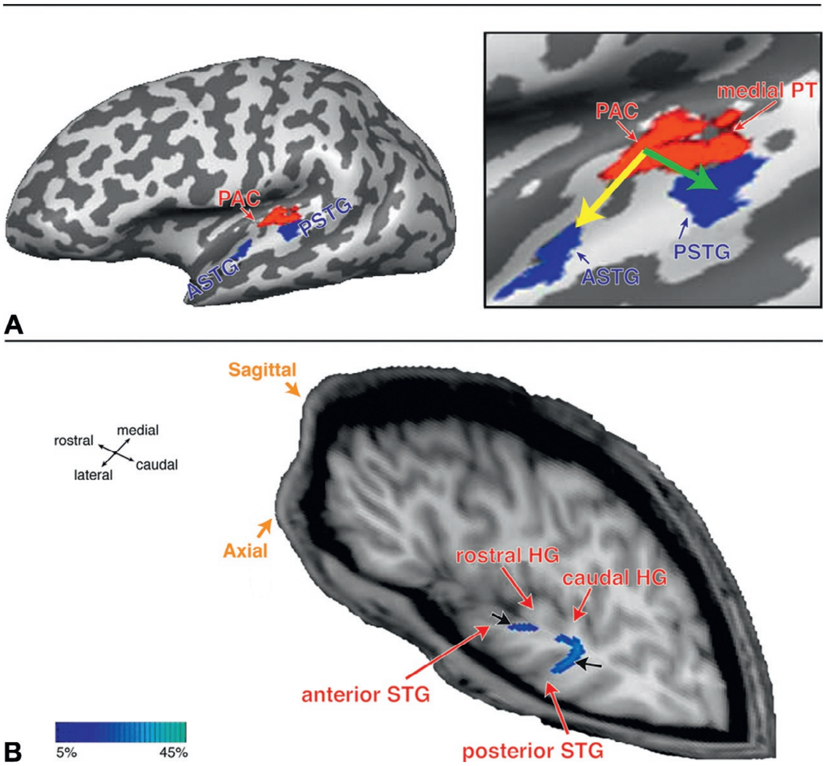

Fig. 10.2. Connectivities in the auditory cortex. (**A**) Effective connectivity in auditory cortex. An effective connectivity map in the auditory cortex is shown for a single subject. The red region corresponds to the reference region in the primary auditory cortex (PAC) as well as the medial regions of the planum temporale (PT), which showed functional connectivity with PAC. Blue regions depict the rostrolateral (lateral planum polare + anterior superior temporal gyrus, referred to as ASTG) and caudolateral (lateral PT + posterior superior temporal gyrus, referred to as PSTG) auditory cortex regions identified as being targets of influence of PAC. (**inset**) An enlarged view of the effective connectivity map is shown on the inflated brain surface. The green arrow depicts a caudal pathway as defined by granger causality mapping (GCM) analysis, and the yellow arrow represents a possible rostral pathway. (**B**) Rostral and caudal fiber pathways in auditory cortex. Two-dimensional probabilistic maps of the rostral and caudal fiber pathways (marked by the black arrows) are shown on sagittal and axial T1-weighted slices. Whereas the caudal pathway projects from more caudal regions of the rostral Heschl's gyrus, the rostral pathway projects from the rostral segments of the same gyrus. The two pathways also have distinct fiber densities or probabilities, as defined by probability values. High fiber density is indicated by light blue-green voxels; low fiber density is indicated by dark blue voxels. (Adapted from Upadhyay et al., 2008.)

Dorsal pathway

The distinction between a dorsal and a ventral pathway connecting the temporal cortex and the frontal cortex is based on the neuroanatomic differentiation in the monkey between the "where" stream, which goes from the auditory cortex to the dorsolateral prefrontal cortex and the ventrally located "what" stream, originally defined by Rauschecker and Tian (2000). The dorsal pathway was initially described as emanating from the planum temporale in the posterior superior temporal region running through the IPL to the dorsal PMC (BA 6) and was seen as responsible for sensory-to-motor mapping in speech processing (Hickok and Poeppel, 2000, 2007; Rauschecker and Scott, 2009).

Structurally, however, the dorsal pathway appears to consist of more than one white-matter fiber bundle (Catani et al., 2005; for a recent review, see Gierhan, 2013). Here, we will discuss two major fiber bundles, which can be differentiated by their termination regions in the frontal cortex and possibly by their particular language subfunctions as well. One dorsal fiber bundle connects the temporal cortex with the PMC through the mediation of the IPL, whereas the other bundle connects the temporal cortex to Broca's area, in particular BA 44 (Perani et al., 2011). Interestingly, this fiber bundle is not yet myelinized in newborns (Fig. 10.5).

Functionally, the dorsal stream has been discussed as being involved in speech repetition, that is, the production and articulation of perceived speech sounds (Hickok and Poeppel, 2000, 2007). A function-based DTI study has shown that the fiber tract terminating in the dorsal PMC can indeed be allocated to sensory-to-motor mapping functions (Saur et al., 2008) (Fig. 10.6).

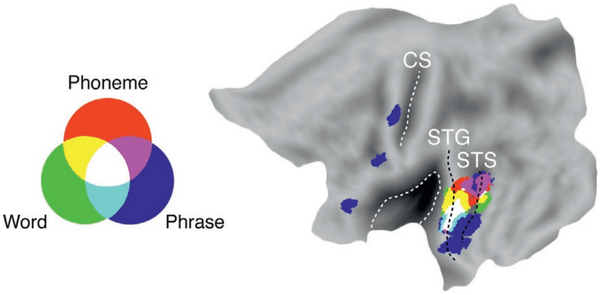

Fig. 10.3. Flat-map presentation of activation likelihood estimation for more than 115 studies on speech perception. Activations for phonemes (red), words (green), and phrases (blue), as well as the overlap (white). CS, central sulcus; STG, superior temporal gyrus; STS, superior temporal sulcus. (Adapted from DeWitt and Rauschecker, 2012.)

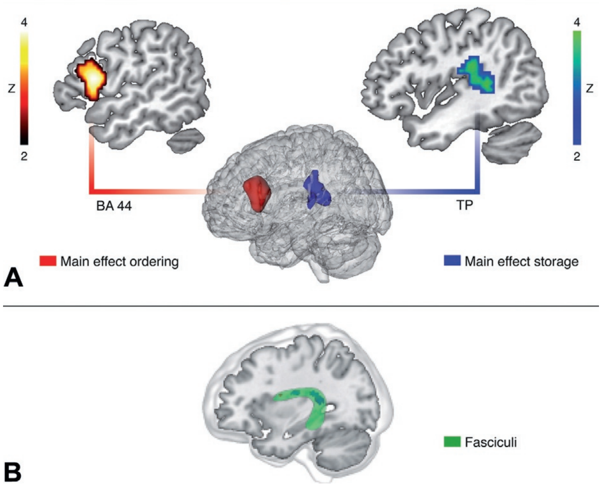

Fig. 10.4. Functional activations (FAs) and connectivity pattern. (**A**) Brain activations for the ordering effect (red cluster) and the storage effect (blue cluster). For the ordering factor, 64.8% of the obtained cluster is in the left BA 44 with a peak at $x = -54$, $y = 10$, $z = 18$ ($z = 3.76$). For the storage factor, the activation is found in the medial left temporoparietal (TP) region, peaking at $x = -42$, $y = -40$, $z = 10$ ($z = 3.66$). (**B**) Correlation of FA values with signal change of the storage effect in left TP region (blue cluster in **A**) as compared to the ordering effect in the BA 44 (red cluster in **A**). The regression analysis resulting from the averaging of the individual fiber tracts was carried out in a volume of 1561 voxels of the arcuate fascicle/superior longitudinal fascicle (green). Clusters were thresholded at pb0.05 and a minimum cluster size of seven suprathreshold voxels to control for family-wise error at pb0.005. (Reproduced from Meyer et al., 2012.)

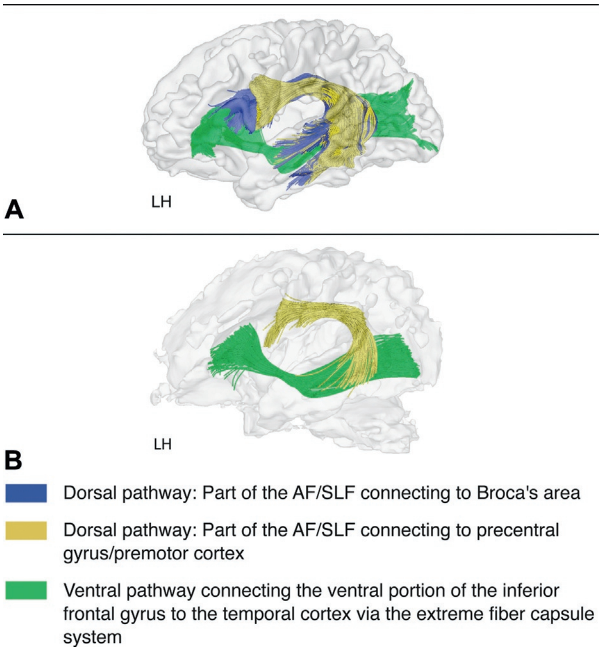

Fig. 10.5. Structural connectivity results. (**A**) Fiber tracking of diffusion tensor imaging data for adults for speech-relevant regions with seed in Broca's area and seed in the precentral gyrus/premotor cortex. Two dorsal pathways are present in adults – one connecting the temporal cortex via the arcuate fascicle (AF) and the superior longitudinal fascicle (SLF) to the inferior frontal gyrus, i.e., Broca's area (blue), and one connecting the temporal cortex via the AF and SLF to the precentral gyrus, i.e., premotor cortex (yellow). The ventral pathway connects the ventral inferior frontal gyrus via the extreme capsule fiber system to the temporal cortex (green). Left hemisphere (LH). (**B**) Fiber tracking for newborns. Dorsally only one pathway can be detected, i.e., the pathway connecting the temporal cortex to the precentral gyrus, i.e. premotor cortex (yellow). The ventral pathway (green) is present in newborns. (Adapted from Perani et al., 2011.)

The second major dorsal fiber tract terminates in BA 44, i.e., in the posterior portion of Broca's area, and connects this area directly with the posterior temporal cortex (Fig. 10.6). This fiber bundle, which connects the language areas Broca's area and Wernicke's area, has long been described as relevant for language processing. It is classically labeled as the arcuate fascicle (AF). Catani et al. (2005) tracked the AF using dMRI and already suggested two dorsal connections, one connecting Broca's region and Wernicke's region directly, and one connecting these regions indirectly. The figure in their publication, however, suggests the latter fiber bundle terminates in the PMC rather than in Broca's area (Fig. 10.7). Nevertheless, this early dMRI work provided some indication of there being two major dorsal connections, a direct one and an indirect one mediated by the IPL.

The neuroanatomic description and the labeling of the dorsally located fiber bundles in the literature are unfortunately somewhat heterogeneous and have even changed over the past decades. Today, the fiber bundles that connect the IPL to the PMC are most commonly named the superior longitudinal fascicle (SLF), which has three subcomponents: SLF I, SLF II, and SLF III,

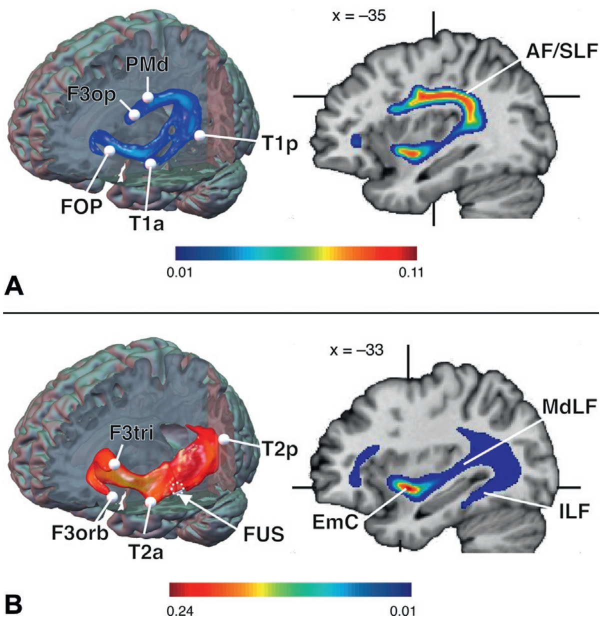

Fig. 10.6. Fiber tracking results. (**A**) Composite fiber networks subserving repetition and (**B**) comprehension computed by averaging the pairwise connections of 33 subjects defined in the repetition and comprehension experiment, respectively. Three-dimensional tractography renderings visualize the spatial orientation of both networks. Crosshairs on sagittal sections indicate the orientation of the coronal and axial sections. Maximum PIBI (probability index-forming part of the bundle of interest) values are given at the top of the color bar. T1a/p, anterior/posterior superior temporal gyrus; T2a/p, anterior/posterior middle temporal gyrus; FUS, fusiform gyrus; F3orb/tri/op, pars orbitalis/triangularis and opercularis of the inferior frontal gyrus; FOP, deep frontal operculum; PMd, dorsal premotor cortex; EmC, extreme capsule; AF/SLF, arcuate and superior longitudinal fascicle; MdLF/ILF, middle and inferior longitudinal fascicle. (Adapted from Saur et al., 2008. Copyright (2008) National Academy of Sciences, U.S.A.)

initially identified in the monkey (Petrides and Pandya, 1984; Schmahmann et al., 2007). SLF I is the most dorsally located bundle connecting the superior parietal cortex with the superior frontal cortex, while SLF II and III are located more inferiorly. SLF III connects the PMC to the IPL. The nomenclature of SLF I–III has been adapted to the human brain, with SLF II and III connecting the PMC to the IPL being highlighted as relevant for language (Makris et al., 2005; Frey et al., 2008; Thiebaut de Schotten et al., 2012). The fiber bundle connecting the IPL to the temporal cortex has been named SLF-tp. The AF, which connects the prefrontal cortex to the posterior STG, runs closely in parallel with SLF II from prefrontal to parietal regions, but differs from the SLF in particular in its posterior portion curving into the temporal posterior cortex. But since the SLF and the AF run in parallel between the prefrontal and parietal cortex, some researchers refer to this fiber tract as AF/SLF.

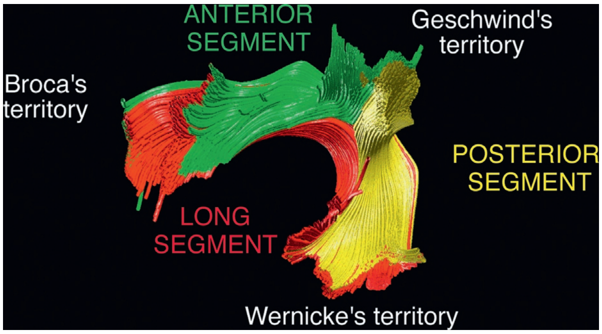

Fig. 10.7. Tractography reconstruction of the arcuate fascicle. Broca's and Wernicke's territories are connected through direct and indirect pathways in the average brain. The direct pathway (long segment shown in red) runs medially and corresponds to classical descriptions of the arcuate fascicle. The indirect pathway runs laterally and is composed of an anterior segment (green) connecting the inferior parietal cortex (Geschwind's territory) and Broca's territory and a posterior segment (yellow) connecting Geschwind's and Wernicke's territories. (Reproduced from Catani et al., 2005.)

The specific function of the AF connecting Broca's area to the posterior temporal cortex is still under debate. One proposed function is that it is particularly involved in processing syntactically complex sequences and sentences. This evidence comes from a number of studies using different approaches to identify the function of this fiber tract in language. First, a function-based dMRI study using probabilistic fiber tracking with seeds in BA 44 argued that it was involved in the processing of syntactically complex sequences and was structurally connected by a dorsal fiber tract to the temporal cortex (Friederici et al., 2006) (Fig. 10.8A).

This suggested that this fiber tract, the AF/SLF, is crucially involved in processing complex syntax. Second, non-fluent primary progressive aphasic patients, who had suffered from lesions in this fiber bundle, were found to be specifically deficient in processing syntactically complex sentences (Wilson et al., 2011) (Fig. 10.9). Third, a study of 7-year-old children found that their AF/SLFs had not yet fully matured and they had problems in processing syntactically complex sentences (Brauer et al., 2011). It is an open question how this pathway supports complex sentence processing, either by computing syntactic relations or via some form of working memory-related mechanism.

Ventral pathway

The language regions in the frontal cortex and in the temporal cortex are also connected to each other by at least two ventrally located pathways. First, the extreme

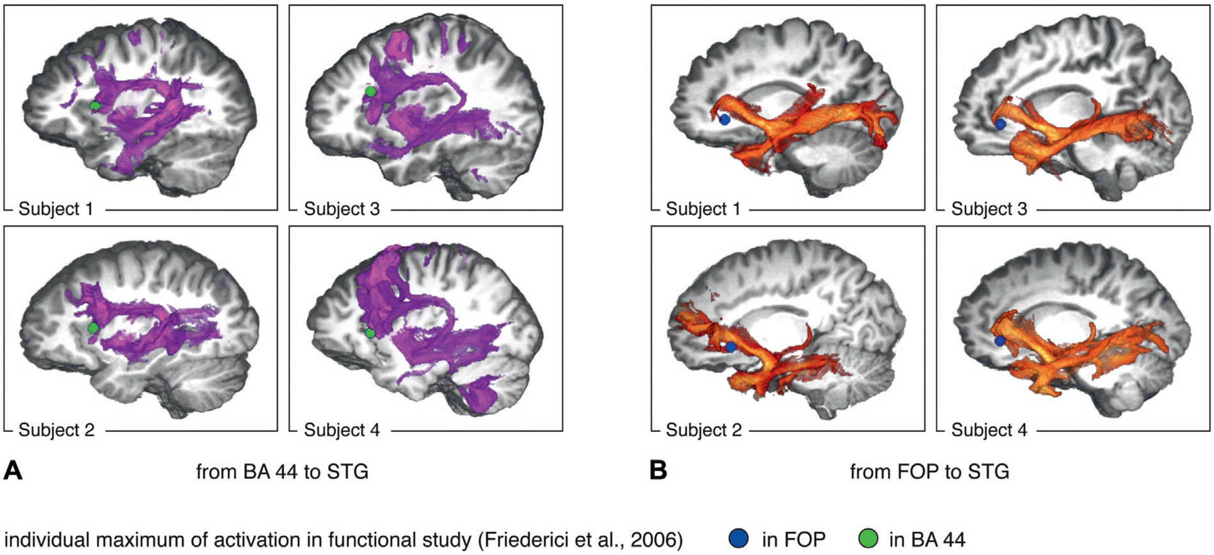

Fig. 10.8. Tractograms for two brain regions: Broca's area and frontal operculum (FOP). Three-dimensional rendering of the distribution of the connectivity values of two start regions with all voxels in the brain volume (purple, tractograms from Broca's area; orange, tractograms from FOP). (**A**) Four representative subjects of the group processing a phrase structure grammar with their individual activation maxima in Broca's area (green) in the critical contrast incorrect vs correct sequences ($P > 0.005$). For all subjects, the tractography detected connections from Broca's area to the posterior and middle portion of the superior temporal region via the fasciculus longitudinalis superior. (**B**) Four representative subjects of the group processing a finite-state grammar with their individual activation maxima in the FOP (blue) in the critical contrast incorrect vs correct sequences ($P > 0.005$). The individual peaks of the functional activation were taken as starting points for the tractography. For all subjects, connections to the anterior temporal lobe via the fasciculus uncinatus were detected. BA, Brodmann's area; STG, superior temporal gyrus. (Adapted from Friederici et al., 2006.)

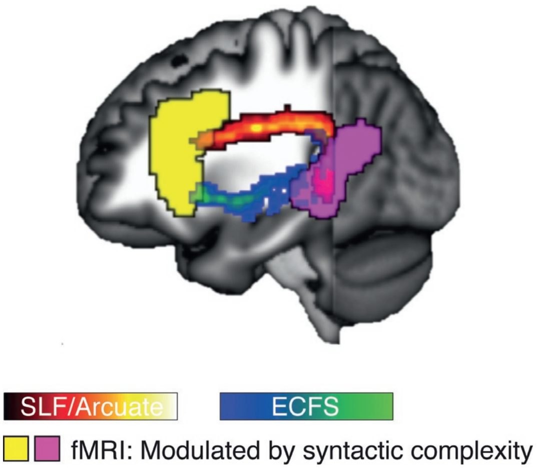

Fig. 10.9. Voxel-based morphometry and functional magnetic resonance imaging (fMRI). The left superior longitudinal fascicle (SLF)/arcuate fascicle (red/orange) and extreme capsule fiber system (ECFS) (blue/green) were constrained to connect the anterior language region (yellow) and posterior language region (magenta) that were modulated by syntactic complexity in normal controls in a previous fMRI study (Wilson et al., 2010a). Functional anisotropy (FA) values in the constrained SLF/arcuate fascicle were associated with syntactic deficits, but FA values in the constrained ECFS were not. (Adapted from Wilson et al., 2011.)

capsule fiber system (ECFS) connects BA 45 and BA 47, which are known to be involved in semantic processes, to the STG/MTG, the MTG, and the occipital cortex. Second, the uncinate fascicle (UF) connects the FOP to the anterior temporal cortex.

The ventral pathway connecting the frontal and temporal cortex ventrally was originally viewed as a unifunctional tract subserving sound-to-meaning mapping (Hickok and Poeppel, 2004, 2007; Rauschecker and Scott, 2009), but later different functions were assigned to subparts of the ventral pathway, specifically the ECFS, also named the inferior-fronto-occipital fascicle (IFOF) (Saur et al., 2008, 2010; Turken and Dronkers, 2011; Sarubbo et al., 2013) and the UF. From these subparts the ECFS/IFOF, with frontal terminations in BA 45, BA 47, and the orbitofrontal cortex and temporal terminations in the MTG, the STG, and the temporoparietal cortex, are seen as the major pathway supporting semantic processes (Saur et al., 2008) (Fig. 10.6).

The specific function of the UF, which connects the FOP and orbitofrontal cortex to the aSTG (Anwander et al., 2007; Hua et al., 2009; Thiebaut de Schotten et al., 2012), is still being debated. Early work proposed that the UF is relevant for language processing in general

(Wise, 2003; Grossman et al., 2004; Catani and Mesulam, 2008; Matsuo et al., 2008). However, Friederici et al. (2006), using function-based dMRI, suggested that the UF connecting the FOP and the aSTG may also be involved in syntactic processing such as the building up of local syntactic phrases through which adjacent elements are combined syntactically. Note that, for syntactic processes, a differentiation is made between local phrase structure building processes which recruit a ventral fiber tract (Fig. 10.8B) and the process of non-local syntactic dependencies in artificial grammar sequences and sentences with non-canonical word order which involve a dorsal pathway (Fig. 10.8A) (all the fMRI studies investigating such complex structures are discussed in a recent review: Friederici, 2011).

Both the proposal of allocating semantic processes to the ventral pathway and the proposal of allocating local phrase structure building to the ventral pathway may be valid since, functionally, the anterior STS has been found to be relevant for the intelligibility of speech in general (Scott et al., 2000; Crinion et al., 2003; Narain et al., 2003; Obleser et al., 2007; Friederici et al., 2010; Obleser and Kotz, 2010) and the aSTG as well as the anterior temporal lobe have been reported to be activated as a function of semantic and syntactic aspects (for a review of the functional studies, see Mazoyer et al., 1993; Stowe et al., 1998; Friederici et al., 2000, 2003; Vandenberghe et al., 2002; Humphries et al., 2005, 2006; Snijders et al., 2009; Friederici, 2011). Thus, both semantic and syntactic combinatorial processes that are elementary for language may involve the anterior temporal cortex.

The combined data suggest that the ventral pathway, with its different subparts, supports elementary semantic processes and local phrase structure building processes. The intraoperative stimulation of the two ventral fiber tracts suggests that the ECFS is more relevant for language than the UF because verbal fluency (naming as many words as possible in a particular category) and performance on a grammatical gender task (matching the article to the noun) were found not to be interrupted when stimulating the UF, but only when stimulating the ECFS (Duffau et al., 2008). However, these tasks may have challenged the semantic system more than the combinatorial system and, thus, do not rule out the possible involvement of the UF in combinatorial processes. It is undisputed that the ECFS/IFOF is language-relevant.

Thus, both the ventral and the dorsal pathway are involved in syntactic processes (Griffiths et al., 2013); however, the dorsal pathway (AF/SLF) is needed for the processing of sentences when they are syntactically complex (Brauer et al., 2011; Wilson et al., 2011).

CONCLUSIONS

The white-matter fiber tracts connecting the language-relevant regions in the frontal and temporal cortices can be classified into dorsal and ventral pathways. Each pathway consists of more than one major fiber tract. Within the ventral pathway one tract connects BA 45/47 with the STG and MTG and the other tract connects the orbitofrontal cortex with the anterior temporal cortex. The former ventral tract supports semantic processes, while the function of the latter is still debated. Within the dorsal pathway, one tract connects the posterior temporal cortex to the PMC and another one connects it to the posterior portion of Broca's area. While the former dorsal pathway is taken to support sensory-to-motor mapping, the latter appears to be relevant for the performance of complex syntactic tasks.

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