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# Fiber anatomy of dorsal and ventral language streams

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ABSTRACT

Recent advances in neuroimaging have led to new insights into the organization of language related networks. Increasing evidence supports the model of dorsal and ventral streams of information flow between language-related areas. Therefore, a review of the descriptions of language-related fiber anatomy in the human and monkey brain was performed. In addition, case studies of macroscopical fiber dissection and polarized light imaging (PLI) with special focus on the ventral stream were done. Several fiber structures can be identified to play a role in language, i.e. the arcuate fasciculus as a part of the superior longitudinal fasciculus, the middle longitudinal fasciculus, the inferior fronto-occipital fasciculus, and extreme and external capsules. Substantial differences between human and monkey fiber architecture have been identified. Despite inconsistencies based on different terminologies used, there can be no doubt that dorsal and ventral language streams have a clear correlation in the structure of white matter tracts.



## 1. Introduction

The classical concept of anatomical language circuitry has been the connection between the temporal sensory region (Wernicke's area) and the frontal motor region (Broca's area) via the arcuate fasciculus (e.g. Geschwind, 1970) – this model has dominated the anatomical comprehension of language over decades (Catani & Mesulam, 2008). However, modern concepts describe the classical dorsal pathway along the arcuate fascicle/superior longitudinal fasciculus that is activated during repetition and a second ventral pathway via the extreme capsule which is activated during auditory comprehension (Saur et al., 2008). Therefore, the concept of a dorsal stream for the integration of sensory percept and internal models and a ventral stream for meaning has been proposed as the backbone language related network (Weiller, Bormann, Saur, Musso, & Rijntjes, 2011).

Although the arcuate fasciculus as the major fiber tract of the dorsal stream is well established, the anatomical existence of a ventral stream fiber tract running via the extreme/external capsule is still a matter of debate. Recent concepts of dorsal and ventral streams of language networks are mainly based on MR data and uncertainty arises if these results are based on real existing anatomical structures or if these may simply be caused by artifacts based on magnification problems of diffusion MRI such as the crossing and kissing fibers problem.

However, white matter architecture and structural connectivity of language related networks in the human brain clearly form the backbone for modern language models (Berthier, Lambon Ralph, Pujol, & Green, 2012; Friederici, 2009). Therefore, this review aims at a literature analysis of the anatomical description of structural fiber systems of the white matter related to language-sensitive areas (especially the arcuate fasciculus (AF), extreme (EmC) and external capsules (EC), the inferior fronto-occipital fasciculus (IFOF), and others) in the human and the monkey brain.

Table 1 shows the fiber tracts and the abbreviations used here. The term 'fasciculus' is generally used as a description of an anatomically defined, larger fiber tract or fiber bundle in the brain, while 'extreme capsule' and 'external capsule' are topographical descriptions of white matter with the extreme capsule (EmC) being located between insula and claustrum and external capsule (EC) being located between claustrum and putamen. Terms like 'stream' or 'pathway' are used mainly in functional imaging studies depicting information flow and are not clearly defined anatomical terms.

A pubmed inquiry, therefore, was performed to search for the following anatomical terms (date: 01-02-2012): 'arcuate fasciculus' with 194 hits, 'inferior fronto occipital fasciculus' with 105 hits, 'external capsule brain' with 466 hits, 'extreme capsule brain' with 70 hits. All abstracts were analyzed regarding anatomical information about fiber anatomy possibly contained. These papers were collected and build the basis of this review. In addition, several historical publications were sighted regarding the anatomical description of these fiber tracts. In addition, we present own case studies

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**Table 1**
Terminology of fiber tracts.

| Fiber tract/white matter structure | Abbreviation |
|---|---|
| Arcuate fasciculus | AF |
| Superior longitudinal fasciculus | SLF |
| Middle longitudinal fascicle | MdLF |
| Inferior fronto-occipital fasciculus | IFOF |
| Uncinate fasciculus | UF |
| Extreme capsule | EmC |
| External capsule | EC |

using macroscopical dissection and polarized light imaging (PLI) of the human brain.

## 2. Human brain

### 2.1. Historical aspects

Recently, the history of the concept of dorsal and ventral routes for speech production was intensively reviewed by Weiller et al. (2011). It is very interesting, that nerve fiber architecture of the ventral stream was seriously discussed in former times, based on observations of Meynert (1866) and especially Wernicke (1874), but then was rejected and lost.

The anatomical substrate of the dorsal pathway of speech production is well known and accepted. The arcuate fasciculus and the superior longitudinal fasciculus are important associative fiber systems of the dorsal stream (Catani & Mesulam, 2008). Early descriptions of the arcuate fasciculus were given by Reil (1809) and Burdach (1822) and subsequently confirmed by Dejerine (1895).

In contrast, associative bundles of fibers located in the region of anterior insula, external or extreme capsules may be important constituting the ventral stream. The uncinate fasciculus of Reil, also termed as fasciculus unciformis (Burdach), must be mentioned in this context. Furthermore, the inferior longitudinal fasciculus must be considered, connecting the occipital cortex with the temporal lobe (Catani & Mesulam, 2008). The inferior longitudinal fasciculus is well known in anatomy and no problems arise concerning its topography.

In contrast, the inferior occipito-frontal fasciculus (IFOF) is a structure, which has not always been clearly defined. In some anatomical textbooks it is not mentioned at all (e.g. Clara, 1942; Kopsch, 1914) and mixed with the uncinate fasciculus.

Nevertheless there is a serious early hint, given by Gordinier (1899), that the uncinate fasciculus can be subdivided into two parts: the uncinate bundle strictly speaking and a posterior part, which has a more horizontal direction. The anterior part contains external fibers, connecting the inferior frontal cortex with the apex of the temporal lobe. These fibers describe a very sharp curve forming the typical uncinate fascicle. The posterior part with the internal fibers demonstrates a more horizontal extension and radiates into the orbital part of the first and third frontal gyri (Gordinier, 1899). Another hint to the inhomogeneity of the uncinate fascicle was given by Testut (1900), who also figures the uncinate fasciculus to be composed of these two parts. The anterior part forms a sharp curve into the temporal pole and a smaller posterior part reaches the middle/posterior region of the temporal lobe. Testut (1900) cited this figure according to Meynert. However, these two parts considered and figured by Gordinier (1899) and Testut (1900) are not differentiated by Obersteiner (1888) and Dejerine (1895).

The posterior part of the uncinate fascicle was investigated more intensively by Curran (1909). Curran introduced the term "inferior occipito-frontal fasciculus" to this structure and stated the discovery of this bundle for himself. Curran (1909) exactly described the topography of his newly introduced and named fascicle. According to this author the fascicle contains fibers which connect the frontal lobe with the occipital lobe but it also contains fibers which join the frontal lobe with the posterior part of the temporal and parietal lobes. It must be emphasized that the fibers of this tract swing to the lower external side of the lenticular nucleus and run in the inferior part of the external capsule. In this region the fascicle forms a compact bundle, which can be separated. Just beneath and somewhat anterior to the inferior occipito-frontal fascicle of Curran the uncinate bundle is positioned. Curran (1909) also presented very impressive specimens in his paper, which are congruent to the preparations of the IFOF presented by Ludwig and Klingler (1956) in dissections performed using their freezing dissection technique.

The IFOF is also mentioned in important textbooks of neuroanatomy (e.g. Rager & Zenker, 2004; Truex & Carpenter, 1969; Villiger & Ludwig, 1940; Zilles, 1987). Especially the description of Villiger and Ludwig (1940) is important, because these remarks are able to explain the difficulties in separating and identifying the IFOF not only in dissections but also in MRI-based fiber studies. Villiger & Ludwig state: "*Denn der Fasciculus uncinatus ist vom Fasciculus frontooccipitalis inferior (Curran) nicht zu trennen. Dieser stellt mit dem Fasciculus uncinatus zusammen einen doppelten Fächer dar, der etwas tiefer liegt als der Fasciculus arcuatus. Seine Fasern sind nach vorne nicht nur in die Orbitalwindungen, sondern auch gegen die Konvexität des Stirnlappens zu verfolgen, nach hinten in den Temporallappen und den Okzipitallappen. Die hintersten Fasern, die in den Stirnlappen eintreten, liegen lateral vom Putamen und sind von den zu diesem Kerne tretenden nicht zu trennen. Die Fasern gegen den Okzipitallappen vermengen sich mit anderen sagittal laufenden Zügen*" (translation by the authors: 'The uncinate fasciculus cannot be isolated from the inferior frontooccipital fasciculus (Curran). This fascicle constitutes together with the uncinate fasciculus a double fan, which is located more deeply than the arcuate fasciculus. Its fibers can be tracked not only into the convexity of the frontal lobe but also backwards into temporal and occipital lobes. The posteriormost fibers running into the frontal lobe are located laterally to the putamen and cannot be separated from those fibers running into this nucleus. The occipital fibers intermingle with other fibers running sagitally.'). The described difficulties in dissecting the IFOF are also mentioned in a recent paper (Türe, Yaşargil, Friedman, & Al-Mefty, 2000).

Zilles (1987) presented a schematically drawing of a frontal section and marks the IFOF as a strong bundle in the caudal part of the extreme capsule just above and minimally lateral to the uncinate fasciculus. According to this scheme he locates the IFOF laterally to the claustrum, which is not exactly congruent to other anatomical descriptions (e.g. Curran, 1909) but fits to the assumed ventral pathway according to the fMRI studies (Saur et al., 2008). Furthermore, Zilles (1987) described the IFOF to connect the fusiform, lingual and inferior temporal gyri, which is also very suitable to the concept. The difficulties concerning the topography of the IFOF located in the inferior part of the external capsule or in the inferior part of the extreme capsule have been solved by Ebeling and von Cramon (1992), who stated that the IFOF runs in both capsules encasing the inferior part of the claustrum.

The IFOF is also mentioned in different dissection guides for the brain (Hultkrantz, 1929; Inke, 1961). In comparative anatomy the IFOF is also suggested, for example by Kappers (1967), who stated, that this structure can be demonstrated in various mammalian brains, such as sheep and dog. Unfortunately the topographical description given in this text is somewhat weak. Kappers (1967) described that the fasciculus passes beneath the lenticular nucleus and the overlying external capsule, which is not completely correct.

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