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Connections for auditory language in the human brain

Sarah M.E. Gierhan *

Max Planck Institute for Human Cognitive and Brain Sciences, Department of Neuropsychology, Leipzig, Germany
Berlin School of Mind and Brain, Humboldt University of Berlin, Berlin, Germany

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ABSTRACT

The white matter bundles that underlie comprehension and production of language have been investigated for a number of years. Several studies have examined which fiber bundles (or tracts) are involved in auditory language processing, and which kind of language information is transmitted by which fiber tract. However, there is much debate about exactly which fiber tracts are involved, their precise course in the brain, how they should be named, and which functions they fulfill. Therefore, the present article reviews the available language-related literature, and educes a neurocognitive model of the pathways for auditory language processing. Besides providing an overview of the current methods used for relating fiber anatomy to function, this article details the precise anatomy of the fiber tracts and their roles in phonological, semantic and syntactic processing, articulation, and repetition.

1. Introduction

For over two decades, neuroscientist and linguists have investigated the cortical areas that enable humans to speak and to comprehend language (see, e.g., Price, 2010, for a recent review). However, a clear picture of how these cortical processing areas are connected for information propagation has remained elusive. As a result, a number of studies have been conducted recently, which investigate the anatomical connections between the cortical areas, and their functions in language processing. However, this has still not resulted in a coherent picture, and it is, as yet, undetermined which connections contribute to language processing and which specific linguistic information they transmit (Friederici, 2009, 2011; Weiller, Bormann, Saur, Musso, & Rijntjes, 2011).

Anatomically, the connections materialize as bundles of white matter, i.e., projections of nerve cells that proceed under the surface from one cortex area to another. The cellular projections bundle during their course, and form so-called *fiber tracts*. These fiber tracts enable cortical areas to communicate with each other by transmitting information. However, there is much debate about the precise course of the tracts: the brain divisions they pass through and the terminating regions. For example, tracts that were previously regarded as one single fiber bundle have been shown, in non-human primates, to actually consist of various separate components that pass through and connect different areas of the brain (e.g., Petrides & Pandya, 1984).

Additionally, it is not only unknown which fiber tracts specifically contribute to language processing, and their precise course, but there is also disagreement about the nomenclature of the fiber tracts and about the functions they subserve during language processing. The present article aims to provide an overview of which fiber tracts support transmission of which linguistic information during auditory language processing.

First, the methods used for exploring fiber tracts and relating anatomy to function will be reviewed (Section 2). Second, the anatomy and nomenclature of the fiber tracts that are discussed as participating in language processing are expounded (Section 3). Last, the language functions will be stated that have been attributed to the different fiber tracts (Section 4). The focus is on auditory language processing and its underlying left-hemispheric long-range association pathways, i.e., the structural connections between the lobes of the left hemisphere.

2. Methods for accessing language fiber tracts

In the following two sections, the methods used for investigating the anatomy and functional roles of fiber tracts in the human brain are outlined. The first section clarifies the methods applied in pure anatomical examinations. The second section outlines the methods applied when relating the anatomy to the underlying function.

2.1. Exploring the anatomy

2.1.1. Dissection

In the exposed brain, dissection of the gray and white matter can be performed (e.g., Martino et al., 2011). This allows the course

* Address: Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1a, D-04103 Leipzig, Germany. Fax: +49 341 9940 2260.
E-mail address: gierhan@cbs.mpg.de

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of the fiber bundles to be uncovered and studied in detail. However, with dissection it is rarely possible to study more than one fiber bundle simultaneously, because dissection is accompanied by discreation of the covering brain structure. Moreover, dissection methods can obviously only be applied post mortem.

2.1.2. Fiber tracking

In the living brain, fiber bundles can be studied when using a specific diffusion weighted sequence in the magnetic resonance (MR) scanner, which measures the diffusivity of water molecules in the brain. Basser, Mattiello, and LeBihan (1994) showed that the principal diffusion direction of water in the brain is parallel to the fiber bundles. This local diffusion direction can be used by a fiber tractography algorithm to reconstruct the fiber bundles which exist in the brain (see Catani, Howard, Pajevic, & Jones, 2002 for one of the first studies using fiber tractography, as well as Catani & Thiebaut de Schotten, 2008). Starting from one or more brain region(s) of interest (ROI), the principal diffusion direction parallel to the fiber direction is traced. If the diffusion of the water molecules is highly parallel, the fibers are likely to be arranged in a bundle.

There are multiple methods for reconstructing the fiber tracts, e.g., deterministic and probabilistic calculations (for details see, e.g., Mori, 2007). In deterministic tractography, one single diffusion direction per voxel is interpolated and followed to reconstruct the tract; in probabilistic tractography, the probability of a diffusion direction per voxel is calculated and a likelihood map of a tract is reconstructed, which shows the probability that a particle traverses the voxels of the tract.

The amount of scientific insight that can be gained when studying the precise anatomy of the fiber tracts is affected by the extent to which the course of the fibers is constrained a priori by ROIs. Moreover, it makes a difference if only one starting region (so-called *seed region*) is used, or if target regions are also used. Other important considerations are, how big the ROIs are, and if the ROIs are terminating regions or bottleneck regions, i.e., an area the fibers of a tract have to pass through if they are constricted by surrounding brain structures. Based on the number of ROIs that researchers use, different tractography approaches have been distinguished:

- Single-ROI approach (one-ROI approach): One single seed ROI is chosen a priori and used for fiber tracking. The ROI can consist of one white matter voxel or a bigger volume of voxels. The ROI can be a terminating region or a bottleneck region of the intended tract. Thus, the course of the resulting fiber is restricted to only one region or even one voxel.
- Double-ROI approach (two-ROI approach): One seed ROI and one big target ROI (i.e., a whole lobe or gyrus) or two small ROIs (used as seed and target alternatively) are defined a priori and used for fiber tracking. Thus, the course of the resulting fiber tract is restricted to the fibers passing through both ROIs. The double-ROI approach is often used for partitioning of a fiber tract into subcomponents.
- Multi-ROI approach (multiple-ROI approach): Two or more ROIs are defined a priori and used for fiber tracking. One seed ROI together with multiple target ROIs, or multiple seed ROIs together with one target ROI (Wakana et al., 2007) are possible. Thus, the course of the resulting fiber tracct is restricted to the fibers passing through all regions or explicitly not passing through some of the regions.

To determine the location of the ROIs for fiber tracking, functional imaging data (see the section "Functional-based fiber tracking" below), data from correlations between gray matter and behavioral performance (e.g., from voxel-based morphometry or cortical thickness analyses) or even a priori knowledge about the course of the fibers is consulted.

2.2. Relating anatomy to function

2.2.1. Inference

One deductive method for investigating the functions of fiber tracts is to compare the fiber tracts or diffusivity parameters of different species (e.g., humans vs. non-human primates), or developmental stages (e.g., children vs. adults), against the background of what these groups are able to do. If a fiber tract is less pronounced in one group compared to another group, its function can be related to the behavioral ability that is less matured in the one group, compared to the other group. Some researchers additionally calculate correlations between structure and function, which makes this method more reliable.

2.2.2. Lesion mapping

The functions that underlie different fiber tracts can also be studied by lesion mapping (e.g., Dronkers, Wilkins, van Valin, Redfern, & Jaeger, 2004; Tyler et al., 2011). To investigate language functions, lesion mapping is applied to patients that exhibit language deficits: patients with speech or language disorders, patients with different types of aphasia, or patients with semantic dementia or schizophrenia. In this method, the white and gray matter damage that causes the clinical symptoms is correlated with the behavioral performance in language tasks.

To reconstruct the damaged fiber tract, an image of the patient's brain is overlaid with fiber tracts from images of healthy participants' brains, or fiber tracking is directly applied to the patient's brain. The function of the damaged tract is then deduced from the ability that the patient lacks. To determine the quantitative relationship between clinical symptoms and the microstructural damage, the patient's behavioral performance is correlated with the diffusivity values (e.g., fractional anisotropy, mean diffusivity, axial/parallel/longitudinal diffusivity, radial diffusivity; see Sundgren et al., 2004, for an overview about different diffusivity values and their application to different diseases).

2.2.3. Functional-based fiber tracking

Possibly the simplest method for mapping function and anatomy of a tract is to infer their functional roles from neuroimaging studies (e.g., Catani, Jones, & Ffytche, 2005). Neuroimaging investigates the functions of cortical areas. Based on the functions of interconnected cortical areas, the functional role of the tract that connects the areas is deduced.

A more reliable way to deduce the functional role of a tract is to perform fiber tracking directly on the data of preceding functional imaging studies (e.g., Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006; Kamada et al., 2007; Saur et al., 2008). In this method, a fiber tract starting in a specific ROI is ascribed the functional role of transmitting the information that is processed in that ROI.

One option for identifying the functionally informed seed region for fiber tracking is to use the white matter adjacent to functional magnetic resonance imaging (fMRI) activations. Ideally, the fMRI and diffusion data are derived from the same subjects so that a direct and precise individual mapping of function and anatomy is possible. However, some studies have also applied group averaged fMRI activations to individual brains, or used fMRI activations from other participants. Another possibility for locating functionally informed seed regions is to use those gray matter regions that show a strong correlation between damage and clinical symptoms in patients, e.g., regions revealed by lesion mapping.

When using functional-based fiber tracking, the relation between structure and function is only indirect, as is the case when