Pathways to language: fiber tracts in the human brain

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The human language function is not only based on the grey matter of circumscribed brain regions in the frontal and the temporal cortex but moreover on the white matter fiber tracts connecting these regions. Different pathways connecting frontal and temporal cortex have been identified. The dorsal pathway projecting from the posterior portion of Broca's area to the superior temporal region seems to be of particular importance for higher-order language functions. This pathway is particularly weak in non-human compared to human primates and in children compared to adults. It is therefore considered to be crucial for the evolution of human language, which is characterized by the ability to process syntactically complex sentences.

White matter, grey matter and language

Knowledge about the language–brain relationship has dramatically improved since the advent of brain imaging techniques. The functional relevance of different regions in the grey matter as revealed by functional magnetic resonance imaging (fMRI) has led to several quite elaborate neurocognitive models on speech and language processing (e.g. Refs [1–5]). These models define functional neural networks for the processing of different aspects of language such as phonology, syntax and semantics which each involve areas in the temporal and the frontal cortex. All models see Wernicke's area, located in the superior temporal gyrus (STG) and middle temporal gyrus (MTG), and Broca's area, located in the inferior frontal gyrus (IFG), as parts of the language network. Although the models vary with respect to the functional allocation of these different areas (Box 1), they agree in viewing circumscribed regions in the grey matter of the frontal and temporal cortex as constituting the neural basis of language. However, the grey matter alone cannot accomplish language processing. Rather, to allow information flow between the different cortical regions, these have to be connected to each other. Neuroanatomically this is guaranteed through white matter fiber bundles which connect adjacent and distance brain regions.

Lesions of these pathways connecting different brain regions have long indicated the importance of specific pathways for language processing [6,7]. More recently, new imaging techniques and analyses allow us to describe these white matter connections in the healthy living brain.

Here, we review the recent literature on the structural connectivity between language-relevant brain areas, namely Broca's and Wernicke's area. Before discussing

the connectivities in more detail, the language relevant areas are briefly characterized with respect to their cytoarchitectonic features. This brief characterization provides an important context for the review of recent findings on white matter pathways between language-relevant areas: subdivisions of the language-related areas are relevant insofar as they coincide with different connectivity patterns, and moreover, functional distinctions.

Subdivisions of the grey matter within the language areas

Broca's area

Subdivisions of the IFG into different 'cytoarchitectonically' defined areas are acknowledged by all scientists, and some even propose a functional separation of these (Box 1). The cytoarchitectonic differentiation proposed by Brodmann [8] was based on the layering of the isocortex and the presence of particular cell types therein (Figure 1). According to these criteria, Broca's area is distinguished into a more posterior part of the inferior frontal gyrus (i.e. Brodmann Area [BA] 44) from the more anteriorly located area BA 45 (see also Ref. [9]).

A neuroanatomical subdivision into BA 44 and BA 45 and the adjacent frontal operculum was also proposed in connectivity-based analyses by means of diffusion tensor imaging (DTI) (Box 2) [10]. The idea behind connectivity-based parcellation is that cortical tissue with similar long-range white matter connectivity combine into an area which can be segregated from neighbouring areas, each of which has a different connectivity profile. With some variance in the relative size of the respective areas, a three-region parcellation into BA 44, BA 45 and frontal operculum has been seen across individuals.

These neuroanatomical differentiations are interesting given the proposed differentiations of language functions within the inferior frontal gyrus [1,3,5] (Box 1).

Wernicke's area

The neuroanatomical subdivision of the temporal cortex of the dominant left hemisphere is less defined. Within the superior temporal gyrus, a large portion of Wernicke's area (BA 22) was differentiated cytoarchitectonically from BA 42 [8]. More recently, BA 42 was further subdivided cytoarchitectonically in at least two subareas [11].

A connectivity-based analysis suggests a subdivision of the superior temporal gyrus and sulcus (STG/STS) into three parts: one located anterior to Heschl's gyrus, one located posterior to Heschl's gyrus and one including Heschl's gyrus [12]. A recent structural and functional

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Box 1. Neurocognitive models of language functions

The degree of functional subdivision of the IFG in the language domain differs among recent neurocognitive models of language. (Note, the existence of functional subdivisions of the prefrontal independent of language, e.g. Ref. [62].) Poeppel and colleagues [4,63] do not clearly subdivide the IFG functionally, but consider it to be involved in synthesizing information in general. According to Hagoort [2], the IFG 'binds' phonological, syntactic and semantic aspects with a function-location mapping from more posterior to anterior, respectively. Bornkessel and Schlesewsky [3] take BA 44 to be responsible for linearization of argument hierarchy during thematic role assignment based on syntactic and semantic features. Friederici [1] proposes a functional subdivision of the IFG into three regions, with BA 44 supporting the processing of hierarchical structures, the adjacent more-ventrally and medially located frontal operculum subserving the processing of local phrase structure and BA 45 subserving controlled semantic processes. Note, that BA 47 located anterior and ventral to BA 45 is considered to have an important role in semantic recall from long term memory [64,65].

Within the latter model, the frontal operculum and BA 44 have been claimed to each be part of separate frontotemporal networks (Figure I), with the frontal operculum, together with the anterior STG, dealing with the structure of phrases (noun phrase, prepositional phrase etc.) and with BA 44/45, together with the posterior STG, being responsible for thematic role assignment [66]. Within the latter network, BA 44 seems to process hierarchical structures independent of semantics (i.e. in natural [51] and semantic-free artificial grammars [44,45]), whereas the posterior STG seems to support the integration of syntactic and semantic information to achieve understanding (that is to understand who is doing what to whom).
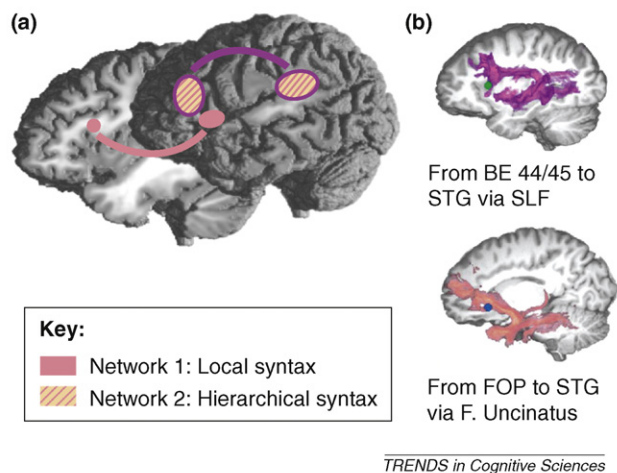

Figure I. Syntactic networks in the human brain. **(a)** Depicts the two neural networks for syntactic processing and their fronto-temporal involvement (function) schematically. **(b)** Shows fiber tracing as revealed by diffusion tensor imaging (DTI) (structure) in an individual subject: top right, with the starting point (green dot) being BA 44 and bottom right, with the starting point (blue dot) being the frontal operculum. The former pathway (top right) is referred to as the dorsal pathway and the latter (bottom right) is referred to as the ventral pathway. Abbreviations: SLF, superior longitudinal fasciculus; STG, superior temporal gyrus; FOP, frontal operculum; F, fasciculus. (b) Reproduced, with permission, from Ref. [44].

Box 2. Diffusion tensor imaging and diffusion spectrum imaging

Diffusion tensor imaging (DTI) enables the quantification of long-range connectivity between different areas in the brain *in vivo*. It is based on the fact that measured diffusivity depends on the orientation of the principle axes of fiber tracts. Diffusion weighted magnetic resonance imaging measures the direction-dependent mobility of water molecules which is influenced by the microscopic architecture of the brain tissue yielding information about the local orientation of the white matter fibers [67–69].

Two approaches are used to provide information about the course of white matter fiber bundles, these being deterministic and probalistic tractography. Deterministic tractography produces maximum likelihood pathways using diffusion weighted magnetic resonance data. Probabilistic approaches take into account the uncertainty of the direction information in each voxel along the tract [70,71]. The basis for probabilistic tractography is the local probability density function generated by a mathematical model of the local diffusivity in which each parameter is characterized by a statistical distribution (e.g. Ref. [18]). Then these local probability density values have to be connected using conditional probabilities.

Note, however, that in a strict sense DTI does not directly map anatomical connectivity. There are limitations, in particular when fibers merge, branch or cross each other [56]. New methods are currently being developed to minimize false positives.

One such method is diffusion spectrum imaging (DSI). DSI has the ability to resolve crossing fibers at the scale of a single MRI (magnetic resonance imaging) voxel. This approach requires a special pulse sequence in the MRI scanner. Diffusion spectrum encoding was described by Wedeen *et al.* [72]. The resolution of these images is amazingly fine grained.

Using DSI, Schmahmann *et al.* [48], for example, were able to distinguish three subcomponents of the SLF projecting from the frontal cortex to the parietal cortex (SLF I-III) in the rhesus monkey, none of which seem to project to the temporal cortex directly. But even with this method, Schmahmann *et al.* [48] acknowledge that they were 'not able to identify with certainty' whether the fibers lying obliquely in the caudal part of the STG were continuous with those that intersect with fibers projecting to the parietal lobe or not (Figure I).
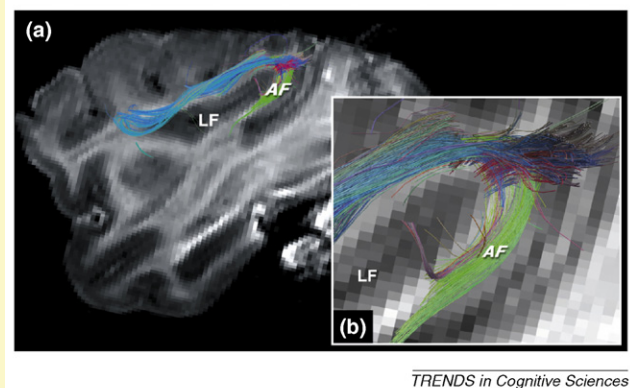

Figure I. Fiber tracts in the rhesus monkey. **(a)** Shows fibers as revealed by DSI that intersect with a sphere placed in the caudal part of the superior temporal gyrus and the inferior parietal lobule. **(b)** A higher magnification view of fibers that arch around the caudal end of the sylvian fissure, in the location of the arcuate fasciculus. Reproduced, with permission, from Ref. [48].

connectivity study focussing on the human auditory cortex identified three functional regions: the Heschl's gyrus (including primary auditory cortex), the posterior STG (including the planum temporale) and anterior STG (including the planum polare) [13]. DTI data revealed two local pathways within the temporal white matter, one projecting from Heschl's to the anterior STG and one to the posterior STG.

This three-part differentiation of the superior temporal regions thus seems to coincide with the proposed functional subdivisions of the STG [14–16].

White matter fiber tracts connecting the language areas
Research trying to identify the fiber pathways between Broca's area and Wernicke's area date back to 1895 when Dejerine [17] defined the arcuate fasciculus (AF) as the
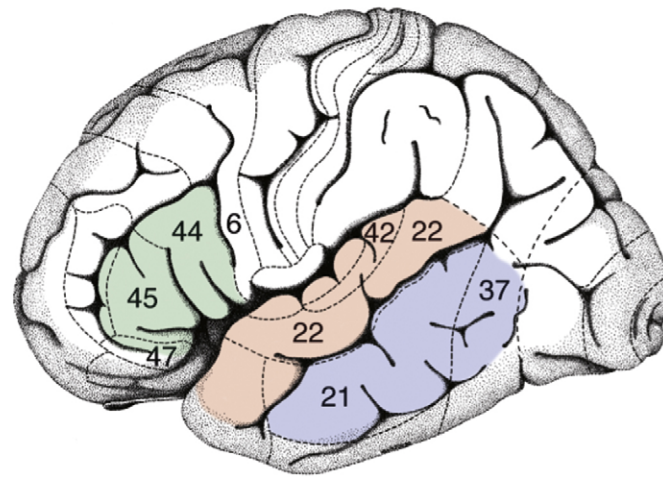
Figure 1. Brodmann areas (BA) in the human left hemisphere. The inferior frontal gyrus (IFG) is shown in green, the superior temporal gyrus (STG) in red and the middle temporal gyrus (MTG) in blue. Adapted, with permission, from Refs [1] and [61].

prominent fiber tract connecting these two areas (see long segment in Figure 2) based on post-mortem dissections.

Today, DTI (Box 2) can be used to investigate fiber pathways *in vivo* in the human brain [18–22]. Two issues are of great importance when considering DTI studies in the language context. The first issue concerns the question of hemispheric differences of language-related fiber tracts. The obvious reason for this consideration is to find out whether the often described left hemipheric functional dominance for language in humans coincides with a structural dominance. The second issue concerns those pathways that are specific to humans compared to non-human primates, as only the former possess the language faculty.

Language pathways in the left hemisphere
Studies on the issue of hemispheric differences in the human brain were triggered by the observation that functional language lateralization to the left hemisphere is found in 95% of right-handers and to the right-hemisphere in 15% of left-handers [23,24]. Those studies which analyzed the volume of the language-related areas reported a leftward asymmetry in the volume of the human planum temporale [25–28] and of Broca's area [27–30].

Comparative studies between human and non-human primates revealed that great apes, similarly to humans, show an asymmetry in the planum temporale [31,32]. Interestingly, however, more fine grained structural analyses revealed that only humans demonstrate a robust asymmetry in the minicolum morphology of the planum polare [33]. To what extent these differences are functionally relevant for language processing must remain speculative.

Those studies which investigated the AF as the white matter pathway connecting Broca's area and Wernicke's area with respect to its lateralization indicate a leftward asymmetry in the degree of anatomical connectivity for the
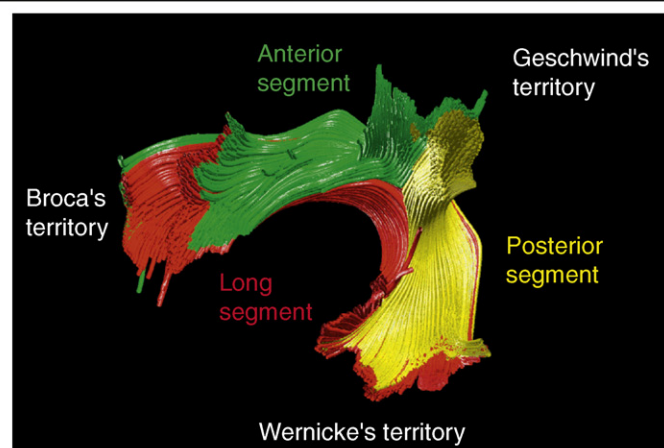
Figure 2. Fiber tracts between Broca's and Wernicke's area. Tractography reconstruction of the arcuate fasciculus using the two-region of interest approach in the human left hemisphere. Broca's and Wernicke's territories are connected through direct and indirect pathways in the average brain. The direct pathway (long segment shown in red) runs medially and corresponds to classical descriptions of the arcuate fasciculus. The indirect pathway runs laterally and is composed of an anterior segment (green), connecting Broca's territory and the inferior parietal cortex (Geschwind's territory), and a posterior segment (yellow), connecting Geschwind's and Wernicke's territories. Adapted, with permission, from Ref. [42].

AF [34,35]. Studies combining fMRI and DTI have tried to establish the relationship between language function and the structure of the AF [36,37]. Although a leftward asymmetry of the AF as measured by DTI was found in these studies, this was only related to functional lateralization or handedness in Ref. [36] but not in Ref. [37]. Further studies are clearly needed to establish the function–brain relationship with respect to lateralization in humans.

When it comes to describing the pathways within the left hemisphere, DTI studies indicate that the AF is not the only white matter tract connecting Broca's area and Wernicke's area, but that there are additional dorsal and ventral pathways. One dorsal pathway runs from Broca's area (in particular BA 44) via the superior longitudinal fasciculus (SLF) to posterior temporal lobe with connectivities to BA 40, the lateral STG and MTG, whereas two more ventrally located routes connect Broca's area (in particular BA 45) via the ventral portion of the extreme capsule and the uncinate fasciculus (UF) to the anterior STG [38,39]. In an analogy to the two pathways that were found in non-human primates [40], the dorsal and the ventral route in humans have been labelled the 'what' stream and the 'where' stream [41].

Because of the limitations of the resolution of the current DTI methods, the two dorsal pathways (i.e. the AF and the SLF) are not reliably separable. The same holds for the two ventral connections, namely the extreme capsule fiber systems (ECFS) and the UF. Today, the available literature indeed indicates more than one dorsal and one ventral route, and the functional significance of each of these pathways is hotly debated [42–49].

Catani and colleagues [42] were the first to report two dorsally located pathways: the AF as the classical 'direct' pathway connecting Broca's and Wernicke's area directly, and a parallel and laterally running 'indirect' pathway projecting from Broca's area to the inferior parietal lobe

and from there to Wernicke's area (Figure 2). The authors take the indirect pathway's function to be semantically based and the direct pathway's function to be phonological. The functional interpretation of the indirect pathway, however, is not necessarily supported by the available functional brain imaging data, which do not indicate an involvement of the parietal cortex in semantic processes (for a review see Ref. [50]).

Glasser and Rilling [43] performed a deterministic tractography analysis of the dorsal projections and compared these with functional imaging studies in the literature. According to their analysis, the AF divides into two segments, one terminating in the posterior STG (BA 22) and one terminating in the MTG (BA 21/BA 37). The posterior STG was seen to connect to Broca's area proper (BA 44 and 45) and the MTG to Broca's area and surrounding cortex (BA 44, 45 and 6, 9). Based on a meta-analysis of functional studies, the authors interpret the STG segment related pathway as being phonological, and the function of the MTG segment related pathway as lexical-semantic.

A recent DTI study differentiated three different pathways connecting the temporal and frontal lobe in humans [10]: a dorsal pathway running from BA 44 to the posterior temporal lobe via the SLF, and two ventral pathways, one from the deep frontal operculum following the UF to the anterior temporal lobe and another pathway running from BA 45 projecting through the ECFS to the temporal lobe anterior to Heschl's gyrus (Figure 3). The differentiation of the two ventral pathways, however, is not easily achieved by the current means of DTI because of their neuroanatomical adjacency and must, therefore, await further empirical support.

Combining functional MRI and DTI, two of these pathways were defined as being relevant for syntactic processes [44]. Functionally, two levels of syntactic processing were distinguished, one dealing with building a local phrase (i.e.
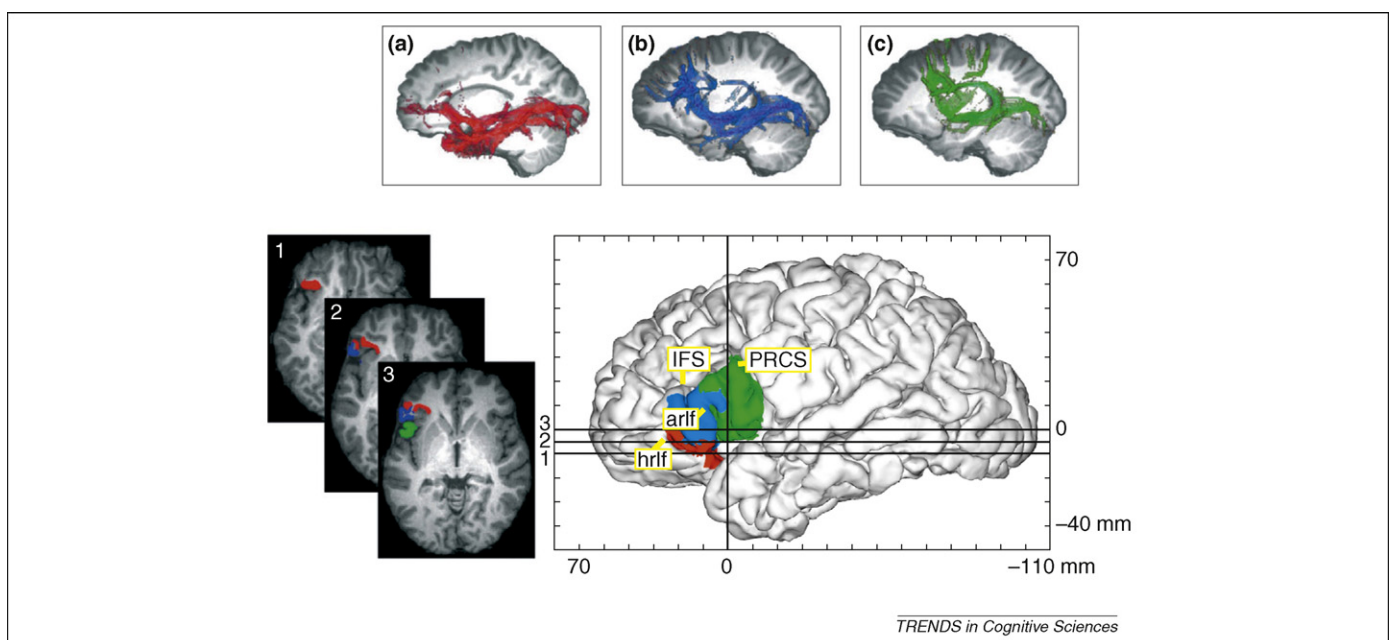

Figure 3. Parcellation and connectivities of the left inferior frontal cortex (IFC). Parcellation and signatures of the left IFC in the example of one subject. Parcellation into frontal operculum (red), BA 45 (blue) and BA 44 (green), and respective connectivity pattern from the area to temporal and parietal cortex **(a)**, **(b)** and **(c)**. Abbreviations: arlf, ascending branch of the lateral fissure; hrlf, horizontal branch of the lateral fissure; IFS, inferior frontal sulcus; PRCS, precentral sulcus. Adapted, with permission, from Ref. [10].

a noun phrase consisting of a determiner and a noun 'the boy') and one dealing with building complex, hierarchically structured sequences (like embedded sentences 'This is the girl who kissed the president'). DTI data [44] revealed that the frontal operculum supporting local phrase structure building [14,44] was connected via the UF to the anterior STG which has been shown to be involved in phrase structure building as well [14]. The dorsal pathway connects BA 44 which supports hierarchical structure processing [42,45], via the SLF to the posterior portion of the STG/STS, which is known to subserve the processing of syntactically complex sentences [51]. This latter network was, therefore, taken to have a crucial role in the processing of syntactically complex, hierarchically structured sentences.

But what could be the function of the other ventrally located pathway running through the extreme capsule and connecting BA 45/47 to the temporal lobe? Given that BA 45 and BA 47 are involved in the processing of semantic information (for a review see Ref. [50]), the pathway running from BA 45/47 through the extreme capsule to the mid portion of the STG/MTG appears to support semantic processes in the adult human brain.

However, a recent combined functional and DTI study [46] has indicated that the ventral route through the extreme capsule is most relevant for language comprehension. This study used language comprehension and sublexical repetition tasks and found the dorsal route to be responsible for aspects of sound-to-meaning mapping, and the ventral route for aspects of language comprehension.

Thus, it seems that the functional interpretation of the pathways supporting language processing as seen in the different studies is not independent of the particular tasks used in the combined functional and DTI studies and/or the respective functional studies considered in the context of DTI studies.

Phylogeny and ontogeny of the language pathways

When considering the importance of these different pathways for language and its evolution, two additional pieces of information are of particular relevance. Because it is impossible to observe language evolution directly, we can only rely on inferences from comparisons between human and non-human primates and on inferences from the language–brain relationship during human ontogeny. Thus, additional information could be gained from considering phylogenetic and ontogenetic data. The comparison between human and non-human DTI data with respect to the pathways that connect the frontal lobe and the temporal lobe have indeed raised the question of whether there are species-specific differences and to what extent these might responsible for the well-known differences in language ability [47].

There are two apparently opposing views. One view holds that the neuroanatomy of the human and the non-human brain is, in principle, the same and that, therefore, fiber tract information of the monkey's brain is directly informative to human language pathways. Using a fine-grained imaging technique (Box 2) in the rhesus monkey, Schmahmann *et al.* [48] question whether the AF has a role in language because their monkey data indicate that the AF does not link the mid superior temporal region to the cortex homologous to Broca's area. Rather, they consider the pathway through the extreme capsule connecting the STG/STS to area 45 and 47 to be crucial for language functions, and not the AF or the SLF.

Rilling *et al.* [49], by contrast, stress that neuroanatomical differences between human and non-human species could be crucial for the evolution of language. Comparing humans, chimpanzees and macaques, they analyzed three pathways; the AF and the SLF as the dorsal connection, and the extreme capsule as the ventral connection. They found the human AF to be smaller in chimpanzees and absent in macaques. The dorsal pathway in humans terminated in the temporal lobe, whereas in chimpanzees, terminations were dominant in the parietal lobe. The ventral pathway running from the ventral portion of the IFG through the extreme capsule to STG was strongest in the macaque and weakest in humans (Figure 4). The authors [49] argue that because humans showed more widespread termination of the dorsal pathway in the MTG than non-human primates, and because the MTG [52] together with BA 45/47 [53] is known to support lexical-semantic processing, the expanded dorsal pathway is crucial for the evolution of language.

However, it has been argued that the processing of syntax (especially the processing of recursive structures), rather than the processing of semantic information, is the crucial ability that differentiates human from non-human species [54]. Functional imaging studies on language (for a meta-analysis see Ref. [55]) indicate that syntactic and semantic processes are supported by distinct networks
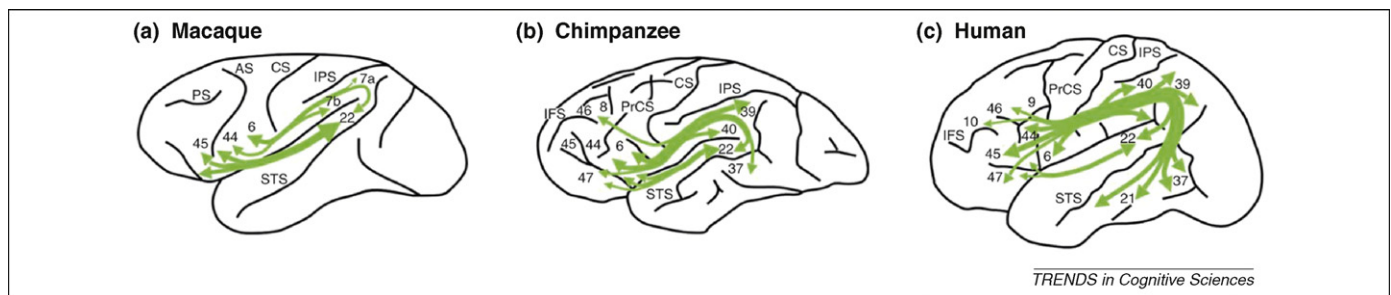

Figure 4. Fiber tracts in human and non-human primates. Average tractography results for **(a)** macaques, **(b)** chimpanzees and **(c)** humans, presented as a schematic summary. Abbreviations: absf, ascending branch of the Sylvian fissure; AOS, anterior occipital sulcus; AS, arcuate sulcus; CS, central sulcus; FOS, fronto-orbital sulcus; hbSF, horizontal branch of the Sylvian fissure; IFS, inferior frontal sulcus; IPS, intraparietal sulcus; ITS, inferior temporal sulcus; LCaS, lateral calcarine sulcus; LuS, lunate sulcus; PoCS, postcentral sulcus; PrCS, precentral sulcus; PS, principal sulcus; SF, Sylvian fissure; SFS, superior frontal sulcus; STS, superior temporal sulcus. Adapted, with permission, from Ref. [49].
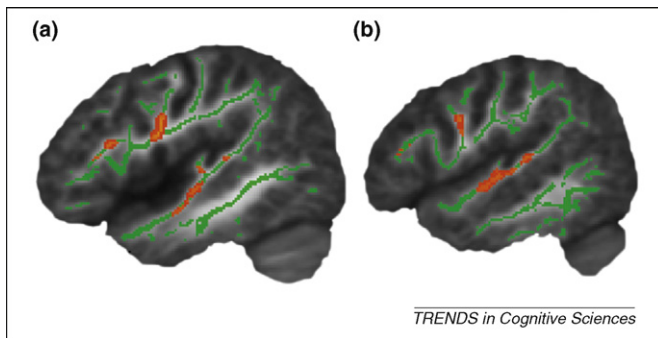
Figure 5. Fiber tracts in adults and children. Differences in fractional anisotropy between adults and 7-year-old children: **(a)** more medial and **(b)** more lateral sagital slices of the left hemisphere. Adapted, with permission, from J. Brauer, PhD thesis, Leipzig University, 2008.

involving areas in the inferior frontal and in the temporal lobe. Although semantic processes involve BA 45/47 and the MTG, the processing of syntactically complex sentences indicative for human language involve BA 44 and the posterior STG/STS. In this context, it is interesting to note that visual inspection of the DTI data comparing human to non-human primates [49] indicate species-specific differences with respect to the number of terminations of the dorsal pathway, not only in the MTG but also in the STS, which, however, remains undiscussed. The role of the posterior STS/STG and the connection to it, however, might be most important because this region supports the comprehension of syntactically complex sentences (for a review see Ref. [55]), an ability specific to humans [56].

Thus, the dorsal connection from BA 44 to the posterior STG/STS might have a crucial role in the evolution of human language. If so, one would predict that in children at an age at which they still demonstrate problems in processing syntactically complex sentences, this dorsal projection should not yet be fully developed. There is ample behavioural evidence that children at the age of 5 years are at chance level when processing object-first sentences (e.g. 'Birds I like.') and still show clear deficits around the age of 7 years [57]. DTI analyses in humans show that the SLF and the AF are among the last to mature [58]. A direct comparison of fiber tracts in children and adults indicates that the dorsal pathway is not fully myelinized even at the age of 7 years (J. Brauer, PhD thesis, Leipzig University, 2008) (Figure 5). A weak myelination of this pathway seems to go hand-in-hand with functional imaging data [59,60] in addition to behavioural data [57]), both indicating that syntactic processes at this age are not yet similar to adults.

Conclusion

The data reviewed indicate that there are several pathways connecting the language-relevant brain areas. They indicate, however, that in particular the dorsal pathway connecting the posterior part of Broca's area (i.e. BA 44) and the posterior STG/STS is crucial for the human language capacity which is characterized by the ability to process complex sentence structures. First, non-human primates which are not able to learn and process hierarchically structured sequences [56] do not seem to possess a strong dorsal connection between the posterior portion of Broca's area (BA 44) and the posterior STG/STS [48,49].

Second, in children at an age at which they are still deficient in processing syntactically complex sentences, the dorsal pathway connecting the language areas is not yet fully myelinized (J. Brauer, PhD thesis, Leipzig University, 2008). Thus, it seems that the evolution of language is tightly related to the maturation of the dorsal pathway connecting those areas which in the adult human brain are involved in the processing of syntactically complex sentences (Box 3).

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