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Current Opinion in Neurobiology

The language network

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Language processing is supported by different regions located in separate parts of the brain. A crucial condition for these regions to function as a network is the information transfer between them. This is guaranteed by dorsal and ventral pathways connecting prefrontal and temporal language-relevant regions. Based on functional brain imaging studies, these pathways' language functions can be assigned indirectly. Dorsally, one pathway connecting the temporal cortex (TC) and premotor cortex supports speech repetition, another one connecting the TC and posterior Broca's area supports complex syntactic processes. Ventrally, the uncinate fascile and the inferior fronto-occipital fascile subserve semantic and basic syntactic processes. Thus, the available evidence points towards a neural language network with at least two dorsal and two ventral pathways.

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Current Opinion in Neurobiology 2012, **23**:xx–yy

This review comes from a themed issue on **Macrocircuits**

Edited by **Steve Petersen** and **Wolf Singer**

http://dx.doi.org/10.1016/j.conb.2012.10.002

Introduction

Macrocircuits in the brain are realized by white matter fiber bundles which are composed of millions of axons. The myelin that surrounds the axons is essential for the fast transmission of electrical impulses and, thus, for the transmission of information during sensory, motor and cognitive functions [1]. With the advent of diffusion weighted magnetic resonance imaging (dMRI), white matter fiber bundles can now be tracked non-invasively, *in vivo* in the human brain (for a review see [2]) by using, for example, functional magnetic resonance imaging (fMRI)-based regions of interest (ROIs) to map the anatomy to the function. Different approaches have been taken to linking language function and brain structure using tractography (for a review see [3]).

The neural circuit supporting language functions must connect the language-relevant brain regions located in the inferior frontal cortex, including Broca's area, and the superior temporal cortex, including Wernicke's area (for reviews see [4•,5•]). For the production of language, motor and premotor regions are relevant, and for language perception, sensory input systems such as the auditory systems for hearing and the visual system for reading must be recruited.

Recent research investigating the structural network underlying language has mainly focused on the core functions of language, that is, semantic and syntactic processes, leaving the sensory–motor interface undiscussed or in the background. Therefore, we will only briefly touch on the input–output aspect of language processing when discussing speech repetition and will mainly focus on those fiber bundles whose functional relevance to semantic and syntactic processing has been demonstrated, either through fMRI-based defined ROIs, through phylogenetic and ontogenetic data or through lesion studies.

The dorsal pathways

The two dorsal long-range fiber bundles discussed in the literature as being most important for language are the arcuate fascile (AF) and parts of the superior longitudinal fascile (SLF), connecting the frontal cortex (FC) and the TC [6,7•,8]. Since the AF and the SLF are not easily distinguishable in their horizontal parts, given the available methods, some researchers use the nomenclature AF/SLF. The AF is the fiber tract which directly connects Broca's area and Wernicke's area. It has been shown to project from the posterior portion of Broca's area (BA 44, pars opercularis) to the posterior and middle superior temporal gyrus (STG) [9,10]. The SLF has been shown to indirectly connect the middle temporal gyrus (MTG) or STG with the dorsal premotor cortex (PMC) via the parietal cortex (PC) [10–12]. The SLF itself consists of more than one fiber bundle. Neuroanatomical data from the macaque have suggested a separation of three parallel SLF components (SLF I, II, III) [13], and also, a similar subdivision of the SLF has recently been proposed for humans [14,15•]. In humans, the SLF II has been shown to connect the FC to the angular gyrus (AG), and the SLF III has been shown to connect the FC to the supramarginal gyrus (SMG), whereas a temporo-parietal bundle, the SLF-tp, has been shown to connect the AG to the TC [16•] (Figure 1).

The dorsal pathways have been described as supporting different functions in language processing [8], with the tract from the MTG/STG to the PMC being relevant for speech repetition [12], and the tract from the STG to Broca's area being relevant for complex syntactic processes [14,17]. We will discuss these functional aspects in turn.

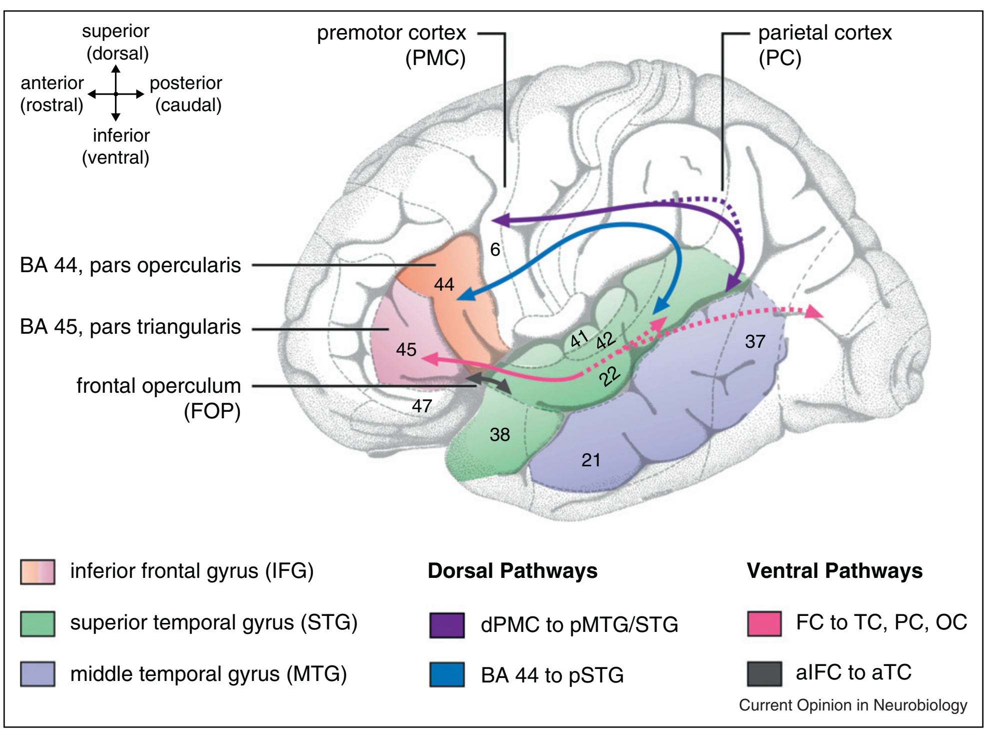
Speech repetition is a multifaceted function that involves the perception of speech, some phonological working memory to hold the perceived information, and aspects of speech production, including articulatory planning and execution. Speech repetition is traditionally used to test for the disconnection syndrome due to brain lesions which lead to conduction aphasia [18]. According to the classical view, auditory-to-motor mapping, as in repetition, is supported by the AF [18], although recent case studies seem to contradict this view [[19]; for a discussion see [20]].

From a functional point of view, lesions in several regions along the dorsal connection between the TC and the FC can cause a speech repetition deficit. This is to be expected given that the cortical network supporting repetition involves the auditory input system in Heschl's gyrus. This system connects the planum temporale (known to support phonological discrimination), to the inferior PC (known to support phonological working memory), and the PMC (in the service of speech output). Breier *et al.* [21] correlated white matter damage with aphasic behavior and showed that a temporo-parietal part, as well as a horizontal part of the pathway, contributes to speech repetition. In addition, white matter deficiencies underlying the SMG itself have been associated with repetition deficits [22].

These findings suggest that both the SLF-tp, connecting the TC to the inferior PC, and the SLF III, connecting the SMG with the posterior inferior FC, and/or the SLF II, connecting the AG to the FC, are involved in repetition.

Processing complex syntactic structures are known to involve Broca's area; in particular its posterior part (BA 44) and the posterior STG [for a recent review see [14]]. Thus, these two regions need a structural connection to allow information transfer; this idea is supported by several functional-based fiber tracking studies. Using an artificial grammar paradigm with a seed in BA 44 as the relevant region for the processing of complex syntactic sequences, a direct fiber connection to the posterior STG, namely the AF, was found [9]. This fiber tract was not only reported to subserve the processing of complex structures in artificial grammar, but also the processing of complex syntactic structures in natural language [17]. The allocation

Figure 1



Language-relevant brain regions and fiber tracts (schematic and condensed view of the left hemisphere). The dorsal pathway connecting dorsal premotor (dPMC) with posterior temporal cortex (pMTG/STG) involves the SLF III and/or the SLF II and the SLF-tp; the dorsal pathway connecting BA 44 with the posterior STG involves the AF. The ventral pathway connecting the frontal cortex (FC), that is, BA 45 and others, with the temporal (TC), the parietal (PC), and the occipital (OC) cortex, involves the IFOF (also called the ECFS); the ventral pathway connecting the anterior inferior FC (aIFC), that is, BA 47 and others, and the FOP, with the anterior TC (aTC), involves the UF.

Please cite this article in press as: Friederici AD, Gierhan SME. The language network, Curr Opin Neurobiol (2012), http://dx.doi.org/10.1016/j.conb.2012.10.002

of the higher-order language function of processing complex syntax to the AF is further supported by phylogenetic and ontogenetic, as well as lesion-based findings: first, the AF is not well developed in non-human primates, which do not possess this syntactic ability [23], second, it is not fully matured in children, who have problems in processing syntactically complex sentences [24] and third, patients with lesions in this fiber tract are deficient in processing complex syntactic structures [17].

A recent model describing the neural language circuit with respect to the information flow [5•] has suggested the particular roles of the two dorsal pathways to be as follows: the pathway connecting the posterior TC to the PMC, probably mediated via the PC, supports input driven auditory-to-motor mapping, as in speech repetition, whereas the pathway connecting Broca's area and posterior STG directly (the AF) supports the processing of syntactically complex sentences, possibly by providing top-down predictions for the incoming input.

Ventral pathways

Ventrally, the FC and the TC are connected via at least two pathways, the uncinate fascile (UF) and another fiber tract, which is either named the extreme capsule fiber system (ECFS) or the inferior-fronto-occipital fascile (IFOF) in the literature, running through the extreme capsule (see also [25]). The UF connects the anterior inferior FC with the anterior TC [9,15•,26,27]. The IFOF connects the FC with posterior parts of the brain, that is, the posterior TC [28,29], the occipital cortex [12,27,30•], and also the PC [29,30].

Semantic processes

Functionally, the ventral pathways connect areas in the anterior inferior frontal cortex which have been found to be activated during semantic processes (BA 45/47), as well as during syntactic processes (frontal operculum, FOP): BA 45 and BA 47 have long been discussed as regions supporting semantic processes [31]; in particular controlled processes at the word-level such as semantic judgment or categorization [32,33], and lexical-semantic access [34], but also aspects of sentence-level semantic plausibility [35]. Also, in the TC, different regions have been found to be involved in semantic processes. The middle temporal gyrus (MTG) has been shown to activate for lexical-semantic processes [36,37•], whereas the anterior and posterior STG, and also the AG, have been indicated to be involved in semantic processing beyond single word meaning [31]: The posterior STG and the AG have been shown to support sentence-level semantics, and the anterior STG has been assumed to be involved in combinatorial aspects [7].

The majority of tractography studies on semantic processing are patient-based and relate semantic processing to the ventral pathways. A study with semantic dementia patients suggested fiber bundles passing through the anterior temporal lobe to be relevant for semantic processes [38]. A study with aphasic stroke patients showed that the IFOF is correlated with semantic processing [39•]. Galantucci *et al.* [16•] delineated the anterior and middle portions of the IFOF to be most relevant for semantic processing when investigating primary progressive aphasia patients. In line with these studies, stimulation of the IFOF elicited semantic paraphasias [40–42], whereas stimulation of other ventral tracts did not [41,43].

Basic syntactic processes

The UF connecting, among others, the FOP and the anterior TC, has been viewed as supporting local phrase structure building; the frontal operculum and the anterior STG were both found to be activated during the processing of violations in the local phrase structure [44], when comparing the processing of meaningless sentences, which only contained syntactic phrase information, to pseudoword lists containing no syntactic structure [45], and when processing local finite state grammar structures in an artificial grammar [9]. In addition, fMRI-based fiber tracking studies have provided supporting evidence for the ventral pathways being involved in syntactic processing [9,46,47].

Thus, two functionally different ventral pathways can be identified as being involved in language processing; namely for processing semantics and syntactically simple sentences, although the structural separation of these pathways is not easy as they both run through the extreme capsule. The IFOF (also called the ECFS) has been discussed as supporting semantic processes and comprehension. The UF has been found to subserve local syntactic processes, rather than semantic processes.

Conclusion

The reviewed studies point towards a neural language network with at least two dorsal and two ventral pathways, each serving a different language function. The two dorsal pathways support auditory-to-motor mapping and the processing of syntactically complex sentences, respectively. The two ventral pathways subserve, on the one hand, semantic and, on the other, basic syntactic processes. However, further studies may provide a more fine-grained picture of the dorsal and ventral pathways of the cortical network underlying language, and may also deliver additional information concerning the connections between cortical and subcortical systems involved in language.

Acknowledgements

A.F. was supported by a grant by the European Research Council (ERC-2010-AdG_20100407 for project 269505 NEUROSYNTAX). S.G. was partly supported by the German Research Foundation as a member of the Berlin School of Mind and Brain, Humboldt University, Berlin, Germany, as well as by the German National Merit Foundation.

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