A taxonomy of the brain's white matter:

Twenty-one major tracts for the twenty-first century

Daniel N. Bullock¹, Elena A. Hayday², Mark D. Grier², *Wei Tang^{1,3}, *Franco Pestilli⁴, *Sarah R. Heilbronner²

*These authors share senior author contribution

1. Department of Psychological and Brain Sciences, Program in Neuroscience, Indiana University Bloomington, Bloomington, IN USA 47405
2. Department of Neuroscience, University of Minnesota, Minneapolis, MN USA 55455
3. Department of Computer Science, Indiana University Bloomington, Bloomington, IN USA 47408
4. Department of Psychology, The University of Texas at Austin, Austin, TX USA 78712

Correspondence:

Sarah R. Heilbronner, PhD

2-164 Jackson Hall

321 Church St SE

Minneapolis, MN 55455

772-285-7021

heilb028@umn.edu

Acknowledgements: SRH was supported by NIH R01MH118257 (SRH); MDG was supported by NIDA T32DA007234 to P. Mermelstein (UMN); DNB was supported by NIMH 5T32MH103213-05 to W. Hetrick (IU); FP was supported by NSF IIS-1636893, NSF BCS-1734853, NSF IIS-1912270, NIH NIBIB 1-R01-EB029272-01, and a Microsoft Investigator Fellowship.

Conflicts: SRH has received teaching fees from Medtronic, Inc. Remaining authors have no conflicts to disclose.

Abstract

The functional and computational properties of brain areas are determined, in large part, by their connectivity profiles. Advances in neuroimaging and network neuroscience allow us to characterize the human brain noninvasively and *in vivo*, but a comprehensive understanding of the human brain demands an account of the anatomy of brain connections. Long-range anatomical connections are instantiated by white matter and organized into tracts. Here, we aim to characterize the connections, morphology, traversal, and functions of the major white matter tracts in the brain. It is clear that there are significant discrepancies across different accounts of white matter tract anatomy, hindering our attempts to accurately map the connectivity of the human brain. We thoroughly synthesize accounts from multiple methods, but especially nonhuman primate tract-tracing and human diffusion tractography. Ultimately, we suggest that our synthesis provides an essential reference for neuroscientists and clinicians interested in brain connectivity and anatomy, allowing for the study of the association of white matter's macro and microstructural properties with behavior, development, and disordered processes.

Table of Contents

INTRODUCTION	4
DEFINING WHITE MATTER	5
<i>WHAT IS A WHITE MATTER TRACT?</i>	<i>5</i>
<i>METHODS USED STUDY WHITE MATTER BUNDLES.....</i>	<i>7</i>
<i>Gross dissection.</i>	<i>7</i>
<i>Tract-tracing</i>	<i>7</i>
<i>Diffusion-weighted MRI</i>	<i>8</i>
<i>Label-free imaging technologies.</i>	<i>10</i>
<i>INTERPRETING CONVERGENT AND DISCORDANT EVIDENCE.....</i>	<i>10</i>
WHITE MATTER TAXONOMY OF THE BRAIN.....	12
<i>CORPUS CALLOSUM.....</i>	<i>13</i>
<i>ANTERIOR COMMISSURE</i>	<i>14</i>
<i>INTERNAL CAPSULE</i>	<i>16</i>
<i>SUPERIOR LONGITUDINAL FASCICULUS.....</i>	<i>18</i>
<i>MIDDLE LONGITUDINAL FASCICULUS.....</i>	<i>20</i>
<i>ARCUATE FASCICULUS.....</i>	<i>21</i>
<i>POSTERIOR ARCUATE FASCICULUS.....</i>	<i>22</i>
<i>VERTICAL OCCIPITAL FASCICULUS</i>	<i>23</i>
<i>TEMPORO-PARIETAL CONNECTIONS TO THE SUPERIOR PARIETAL LOBULE</i>	<i>24</i>
<i>INFERIOR LONGITUDINAL FASCICULUS</i>	<i>25</i>
<i>INFERIOR FRONTO-OCCIPITAL FASCICULUS</i>	<i>26</i>
<i>CINGULUM BUNDLE.....</i>	<i>27</i>
<i>UNCINATE FASCICULUS.....</i>	<i>29</i>
<i>CORTICO-STRIATAL CONNECTIONS: MURATOFF'S BUNDLE AND THE EXTERNAL CAPSULE.....</i>	<i>30</i>
<i>EXTREME CAPSULE</i>	<i>31</i>
<i>SUPERIOR FRONTO-OCCIPITAL FASCICULUS</i>	<i>32</i>
<i>OPTIC RADIATION</i>	<i>32</i>
<i>FORNIX</i>	<i>33</i>
<i>MEDIAL FOREBRAIN BUNDLE</i>	<i>34</i>
<i>VENTRAL AMYGDALOFUGAL PATHWAY.....</i>	<i>35</i>
CONCLUSION	36
REFERENCES	38

Introduction

The brain acts as an ensemble of distal computing centers located in both cortical and subcortical structures (Bullmore and Sporns, 2009). The functions and computational profiles of these brain areas are determined not only by the local properties but, importantly, by their connectivity profiles. Long range-connectivity is composed of ensembles of axonal projections wrapped in myelin, generally referred to as white bundles or tracts.

Early on, these long-range tracts were thought to be a passive cabling system. The role of myelinated bundles in cognition and disease had been overlooked to ‘simply’ allow fast and reliable long-distance communication between brain areas. Modern measurements show that white matter axons and glia respond to experience, and that the tissue properties of the white matter are transformed during development and following training. The white matter pathways comprise a set of active wires, and the responses and properties of these wires predict human cognitive and emotional abilities in health and disease (Fields and Douglas Fields, 2008; Filley and Fields, 2016; Wandell, 2016). We can now confidently predict that to fully understand the functions of the human brain, neuroscientists will have to develop an account of the connections and tissue properties of these active wires. Indeed, it has been proposed that some brain disorders are best considered as disruptions of connectivity (Geschwind, 1965; Catani and Ffytche, 2005; Catani and Mesulam, 2008a).

The recent expansion of network neuroscience and neuroimaging has brought renewed interest to the study of long-range white-matter bundles and brain connectivity. Yet, despite the theoretical expansion of our understanding of the brain, there is a major roadblock ahead: we must first build an anatomically accurate connectivity map of the human brain. Unfortunately, a complete map of the brain connections is not yet available. However, deep knowledge of major white matter bundles exists, but it is mostly dispersed across sub-fields of neuroscience spanning comparative tract-tracing, dissections, medicine, and neuroimaging.

Here, we have curated and synthesized information about white matter tract organization across different fields and methodologies. In doing so, we are able to make inferences both about each tract’s connections and gross morphology. We are particularly interested in how tract-tracing, tractography, and dissection results bear on one another. The present review provides an intermediate solution along the continuum of the complete coverage that a book can provide and the narrow description individual papers can cover when reporting on individual aspects of the white matter and brain connectivity. The review is meant to provide a primer, a lookup table for students, educators and researchers interested in white matter by providing an introduction without dwelling on the technical aspects of any of the specific subfields that are involved in continuously contributing knowledge to understanding white matter. It is our hope that we are able to facilitate the expedited formation of a consensus white matter taxonomy (Schilling et al., 2020a). We suggest, as others

have, that the formation of such a consensus is an important and necessary precursor to the widespread adoption of investigations of white matter as a standard component of neurobiological accounts of behavior, brain disorders, and changes in cognition across the lifespan.

Defining white matter

White matter is a prominent and conspicuous feature of brain architectures: nearly fifty percent of total brain volume is composed of white matter tissue. Notably, the total brain volume occupied by gray and white matter scales universally across mammalian species and is related to the complexity in cortical folding (Azevedo et al., 2009; Herculano-Houzel et al., 2010; Herculano-Houzel, 2014). In order to achieve selective conduction of neural information, and to balance the spatial constraints incurred by the axons themselves, the white matter is further subdivided into smaller substructures, often referred to as “tracts”

What is a white matter tract?

The brain’s gray matter cortical and subcortical structures can be divided into regions and subregions on the basis of cytoarchitecture, neurotransmitter and neuromodulator distribution, ontogeny, and function. These are not simply used as delineations of convenience, but are instead taken to reflect meaningful biological units with distinct functional profiles. Can the same be said of white matter?

It is generally accepted that the taxonomic analogue of a gray matter brain region is a white matter tract or bundle: a collection of myelinated axons that share a meaningful combination of properties which may include connectivity, volume, gross morphology, trajectory, ontogeny, phylogeny, function, and susceptibility to disease or injury processes. Although this specification is broadly accepted, the actual implementation of this notion appears to be bifurcated into two implicitly distinct approaches to delineating white matter tracts.

One of the principles that can define white matter tracts is their **volumetric** characteristics, such that a tract is defined as coursing through a specific white matter volume. For example, the internal capsule could be considered the white matter lateral to the caudate and thalamus but medial to the putamen and globus pallidus. Somewhat distinct from this is a second set of principles used to define tracts: namely, their **connective** characteristics. With this approach, the defining features are the regions that the tract connects to--“origins” or “terminations.” For example, the internal capsule could be considered the majority of the neuronal projections between the cortex and the thalamus, subthalamic nucleus, brainstem, and spinal cord. Sometimes these two approaches conflict: there are striato-pallidal axons that traverse the volume occupied by the internal capsule, but are these part of the internal capsule itself?

As will be noted in many of the white matter structure characterizations that follow, most of the definitions comprise some combination of both volumetric and connective features. However, it is our contention that, both

in existing accounts of white matter structures (and thus as a matter of practice) and in the idealized specifications of white matter structures (and thus as a matter of fact) either **volumetric** or **connective** characteristics tend to be most salient to particular tracts. To foreshadow several discussions that will follow in this review, many of the controversies surrounding the definition of a tract may be the result of unacknowledged tensions between preferences or investigative foci held by investigators. Notably, even though some amount of description of both the volumetric *and* connective characteristics of white matter structures is typically found in all accounts, there is rarely, if ever, a justification of *why* a **volumetric** or **connective** approach is appropriate for the delineation of white matter structures.

Though it involves an element of speculation, within the context of the practice of science in this domain, there are many reasons why a given group of scientists may lean toward volume or connectivity-centric accounts of white matter structures. The volume-based definitions may stem from the common practice of using volumetric boundaries to delineate the boundaries of gray matter brain regions. Of course, this approach faces challenges in the many volumes in the brain with crossing fibers. Moreover, in the context of volumetric approaches to tract definition, mapping a white matter tract entails the exhaustive cataloguing of connections running through the volume. This is not seen as violating or altering the definition of the tract, because the essence of “the tract” is volumetric in nature. From this, it follows that, in the case of the volumetric framework, a tract has been *fully and completely* characterized when all distinct subcomponents within a volume have been documented.

Connectivity-based approaches to white matter structure delineation, though also present in historical dissections and tract-tracer studies, are becoming more prominent with the rise of diffusion tractography. This may be attributable to the availability of computational tools allowing for the use of cortical regions as endpoint criteria to ascribe identities. For connectivity-based approaches, the act of “diving deeper” for a particular tract entails the exhaustive cataloguing of distinct, but nonetheless coherent, sub-component connectivity profiles. Thus, new anatomical insight from connective approaches often comes in the form of descriptions of *novel* (and increasingly granular) sub-components of a tract (Schotten et al., 2011; Sarubbo et al., 2013; Makris et al., 2017). This is not seen as violating or altering the definition of the tract, because the overarching connectivity motif is not violated. Instead, the tract characterization is made more nuanced. In the case of the connective framework, a structure is *fully and completely* characterized only after the connectivity of all distinct subcomponents (as defined by origins and terminations) have been determined.

Finally, there are other terms relevant to white matter organization, many of which can have multiple definitions within the field. For example, a **bundle**, **connection** or **tract** may refer to a white matter structure or a particular subset of connectivity within a larger structure. For example, the cingulum bundle is a bundle (or tract) unto itself, but at the same time the axons connecting the subgenual anterior cingulate cortex with the posterior cingulate cortex (which constitutes just a subcomponent of the cingulum bundle) are also a bundle (or

tract). Pathway is a more (but not exclusively) connectivity-based term (for example, the ventral amygdalofugal pathway). Individual axons can also be referred to as fibers; in a tractography setting, connections are expressed as streamlines, but these are not equivalent to single axons.

Methods used study white matter bundles

Understanding white matter necessitates bridging gaps between nonhuman animal model species and humans. As a result, the process of mapping white matter inevitably involves different measurement modalities, and each modality comes with opportunities and challenges.

Gross dissection.

Scientists have been dissecting brain tissue for centuries; however, the Klingler technique for white matter dissection was only developed in the 1930s (Silva and Andrade, 2016). This *ex vivo* technique requires brain fixation, freezing, and thawing. The formation of ice loosens axons, allowing them to be pulled apart while maintaining their structural integrity. This technique can be applied to both human and nonhuman animal brains. Because this is not the case for tract-tracing (see below), it provides an important complement to diffusion tractography. Dissection has been highly useful for determining the broad shapes of the largest, most prominent white matter bundles. However, it was never meant or understood to be a highly accurate or thorough technique for establishing point-to-point connectivity estimates. Dissection cannot distinguish directionality of fibers and has trouble determining details of where, precisely, fibers originate and terminate (Beever and Ferrier, 1891). Furthermore, dissection is limited to major structures, as it cannot identify the areas of termination of white matter bundles beyond reporting major areas of global projections. Finally, it is likely that the Klingler method is biased towards the dominant bundle within a volume of white matter. In other words, it is likely that the minor fibers crossing within a certain region of white matter are invisible to the Klingler method. This is a problem similar to that attributed to deterministic tractography based on the diffusion tensor model method (Pestilli et al., 2014; Takemura et al., 2016a; Caiafa and Pestilli, 2017).

Tract-tracing.

Neuroanatomists of the 20th century devoted considerable effort to developing methods for precisely determining region-to-region connectivity in the brain (Nauta and Gygax, 1951, 1954; Fink and Heimer, 1967; Heimer, 1970; Wouterlood and Groenewegen, 1991; Nauta, 1993). Modern day tract-tracing techniques rely on dyes (or, more recently, viruses, Cushnie et al., 2020; Lanciego and Wouterlood, 2020) that are taken up by cells and/or terminating axons and actively transported retrogradely (from the terminal field to the cell body) or anterogradely (from the cell body to terminal fields). This reliance on active transport means that most tract-

tracing requires a delay period of days to weeks during which the tracer remains in the live brain. Because of this combination of intracranial surgery and timed sacrifice, tract-tracing is impossible in the human brain.

Furthermore, because of the focus of this review, it is worth noting that uptake of tract-tracers within white matter is unreliable; thus, one generally cannot inject part of a bundle in order to understand which connections it carries. Our understanding of the fine details of white matter anatomical organization is therefore due in large part to the combination of hundreds of tract-tracing cases from injections into specific gray matter regions, across many laboratories. A downside to this approach is that it is decidedly not “whole-brain.” In addition, common laboratory animal models like mice and rats tell us little about human white matter organization, because their tracts appear to be very different (Coizet et al., 2017). This leaves us with costly and limited nonhuman primate experiments (Heilbronner and Chafee, 2019). Another major limitation to tract-tracing is that negative results (meaning absent connections) are difficult to interpret without a large number of supporting studies, as opposed to positive results (meaning found connections), which are considered much more decisive. That is, a tract-tracing study may fail to find a connection between two specific regions, but it may be that another part or layer of the region does make the connection. Only with overwhelming evidence from many cases across laboratories are we confident in a true lack of connection. In other words, “Absence of evidence is not evidence of absence.”

Diffusion-weighted MRI.

With tract-tracing limited to nonhuman animals and gross dissection lacking detail and resolution, there has been a longstanding need for a noninvasive method of determining white matter organization in humans. Neuroimaging, and specifically diffusion-weighted MRI (dMRI) has presented itself as a viable means of meeting this need. DMRI is sensitive to water molecule displacement (diffusion) within the fluids in brain tissue. The displacement of water molecules is understood to be constrained by the microscopic tissue structure of the brain, and in particular the myelin-wrapped, long-range axonal projections (Basser and Pierpaoli, 1996; Le Bihan and lima, 2015). Moreover, this imaging modality is sensitive to a combination of white matter tissue features including axonal configuration (e.g., axonal direction and crossing) as well as the packing density of said axons and the properties of the myelin tissue itself (Basser and Pierpaoli, 1996; Assaf and Pasternak, 2008; Tournier et al., 2008).

Multiple computational models have been developed to represent the process of water diffusion within brain tissue (Panagiotaki et al., 2012; Wandell, 2016; Jelescu and Budde, 2017; Rokem et al., 2017; Shi and Toga, 2017). Among these is the diffusion-tensor imaging model (DTI; (Sakuma et al., 1991; Pierpaoli et al., 1996; Basser and Pierpaoli, 1998) which represents water-diffusion as a *single* gaussian process in three-dimensional space. Although quite elegant, DTI is one of the simplest models, a property that limits the complexity of bundle configurations that can be modeled by this method. For example, DTI cannot distinguish among crossing, “kissing,” and fanning fiber configurations (Tournier et al., 2007, 2012; Jeurissen et al., 2013),

as these configurations would need additional parameters and diffusion distributions to be represented. This is a limitation similar to that mentioned above for the Klingler method. More recent and complex models such as constrained-spherical deconvolution (CSD; Tournier et al., 2007) or constant solid angle (CSA; Aganj et al., 2010), can capture nuanced aspects of diffusion processes, and thereby model more complex white matter configurations.

To reconstruct the long-range axonal fibers using dMRI, the discrete, voxel-wise output features from a diffusion model must be interpolated to model the contiguous white matter as streamlines. The systematic production of such elements corresponds to the process of tractography generation, which, when performed for the entire volume of the white matter, results in a whole brain tractogram. A variety of methods have been proposed to generate fiber tractography (Mori et al., 1999; Jiang et al., 2006; Descoteaux et al., 2009; Smith et al., 2012; Tournier et al., 2012; Takemura et al., 2016a; Sarwar et al., 2019). Among the many distinguishing characteristics of such models is whether they approach tractography generation in a probabilistic or deterministic fashion. Deterministic tractography uses the parameters from diffusion models to fit the signal of individual voxels in such a way that starting in the same voxel always proceeds along the same path. Probabilistic tractography instead chooses from a distribution of potential paths with each step, and therefore can result in different outcomes from within the same voxel. In this way it captures the inherent uncertainty regarding aggregate local fiber distributions and allows the fiber tracking process, through stochastic variation, to eventually model the range of possible configurations.

DMRI is typically collected at a resolution in the range of 1.5-2 mm³ (Van Essen et al., 2012; Sotiropoulos et al., 2013). By contrast, the typical axon diameter is less than 1µm. Because of this, and because of the number of presumptions made in models of diffusion, tractography is necessarily an indirect and inferential method. In turn, fiber pathway identification can suffer from a number of issues which undermine the biological plausibility of the aggregate tractogram, unless informed by relevant anatomical priors. Without these priors, tractography may suggest pathways that are nonexistent (*false positives*), or miss pathways that do, in fact, exist (*false negatives*) (Figure 1). Of particular concern is the appropriate reproduction of unknown connections (Maier-Hein et al., 2019) and the biased density of the coverage and penetration of the cortical mantle by tractography (Thomas et al., 2014; Jbabdi et al., 2015; Reveley et al., 2015; Schilling et al., 2018; Grier et al., 2020). Nevertheless, dMRI-based techniques and tractography are the only methods available to track major fiber bundles in living human brains. Indeed, with careful additional work, some of the limitations of tractography can be countered by statistical evaluation (Pestilli et al., 2014; Daducci et al., 2015; Rheault et al., 2020) or by using anatomically based heuristics to eliminate biologically implausible features of bundles (Wassermann et al., 2016; Bullock et al., 2019; Schilling et al., 2020b). Unfortunately, where there is no rich account of a white matter

structure's morphology and anatomy available, the accuracy of the output of tractography is uncertain. It is for this reason that better anatomical models are paramount to understanding brain connectivity.

One of the primary uses of dMRI in the literature is to understand the relationship between white matter properties and human behavior, development, aging, and disease (Sullivan and Pfefferbaum, 2003; Clark et al., 2011; Thomason and Thompson, 2011). For example, fractional anisotropy refers to the degree of anisotropic diffusion, and is often roughly interpreted as white matter integrity. Here, we are concerned primarily with using dMRI to determine anatomical connectivity, not to assess how these values are different across populations. However, the two goals can be mutually beneficial, such that more accurate connectivity maps make specific white matter abnormalities more meaningful.

Label-free imaging technologies.

Polarization-sensitive optical coherence tomography (PS-OCT) and polarized light imaging (PLI) both take advantage of birefringence in brain tissue to differentiate between axons that are parallel vs perpendicular to the plane of light (Larsen et al., 2007; Axer et al., 2016; Wang et al., 2016a; Jones et al., 2020). PS-OCT is undistorted, whereas PLI is performed on distorted histological slices. Both are *ex-vivo* techniques that can be performed on unlabeled human tissue. Spatial resolution tends to be between tract-tracing and dMRI, in the tens to hundreds of microns range (Axer et al., 2011; Schmitz et al., 2018). Thus, while too big to visualize single axons, PLI and PS-OCT provide a valuable intermediate step between the spatial resolutions of tract-tracing and dMRI/dissection. Thus, they can miss some important details (like particular termination points or crossing fibers) present in tract-tracing but detect many missed by dMRI.

Interpreting convergent and discordant evidence

Mapping anatomical connectivity of the human brain remains an urgent challenge, and no single method can achieve this goal. However, combining evidence from multiple methods allows us to come much closer to determining truth. In particular, without the guidance from anatomical priors, tractography generation algorithms may suggest pathways that are nonexistent (false positives) or miss the pathways that do exist (false negatives) (Schilling et al., 2020b). Integrating anatomical knowledge from human and monkey work (both post-mortem and *in vivo*) into tractography offers the best path forward to accurately map human brain connectivity.

Figure 1. Using tractography to establish brain connectivity. **A-C.** Depictions of (A) dMRI data, modeling of the diffusion processes giving rise to these data (B), and the generation of streamline tractography using these models (C). The generation of streamline tractography models of white matter is an inherently iterative and inferential process. This process, framed as a signal detection problem, can result in the accurate generation of streamlines (green streamline, panel C) as well as the accurate failure to generate streamlines (blue outline, panel C), but also the generation of inaccurate streamlines (yellow streamline, panel C) as well as inaccurate failures to generate streamlines (red outline, panel C). (D) Distinct tractography generation approaches (e.g., models, parameters, thresholds, priors, etc.) result in different levels of specificity and sensitivity for detecting white matter anatomy connectivity. The resultant tractomes (represented by the three bar columns) can be composed of streamlines and tracts with varying levels of validity, and thus reflects a signal detection problem. Assessing these qualities remains a challenge, and there is currently no known perfect tractography method.

Unsurprisingly, there are major challenges with identifying the potential source of discrepancies across accounts of tracts as attributable to species vs methodological differences. This is largely because the most common method used in nonhuman primates is tract-tracing, whereas noninvasive tractography is commonly used in humans. In other words, when tract-tracing in monkeys vs tractography in humans identify apparent topological or morphological discrepancies between putatively homologous structures, it is difficult to know how to interpret this difference. Should this be assumed to reflect a species difference or a methodological error? One crucial step is to examine tractography results in monkeys. In some cases, the tractography in monkeys is consistent with the results seen in humans, but not with tract-tracing in monkeys. In such a case, under the assumption of homology between species, we can infer that the mismatch between human tractography and monkey tract-tracing is due to a methodological error in tractography, not a species difference. By contrast, if tractography in monkeys matches tract-tracing in monkeys (but not tractography in humans), there may be a true species difference at work leading to the novel human tractography result. A similar logic would be true when comparing tract-tracing and dissection.

BOX 1

Implications for human health and interventions: Neuromodulation of white matter. Targeted changes to axonal bundles have been used to try to treat brain disorders, including both neurological diseases and mental illness. Ablation of the white matter of the internal capsule, for example, is known as a capsulotomy, and has been used to treat major depressive disorder and obsessive-compulsive disorder (Oliver et al., 2003; Christmas et al., 2011; Hurwitz et al., 2012; Pepper et al., 2019). Deep brain stimulation is a treatment used widely for movement disorders and sparingly for psychiatric disorders (Perlmutter and Mink, 2006; Heilbronner et al., 2016). It requires placing an electrode semi-permanently in the brain. Although initially conceived of as operating on nearby cell bodies, we now understand that the efficacy of DBS is mostly dependent on stimulating myelinated axons (Ashkan et al., 2017). Advances in electrode technology mean that neurosurgeons can not only target different physical locations but also steer current to selectively stimulate axons of different orientations (Chaturvedi et al., 2012).

BOX 2

Implications for human health and interventions: The effect of eye and visual disease on the brain's white matter. Recently, researchers interested in diseases and disorders of the human eye have reported associations between these conditions and changes to brain white matter tissue. In this way, such disorders uniquely demonstrate how the alteration of external sensory organs (and thus the signals they transduce), can result in downstream alterations, a demonstration of plasticity. Indeed, investigations of a diverse array of pathogenic processes involving eye motor coordination (Allen et al., 2015; Ashkan et al., 2017), intraocular pressure (Hanekamp et al., 2021), and the retina itself (Ogawa et al., 2014; Yoshimine et al., 2018) have demonstrated that a reduction in sensory inputs results in alterations of the brain's white matter tissue. Understanding the extent to which such changes are reversible will be key to identifying viable and effective paths to intervention. For example, is it the case that once the white matter tissue is affected as a result of sensory disease, no rehabilitation will allow effective recovery of function?

White matter taxonomy of the brain

For each white matter structure in the brain, we will review what is known about: location, fiber orientation(s), anatomical composition (meaning which specific connections are present in each structure, including origins and terminations), and reconstruction using dMRI. Where possible, we briefly touch on functions, abnormalities in brain disorders, and any potential neuromodulatory treatments targeted at the bundle.

Corpus callosum

Perhaps one of the best-studied and best-understood white matter structures, the corpus callosum (Figure 2) connects the left and right cerebral cortices (although not all of the cerebral cortex: see description of the anterior commissure below). Its rostral end is termed the genu; its caudal end is termed the splenium; finally, its central portion is the body. The location and fiber orientations of this structure are easily reconstructed in an automated fashion using dMRI (Yendiki et al., 2011).

The corpus callosum has a strong topographic organization, such that it contains, in order from rostral to caudal: frontal lobe fibers, parietal lobe fibers, temporal lobe fibers, and occipital lobe fibers (Sunderland, 1940; Pandya et al., 1971; de Lacoste et al., 1985). A dMRI study in which analyses were matched for rhesus macaques and humans found strikingly similar organization across the two species (Hofer et al., 2008). Callosal organization becomes increasingly precise as one considers more restricted regions. For example, Barbas & Pandya (Barbas and Pandya, 1984) argue that agranular parts of the monkey prefrontal cortex travel through a different zone than granular regions do.

Crossing fibers utilizing the corpus callosum have several targets. First, they target homotopical cortex (the mirror image location) very strongly. Second, they target heterotopical cortex (other cortical locations on the contralateral side), generally with the same pattern (region and strength) as seen in the ipsilateral cortical connections. Finally, some fibers do travel through the corpus callosum to reach contralateral subcortical targets, including the striatum and claustrum, though likely not the thalamus (Locke et al., 1964; Jones and Powell, 1969; Cavada and Goldman-Rakic, 1991).

The broad pattern of rostro-caudal topography through the corpus callosum can be straightforwardly reconstructed in human dMRI. However, early, tractography-based examples of the corpus callosum (Catani et al., 2002; Abe et al., 2004; Huang et al., 2005; Hofer and Frahm, 2006; Catani and Thiebaut de Schotten, 2008) were often not whole-brain, were generated using deterministic tractography, and/or were focused on an extended U-shaped morphology (see Catani et al., 2002 Figure 12, Abe et al., 2004 Figures 4 and 5, Huang et al., 2005 Figure 4, Hofer and Frahm, 2006 Figure 1, and Catani and Thiebaut de Schotten, 2008 Figure 3). Consequently, resultant tractography models of the corpus callosum were biased toward homotopic connections. A more recent and comprehensive dMRI investigation of connection motifs of the corpus callosum by de Benedictis et al. explores more complex pathways of the corpus callosum, using the frontal pole as an exemplar. The authors note the challenge this constrained conception has posed on investigations of the corpus callosum, and suggest the cause may be attributed to the use of early tractography algorithms (De Benedictis et al., 2016) and/or early dissection-based definitions of the structure. Even so, even recent segmentations do not always reflect this more nuanced conception of the corpus callosum.

Agenesis of the corpus callosum, a condition in which the corpus callosum never develops, and split brain patients, in whom the corpus callosum has been severed, provide unique opportunities to study the functions and plasticity of this bundle. Both sets of subjects demonstrate “disconnection syndrome,” which involves a lack of interhemispheric transfer of sensory information, as well as difficulties with performance of bilaterally coordinated motor tasks (Zaidel and Sperry, 1977). However, there are important differences, not only in these manifestations, but in cognitive and emotional symptoms, depending on the age of commissurotomy/agenesis, implying the existence of significant developmental compensations (Paul et al., 2007), perhaps in the form of the superior fronto-occipital fasciculus (see below).

Extensive work performed by Sperry and Gazzaniga demonstrated fascinating cognitive and behavioral consequences of callosotomy (Gazzaniga, 2005). For example, with the lateralized function of language production, a callosotomy subject (left-handed) was able to generate speech from their left hemisphere, but generate written language with their right (Baynes et al., 1998). Additionally, separate attentional foci can operate in each hemisphere, resulting in faster search times for bilateral stimulus arrays (Luck et al., 1989). Callosal involvement in higher order processes like causation inference and “self awareness” has also been demonstrated as well.

Finally, because of the strong topography present in the corpus callosum, the location of a callosal abnormality can and has been used to infer which parts, broadly speaking, of the cortex are involved in a particular brain condition. For example, obsessive-compulsive disorder is associated with reduced fractional anisotropy in a restricted portion of the rostral body of the corpus callosum (Nakamae et al., 2011), an area that carries crossing fibers from the dorsolateral prefrontal and mid-cingulate cortices. By contrast, schizophrenia is associated with reduced fractional anisotropy in the genu of the corpus callosum, implicating a very different set of crossing cortical fibers in this disorder (Foong et al., 2000).

Anterior commissure

After the corpus callosum, the anterior commissure (Figure 2) is the second-largest cerebral commissure. Its decussation is a prominent landmark in the brain, and crosses through the rostral striatum and anterior limb of the internal capsule. Moving caudally, it is situated lateral and ventral to the striatum, medial to the claustrum, and ventral to the external capsule, from which it remains segregated.

The anterior commissure is responsible for carrying crossing fibers from the basal surface of the cerebral cortex, from the zone extending from the temporal pole and caudal orbitofrontal cortex to the occipitotemporal boundary (Jouandet and Gazzaniga, 1979; Barbas and Pandya, 1984). The dorsal boundary for its component fibers is the inferior half of the insula. Although most areas that send crossing fibers through the anterior commissure do so exclusively, the posterior basal temporal lobe does appear to send crossing fibers through

both the splenium of the corpus callosum and through the anterior commissure (Zeki, 1973). Unlike the corpus callosum, the anterior commissure appears to have only a weak topography (Schmahmann and Pandya, 2006).

Finally, the anterior commissure can be reconstructed in human dMRI using ROIs around its lateral branches, excluding the most lateral areas to avoid contamination with the uncinate fasciculus, inferior fronto-occipital fasciculus, and external capsule (Catani and Thiebaut de Schotten, 2008). Alternative reconstruction methods using the third ventricle as a landmark have also been presented (Wang et al., 2008). A uniting feature of these approaches is that the reconstruction methods used targeted seeding-based approaches, as opposed to whole brain tractography. This trend may be explained by the likely difficulty of reconstructing a very small tract (the anterior commissure is only ~1% the size of the corpus callosum). As such, whole brain tractography approaches to segmentation do not typically include this tract.

Studies of patients with an intact anterior commissure but a severed corpus callosum have been used to infer the functions of the anterior commissure (those interhemispheric functions that are spared). Oddly, in one study, each patient demonstrated some combination of intact visual, auditory, and olfactory functioning, but never all three at the same time (Risse et al., 1978). Fibers from auditory association areas, for example, are known to use a combination of the corpus callosum (caudal areas) and anterior commissure (rostral areas) to cross hemispheres (Pandya et al., 1969). This suggests that, in the absence of a corpus callosum, the anterior commissure has some capacity for multimodal sensory interhemispheric communication (Barr and Corballis, 2002; Aralasmak et al., 2006).

Figure 2. The corpus callosum and anterior commissure. (A) A sagittal view of a tractography model of the corpus callosum (orange), along with a (B) corresponding midline voxel mask indicating a volumetric criterion for it. Even for the well-understood corpus callosum, it is clear that the terminology may be used differently across investigations. “Corpus callosum” may refer to only the volumes at the midline of the brain (B), or might extend to include the entirety of the axons traversing that region (A). (C). A sagittal view of a tractography model of the anterior commissure. Tractography models derived from TractSeg (Wasserthal et al., 2018) for this and all figures unless otherwise indicated.

Internal capsule

In primates, including humans, the internal capsule (Figure 3) is positioned between the caudate and thalamus medially and the putamen and globus pallidus laterally. Its fibers are oriented at an angle such that they run mainly rostro-caudally and dorsal-ventrally, while also moving somewhat medial-laterally. The internal capsule can be divided into two portions: the anterior limb and the posterior limb. The dividing line is the genu, which in a transverse brain slice is shaped like a “V.”

The internal capsule is a major ascending and descending fiber structure, carrying fibers between the cortex and the thalamus, brainstem, spinal cord, and subthalamic nucleus. This means that the internal capsule includes subcomponents or the entirety of many bundles and connections with their own, distinct terminology in the literature: thalamic radiations (which are simply corticothalamic and thalamocortical fibers), pyramidal tracts (a term usually used to refer to descending projections from upper motor neurons to the brainstem and spinal cord), and the corticospinal and corticobulbar tracts (which together make up the pyramidal tracts). Furthermore, the *corona radiata* is typically considered the dorsal extension (positioned nearer to the cerebral cortex) of the internal capsule. Finally, although many brainstem-cortical connections traverse the internal capsule, others do not, such as those that use the medial forebrain bundle. As such, the internal capsule resists standard conceptions of a “bundle,” as it contains shared and unshared connections that use both shared and unshared volumes.

Like the corpus callosum, the internal capsule is topographic. For the anterior limb of the internal capsule, the cortical fibers originate/terminate in the prefrontal cortex; for the posterior limb, the cortical fibers originate/terminate outside the prefrontal cortex. The posterior limb contains the majority of the pyramidal tracts—the axons connecting cortical motor neurons with the brainstem and spinal cord (Beevor and Horsley, 1890; Ross, 1980). Importantly, to our knowledge, fibers in the internal capsule are associated with the ipsilateral cortex only (see for example, (Aggleton et al., 1986; Stanton et al., 1988; Smith et al., 1990; Morecraft et al., 2002). (Although fibers do project between the cortex and the contralateral thalamus and brainstem, they do so inside white matter bundles contained within these structures, rather than through the contralateral internal capsule.) Capsule fibers also travel outside of the main outline of the bundle, in small fascicles embedded within the central striatum, globus pallidus, anterior commissure, and basal forebrain (Lehman et al., 2011). Whether these axons should rightfully be considered part of the internal capsule *per se* harkens back to volumetric vs connectionist approaches to tract delineation, discussed above.

A series of anatomical and dMRI studies have demonstrated the relatively strict topography of the anterior limb of the internal capsule (Lehman et al., 2011; Jbabdi et al., 2013; Safadi et al., 2018). This bundle is organized according to dorsal-ventral, anterior-posterior, and medial-lateral points of origin in the prefrontal cortex, although there are complex interaction effects between axes. In anatomical tract-tracing studies in monkeys, it is clear

that dorsal prefrontal cortical fibers travel dorsally within the anterior limb of the internal capsule to ventral prefrontal cortical fibers. Ventral, anterior prefrontal fibers travel ventrally to ventral, posterior prefrontal fibers; however, the reverse is true for fibers originating in the dorsal prefrontal cortex. Medial, dorsal fibers travel medially within the bundle to lateral, dorsal fibers (although there is considerable compression/overlap). Medial fibers from the ventral surface travel ventrally to lateral fibers from the ventral surface. For the most part, dMRI in monkeys and humans is able to replicate this topography. One manner in which tractography struggles is in capturing ventromedial prefrontal cortical fibers that use small fascicles embedded in larger structures mentioned above as their portion of the anterior limb of the internal capsule (Lehman et al., 2011). Tractography is unable to correctly follow such small bundles and identifies inaccurate ventromedial prefrontal cortical connections to the thalamus and brainstem (Jbabdi et al., 2013).

In addition to the fine topography of the anterior limb of the internal capsule, tractography can accurately map the topography and connections of the posterior limb. Its ability to do so has been greatly improved over time due to the advent of probabilistic tractography methods (Parker et al., 2002; Behrens et al., 2007; Sherbondy et al., 2008; Descoteaux et al., 2009; Tournier et al., 2012) and high-angular resolution data (Frank, 2002). Whereas early mapping of the corticospinal tract using deterministic tracing based on tensor models failed to represent the full extent of the tract (reconstructing only the vertical fibers: (Yeatman et al., 2012b), (Basser et al., 2000), (Lazar et al., 2003), more recent data and tractography methods allow a more complete mapping of the corticospinal tract that represent fibers spanning the full extent of motor cortex (Behrens et al., 2007; Smith et al., 2015; Takemura et al., 2016a; Aydogan and Shi, 2021).

With such a wide array of cortical-subcortical projections, the internal capsule's functions are diverse, ranging from movement to cognitive control and language skills (Damasio et al., 1982; Sullivan et al., 2010; Widge et al., 2019). The anterior limb of the internal capsule has been used as a target of neuromodulatory therapies (capsulotomy and deep brain stimulation) for obsessive-compulsive disorder, major depressive disorder, and Tourette Syndrome (Flaherty et al., 2005; Greenberg et al., 2010; Hurwitz et al., 2012). Because of the highly topographic nature of the internal capsule, stimulation or lesion therapy will affect a very different set of fibers depending on where treatment is applied. Ventral anterior limb stimulation will affect ascending and descending fibers of the orbitofrontal cortex and ventromedial prefrontal cortex; central anterior limb stimulation will affect fibers of the orbitofrontal and anterior cingulate cortex; dorsal anterior limb stimulation will affect fibers of the dorsal prefrontal cortex.

In addition, like the corpus callosum, the topography of the internal capsule may help us to deduce *which* specific sets of fibers are abnormal in disorders. For example, the aforementioned cross species tract-tracing and tractography studies were used to pinpoint that it is ventrolateral prefrontal cortex projections to and from

the thalamus and brainstem that are abnormal in patients with bipolar disorder, based on a very regionally specific fractional anisotropy reduction (Safadi et al., 2018).

Figure 3: The internal capsule. (A) A sagittal view of the internal capsule. This depiction excludes some known fibers from the ventral prefrontal cortex. **(B)** A segmentation of the anterior limb of the internal capsule according to constituent prefrontal cortical fibers, reprinted from (Safadi et al., 2018). Red=ventromedial prefrontal cortex/orbitofrontal cortex; yellow=dorsal anterior cingulate cortex; green=dorsomedial prefrontal cortex; teal=ventrolateral prefrontal cortex; blue=dorsolateral prefrontal cortex.

Superior longitudinal fasciculus

The superior longitudinal fasciculus (SLF, Figure 4) runs rostro-caudally through the white matter of the dorsal parietal and frontal lobes. It has multiple separable components, although how many is a matter of dispute. The terms SLF and IV and V are sometimes used to refer to what we (and others) call the arcuate fasciculus and posterior arcuate fasciculus, respectively (Wu et al., 2016b; Mandonnet et al., 2018; Panesar and Fernandez-Miranda, 2019). Easily identified across species and techniques are the SLF II and III. Tract-tracing in monkeys shows that the SLF II contains fibers from the caudal inferior parietal lobule (in humans, the angular gyrus), the intraparietal sulcus, and the middle portion of the lateral prefrontal cortex, while the SLF III (lateral and ventral to SLF II) contains fibers from the rostral inferior parietal lobule (in humans, the supramarginal gyrus), the parietal operculum, and the ventrolateral prefrontal cortex (Schmahmann and Pandya, 2006).

More controversial of these is the SLF I. Schmahmann and Pandya (2006) claim that, in monkeys, it is the longest, most dorsal, and most medial component of the SLF, sitting above the cingulum bundle and cingulate cortex (also see (Petrides and Pandya, 1984). According to this account, SLF I contains fibers from the precuneus, caudal superior parietal lobule, supplementary motor area, and dorsomedial frontal cortex. Some early human tractography studies concur (Makris et al., 2005). However, more recent human tractography and dissection studies have failed to find a long rostro-caudal bundle in the dorsomedial cortex where the SLF I is thought to be (Wang et al., 2016b; Mandonnet et al., 2019). Others show that the so-called “SLF I” is continuous with and identical to (connectivity-wise) the cingulum bundle, and thus should not be considered its own tract.

This seems to broadly agree with the monkey tract-tracing data, which show continuity of connectivity between the cingulum bundle and the “SLF I” (see commentary in Panesar and Fernandez-Miranda, 2019). Nevertheless, the SLF I *could* be considered separable from the cingulum bundle volumetrically, and the debate is not fully resolved.

In humans, the SLF complex is associated primarily with language, but also with musical ability (Oechslin et al., 2009), tool use (Hecht et al., 2015), and working memory (Karlsgodt et al., 2008; Vestergaard et al., 2011; Rizio and Diaz, 2016). The SLF may act, via the supramarginal gyrus, as a relay between frontal and temporal language regions (Catani et al., 2005; Catani and Mesulam, 2008b). In an unusual microstimulation study of the human SLF, Maldonado et al. (Maldonado et al., 2011) conclude that the caudal SLF is involved in articulatory processing, but not semantic processing. SLF integrity (FA) is associated with language performance (Madhavan et al., 2014). Finally, patients with schizophrenia have reduced FA values in the SLF (Karlsgodt et al., 2008; Davenport et al., 2010), which is consistent with the broad fronto-parietal abnormalities observed in this disorder (Chang et al., 2014; Sheffield et al., 2016).

Figure 4. A tractography model of the Superior Longitudinal Fasciculus (SLF). (A) Depicts a sagittal view of the three subcomponents of the SLF (I, pink; II, green; III, blue). (B) Depicts A-P positions from which slices in (C) are drawn. (C) Depicts coronal views of the cores of the subcomponents, using the same color convention.

Middle longitudinal fasciculus

The middle longitudinal fasciculus (MdLF, Figure 5) connects the parietal and temporal lobes, traversing the white matter medial to the lateral fissure. The details of its constituent connections, however, have historically been the subject of debate. Early tractography reports of the MdLF alternatively depicted it as primarily extending to *either* the superior parietal lobule (Oishi et al., 2008; Maldonado et al., 2013; Wang et al., 2013; Jang et al., 2015; Wu et al., 2016b) or inferior parietal lobule (Makris et al., 2009; Martino et al., 2013a; Menjot de Champfleury et al., 2013) (but not both). Indeed, much of the early investigative energy applied to this structure appears to have been attempts to bolster claims specific to one parietal lobule or the other. Subsequent studies synthesized these reports and presented findings indicating the presence of terminations in both parietal lobules (Makris et al., 2013; Kamali et al., 2014a, 2014b; Bajada et al., 2015, 2017; Bullock et al., 2019). More recently, investigations of this tract have revealed an even finer grained connectivity profile (Kalyvas et al., 2020).

The superior vs inferior parietal lobule debate bears on questions about direct anatomical connectivity and species differences. Tract-tracing studies do *not* show strong anatomical projections between the superior temporal cortex and the superior parietal lobule in monkeys; by contrast, the connectivity between the superior temporal cortex and the inferior parietal lobule is consistently reported and strong (Seltzer and Pandya, 1978, 1984, 1991, 1994; Petrides and Pandya, 1984; Padberg et al., 2019). This raises the possibility that the often-observed connectivity between the superior temporal cortex and the superior parietal lobule in human tractography and dissection may be a false positive. However, matched cross-species tractography and dissection studies would be needed to confirm or deny such an assertion. There has been one study of the MdLF in which tractography methods were applied consistently across multiple primate species (Roumazeilles et al., 2020). However, these authors do not note a superior parietal lobule connection in humans (putting them firmly in the inferior parietal lobule camp of the debate), limiting how much we can say about potential species differences with regard to MdLF connectivity. As an example of this logic: to our knowledge, there has not been a Klingler dissection study in monkeys equivalent to Kalyvas et al. (Kalyvas et al., 2020), which found evidence of a superior parietal lobule component, that could be compared with the monkey tract-tracing data. Because dissections may miss endpoints and conflate nearby tracts, and multiple tract-tracing studies have failed to find a pathway between the superior parietal lobule and the superior temporal gyrus, if a novel monkey MdLF dissection study were to reveal one, it would be taken as a false positive in both species. However, if a monkey MdLF dissection study showed a tract stopping at the inferior parietal lobule, there may be a uniquely human component to the MdLF.

The middle longitudinal fasciculus may, along with the arcuate fasciculus, connect the major language areas of Wernicke's area and the angular gyrus (Makris et al., 2009). Indeed, this bundle does seem to show a left lateralization (Menjot de Champfleury et al., 2013), as would be expected for a language tract. However, electrical stimulation of the MdLF did not appear to interfere with language (De Witt Hamer et al., 2011). Other possible functions include attentional processing (Makris et al., 2009), auditory perception, and/or auditory-visual integration (Kalyvas et al., 2020).

Arcuate fasciculus

The arcuate ("arched") fasciculus (Figure 5), alternatively referred to as the SLF IV and direct SLF (Catani et al., 2005; Bernal and Altman, 2010; De Benedictis and Duffau, 2011; Mandonnet et al., 2018; Panesar and Fernandez-Miranda, 2019), is a relatively long, rostro-caudally directed bundle. It runs laterally in the temporal, parietal, and frontal lobes. It carries fibers between the temporal cortex (as opposed to the parietal cortex, like the superior longitudinal fasciculus) and some parts of the frontal lobe (see below).

Matched tractography in macaques and humans shows a species difference in the specific connections constituting the arcuate fasciculus, with more extensive temporal (middle and inferior temporal gyri) and frontal (ventrolateral prefrontal cortex) connectivity in the human than the macaque (Rilling et al., 2008). These extensive human tractography connections have been replicated multiple times (Babo-Rebelo et al., 2020; Schilling et al., 2020a). Furthermore, the monkey tractography seems to closely match the tract-tracing results (Schmahmann and Pandya, 2006). Thus, it seems quite likely that the human arcuate fasciculus does indeed carry connections that do not exist in the macaque.

The more extensive connectivity in the human (vs macaque) arcuate fasciculus described above is also observed for human vs chimpanzee, and is more pronounced in the left hemisphere (Rilling et al., 2008). Because of the combination of species and laterality differences, and the proximity of the bundle to traditional language areas in humans (Wernicke's and Broca's areas), the arcuate fasciculus is thought to be essential for language function. Indeed, the arcuate fasciculus has been associated with conduction aphasia(s) (Geschwind, 1965; Anderson et al., 1999; Catani et al., 2005; Catani and Mesulam, 2008b; Bernal and Ardila, 2009; Dick and Tremblay, 2012), a stereotyped form of aphasia with etiology associated with tissue damage in the perisylvian area of the brain, and lesions of the arcuate fasciculus following stroke result in language deficits (Marchina et al., 2011). FA values and number of streamlines in the arcuate fasciculus predict degree of aphasia in stroke patients (Hosomi et al., 2009). The arcuate fasciculus has also been related to reading performance (Klingberg et al., 2000; Dehaene et al., 2010; Wandell, 2011; Yeatman et al., 2011, 2012a) and reading interventions have been shown to change the properties of the white matter (Thiebaut de Schotten et al., 2012a).

Figure 5. A tractography model of the middle longitudinal fasciculus (MdLF) and arcuate fasciculus (Arc). (A) Depicts a sagittal view of the MdLF (pink) and AF (gold). (B) Depicts A-P positions from which slices in (C) are drawn. (C) Depicts coronal views of the cores of the subcomponents, using the same color convention.

Posterior arcuate fasciculus

Although its connectivity is often characterized as being part of structures like the middle longitudinal fasciculus (Frey et al., 2008), arcuate fasciculus, and inferior longitudinal fasciculus (Schmahmann and Pandya, 2006; Frey et al., 2008), there is evidence of a separate, vertically oriented bundle, termed the posterior arcuate fasciculus (pArc, Figure 6). This bundle connects the inferior parietal lobule with the middle and inferior temporal lobes (Catani et al., 2005; Catani and Mesulam, 2008b; Kamali et al., 2014a, 2014b; Weiner et al., 2017). Previous work has referred to this tract using a multitude of names including, the SLF-V (Koutsarnakis et al., 2015; Wu et al., 2016b), SLF temporo-parietal connection with the inferior parietal lobule (Makris et al., 2005; Kamali et al., 2014a, 2014b), vertical arcuate fasciculus (Makris et al., 2005; Panesar et al., 2019), vertical SLF (Martino et al., 2013a; Martino and De Lucas, 2014), perisylvian SLF (Catani and Ffytche, 2005; Martino et al., 2013b), posterior SLF (Martino et al., 2013b), indirect arcuate fasciculus (Turken and Dronkers, 2011), temporo-parietal aslant tract (Panesar et al., 2019), parieto temporal long association fibers (Oishi et al., 2008), anterior vertical occipital fasciculus (Choi et al., 2020), and “U-fiber” (Lin et al., 2020). Given all of the labels attached to the pArc, this bundle has clear nomenclature issues that may have stymied progress in its study. Additionally, it has received reduced attention in nonhuman animal work.

The pArc’s dorsal terminations are in the inferior parietal lobule and superior to the posterior portion of the lateral fissure. It has been subdivided into at least two subcomponents (Panesar et al., 2019; Nakajima et al., 2020). The ventral terminations occur throughout the posterior and middle temporal lobe, specifically in the

middle and inferior temporal gyrus (as compared with the superior temporal gyrus, and more anterior terminations of the MdLF). The pArc runs roughly parallel (in the rostro-caudal plane) to the ventral occipital fasciculus (and the two bundles are often confused with each other), but is located more anteriorly (Weiner et al., 2017). Previous work has linked the pArc to speech perception (Vandermosten et al., 2012) as well as particular forms of alexia (Catani and Mesulam, 2008b; Epelbaum et al., 2008).

Vertical occipital fasciculus

The vertical occipital fasciculus (VOF, Figure 6) (Yeatman et al., 2014; Takemura et al., 2016b, 2017), identifiable in both human and macaque dMRI, is a dorsal-ventrally running tract lateral to the calcarine sulcus and the optic radiation. It connects dorsal and ventral regions of the occipital lobe (Takemura et al., 2016b, 2017). More specifically, it connects the dorsal and ventral quadrants of early visual field maps, such as V2 and V3. Downstream (with respect to visual processing areas) of that, it connects hV4, LO-1 and 2 and VO-1 and 2 in the ventral-occipital cortex with V3A/B in the dorsal occipital cortex. The fact that the VOF connects primarily cortical structures *within* the occipital lobe distinguishes it from several other bundles discussed here, which typically connect cortical structures spanning relatively distal portions of the brain. It is also one of the shortest bundles in our review (similar to the uncinate fasciculus in length). The VOF has had a circuitous history (Yeatman et al., 2014), with an early appearance, sustained absence, then recent reappearance in the literature (Yeatman et al., 2014; Takemura et al., 2016b). Even in recent years, the definition of the VOF has sparked substantial debate. For example, efforts have been made to differentiate the VOF from the pARC (Weiner et al., 2017). Interestingly, this issue is predicated upon the assumption that the VOF extends outside the occipital lobe, potentially contrary to its nomenclature. A series of other white matter bundles connecting the parietal cortex and ventral cortex have also been clarified (Kamali et al., 2014a, 2014b; Bullock et al., 2019; Panesar et al., 2019) (e.g. posterior arcuate, temporo parietal connection to the superior lobule). The clarification of these tracts delineate these structures from the VOF, suggesting that the VOF is indeed constrained to within the occipital cortex. More broadly, although connections between the dorsal and ventral early visual cortex have been reported in major tract-tracing work (Felleman and Van Essen, 1991; Ungerleider et al., 2007), there has been a relative dearth of investigation of this bundle as its own entity.

The VOF may help to connect the early dorsal visual stream, which is associated with the representation of space, and the ventral visual stream, which is responsible for object identification (Mishkin and Ungerleider, 1982; Goodale and Milner, 1992).

Temporo-parietal connections to the superior parietal lobule

The temporo-parietal connection to the superior lobule (TP-SPL, also referred to as the temporo-parietal connection Wu et al., 2016b; SLF TP (SPL) Kamali et al., 2014a, 2014b; IPS-FG Jitsuishi and Yamaguchi, 2020) is a vertically oriented tract connecting the superior parietal lobule to the fusiform gyrus and posterior inferior temporal gyrus. The TP-SPL's superior and inferior terminations are generally located medially to the pArc, while its trunk exhibits extensive volumetric overlap with that tract. Its relative positioning with the pArc mirrors (at least in the dorsal white matter) the relationship between the angular gyrus and putative superior parietal lobule components of the MdLF. In the ventral white matter however, the pArc and TP-SPL are both found to have terminations posterior to the MdLF subcomponents, distinguishing the two pairings. In this way, the structure of the pArc, TP-SPL and MdLF constitutes an interesting motif for brain connectivity between the posterior dorsal and ventral cortices that has been postulated to play a role in the development of the dorsal and ventral pathways of visual information processing (Choi et al., 2020; Vinci-Booher et al., 2021). This dorsal bifurcation is noted to also be consistent with the bifurcation of the VOF (Bugain et al., 2020), suggesting (minimally) a morphological consistency between the MdLF, pArc, TP-SPL and VOF, and may have further relevance to the the distinct parietal mappings of the subcomponents of the SLF (Schotten et al., 2011). The functional implications of this architecture have yet to be determined.

Figure 6. A tractography model of the posterior arcuate fasciculus (pArc), vertical occipital fasciculus (VOF), and Temporo-Parietal connections to the superior parietal lobule (TP-SPL). (A) Depicts a sagittal view of the pArc (red), VOF (light pink) and TP-SPL (dark pink). (B) Depicts D-V positions from which slices in (C) are drawn. (C) Depicts horizontal views of the cores of the subcomponents, using the same color convention. Images derived from WMA_segmentation available on brainlife.io

Inferior longitudinal fasciculus

The definition of the inferior longitudinal fasciculus (ILF, Figure 7) has been the subject of confusion and contradiction, both historically and in the modern day. Historically, extant views (Bajada et al., 2015) include: that the ILF is not a long association bundle, but instead consists of a series of short U-fibers that interconnect nearby regions (Tusa and Ungerleider, 1985), and thus cannot be properly considered a bundle at all, and that the bundle consists of fibers descending to subcortical regions (Redlich, 1905). We are now certain that the ILF is a long rostro-caudal association (cortical-cortical) bundle with embedded short fibers (Dejerine and Dejerine-Klumpke, 1895). However, which particular cortical connections define the ILF, as well as its precise location, remain in dispute.

In their comprehensive tract-tracing study in monkeys, Schmahmann and Pandya (2006) did see many examples of long cortico-cortical association axons in the ILF, connecting the parietal, occipital, and temporal lobes, in addition to U-fibers, but no subcortically-projecting fibers. However, their definition of both the placement (volume) of the ILF and its connectivity are somewhat unique in the literature. All authors agree that the ILF carries temporo-occipital fibers. More controversial (Mandonnet et al., 2018) is whether parietal fibers belong to this bundle. Tract-tracing makes clear that there are connections between the parietal cortex and inferior temporal cortex, and that some of those axons occupy the same volume as canonical ILF temporo-occipital fibers. Schmahmann & Pandya (2006) include these fibers, as well as a vertical branch that impinges upon the white matter of the parietal lobe, in their definition of the ILF (see also (Seltzer and Pandya, 1984). Some others (who cite Seltzer and Pandya, 1984) also do show more dorsal cortical connections at the caudal end, including to the angular gyrus (Rushworth et al., 2006; Frey et al., 2008; Seghier, 2013). By contrast, some authors would argue that these more vertically oriented tracts belong to the MdLF and pArc (Davis, 1921; Catani et al., 2002, 2003; Catani and Thiebaut de Schotten, 2008; Turken and Dronkers, 2011). They likely would not argue that there are no connections between the parietal and inferior temporal lobes; but rather, they would argue that the dorsal, vertically oriented fibers are not part of the ILF. On such an account, the ILF would be located in the ventral temporal lobe and would exclusively contain rostro-caudally oriented temporo-occipital fibers. This is a clear case of tension between a volume vs connection approach to tract definition (see above, *Approaches to white matter tract definition*). Finally, the ILF's temporo-occipital fibers likely connect the entire occipital lobe (Martino et al., 2013a; Wang et al., 2013; De Benedictis et al., 2014; Kamali et al., 2014a), rather than just the ventral occipital lobe (Catani et al., 2002, 2003; Catani and Thiebaut de Schotten, 2008; Turken and Dronkers, 2011; Menjot de Champfleury et al., 2013).

Functions of the ILF map to known functions of the ventral visual stream (Herbet et al., 2018). For example, lesions or degeneration of the ILF lead to deficits in object recognition (Benson et al., 1974; Meichtry et al., 2018), alexia (Gaillard et al., 2006; Epelbaum et al., 2008), and visual memory (Shinoura et al., 2007). The

ILF is likely also involved in face recognition, which depends upon intact connections between the occipital face area and the fusiform face area (Herbet et al., 2018).

Inferior fronto-occipital fasciculus

The inferior fronto-occipital fasciculus (IFOF, Figure 7) has had a contentious history in the literature, particularly as it relates to cross species considerations. Putatively, it is located medial to the insula and ventral to the extreme capsule and runs from the occipital lobe to the frontal lobe. It is thought to directly connect ventral visual cortices with the frontal lobe. One challenge with understanding the history of this tract is purely terminological: it is alternately referred to as inferior occipitofrontal fasciculus (Kier et al., 2004; Wang et al., 2008; Dick and Tremblay, 2012), the extreme capsule fiber complex (Mars et al., 2016; Bajada et al., 2017), and (more commonly) the inferior fronto-occipital fasciculus (Catani and Thiebaut de Schotten, 2008; Menjot de Champfleury et al., 2013; Mandonnet et al., 2018; Sarubbo et al., 2019). It is abbreviated as IOF, IFOF, IOFF (Seghier, 2013; Oestreich et al., 2016) and IFO (Wakana et al., 2007). In keeping with the trend associated with the evolution of tractographic studies in humans (discussed above, *Approaches to white matter tract definition*), authors have generated increasingly granular accounts of IFOF connectivity and subdivisions (Wu et al., 2016a; Panesar et al., 2017; Conner et al., 2018; Rollans and Cummine, 2018; Sarubbo et al., 2019).

An additional challenge is the status of the IFOF in monkeys. Based on their monkey tract-tracing data, Schmahmann and Pandya (Schmahmann and Pandya, 2006, 2007a) assert that the IFOF does not exist, at least in monkeys. They observed no direct connections between the ventral visual cortices and the basal frontal cortex. Therefore, they believe the IFOF to be a false positive when identified in tractography, a nonexistent tract. Although they themselves did not explicitly consider the existence of the IFOF in humans, their statements were cited in subsequent literature as evidence of a potential species difference: perhaps the IFOF exists in humans but not in monkeys (Catani, 2007; Sarubbo et al., 2013; Forkel et al., 2014).

When tractography and dissection techniques have been more recently applied to monkey data, a tract that clearly matches the human IFOF emerges (Mars et al., 2016; Feng et al., 2017; Decramer et al., 2018; Sarubbo et al., 2019; Bryant et al., 2020), arguing against a species difference. This raises the distinct possibility that the IFOF is a false positive of dMRI. Perhaps tractography and dissection studies are essentially fusing two (or more) distinct bundles (potentially the uncinate fasciculus and inferior longitudinal fasciculus), creating a polysynaptic pathway between the frontal and occipital lobes (Sarubbo et al., 2019). To be explicit, we would *not* consider a series of polysynaptic connections to constitute a discrete bundle, nor have such connectivity profiles been considered coherent white matter tracts historically.

However, evolving endpoint definitions complicate this view. Early tractographic depictions of the IFOF, primarily derived from deterministic tractography algorithms, depict an IFOF tract which features posterior

endpoints in the ventral occipital and frontal lobes (Catani and Thiebaut de Schotten, 2008; Menjot de Champfleury et al., 2013). More recent studies reflect increasingly permissive definitions of ventral occipito-frontal connectivity, resulting in broader connectivity profiles between these regions as compared to earlier accounts of the structure (Panesar et al., 2017; Conner et al., 2018; Sarubbo et al., 2019). This broadening is relevant because direct anatomical connections (as shown with monkey tract-tracing) are known to exist between lateral frontal cortex (such as the frontal eye fields) and occipital areas (such as V2 and V4) (Gerbella et al., 2010; Markov et al., 2014). Other bundles terminating in the frontal eye fields or ventral visual areas do not provide an obvious route for a direct connection between the two. Resolving these issues will likely require meticulous tractography, tract-tracing, and dissection studies across species.

Figure 7. A tractography model of the inferior longitudinal fasciculus (ILF) and inferior fronto-occipital fasciculus (IFOF). (A) Depicts a sagittal view of the ILF (lime green) and IFOF (light purple). (B) Depicts A-P coordinates from which slices in (C) are drawn. (C) Depicts coronal views of the cores of the subcomponents, using the same color convention.

Cingulum bundle

The cingulum bundle (Figure 8) is another of the brain's major rostro-caudal bundles, and is intimately tied to limbic circuitry (Mufson and Pandya, 1984). In a recent paper (Heilbronner and Haber, 2014), we used monkey tract-tracing data to define the cingulum bundle as including not only its prominent dorsal component, but also a subgenual component curving around the genu of the corpus callosum and continuing caudally, tucked up against the gray matter of the subgenual cingulate cortex, as well as a temporal component, curving around the splenium and extending rostrally into the most medial white matter of the medial temporal lobe (Seltzer and

Pandya, 1984). According to our work, the volume associated with the cingulum bundle contains three different types of connections. First, fibers from the adjacent regions of cortex that travel short distances (or not at all) rostro-caudally within the cingulum bundle, but must nevertheless cross through it in order to reach their targets. From a connectivity approach, we would not consider these to be properly part of the cingulum bundle, but they cannot be ignored because of their shared volumes. Second, the bundle contains rostro-caudally directed cingulate fibers (to and from anterior cingulate, posterior cingulate, and retrosplenial cortices): those emanating from the cingulate, those traveling to the cingulate, and both. Third, there are some fibers traveling long distances within the cingulum bundle with no relationship to the cingulate cortex itself (those that travel between subcortical regions and the dorsomedial prefrontal cortex, for example). These connections allowed us to segment the cingulum bundle into four separable components in monkeys: a subgenual, a rostral dorsal, a caudal dorsal, and a temporal. Many connections use all or most of these segments; however, some do not. For example, basolateral amygdala fibers are not present in the caudal dorsal cingulum bundle, and prefrontal fibers are not found in the temporal cingulum bundle. This segmentation does not preclude additional, finer-grained segmentations with more components, based especially on additional subcortical and temporal fibers that were not included in the original analysis.

Tractography reconstructions of the cingulum bundle can also capture its full length in humans (Jones et al., 2013), including its temporal and subgenual components. Nevertheless, the cingulum bundle poses significant challenges for tractography. Fibers appear to enter and exit the bundle at different points rostro-caudally, but then do not occupy distinct zones medio-laterally or dorso-ventrally as they travel within the bundle. Thus, endpoints for particular connections may be difficult to track, as there is no distinct topography to connections once they have joined the bundle, and any given voxel contains a heterogeneous composition of connectivity profiles.

Two different components of the cingulum bundle, the dorsal and the subgenual, are targets for neuromodulatory treatments of psychiatric disorders and chronic pain. The rostral dorsal component is a target for lesions (cingulotomies) of treatment-resistant patients with major depressive disorder, obsessive-compulsive disorder, and chronic pain. More anteriorly placed lesions are associated with better response to cingulotomy in major depressive disorder (Steele et al., 2008). Based on the monkey tract-tracing data, this location would involve more amygdala and lateral orbitofrontal cortex than its more caudal neighbors. The subgenual cingulum bundle is the target of deep brain stimulation for major depressive disorder (Mayberg et al., 2005). Although originally conceived of as correcting a hyperactive subgenual cingulate cortex in patients (Mayberg et al., 1999), it is now clear that this target involves electrical stimulation of the white matter of the subgenual cingulum bundle, along with fibers from the uncinate fasciculus and corpus callosum (Riva-Posse et al., 2014).

Uncinate fasciculus

The uncinate fasciculus (Figure 8) connects the prefrontal cortex with the anterior temporal lobe (Ebeling and von Cramon, 1992). It is noted for hook or arc-like shape, reminiscent of the arcuate fasciculus, though considerably smaller. At its rostral and superior end, the uncinate fasciculus is situated dorsal to the gray matter of the orbitofrontal cortex. Progressing caudally and inferiorly, it moves laterally around the striatum, situated underneath the external and extreme capsules, before curving ventrally into the temporal lobe. It is well-known for bidirectionally connecting the prefrontal cortex with the amygdala and rostral temporal cortex. In addition, the portion of the uncinate fasciculus sitting dorsally to the orbitofrontal cortex carries fibers traveling within the ventral prefrontal cortex (Lehman et al., 2011). These patterns of connectivity have been captured using tract-tracing and tractography in monkeys, as well as dissections and tractography in humans (Folloni et al., 2019).

One point of contention is whether the uncinate fasciculus extends caudally enough to connect the prefrontal cortex with the hippocampal formation (Pribram et al., 1950), or whether such fibers are carried by the nearby inferior longitudinal fasciculus. In addition, some papers refer to the connection as being primarily one between the temporal lobe and the orbitofrontal cortex, rather than the prefrontal cortex more broadly (Thiebaut de Schotten et al., 2012b). Other accounts have divided the hook-like superstructure of the uncinate into a layered organized series of sub-components with distinct topographical connectivity profiles (Hau et al., 2017) .

The specific functions of the uncinate fasciculus have received more attention than for other bundles. Von Der Heide and colleagues (Von Der Heide et al., 2013), after noting a wide range of associations with functional processes and disorders, suggest that the function of the uncinate is to allow mnemonic information (from the anterior temporal lobe) to influence valence for decision-making (from the orbitofrontal cortex), and vice versa. Injury to the uncinate fasciculus can cause isolated retrograde amnesia (Levine et al., 1998). dMRI has also demonstrated reduced fractional anisotropy in the uncinate fasciculus in Alzheimer's disease patients, a change that may be related to memory deficits (Yasmin et al., 2008).

Figure 8. Cingulum bundle and uncinate fasciculus. (A) Depicts a sagittal view of the cingulum bundle (orange). (B) A segmentation of the cingulum bundle in the macaque according to constituent fibers. Many fibers use all four subcomponents of the cingulum bundle; others (in boxes) are only present in a subset. Reproduced from (Heilbronner and Haber, 2014) (C) Depicts a sagittal view of the uncinate fasciculus (cyan).

Cortico-striatal connections: Muratoff's bundle and the external capsule

Nearly the entire cerebral cortex projects to the striatum, the entryway to the basal ganglia. Cortico-striatal bundles use many routes to reach their targets, but the majority at some point use the external capsule and/or Muratoff's bundle (Figure 9). The external capsule is located just lateral to the caudate nucleus. Curving around the lateral edge of the putamen, the external capsule is separated from its more lateral partner, the extreme capsule, by the claustrum (Berke, 1960; Petrides and Pandya, 2006). The architecture of this structure is similar to that of the uncinate fasciculus, and it has thus been proposed that the external capsule may be a sub-component of that structure (Hau et al., 2017).

Muratoff's bundle is situated dorsal to the caudate nucleus, curving around its upper edge. Monkey tract-tracing studies have identified fibers bound for the striatum originating in preoccipital cortices (Yeterian and Pandya, 2010), anterior and posterior cingulate cortices (Heilbronner and Haber, 2014), dorsal prefrontal cortex, and other association and limbic areas (Schmahmann and Pandya, 2006). Although both bundles carry fibers from the cortex to the striatum, fibers passing through the external capsule more commonly terminate in the putamen, whereas fibers passing through Muratoff's Bundle more commonly terminate in the caudate nucleus. However, this rule is not strictly observed, and axons do transfer between these two bundles as well. There is not an extensive literature on reconstruction of Muratoff's bundle using dMRI, aside from differentiating it from the putative superior frontal occipital fasciculus (SFOF, see below). Although occasionally equated with one another, Muratoff's bundle can be distinguished from the putative SFOF based on their respective topographic locations: while Muratoff's bundle travels above the lateral ventricle and beneath the corpus callosum, the putative SFOF has been depicted as lateral to the upper corner of the lateral ventricle (Makris et al., 2007).

Extreme capsule

The extreme capsule is situated between the insula and claustrum (Figure 9). Although the claustrum is traditionally used as the boundary between the external and extreme capsules, tract-tracing shows that the boundaries across the three structures are not strict, and both capsules also send fibers streaming across the claustrum (Lehman et al., 2011). The extreme capsule primarily runs rostro-caudally. However, the volumes occupied by the extreme capsule also contain many fibers traveling to and from the insula, simply because of its position. As with the cingulum bundle, from a connectionist perspective, we would not consider these to be part of the extreme capsule. Instead, monkey tract-tracing demonstrates that the extreme capsule connects the frontal cortex with the superior temporal gyrus and sulcus (Schmahmann and Pandya, 2006). It targets relatively more dorsal aspects of the frontal cortex and caudal aspects of the temporal cortex than the uncinate fasciculus does.

Diffusion MRI investigations of the extreme capsule in humans as well as monkeys have replicated the connections found in monkey tract-tracing (Frey et al., 2008; Mars et al., 2016), but also suggested that the bundle reaches back to the visual cortex (Mars et al., 2016). Importantly, the relationship between the extreme capsule and the inferior fronto occipital fasciculus (IFOF, see below) is not clear (Bajada et al., 2015), not least because some investigators use the term *extreme capsule fiber complex*, which may be broader than just the extreme capsule. One parsimonious explanation of the various discrepancies is that the IFOF and extreme capsule are separable bundles (the IFOF, and in particular its “neck,” is positioned ventrally to the extreme capsule), with the IFOF reaching back to the occipital cortex, and the extreme capsule terminating in the superior temporal cortex. However, given the controversies surrounding the IFOF, further study on the differentiation between these two bundles is necessary (Makris and Pandya, 2009), as there are few studies of the extreme capsule itself using tractography.

Figure 9. External capsule, Muratoff's bundle, and extreme capsule. Volumetric locations shown on high-resolution brain from (Edlow et al., 2019).

Superior fronto-occipital fasciculus

Schmahmann and Pandya (2006) described a bundle in monkeys, which they refer to as the fronto-occipital fasciculus (which here we will refer to as the superior fronto-occipital fasciculus, SFOF, to distinguish it from the IFOF), as adjacent to the corpus callosum, SLF II, Muratoff's bundle, and cingulum bundle. It carries fibers between the parietal and dorsal frontal lobes. Older dissection studies on human brains were mixed in their descriptions of this bundle (Forel, 1881; Dejerine and Dejerine-Klumpke, 1895; Schröder and P., 1901). Importantly, modern human investigations, using both tractography and Klingler dissections (Türe et al., 1997; Forkel et al., 2014; Meola et al., 2015; Liu et al., 2020), have failed to replicate this structure. Instead, a structure consistent with descriptions of the SFOF can be found in individuals with agenesis of the corpus callosum, but this observation in abnormal cases may not apply to white matter architecture in neurotypical individuals (Schmahmann and Pandya, 2006, 2007b; Forkel et al., 2014). Furthermore, it is interesting that even Schmahmann & Pandya (2006) do not identify occipital connections of the SFOF; instead, the connectivity of their bundle appears quite similar to that of the SLF II, by their own account. Even in cases where a structure resembling accounts of the SFOF can be reconstructed in humans via tractographic approaches (e.g., Makris et al., 2007 Figure 7; Uddin et al., 2010 Figure 5; Liu et al., 2020 Figure 6), the posterior connectivity observed is with the parietal lobe (and thus more consistent with accounts of the SLF II), and not with the occipital lobe as would presumably be required of a fronto *occipital* fasciculus (Mandonnet et al., 2018). One possibility is that the SLF II extends more medially in the monkey than in the human, generating the observed tract-tracing results. Perhaps there are constituent frontal or parietal connections that distinguish the SFOF from the SLF II. Regardless, it is unclear whether there is a separate, distinct bundle with its own connectivity patterns in either species that should be referred to as the SFOF, or what criteria would be used to distinguish these adjacent bundles.

Optic radiation

The optic radiation is the primary white matter structure consisting of feed-forward axonal projections connecting the lateral geniculate nucleus of the thalamus (LGN) with the visual cortex (Ebeling and Reulen, 1988) (Figure 10). It is deeply embedded in the corona radiata and sagittal stratum. There is also evidence that fibers to/from structures other than the LGN and V1 (such as the pulvinar, V2, V3) contribute small numbers of axons to this structure (Párraga et al., 2012); (Yoshida and Benevento, 1981; Alvarez et al., 2015); such fibers account for less than 5% of the total fibers.

Some degree of terminological ambiguity exists in the subdivision and nomenclature of the components of the optic radiation. A characteristic morphological aspect of the OR corresponds to the fibers in the anterior portion which progress with a sharp turn as they move towards the posterior of the brain. These fibers have been associated with the term "Meyer's loop" by many anatomists (e.g., (Ebeling and Reulen, 1988). Some have used

the term Meyer's loop to define only the more anteriorly arching, morphological feature of the Optic Radiation (Ebeling and Reulen, 1988; Sarubbo et al., 2015), while others use the same term to refer to the entire length of the axons that traverse the anterior of the thalamus, which includes their posterior expanse as well (Párraga et al., 2012; Pescatori et al., 2017).

Another interesting terminological phenomenon has been associated with the posterior / dorsal component of the optic radiation. As noted by (Knipe et al., 2021), a number of recent publications (including, most notably, the 2019 edition of Gray's Surgical anatomy, Brennan et al., 2019) have made reference to this structure as the eponymously named "Baum's loop". This term is here noted to exhibit two-fold parity with the term "Meyer's loop" in that it is (1) an eponym and (2) utilizes the descriptor "loop", and thereby appears to be a valid and plausible term. Though this structure may in fact exhibit a dorsal arc to it, and thus be sensibly labeled as a "loop", the actual provenance of this full term is decidedly suspicious. Indeed, in their investigation of the origin of the term, (Knipe et al., 2021) appear to have traced its source to a 2009 edit to the wikipedia article for "optic radiation" (specific edit [here](#)), and perhaps even more stunningly, may have even traced it to the apparent individual who coined the eponym implicitly referencing themselves.

The optic radiation has been routinely studied for its involvement in supporting vision in humans and the recent evidence shows major effects to the white matter of the optic radiation due to eye and visual disease (See BOX 2).

Figure 10. A tractography model of the optic radiation (OR) (A) Depicts a sagittal view of the OR (blue). (B) Depicts A-P coordinates from which slices in (C) are drawn. (C) Depicts coronal views of the OR core.

Fornix

A complex, C-shaped structure with three major components (crus, body, and columns), the fornix is situated at the brain's midline and is the major output structure for the hippocampus (Saunders and Aggleton, 2007) (although it also contains hippocampal afferents) (Figure 11). Fibers leave the hippocampus, course

underneath the lateral ventricle, and form the fornix. At the level of the splenium, these fibers form the crus of the fornix (plural: crura); these run beneath the corpus callosum and eventually form the body of the fornix; fibers then descend near the anterior commissure to form columns (Poletti and Creswell, 1977). The fornix contains both crossing fibers (at the body) and ipsilateral projection fibers. Through the fornix, hippocampal formation fibers reach subcortical structures like the mammillary bodies, anterior thalamic nuclei, and the septum.

The fornix can be reconstructed with tractography using targeted approaches (Rheault et al., 2018; Milton et al., 2020), as opposed to whole brain tractography. Observed difficulties in obtaining viable models of the fornix from whole brain tractography have been attributed to several characteristics particular to the fornix. For example, its cross-sectional area in some locations has been estimated to be approximately 2 mm, which is challenging for non-targeted tractography methods, particularly given the curvature of the structure. Furthermore, there is evidence that adjacent cerebrospinal fluid (CSF) might contaminate the signal, such that performing CSF suppression improves reliability (Concha et al., 2005), an example of a partial voluming effect (Alexander et al., 2001). Perhaps for this reason, the fornix has received little attention in the tractography literature, especially relative to what one might expect given its well established structural characteristics and role in memory. Therefore, it is difficult to assess whether there are potential methodological and/or species differences associated with this bundle.

The fornix is central to the classic Papez circuit (Papez, 1937) responsible for emotion, learning and memory (Delay and Brion, 1969). Fornix damage is well-known to result in deficits in these processes (see (Thomas et al., 2011). For example, fornix injury has resulted in anterograde amnesia (Gaffan et al., 1991). Diffusion imaging of the fornix often shows significant differences from healthy controls in a multitude of diseases, including Alzheimer's Disease, multiple sclerosis and schizophrenia (Douet and Chang, 2014).

Medial forebrain bundle

The medial forebrain bundle is a complex network of fibers connecting parts of the brainstem and basal forebrain with the frontal cortex (Garver and Sladek, 1976; Moore and Bloom, 1978; Felten and Sladek, 1983; Oades and Halliday, 1987; Parent et al., 2011) (Figure 11). It is not technically white matter, because its axons tend to be unmyelinated or lightly myelinated, but we will review it here because of widespread interest. This bundle's axons ascend from the brainstem and course through the basal forebrain, ventral to the decussation of the anterior commissure, collecting fibers along the way. Notably, the medial forebrain bundle contains many dopaminergic fibers, although not exclusively.

There is substantial confusion in the dMRI literature regarding the position of the medial forebrain bundle (Haber et al., 2020). This bundle does not ascend into the internal capsule; instead, it remains ventrally positioned until reaching its targets in the frontal lobe. Seeding certain brainstem regions that contribute to the

medial forebrain bundle results in internal capsule connectivity; however, this is because of the complexity of the brainstem-cortical connection. For example, dopaminergic fibers do not traverse the internal capsule, but use the medial forebrain bundle to reach their targets.

The medial forebrain bundle is widely known for effective self-stimulation in rodents (Olds and Milner, 1954); this is likely due in part to the stimulation of dopaminergic fibers within the bundle. More recently, it has come to the attention of clinicians interested in deep brain stimulation (DBS). However, because of the previously mentioned issues with tracking brainstem fibers, there is a widespread misunderstanding of the types of connections DBS in different locations can affect. DBS of the internal capsule is *not* capturing the medial forebrain bundle, and therefore not capturing dopaminergic axons (Coenen et al., 2009; Haber et al., 2020).

Ventral amygdalofugal pathway

The ventral amygdalofugal pathway contains afferent and efferent fibers connecting the amygdala with the rest of the brain (Nauta, 1961; Aggleton et al., 1980; Porrino et al., 1981; Amaral and Price, 1984; Mori et al., 2017) (Figure 11). It is a spatially distinct pathway from the uncinate fasciculus and stria terminalis, although all carry amygdala connections. A careful study comparing anatomical tract-tracing in macaques, diffusion tractography in macaques, and diffusion tractography in humans found broad consistency in the location and connectivity of the ventral amygdalofugal pathway (Folloni et al., 2019). This tract exits the amygdala, ascends dorsally and medially, and travels ventral to the anterior commissure and striatum and medial to the uncinate fasciculus. At its most medial projection, the pathway bifurcates into ascending and descending branches. The ascending branch enters the nucleus accumbens, followed by the prefrontal cortex. The descending branch projects to the anterior hypothalamic nuclei (Kamali et al., 2016). At frontal locations, it is interwoven with the uncinate fasciculus.

The functions of the ventral amygdalofugal pathway are no less complex than those of the amygdala itself. This pathway has been implicated in fear, reward learning, and drug abuse, to name just a few (Hamm and Weike, 2005; Gray et al., 2018). For example, dMRI studies on patients addicted to prescription opioids have demonstrated reduced fractional anisotropy in the ventral amygdalofugal pathway (Upadhyay et al., 2010).

Figure 11. Fornix, medial forebrain bundle (MFB), ventral amygdalofugal pathway (VAF), and uncinate fasciculus (UF). Volumetric locations shown on high-resolution brain from (Edlow et al., 2019). (A) Sagittal view; (B) Coronal view.

Conclusion

In compiling this review, we, as a collection of neuroanatomy and neuroimaging specialists, working across multiple species and methods, came to a number of important realizations. Our underlying assumptions about the connections constituting any given tract and the volumes it might traverse were often different from one another, occasionally dramatically so. We noted that our distinct but intersecting fields of knowledge, drawn from both our own experiences with data and our readings of our domains' literature, had led to different understandings of tract definitions. We were struck by how *challenging* it is to create a consensus-based characterization of white matter architecture. Perhaps our experience is a microcosm of the field more broadly.

Much of the challenge relates to how difficult it is to discern the objective truth of white matter morphology and architecture. Tract-tracing and dissection studies provide a special class of data: rare, expensive, and difficult to come by. Collecting data of this sort requires analyzing donated human brains or many sacrificed animals (with the attendant critical ethical concerns). The work is labor-intensive and highly skilled. Attempts have been made to streamline and advance high-throughput anatomical data acquisition (Shen et al., 2012; Amunts et al., 2013) to lower barriers to doing big data neuroinformatics. Despite these substantial efforts, it remains inarguable that we do not have a complete map of human brain connections. This stands as a major obstacle for turning our field's already appreciable collective anatomical knowledge into actionable insights for understanding human behavior, development, and disordered processes.

As emphasized by our discussion here, one additional challenge we will be forced to face as a field is a reconsideration of what it is we actually *know* and what is instead a matter of convention. By annealing our diverse methodological backgrounds, we have come to realize that understanding can become siloed, cut off from contributing to the formation of a discipline-wide synthesis. In other words, we strive to understand white matter anatomy, agnostic of approach or method. Unfortunately, current accounts are occasionally divergent or

even inconsistent. Moreover, it is not always clear if divergent accounts can accommodate one another. This raises the uncomfortable possibility that some amount of research work, perhaps even non-trivial amounts thereof, may ultimately need to be reconsidered. On an optimistic note, though, this necessary self-reflection may also stand as an opportunity to learn about how anatomical evidence accumulates and evolves, and could thereby help shape more advanced forms of anatomical investigation of white matter. Additionally and more conservatively, although we may have reservations about the ability of our various methods to detect valid connections (i.e. “True positives” Figure 1), via the accumulation of substantial amounts of evidence from diverse lines of investigation, and thus consilience, we can nonetheless feel some confidence as we rule out invalid connections (i.e. “True negatives” Figure 1). In this way, we may come to develop a foundational understanding in our field via an exclusionary process, albeit slowly. This may prove to be logistically intensive, and require the investment of substantial additional resources. Such investments will be critical for advancing the field, and for developing applications that can be used *in-vivo*.

References

- Abe O, Masutani Y, Aoki S, Yamasue H, Yamada H, Kasai K, Mori H, Hayashi N, Masumoto T, Ohtomo K (2004) Topography of the human corpus callosum using diffusion tensor tractography. *J Comput Assist Tomogr* 28:533–539.
- Aganj I, Lenglet C, Sapiro G, Yacoub E, Ugurbil K, Harel N (2010) Reconstruction of the orientation distribution function in single- and multiple-shell q-ball imaging within constant solid angle. *Magn Reson Med* 64:554–566.
- Aggleton JP, Burton MJ, Passingham RE (1980) Cortical and subcortical afferents to the amygdala of the rhesus monkey (*Macaca mulatta*). *Brain Res* 190:347–368.
- Aggleton JP, Desimone R, Mishkin M (1986) The origin, course, and termination of the hippocampothalamic projections in the macaque. *J Comp Neurol* 243:409–421.
- Alexander AL, Hasan KM, Lazar M, Tsuruda JS, Parker DL (2001) Analysis of partial volume effects in diffusion-tensor MRI. *Magn Reson Med* 45:770–780.
- Allen B, Spiegel DP, Thompson B, Pestilli F, Rokers B (2015) Altered white matter in early visual pathways of humans with amblyopia. *Vision Res* 114:48–55.
- Alvarez I, Schwarzkopf DS, Clark CA (2015) Extrastriate projections in human optic radiation revealed by fMRI-informed tractography. *Brain Struct Funct* 220:2519–2532.
- Amaral DG, Price JL (1984) Amygdalo-cortical projections in the monkey (*Macaca fascicularis*). *J Comp Neurol* 230:465–496.
- Amunts K, Lepage C, Borgeat L, Mohlberg H, Dickscheid T, Rousseau M-É, Bludau S, Bazin P-L, Lewis LB, Oros-Peusquens A-M, Shah NJ, Lippert T, Zilles K, Evans AC (2013) BigBrain: an ultrahigh-resolution 3D human brain model. *Science* 340:1472–1475.
- Anderson JM, Gilmore R, Roper S, Crosson B, Bauer RM, Nadeau S, Beversdorf DQ, Cibula J, Rogish M 3rd, Kortencamp S, Hughes JD, Gonzalez Rothi LJ, Heilman KM (1999) Conduction aphasia and the arcuate fasciculus: A reexamination of the Wernicke-Geschwind model. *Brain Lang* 70:1–12.
- Aralasmak A, Ulmer JL, Kocak M, Salvan CV, Hillis AE, Yousem DM (2006) Association, commissural, and projection pathways and their functional deficit reported in literature. *J Comput Assist Tomogr* 30:695–715.
- Ashkan K, Rogers P, Bergman H, Ughratdar I (2017) Insights into the mechanisms of deep brain stimulation. *Nat Rev Neurol* 13:548–554.
- Assaf Y, Pasternak O (2008) Diffusion tensor imaging (DTI)-based white matter mapping in brain research: a review. *J Mol Neurosci* 34:51–61.
- Axer M, Grässel D, Kleiner M, Dammers J, Dickscheid T, Reckfort J, Hütz T, Eiben B, Pietrzyk U, Zilles K, Amunts K (2011) High-resolution fiber tract reconstruction in the human brain by means of three-dimensional polarized light imaging. *Front Neuroinform* 5:34.
- Axer M, Strohmer S, Gräßel D, Bückner O, Dohmen M, Reckfort J, Zilles K, Amunts K (2016) Estimating Fiber Orientation Distribution Functions in 3D-Polarized Light Imaging. *Front Neuroanat* 10:40.
- Aydogan DB, Shi Y (2021) Parallel Transport Tractography. *IEEE Trans Med Imaging* 40:635–647.

- Azevedo FAC, Carvalho LRB, Grinberg LT, Farfel JM, Ferretti REL, Leite REP, Filho WJ, Lent R, Herculano-Houzel S (2009) Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain. *The Journal of Comparative Neurology* 513:532–541 Available at: <http://dx.doi.org/10.1002/cne.21974>.
- Babo-Rebello M, Puce A, Bullock D, Hugueville L, Pestilli F, Adam C, Lehongre K, Lambrecq V, Dinkelacker V, George N (2020) Visual information routes in the posterior dorsal and ventral face network studied with intracranial neurophysiology, and white matter tract endpoints. Cold Spring Harbor Laboratory:2020.05.22.102046 Available at: <https://www.biorxiv.org/content/10.1101/2020.05.22.102046v2> [Accessed March 16, 2021].
- Bajada CJ, Haroon HA, Azadbakht H, Parker GJM, Lambon Ralph MA, Cloutman LL (2017) The tract terminations in the temporal lobe: Their location and associated functions. *Cortex* 97:277–290.
- Bajada CJ, Lambon Ralph MA, Cloutman LL (2015) Transport for language south of the Sylvian fissure: The routes and history of the main tracts and stations in the ventral language network. *Cortex* 69:141–151.
- Barbas H, Pandya DN (1984) Topography of commissural fibers of the prefrontal cortex in the rhesus monkey. *Exp Brain Res* 55:187–191.
- Barr MS, Corballis MC (2002) The role of the anterior commissure in callosal agenesis. *Neuropsychology* 16:459–471.
- Basser PJ, Pajevic S, Pierpaoli C, Duda J, Aldroubi A (2000) In vivo fiber tractography using DT-MRI data. *Magn Reson Med* 44:625–632.
- Basser PJ, Pierpaoli C (1996) Microstructural and physiological features of tissues elucidated by quantitative-diffusion-tensor MRI. *J Magn Reson B* 111:209–219.
- Basser PJ, Pierpaoli C (1998) A simplified method to measure the diffusion tensor from seven MR images. *Magn Reson Med* 39:928–934.
- Baynes K, Eliassen JC, Lutsep HL, Gazzaniga MS (1998) Modular organization of cognitive systems masked by interhemispheric integration. *Science* 280:902–905.
- Beevor CE, Ferrier D (1891) VIII. On the course of the fibres of the cingulum and the posterior parts of the corpus callosum and of the fornix in the Marmoset monkey. *Proc R Soc Lond* 48:271–273.
- Beevor CE, Horsley VAH (1890) III. An experimental investigation into the arrangement of the excitable fibres of the internal capsule of the bonnet monkey (*macacus sinicus*). *Philosophical Transactions of the Royal Society of London (B)* 181:49–88.
- Behrens TEJ, Berg HJ, Jbabdi S, Rushworth MFS, Woolrich MW (2007) Probabilistic diffusion tractography with multiple fibre orientations: What can we gain? *Neuroimage* 34:144–155.
- Benson DF, Segarra J, Albert ML (1974) Visual agnosia-prosopagnosia. A clinicopathologic correlation. *Arch Neurol* 30:307–310.
- Berke JJ (1960) The claustrum, the external capsule and the extreme capsule of *Macaca mulatta*. *J Comp Neurol* 115:297–331.
- Bernal B, Altman N (2010) The connectivity of the superior longitudinal fasciculus: a tractography DTI study. *Magn Reson Imaging* 28:217–225.

- Bernal B, Ardila A (2009) The role of the arcuate fasciculus in conduction aphasia. *Brain* 132:2309–2316.
- Brennan P, Standring S, Wiseman S (2019) *Gray's Surgical Anatomy*. Elsevier.
- Bryant KL, Li L, Eichert N, Mars RB (2020) A comprehensive atlas of white matter tracts in the chimpanzee. *bioRxiv:2020.01.24.918516* Available at: <https://www.biorxiv.org/content/10.1101/2020.01.24.918516v2> [Accessed April 13, 2021].
- Bugain M, Dimech Y, Torzhenskaya N, de Schotten MT, Caspers S, Muscat R, Bajada CJ (2020) Occipital Intralobar fasciculi and a novel description of three forgotten tracts. *bioRxiv:2020.07.07.191767* Available at: <https://www.biorxiv.org/content/10.1101/2020.07.07.191767v1> [Accessed March 30, 2021].
- Bullmore E, Sporns O (2009) Complex brain networks: graph theoretical analysis of structural and functional systems. *Nat Rev Neurosci* 10:186–198.
- Bullock D, Takemura H, Caiafa CF, Kitchell L, McPherson B, Caron B, Pestilli F (2019) Associative white matter connecting the dorsal and ventral posterior human cortex. *Brain Struct Funct* 224:2631–2660.
- Caiafa CF, Pestilli F (2017) Multidimensional encoding of brain connectomes. *Sci Rep* 7:11491.
- Catani M (2007) From hodology to function. *Brain* 130:602–605.
- Catani M, Ffytche DH (2005) The rises and falls of disconnection syndromes. *Brain* 128:2224–2239.
- Catani M, Howard RJ, Pajevic S, Jones DK (2002) Virtual in vivo interactive dissection of white matter fasciculi in the human brain. *Neuroimage* 17:77–94.
- Catani M, Jones DK, Donato R, Ffytche DH (2003) Occipito-temporal connections in the human brain. *Brain* 126:2093–2107.
- Catani M, Jones DK, Ffytche DH (2005) Perisylvian language networks of the human brain. *Ann Neurol* 57:8–16.
- Catani M, Mesulam M (2008a) What is a disconnection syndrome? *Cortex* 44:911–913 Available at: <http://dx.doi.org/10.1016/j.cortex.2008.05.001>.
- Catani M, Mesulam M (2008b) The arcuate fasciculus and the disconnection theme in language and aphasia: history and current state. *Cortex* 44:953–961.
- Catani M, Thiebaut de Schotten M (2008) A diffusion tensor imaging tractography atlas for virtual in vivo dissections. *Cortex* 44:1105–1132.
- Cavada C, Goldman-Rakic PS (1991) Topographic segregation of corticostriatal projections from posterior parietal subdivisions in the macaque monkey. *Neuroscience* 42:683–696.
- Chang X, Shen H, Wang L, Liu Z, Xin W, Hu D, Miao D (2014) Altered default mode and fronto-parietal network subsystems in patients with schizophrenia and their unaffected siblings. *Brain Res* 1562:87–99.
- Chaturvedi A, Foutz TJ, McIntyre CC (2012) Current steering to activate targeted neural pathways during deep brain stimulation of the subthalamic region. *Brain Stimul* 5:369–377.
- Choi S-H, Jeong G, Kim Y-B, Cho Z-H (2020) Proposal for human visual pathway in the extrastriate cortex by fiber tracking method using diffusion-weighted MRI. *Neuroimage* 220:117145.

- Christmas D, Eljamel MS, Butler S, Hazari H, MacVicar R, Steele JD, Livingstone A, Matthews K (2011) Long term outcome of thermal anterior capsulotomy for chronic, treatment refractory depression. *J Neurol Neurosurg Psychiatry* 82:594–600.
- Clark KA, Nuechterlein KH, Asarnow RF, Hamilton LS, Phillips OR, Hageman NS, Woods RP, Alger JR, Toga AW, Narr KL (2011) Mean diffusivity and fractional anisotropy as indicators of disease and genetic liability to schizophrenia. *J Psychiatr Res* 45:980–988.
- Coenen VA, Honey CR, Hurwitz T, Rahman AA, McMaster J, Bürgel U, Mädler B (2009) Medial forebrain bundle stimulation as a pathophysiological mechanism for hypomania in subthalamic nucleus deep brain stimulation for Parkinson's disease. *Neurosurgery* 64:1106–1114; discussion 1114–1115.
- Coizet V, Heilbronner SR, Carcenac C, Mailly P, Lehman JF, Savasta M, David O, Deniau J-M, Groenewegen HJ, Haber SN (2017) Organization of the Anterior Limb of the Internal Capsule in the Rat. *J Neurosci* 37:2539–2554.
- Concha L, Gross DW, Beaulieu C (2005) Diffusion tensor tractography of the limbic system. *AJNR Am J Neuroradiol* 26:2267–2274.
- Conner AK, Briggs RG, Sali G, Rahimi M, Baker CM, Burks JD, Glenn CA, Battiste JD, Sughrue ME (2018) A Connectomic Atlas of the Human Cerebrum-Chapter 13: Tractographic Description of the Inferior Fronto-Occipital Fasciculus. *Oper Neurosurg (Hagerstown)* 15:S436–S443.
- Cushnie AK, El-Nahal HG, Bohlen MO, May PJ, Basso MA, Grimaldi P, Wang MZ, de Velasco Ezequiel MF, Sommer MA, Heilbronner SR (2020) Using rAAV2-retro in rhesus macaques: Promise and caveats for circuit manipulation. *J Neurosci Methods* 345:108859.
- Daducci A, Canales-Rodríguez EJ, Zhang H, Dyrby TB, Alexander DC, Thiran J-P (2015) Accelerated Microstructure Imaging via Convex Optimization (AMICO) from diffusion MRI data. *Neuroimage* 105:32–44.
- Damasio AR, Damasio H, Rizzo M, Varney N, Gersh F (1982) Aphasia with nonhemorrhagic lesions in the basal ganglia and internal capsule. *Arch Neurol* 39:15–24.
- Davenport J, Bore M, Campbell J (2010) Changes in personality in pre- and post-dialectical behaviour therapy borderline personality disorder groups: A question of self-control. *Aust Psychol* 45:59–66.
- Davis LE (1921) AN ANATOMIC STUDY OF THE INFERIOR LONGITUDINAL FASCICULUS. *Arch Neuropsych* 5:370–381.
- De Benedictis A, Duffau H (2011) Brain homotopy: from esoteric concept to practical surgical applications. *Neurosurgery* 68:1709–1723; discussion 1723.
- De Benedictis A, Duffau H, Paradiso B, Grandi E, Balbi S, Granieri E, Colarusso E, Chioffi F, Marras CE, Sarubbo S (2014) Anatomico-functional study of the temporo-parieto-occipital region: dissection, tractographic and brain mapping evidence from a neurosurgical perspective. *J Anat* 225:132–151.
- De Benedictis A, Petit L, Descoteaux M, Marras CE, Barbareschi M, Corsini F, Dallabona M, Chioffi F, Sarubbo S (2016) New insights in the homotopic and heterotopic connectivity of the frontal portion of the human corpus callosum revealed by microdissection and diffusion tractography. *Hum Brain Mapp* 37:4718–4735.
- Decramer T, Swinnen S, van Loon J, Janssen P, Theys T (2018) White matter tract anatomy in the rhesus

- monkey: a fiber dissection study. *Brain Struct Funct* 223:3681–3688.
- Dehaene S, Pegado F, Braga LW, Ventura P, Nunes Filho G, Jobert A, Dehaene-Lambertz G, Kolinsky R, Morais J, Cohen L (2010) How learning to read changes the cortical networks for vision and language. *Science* 330:1359–1364.
- Dejerine J, Dejerine-Klumpke A (1895) *Anatomie des centres nerveux*. Rueff.
- de Lacoste MC, Kirkpatrick JB, Ross ED (1985) Topography of the human corpus callosum. *J Neuropathol Exp Neurol* 44:578–591.
- Delay J, Brion S (1969) *Le syndrome de Korsakoff*. Masson.
- Descoteaux M, Deriche R, Knösche TR, Anwander A (2009) Deterministic and probabilistic tractography based on complex fibre orientation distributions. *IEEE Trans Med Imaging* 28:269–286.
- De Witt Hamer PC, Moritz-Gasser S, Gatignol P, Duffau H (2011) Is the human left middle longitudinal fascicle essential for language? A brain electrostimulation study. *Hum Brain Mapp* 32:962–973.
- Dick AS, Tremblay P (2012) Beyond the arcuate fasciculus: consensus and controversy in the connectional anatomy of language. *Brain* 135:3529–3550.
- Douet V, Chang L (2014) Fornix as an imaging marker for episodic memory deficits in healthy aging and in various neurological disorders. *Front Aging Neurosci* 6:343.
- Ebeling U, Reulen HJ (1988) Neurosurgical topography of the optic radiation in the temporal lobe. *Acta Neurochir* 92:29–36.
- Ebeling U, von Cramon D (1992) Topography of the uncinate fascicle and adjacent temporal fiber tracts. *Acta Neurochir* 115:143–148.
- Edlow BL, Mareyam A, Horn A, Polimeni JR, Witzel T, Dylan Tisdall M, Augustinack J, Stockmann JP, Diamond BR, Stevens A, Tirrell LS, Folkerth RD, Wald LL, Fischl B, van der Kouwe A (2019) 7 Tesla MRI of the ex vivo human brain at 100 micron resolution. Available at: <http://dx.doi.org/10.1101/649822>.
- Epelbaum S, Pinel P, Gaillard R, Delmaire C, Perrin M, Dupont S, Dehaene S, Cohen L (2008) Pure alexia as a disconnection syndrome: new diffusion imaging evidence for an old concept. *Cortex* 44:962–974.
- Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex* 1:1–47.
- Felten DL, Sladek JR Jr (1983) Monoamine distribution in primate brain V. Monoaminergic nuclei: anatomy, pathways and local organization. *Brain Res Bull* 10:171–284.
- Feng L, Jeon T, Yu Q, Ouyang M, Peng Q, Mishra V, Pletikos M, Sestan N, Miller MI, Mori S, Hsiao S, Liu S, Huang H (2017) Population-averaged macaque brain atlas with high-resolution ex vivo DTI integrated into in vivo space. *Brain Struct Funct* 222:4131–4147.
- Fields RD, Douglas Fields R (2008) White matter in learning, cognition and psychiatric disorders. *Trends in Neurosciences* 31:361–370 Available at: <http://dx.doi.org/10.1016/j.tins.2008.04.001>.
- Filley CM, Fields RD (2016) White matter and cognition: making the connection. *J Neurophysiol* 116:2093–2104.

- Fink RP, Heimer L (1967) Two methods for selective silver impregnation of degenerating axons and their synaptic endings in the central nervous system. *Brain Research* 4:369–374 Available at: [http://dx.doi.org/10.1016/0006-8993\(67\)90166-7](http://dx.doi.org/10.1016/0006-8993(67)90166-7).
- Flaherty AW, Williams ZM, Amirnovin R, Kasper E, Rauch SL, Cosgrove GR, Eskandar EN (2005) Deep brain stimulation of the anterior internal capsule for the treatment of Tourette syndrome: technical case report. *Neurosurgery* 57:E403; discussion E403.
- Folloni D, Sallet J, Khrapitchev AA, Sibson N, Verhagen L, Mars RB (2019) Dichotomous organization of amygdala/temporal-prefrontal bundles in both humans and monkeys. *Elife* 8 Available at: <http://dx.doi.org/10.7554/eLife.47175>.
- Foong J, Maier M, Clark CA, Barker GJ, Miller DH, Ron MA (2000) Neuropathological abnormalities of the corpus callosum in schizophrenia: a diffusion tensor imaging study. *J Neurol Neurosurg Psychiatry* 68:242–244.
- Forel A (1881) Fall von Mangel des Balkens in einem Idiotenhirn. *Tageblatt d. 54. Versammlung Deutscher Naturforscher und Aerzte, Salzburg*. *Tageblatt* 54:186.
- Forkel SJ, Thiebaut de Schotten M, Kawadler JM, Dell'Acqua F, Danek A, Catani M (2014) The anatomy of fronto-occipital connections from early blunt dissections to contemporary tractography. *Cortex* 56:73–84.
- Frank LR (2002) Characterization of anisotropy in high angular resolution diffusion-weighted MRI. *Magn Reson Med* 47:1083–1099.
- Frey S, Campbell JSW, Pike GB, Petrides M (2008) Dissociating the human language pathways with high angular resolution diffusion fiber tractography. *J Neurosci* 28:11435–11444.
- Gaffan EA, Gaffan D, Hodges JR (1991) Amnesia following damage to the left fornix and to other sites. A comparative study. *Brain* 114 (Pt 3):1297–1313.
- Gaillard R, Naccache L, Pinel P, Clémenceau S, Volle E, Hasboun D, Dupont S, Baulac M, Dehaene S, Adam C, Cohen L (2006) Direct intracranial, fMRI, and lesion evidence for the causal role of left inferotemporal cortex in reading. *Neuron* 50:191–204.
- Garver DL, Sladek JR (1976) Monoamine distribution in primate brain. II. Brain stem catecholaminergic pathways in *Macaca speciosa* (arctoides). *Brain Res* 103:176–182.
- Gazzaniga MS (2005) Forty-five years of split-brain research and still going strong. *Nat Rev Neurosci* 6:653–659.
- Gerbella M, Belmalih A, Borra E, Rozzi S, Luppino G (2010) Cortical connections of the macaque caudal ventrolateral prefrontal areas 45A and 45B. *Cereb Cortex* 20:141–168.
- Geschwind N (1965) Disconnexion syndromes in animals and man. II. *Brain* 88:585–644.
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15:20–25.
- Gray DT, Umapathy L, Burke SN, Trouard TP, Barnes CA (2018) Tract-Specific White Matter Correlates of Age-Related Reward Devaluation Deficits in Macaque Monkeys. *J Neuroimaging Psychiatry Neurol* 3:13–26.

- Greenberg BD et al. (2010) Deep brain stimulation of the ventral internal capsule/ventral striatum for obsessive-compulsive disorder: worldwide experience. *Mol Psychiatry* 15:64–79.
- Grier MD, Zimmermann J, Heilbronner SR (2020) Estimating Brain Connectivity With Diffusion-Weighted Magnetic Resonance Imaging: Promise and Peril. *Biol Psychiatry Cogn Neurosci Neuroimaging* 5:846–854.
- Haber SN, Yendiki A, Jbabdi S (2020) Four Deep Brain Stimulation Targets for Obsessive-Compulsive Disorder: Are They Different? *Biol Psychiatry* Available at: <http://dx.doi.org/10.1016/j.biopsych.2020.06.031>.
- Hamm AO, Weike AI (2005) The neuropsychology of fear learning and fear regulation. *Int J Psychophysiol* 57:5–14.
- Hanekamp S, Ćurčić-Blake B, Caron B, McPherson B, Timmer A, Prins D, Boucard CC, Yoshida M, Ida M, Hunt D, Jansonius NM, Pestilli F, Cornelissen FW (2021) White matter alterations in glaucoma and monocular blindness differ outside the visual system. *Sci Rep* 11:6866.
- Hau J, Sarubbo S, Houde JC, Corsini F, Girard G, Deledalle C, Crivello F, Zago L, Mellet E, Jobard G, Joliot M, Mazoyer B, Tzourio-Mazoyer N, Descoteaux M, Petit L (2017) Revisiting the human uncinate fasciculus, its subcomponents and asymmetries with stem-based tractography and microdissection validation. *Brain Struct Funct* 222:1645–1662.
- Hecht EE, Gutman DA, Bradley BA, Preuss TM, Stout D (2015) Virtual dissection and comparative connectivity of the superior longitudinal fasciculus in chimpanzees and humans. *Neuroimage* 108:124–137.
- Heilbronner SR, Chafee MV (2019) Learning How Neurons Fail Inside of Networks: Nonhuman Primates Provide Critical Data for Psychiatry. *Neuron* 102:21–26.
- Heilbronner SR, Haber SN (2014) Frontal cortical and subcortical projections provide a basis for segmenting the cingulum bundle: implications for neuroimaging and psychiatric disorders. *J Neurosci* 34:10041–10054.
- Heilbronner SR, Safadi Z, Haber SN (2016) Neurocircuits commonly involved in psychiatric disorders and their stimulation and lesion therapies. *Neuromodulation in Psychiatry*:27–48 Available at: <http://dx.doi.org/10.1002/9781118801086.ch3>.
- Heimer L (1970) Bridging the Gap between Light and Electron Microscopy in the Experimental Tracing of Fiber Connections. *Contemporary Research Methods in Neuroanatomy*:162–172 Available at: http://dx.doi.org/10.1007/978-3-642-85986-1_8.
- Herbet G, Zemmoura I, Duffau H (2018) Functional Anatomy of the Inferior Longitudinal Fasciculus: From Historical Reports to Current Hypotheses. *Front Neuroanat* 12:77.
- Herculano-Houzel S (2014) The glia/neuron ratio: how it varies uniformly across brain structures and species and what that means for brain physiology and evolution. *Glia* 62:1377–1391.
- Herculano-Houzel S, Mota B, Wong P, Kaas JH (2010) Connectivity-driven white matter scaling and folding in primate cerebral cortex. *Proc Natl Acad Sci U S A* 107:19008–19013.
- Hofer S, Frahm J (2006) Topography of the human corpus callosum revisited--comprehensive fiber tractography using diffusion tensor magnetic resonance imaging. *Neuroimage* 32:989–994.

- Hofer S, Merboldt K-D, Tammer R, Frahm J (2008) Rhesus monkey and human share a similar topography of the corpus callosum as revealed by diffusion tensor MRI in vivo. *Cereb Cortex* 18:1079–1084.
- Hosomi A, Nagakane Y, Yamada K, Kuriyama N, Mizuno T, Nishimura T, Nakagawa M (2009) Assessment of arcuate fasciculus with diffusion-tensor tractography may predict the prognosis of aphasia in patients with left middle cerebral artery infarcts. *Neuroradiology* 51:549–555.
- Huang H, Zhang J, Jiang H, Wakana S, Poetscher L, Miller MI, van Zijl PCM, Hillis AE, Wytik R, Mori S (2005) DTI tractography based parcellation of white matter: application to the mid-sagittal morphology of corpus callosum. *Neuroimage* 26:195–205.
- Hurwitz TA, Honey CR, Allen J, Gosselin C, Hewko R, Martzke J, Bogod N, Taylor P (2012) Bilateral anterior capsulotomy for intractable depression. *J Neuropsychiatry Clin Neurosci* 24:176–182.
- Jang SH, Kim SH, Kwon HG (2015) The Safe Area in the Parieto-Occipital Lobe in the Human Brain: Diffusion Tensor Tractography. *World Neurosurg* 83:982–986.
- Jbabdi S, Lehman JF, Haber SN, Behrens TE (2013) Human and monkey ventral prefrontal fibers use the same organizational principles to reach their targets: tracing versus tractography. *J Neurosci* 33:3190–3201.
- Jbabdi S, Sotiropoulos SN, Haber SN, Van Essen DC, Behrens TE (2015) Measuring macroscopic brain connections in vivo. *Nat Neurosci* 18:1546–1555.
- Jelescu IO, Budde MD (2017) Design and validation of diffusion MRI models of white matter. *Front Phys* 28 Available at: <http://dx.doi.org/10.3389/fphy.2017.00061>.
- Jeurissen B, Leemans A, Tournier J-D, Jones DK, Sijbers J (2013) Investigating the prevalence of complex fiber configurations in white matter tissue with diffusion magnetic resonance imaging. *Hum Brain Mapp* 34:2747–2766.
- Jiang H, van Zijl PCM, Kim J, Pearlson GD, Mori S (2006) DtiStudio: resource program for diffusion tensor computation and fiber bundle tracking. *Comput Methods Programs Biomed* 81:106–116.
- Jitsuishi T, Yamaguchi A (2020) Identification of a distinct association fiber tract “IPS-FG” to connect the intraparietal sulcus areas and fusiform gyrus by white matter dissection and tractography. *Sci Rep* 10:15475.
- Jones DK, Christiansen KF, Chapman RJ, Aggleton JP (2013) Distinct subdivisions of the cingulum bundle revealed by diffusion MRI fibre tracking: implications for neuropsychological investigations. *Neuropsychologia* 51:67–78.
- Jones EG, Powell TP (1969) Connexions of the somatic sensory cortex of the rhesus monkey. II. Contralateral cortical connexions. *Brain* 92:717–730.
- Jones R, Grisot G, Augustinack J, Magnain C, Boas DA, Fischl B, Wang H, Yendiki A (2020) Insight into the fundamental trade-offs of diffusion MRI from polarization-sensitive optical coherence tomography in ex vivo human brain. *Neuroimage* 214:116704.
- Jouandet ML, Gazzaniga MS (1979) Cortical field of origin of the anterior commissure of the rhesus monkey. *Exp Neurol* 66:381–397.
- Kalyvas A, Koutsarnakis C, Komaitis S, Karavasilis E, Christidi F, Skandalakis GP, Liouta E, Papakonstantinou

- O, Kelekis N, Duffau H, Stranjalis G (2020) Mapping the human middle longitudinal fasciculus through a focused anatomo-imaging study: shifting the paradigm of its segmentation and connectivity pattern. *Brain Struct Funct* 225:85–119.
- Kamali A, Flanders AE, Brody J, Hunter JV, Hasan KM (2014a) Tracing superior longitudinal fasciculus connectivity in the human brain using high resolution diffusion tensor tractography. *Brain Struct Funct* 219:269–281.
- Kamali A, Sair HI, Blitz AM, Riascos RF, Mirbagheri S, Keser Z, Hasan KM (2016) Revealing the ventral amygdalofugal pathway of the human limbic system using high spatial resolution diffusion tensor tractography. *Brain Struct Funct* 221:3561–3569.
- Kamali A, Sair HI, Radmanesh A, Hasan KM (2014b) Decoding the superior parietal lobule connections of the superior longitudinal fasciculus/arcuate fasciculus in the human brain. *Neuroscience* 277:577–583.
- Karlsgodt KH, van Erp TGM, Poldrack RA, Bearden CE, Nuechterlein KH, Cannon TD (2008) Diffusion tensor imaging of the superior longitudinal fasciculus and working memory in recent-onset schizophrenia. *Biol Psychiatry* 63:512–518.
- Kier EL, Staib LH, Davis LM, Bronen RA (2004) MR imaging of the temporal stem: anatomic dissection tractography of the uncinate fasciculus, inferior occipitofrontal fasciculus, and Meyer's loop of the optic radiation. *AJNR Am J Neuroradiol* 25:677–691.
- Klingberg T, Hedehus M, Temple E, Salz T, Gabrieli JD, Moseley ME, Poldrack RA (2000) Microstructure of temporo-parietal white matter as a basis for reading ability: evidence from diffusion tensor magnetic resonance imaging. *Neuron* 25:493–500.
- Knipe HC, Bell DJ, Gaillard F (2021) Letter to the editor: the origin of “Baum's loop.” *Surg Radiol Anat* 43:307–307.
- Koutsarnakis C, Liakos F, Kalyvas AV, Sakas DE, Stranjalis G (2015) A Laboratory Manual for Stepwise Cerebral White Matter Fiber Dissection. *World Neurosurg* 84:483–493.
- Lanciego JL, Wouterlood FG (2020) Neuroanatomical tract-tracing techniques that did go viral. *Brain Struct Funct* 225:1193–1224.
- Larsen L, Griffin LD, Grässel D, Witte OW, Axer H (2007) Polarized light imaging of white matter architecture. *Microsc Res Tech* 70:851–863.
- Lazar M, Weinstein DM, Tsuruda JS, Hasan KM, Arfanakis K, Meyerand ME, Badie B, Rowley HA, Haughton V, Field A, Alexander AL (2003) White matter tractography using diffusion tensor deflection. *Hum Brain Mapp* 18:306–321.
- Le Bihan D, Lima M (2015) Diffusion Magnetic Resonance Imaging: What Water Tells Us about Biological Tissues. *PLoS Biol* 13:e1002203.
- Lehman JF, Greenberg BD, McIntyre CC, Rasmussen SA, Haber SN (2011) Rules ventral prefrontal cortical axons use to reach their targets: implications for diffusion tensor imaging tractography and deep brain stimulation for psychiatric illness. *J Neurosci* 31:10392–10402.
- Levine B, Black SE, Cabeza R, Sinden M, McIntosh AR, Toth JP, Tulving E, Stuss DT (1998) Episodic memory and the self in a case of isolated retrograde amnesia. *Brain* 121 (Pt 10):1951–1973.

- Lin Y-H, Young IM, Conner AK, Glenn CA, Chakraborty AR, Nix CE, Bai MY, Dhanaraj V, Fonseka RD, Hormovas J, Tanglay O, Briggs RG, Sughrue ME (2020) Anatomy and White Matter Connections of the Inferior Temporal Gyrus. *World Neurosurg* 143:e656–e666.
- Liu X, Kinoshita M, Shinohara H, Hori O, Ozaki N, Nakada M (2020) Does the superior fronto-occipital fascicle exist in the human brain? Fiber dissection and brain functional mapping in 90 patients with gliomas. *Neuroimage Clin* 25:102192.
- Locke S, Kruper DC, Yakovlev PI (1964) LIMBIC NUCLEI OF THALAMUS AND CONNECTIONS OF LIMBIC CORTEX. 7. TRANSCALLOSAL CONNECTIONS OF CEREBRAL HEMISPHERE WITH STRIATUM IN MONKEY AND MAN. *Arch Neurol* 11:571–582.
- Luck SJ, Hillyard SA, Mangun GR, Gazzaniga MS (1989) Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature* 342:543–545.
- Madhavan KM, McQueeney T, Howe SR, Shear P, Szaflarski J (2014) Superior longitudinal fasciculus and language functioning in healthy aging. *Brain Res* 1562:11–22.
- Maier-Hein KH et al. (2019) Author Correction: The challenge of mapping the human connectome based on diffusion tractography. *Nat Commun* 10:5059.
- Makris N, Kennedy DN, McInerney S, Sorensen AG, Wang R, Caviness VS Jr, Pandya DN (2005) Segmentation of subcomponents within the superior longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Cereb Cortex* 15:854–869.
- Makris N, Pandya DN (2009) The extreme capsule in humans and rethinking of the language circuitry. *Brain Struct Funct* 213:343–358.
- Makris N, Papadimitriou GM, Kaiser JR, Sorg S, Kennedy DN, Pandya DN (2009) Delineation of the middle longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Cereb Cortex* 19:777–785.
- Makris N, Papadimitriou GM, Sorg S, Kennedy DN, Caviness VS, Pandya DN (2007) The occipitofrontal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Neuroimage* 37:1100–1111.
- Makris N, Preti MG, Wassermann D, Rath Y, Papadimitriou GM, Yergatian C, Dickerson BC, Shenton ME, Kubicki M (2013) Human middle longitudinal fascicle: segregation and behavioral-clinical implications of two distinct fiber connections linking temporal pole and superior temporal gyrus with the angular gyrus or superior parietal lobule using multi-tensor tractography. *Brain Imaging Behav* 7:335–352.
- Makris N, Zhu A, Papadimitriou GM, Mouradian P, Ng I, Scaccianoce E, Baselli G, Baglio F, Shenton ME, Rath Y, Dickerson B, Yeterian E, Kubicki M (2017) Mapping temporo-parietal and temporo-occipital cortico-cortical connections of the human middle longitudinal fascicle in subject-specific, probabilistic, and stereotaxic Talairach spaces. *Brain Imaging Behav* 11:1258–1277.
- Maldonado IL, de Champfleury NM, Velut S, Destrieux C, Zemmoura I, Duffau H (2013) Evidence of a middle longitudinal fasciculus in the human brain from fiber dissection. *J Anat* 223:38–45.
- Maldonado IL, Moritz-Gasser S, Duffau H (2011) Does the left superior longitudinal fascicle subserve language semantics? A brain electrostimulation study. *Brain Struct Funct* 216:263–274.
- Mandonnet E, Sarubbo S, Petit L (2018) The Nomenclature of Human White Matter Association Pathways: Proposal for a Systematic Taxonomic Anatomical Classification. *Front Neuroanat* 12:94.

- Mandonnet E, Sarubbo S, Petit L (2019) Response: Commentary: The Nomenclature of Human White Matter Association Pathways: Proposal for a Systematic Taxonomic Anatomical Classification. *Front Neuroanat* 13:91.
- Marchina S, Zhu LL, Norton A, Zipse L, Wan CY, Schlaug G (2011) Impairment of speech production predicted by lesion load of the left arcuate fasciculus. *Stroke* 42:2251–2256.
- Markov NT, Vezoli J, Chameau P, Falchier A, Quilodran R, Huissoud C, Lamy C, Misery P, Giroud P, Ullman S, Barone P, Dehay C, Knoblauch K, Kennedy H (2014) Anatomy of hierarchy: feedforward and feedback pathways in macaque visual cortex. *J Comp Neurol* 522:225–259.
- Mars RB, Foxley S, Verhagen L, Jbabdi S, Sallet J, Noonan MP, Neubert F-X, Andersson JL, Croxson PL, Dunbar RIM, Khrapitchev AA, Sibson NR, Miller KL, Rushworth MFS (2016) The extreme capsule fiber complex in humans and macaque monkeys: a comparative diffusion MRI tractography study. *Brain Struct Funct* 221:4059–4071.
- Martino J, da Silva-Freitas R, Caballero H, Marco de Lucas E, García-Porrero JA, Vázquez-Barquero A (2013a) Fiber dissection and diffusion tensor imaging tractography study of the temporoparietal fiber intersection area. *Neurosurgery* 72:87–97; discussion 97–98.
- Martino J, De Lucas EM (2014) Subcortical anatomy of the lateral association fascicles of the brain: A review. *Clin Anat* 27:563–569.
- Martino J, De Witt Hamer PC, Berger MS, Lawton MT, Arnold CM, de Lucas EM, Duffau H (2013b) Analysis of the subcomponents and cortical terminations of the perisylvian superior longitudinal fasciculus: a fiber dissection and DTI tractography study. *Brain Struct Funct* 218:105–121.
- Mayberg HS, Liotti M, Brannan SK, McGinnis S, Mahurin RK, Jerabek PA, Silva JA, Tekell JL, Martin CC, Lancaster JL, Fox PT (1999) Reciprocal limbic-cortical function and negative mood: converging PET findings in depression and normal sadness. *Am J Psychiatry* 156:675–682.
- Mayberg HS, Lozano AM, Voon V, McNeely HE, Seminowicz D, Hamani C, Schwalb JM, Kennedy SH (2005) Deep brain stimulation for treatment-resistant depression. *Neuron* 45:651–660.
- Meichtry JR, Cazzoli D, Chaves S, von Arx S, Pflugshaupt T, Kalla R, Bassetti CL, Gutbrod K, Müri RM (2018) Pure optic ataxia and visual hemiagnosia - extending the dual visual hypothesis. *J Neuropsychol* 12:271–290.
- Menjot de Champfleury N, Lima Maldonado I, Moritz-Gasser S, Machi P, Le Bars E, Bonafé A, Duffau H (2013) Middle longitudinal fasciculus delineation within language pathways: a diffusion tensor imaging study in human. *Eur J Radiol* 82:151–157.
- Meola A, Comert A, Yeh F-C, Stefanescu L, Fernandez-Miranda JC (2015) The controversial existence of the human superior fronto-occipital fasciculus: Connectome-based tractographic study with microdissection validation: The Superior Fronto-Occipital Fasciculus. *Hum Brain Mapp* 36:4964–4971.
- Milton CK, Palejwala AH, O'Connor KP, McCoy TM, Conner AK, Glenn CA (2020) Diffusion Tensor Imaging Tractography for Fornix Identification in Intraventricular Tumor Surgery: A Case Series. *Neurosurgery Open* 1 Available at: <https://academic.oup.com/neurosurgeryopen/article/1/3/okaa005/5866286> [Accessed April 20, 2021].
- Mishkin M, Ungerleider LG (1982) Contribution of striate inputs to the visuospatial functions of parieto-

- preoccipital cortex in monkeys. *Behav Brain Res* 6:57–77.
- Moore RY, Bloom FE (1978) Central Catecholamine Neuron Systems: Anatomy and Physiology of the Dopamine Systems. *Annu Rev Neurosci* 1:129–169.
- Morecraft RJ, Herrick JL, Stilwell-Morecraft KS, Louie JL, Schroeder CM, Ottenbacher JG, Schoolfield MW (2002) Localization of arm representation in the corona radiata and internal capsule in the non-human primate. *Brain* 125:176–198 Available at: <http://dx.doi.org/10.1093/brain/awf011>.
- Mori S, Crain BJ, Chacko VP, van Zijl PC (1999) Three-dimensional tracking of axonal projections in the brain by magnetic resonance imaging. *Ann Neurol* 45:265–269.
- Mori S, Kageyama Y, Hou Z, Aggarwal M, Patel J, Brown T, Miller MI, Wu D, Troncoso JC (2017) Elucidation of White Matter Tracts of the Human Amygdala by Detailed Comparison between High-Resolution Postmortem Magnetic Resonance Imaging and Histology. *Front Neuroanat* 11:16.
- Mufson EJ, Pandya DN (1984) Some observations on the course and composition of the cingulum bundle in the rhesus monkey. *J Comp Neurol* 225:31–43.
- Nakajima R, Kinoshita M, Shinohara H, Nakada M (2020) The superior longitudinal fascicle: reconsidering the fronto-parietal neural network based on anatomy and function. *Brain Imaging Behav* 14:2817–2830.
- Nakamae T, Narumoto J, Sakai Y, Nishida S, Yamada K, Nishimura T, Fukui K (2011) Diffusion tensor imaging and tract-based spatial statistics in obsessive-compulsive disorder. *J Psychiatr Res* 45:687–690.
- Nauta WJ (1961) Fibre degeneration following lesions of the amygdaloid complex in the monkey. *J Anat* 95:515–531.
- Nauta WJ (1993) Some early travails of tracing axonal pathways in the brain. *The Journal of Neuroscience* 13:1337–1345 Available at: <http://dx.doi.org/10.1523/jneurosci.13-04-01337.1993>.
- Nauta WJ, Gygax PA (1954) Silver impregnation of degenerating axons in the central nervous system: a modified technic. *Stain Technol* 29:91–93.
- Nauta WJH, Gygax PA (1951) Silver impregnation of degenerating axon terminals in the central nervous system: (1) Technic. (2) Chemical notes. *Stain Technol* 26:5–11.
- Oades RD, Halliday GM (1987) Ventral tegmental (A10) system: neurobiology. 1. Anatomy and connectivity. *Brain Res* 434:117–165.
- Oechslin MS, Imfeld A, Loenneker T, Meyer M, Jäncke L (2009) The plasticity of the superior longitudinal fasciculus as a function of musical expertise: a diffusion tensor imaging study. *Front Hum Neurosci* 3:76.
- Oestreich LKL, McCarthy-Jones S, Australian Schizophrenia Research Bank, Whitford TJ (2016) Decreased integrity of the fronto-temporal fibers of the left inferior occipito-frontal fasciculus associated with auditory verbal hallucinations in schizophrenia. *Brain Imaging Behav* 10:445–454.
- Ogawa S, Takemura H, Horiguchi H, Terao M, Haji T, Pestilli F, Yeatman JD, Tsuneoka H, Wandell BA, Masuda Y (2014) White matter consequences of retinal receptor and ganglion cell damage. *Invest Ophthalmol Vis Sci* 55:6976–6986.
- Oishi K, Zilles K, Amunts K, Faria A, Jiang H, Li X, Akhter K, Hua K, Woods R, Toga AW, Pike GB, Rosa-Neto P, Evans A, Zhang J, Huang H, Miller MI, van Zijl PCM, Mazziotta J, Mori S (2008) Human brain white

- matter atlas: identification and assignment of common anatomical structures in superficial white matter. *Neuroimage* 43:447–457.
- Olds J, Milner P (1954) Positive reinforcement produced by electrical stimulation of septal area and other regions of rat brain. *J Comp Physiol Psychol* 47:419–427.
- Oliver B, Gascón J, Aparicio A, Ayats E, Rodriguez R, de León JLM, García-Bach M, Soler PA (2003) Bilateral Anterior Capsulotomy for Refractory Obsessive-Compulsive Disorders. *Stereotactic and Functional Neurosurgery* 81:90–95 Available at: <http://dx.doi.org/10.1159/000075110>.
- Padberg J, Cooke DF, Cerkevich CM, Kaas JH, Krubitzer L (2019) Cortical connections of area 2 and posterior parietal area 5 in macaque monkeys. *J Comp Neurol* 527:718–737.
- Panagiotaki E, Schneider T, Siow B, Hall MG, Lythgoe MF, Alexander DC (2012) Compartment models of the diffusion MR signal in brain white matter: a taxonomy and comparison. *Neuroimage* 59:2241–2254.
- Pandya DN, Hallett M, Kmukherjee SK (1969) Intra- and interhemispheric connections of the neocortical auditory system in the rhesus monkey. *Brain Res* 14:49–65.
- Pandya DN, Karol EA, Heilbronn D (1971) The topographical distribution of interhemispheric projections in the corpus callosum of the rhesus monkey. *Brain Res* 32:31–43.
- Panesar SS, Belo JTA, Yeh F-C, Fernandez-Miranda JC (2019) Structure, asymmetry, and connectivity of the human temporo-parietal aslant and vertical occipital fasciculi. *Brain Struct Funct* 224:907–923.
- Panesar SS, Fernandez-Miranda J (2019) Commentary: The Nomenclature of Human White Matter Association Pathways: Proposal for a Systematic Taxonomic Anatomical Classification. *Front Neuroanat* 13:61.
- Panesar SS, Yeh F-C, Deibert CP, Fernandes-Cabral D, Rowthu V, Celtikci P, Celtikci E, Hula WD, Pathak S, Fernández-Miranda JC (2017) A diffusion spectrum imaging-based tractographic study into the anatomical subdivision and cortical connectivity of the ventral external capsule: uncinate and inferior fronto-occipital fascicles. *Neuroradiology* 59:971–987.
- Papez JW (1937) A PROPOSED MECHANISM OF EMOTION. *Arch Neuropsych* 38:725–743.
- Parent M, Wallman M-J, Gagnon D, Parent A (2011) Serotonin innervation of basal ganglia in monkeys and humans. *J Chem Neuroanat* 41:256–265.
- Parker GJM, Stephan KE, Barker GJ, Rowe JB, MacManus DG, Wheeler-Kingshott CAM, Ciccarelli O, Passingham RE, Spinks RL, Lemon RN, Turner R (2002) Initial demonstration of in vivo tracing of axonal projections in the macaque brain and comparison with the human brain using diffusion tensor imaging and fast marching tractography. *Neuroimage* 15:797–809.
- Párraga RG, Ribas GC, Welling LC, Alves RV, de Oliveira E (2012) Microsurgical anatomy of the optic radiation and related fibers in 3-dimensional images. *Neurosurgery* 71:160–171; discussion 171–172.
- Paul LK, Brown WS, Adolphs R, Tyszka JM, Richards LJ, Mukherjee P, Sherr EH (2007) Agenesis of the corpus callosum: genetic, developmental and functional aspects of connectivity. *Nat Rev Neurosci* 8:287–299.
- Pepper J, Zrinzo L, Hariz M (2019) Anterior capsulotomy for obsessive-compulsive disorder: a review of old and new literature. *J Neurosurg*:1–10.

- Perlmutter JS, Mink JW (2006) DEEP BRAIN STIMULATION. *Annual Review of Neuroscience* 29:229–257
Available at: <http://dx.doi.org/10.1146/annurev.neuro.29.051605.112824>.
- Pescatori L, Tropeano MP, Manfreda A, Delfini R, Santoro A (2017) Three-Dimensional Anatomy of the White Matter Fibers of the Temporal Lobe: Surgical Implications. *World Neurosurg* 100:144–158.
- Pestilli F, Yeatman JD, Rokem A, Kay KN, Wandell BA (2014) Evaluation and statistical inference for human connectomes. *Nat Methods* 11:1058–1063.
- Petrides M, Pandya DN (1984) Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *J Comp Neurol* 228:105–116.
- Petrides M, Pandya DN (2006) Efferent association pathways originating in the caudal prefrontal cortex in the macaque monkey. *J Comp Neurol* 498:227–251.
- Pierpaoli C, Jezzard P, Basser PJ, Barnett A, Di Chiro G (1996) Diffusion tensor MR imaging of the human brain. *Radiology* 201:637–648.
- Poletti CE, Creswell G (1977) Fornix system efferent projections in the squirrel monkey: an experimental degeneration study. *J Comp Neurol* 175:101–128.
- Porrino LJ, Crane AM, Goldman-Rakic PS (1981) Direct and indirect pathways from the amygdala to the frontal lobe in rhesus monkeys. *J Comp Neurol* 198:121–136.
- Pribram KH, Lennox MA, Dunsmore RH (1950) Some connections of the orbito-fronto-temporal, limbic and hippocampal areas of *Macaca mulatta*. *J Neurophysiol* 13:127–135.
- Redlich E (1905) Zur vergleichenden Anatomie der Assoziationssysteme des Gehirns der Säugetiere. *Arbeiten aus dem Neurologischen Institute (Institut für Anatomic und Physiologie des Centralnervensystems) an der Wiener Universität* 12:109.
- Reveley C, Seth AK, Pierpaoli C, Silva AC, Yu D, Saunders RC, Leopold DA, Ye FQ (2015) Superficial white matter fiber systems impede detection of long-range cortical connections in diffusion MR tractography. *Proc Natl Acad Sci U S A* 112:E2820–E2828.
- Rheault F et al. (2020) Tractostorm: The what, why, and how of tractography dissection reproducibility. *Hum Brain Mapp* 41:1859–1874.
- Rheault F, Roy M, Cunnane S, Descoteaux M (2018) Bundle-specific fornix reconstruction for dual-tracer PET-tractometry. *bioRxiv*:423459 Available at: <https://www.biorxiv.org/content/10.1101/423459v1> [Accessed April 20, 2021].
- Rilling JK, Glasser MF, Preuss TM, Ma X, Zhao T, Hu X, Behrens TEJ (2008) The evolution of the arcuate fasciculus revealed with comparative DTI. *Nat Neurosci* 11:426–428.
- Risse GL, LeDoux J, Springer SP, Wilson DH, Gazzaniga MS (1978) The anterior commissure in man: functional variation in a multisensory system. *Neuropsychologia* 16:23–31.
- Riva-Posse P, Choi KS, Holtzheimer PE, McIntyre CC, Gross RE, Chaturvedi A, Crowell AL, Garlow SJ, Rajendra JK, Mayberg HS (2014) Defining critical white matter pathways mediating successful subcallosal cingulate deep brain stimulation for treatment-resistant depression. *Biol Psychiatry* 76:963–969.
- Rizio AA, Diaz MT (2016) Language, aging, and cognition: frontal aslant tract and superior longitudinal

- fasciculus contribute toward working memory performance in older adults. *Neuroreport* 27:689–693.
- Rokem A, Takemura H, Bock AS, Scherf KS, Behrmann M, Wandell BA, Fine I, Bridge H, Pestilli F (2017) The visual white matter: The application of diffusion MRI and fiber tractography to vision science. *J Vis* 17:4.
- Rollans C, Cummine J (2018) One tract, two tract, old tract, new tract: A pilot study of the structural and functional differentiation of the inferior fronto-occipital fasciculus. *J Neurolinguistics* 46:122–137.
- Ross ED (1980) Localization of the pyramidal tract in the internal capsule by whole brain dissection. *Neurology* 30:59–64.
- Roumazeilles L, Eichert N, Bryant KL, Folloni D, Sallet J, Vijayakumar S, Foxley S, Tendler BC, Jbabdi S, Reveley C, Verhagen L, Dershowitz LB, Guthrie M, Flach E, Miller KL, Mars RB (2020) Longitudinal connections and the organization of the temporal cortex in macaques, great apes, and humans. *PLoS Biol* 18:e3000810.
- Rushworth MFS, Behrens TEJ, Johansen-Berg H (2006) Connection patterns distinguish 3 regions of human parietal cortex. *Cereb Cortex* 16:1418–1430.
- Safadi Z, Grisot G, Jbabdi S, Behrens TE, Heilbronner SR, McLaughlin NCR, Mandeville J, Versace A, Phillips ML, Lehman JF, Yendiki A, Haber SN (2018) Functional Segmentation of the Anterior Limb of the Internal Capsule: Linking White Matter Abnormalities to Specific Connections. *J Neurosci* 38:2106–2117.
- Sakuma H, Nomura Y, Takeda K, Tagami T, Nakagawa T, Tamagawa Y, Ishii Y, Tsukamoto T (1991) Adult and neonatal human brain: diffusional anisotropy and myelination with diffusion-weighted MR imaging. *Radiology* 180:229–233.
- Sarubbo S, De Benedictis A, Maldonado IL, Basso G, Duffau H (2013) Frontal terminations for the inferior fronto-occipital fascicle: anatomical dissection, DTI study and functional considerations on a multi-component bundle. *Brain Struct Funct* 218:21–37.
- Sarubbo S, De Benedictis A, Milani P, Paradiso B, Barbareschi M, Rozzanigo U, Colarusso E, Tugnoli V, Farneti M, Granieri E, Duffau H, Chioffi F (2015) The course and the anatomo-functional relationships of the optic radiation: a combined study with “post mortem” dissections and “in vivo” direct electrical mapping. *J Anat* 226:47–59.
- Sarubbo S, Petit L, De Benedictis A, Chioffi F, Ptito M, Dyrby TB (2019) Uncovering the inferior fronto-occipital fascicle and its topological organization in non-human primates: the missing connection for language evolution. *Brain Struct Funct* 224:1553–1567.
- Sarwar T, Ramamohanarao K, Zalesky A (2019) Mapping connectomes with diffusion MRI: deterministic or probabilistic tractography? *Magn Reson Med* 81:1368–1384.
- Saunders RC, Aggleton JP (2007) Origin and topography of fibers contributing to the fornix in macaque monkeys. *Hippocampus* 17:396–411.
- Schilling KG et al. (2020a) Tractography dissection variability: what happens when 42 groups dissect 14 white matter bundles on the same dataset? Cold Spring Harbor Laboratory:2020.10.07.321083 Available at: <https://www.biorxiv.org/content/10.1101/2020.10.07.321083v1> [Accessed March 16, 2021].
- Schilling K, Gao Y, Janve V, Stepniewska I, Landman BA, Anderson AW (2018) Confirmation of a gyral bias in diffusion MRI fiber tractography. *Hum Brain Mapp* 39:1449–1466.

- Schilling KG, Petit L, Rheault F, Remedios S, Pierpaoli C, Anderson AW, Landman BA, Descoteaux M (2020b) Brain connections derived from diffusion MRI tractography can be highly anatomically accurate-if we know where white matter pathways start, where they end, and where they do not go. *Brain Struct Funct* 225:2387–2402.
- Schmahmann JD, Pandya DN (2006) Fiber Pathways of the Brain. Available at: <http://dx.doi.org/10.1093/acprof:oso/9780195104233.001.0001>.
- Schmahmann JD, Pandya DN (2007a) The complex history of the fronto-occipital fasciculus. *J Hist Neurosci* 16:362–377.
- Schmahmann JD, Pandya DN (2007b) Cerebral white matter--historical evolution of facts and notions concerning the organization of the fiber pathways of the brain. *J Hist Neurosci* 16:237–267.
- Schmitz D, Muenzing SEA, Schober M, Schubert N, Minnerop M, Lippert T, Amunts K, Axer M (2018) Derivation of Fiber Orientations From Oblique Views Through Human Brain Sections in 3D-Polarized Light Imaging. *Front Neuroanat* 12:75.
- Schotten MT de, de Schotten MT, Dell'Acqua F, Forkel S, Simmons A, Vergani F, Murphy DGM, Catani M (2011) A Lateralized Brain Network for Visuo-Spatial Attention. *Nature Precedings* Available at: <http://dx.doi.org/10.1038/npre.2011.5549.1>.
- Schröder, P. (1901) Das fronto-occipitale Associationsbündel. *Eur Neurol* 9:81–99.
- Seghier ML (2013) The angular gyrus: multiple functions and multiple subdivisions. *Neuroscientist* 19:43–61.
- Seltzer B, Pandya DN (1978) Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. *Brain Res* 149:1–24.
- Seltzer B, Pandya DN (1984) Further observations on parieto-temporal connections in the rhesus monkey. *Exp Brain Res* 55:301–312.
- Seltzer B, Pandya DN (1991) Post-rolandic cortical projections of the superior temporal sulcus in the rhesus monkey. *J Comp Neurol* 312:625–640.
- Seltzer B, Pandya DN (1994) Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer study. *J Comp Neurol* 343:445–463.
- Sheffield JM, Repovs G, Harms MP, Carter CS, Gold JM, MacDonald AW 3rd, Ragland JD, Silverstein SM, Godwin D, Barch DM (2016) Evidence for Accelerated Decline of Functional Brain Network Efficiency in Schizophrenia. *Schizophr Bull* 42:753–761.
- Shen EH, Overly CC, Jones AR (2012) The Allen Human Brain Atlas. *Trends in Neurosciences* 35:711–714 Available at: <http://dx.doi.org/10.1016/j.tins.2012.09.005>.
- Sherbondy AJ, Dougherty RF, Ben-Shachar M, Napel S, Wandell BA (2008) ConTrack: finding the most likely pathways between brain regions using diffusion tractography. *J Vis* 8:15.1–16.
- Shinoura N, Suzuki Y, Tsukada M, Katsuki S, Yamada R, Tabei Y, Saito K, Yagi K (2007) Impairment of inferior longitudinal fasciculus plays a role in visual memory disturbance. *Neurocase* 13:127–130.
- Shi Y, Toga AW (2017) Connectome imaging for mapping human brain pathways. *Molecular Psychiatry* 22:1230–1240 Available at: <http://dx.doi.org/10.1038/mp.2017.92>.

- Silva SM, Andrade JP (2016) Neuroanatomy: The added value of the Klingler method. *Ann Anat* 208:187–193.
- Smith RE, Tournier J-D, Calamante F, Connelly A (2012) Anatomically-constrained tractography: improved diffusion MRI streamlines tractography through effective use of anatomical information. *Neuroimage* 62:1924–1938.
- Smith RE, Tournier J-D, Calamante F, Connelly A (2015) SIFT2: Enabling dense quantitative assessment of brain white matter connectivity using streamlines tractography. *Neuroimage* 119:338–351.
- Smith Y, Hazrati LN, Parent A (1990) Efferent projections of the subthalamic nucleus in the squirrel monkey as studied by the PHA-L anterograde tracing method. *J Comp Neurol* 294:306–323.
- Sotiropoulos SN, Jbabdi S, Xu J, Andersson JL, Moeller S, Auerbach EJ, Glasser MF, Hernandez M, Sapiro G, Jenkinson M, Feinberg DA, Yacoub E, Lenglet C, Van Essen DC, Ugurbil K, Behrens TEJ, WU-Minn HCP Consortium (2013) Advances in diffusion MRI acquisition and processing in the Human Connectome Project. *Neuroimage* 80:125–143.
- Stanton GB, Goldberg ME, Bruce CJ (1988) Frontal eye field efferents in the macaque monkey: I. Subcortical pathways and topography of striatal and thalamic terminal fields. *J Comp Neurol* 271:473–492.
- Steele JD, Christmas D, Eljamel MS, Matthews K (2008) Anterior cingulotomy for major depression: clinical outcome and relationship to lesion characteristics. *Biol Psychiatry* 63:670–677.
- Sullivan EV, Pfefferbaum A (2003) Diffusion tensor imaging in normal aging and neuropsychiatric disorders. *Eur J Radiol* 45:244–255.
- Sullivan EV, Zahr NM, Rohlfing T, Pfefferbaum A (2010) Fiber tracking functionally distinct components of the internal capsule. *Neuropsychologia* 48:4155–4163.
- Sunderland S (1940) THE DISTRIBUTION OF COMMISSURAL FIBRES IN THE CORPUS CALLOSUM IN THE MACAQUE MONKEY. *J Neurol Psychiatry* 3:9–18.
- Takemura H, Caiafa CF, Wandell BA, Pestilli F (2016a) Ensemble Tractography. *PLoS Comput Biol* 12:e1004692.
- Takemura H, Pestilli F, Weiner KS, Keliris GA, Landi SM, Sliwa J, Ye FQ, Barnett MA, Leopold DA, Freiwald WA, Logothetis NK, Wandell BA (2017) Occipital White Matter Tracts in Human and Macaque. *Cereb Cortex* 27:3346–3359.
- Takemura H, Rokem A, Winawer J, Yeatman JD, Wandell BA, Pestilli F (2016b) A Major Human White Matter Pathway Between Dorsal and Ventral Visual Cortex. *Cereb Cortex* 26:2205–2214.
- Thiebaut de Schotten M, Cohen L, Amemiya E, Braga LW, Dehaene S (2012a) Learning to Read Improves the Structure of the Arcuate Fasciculus. *Cereb Cortex* 24:989–995.
- Thiebaut de Schotten M, Dell'Acqua F, Valabregue R, Catani M (2012b) Monkey to human comparative anatomy of the frontal lobe association tracts. *Cortex* 48:82–96.
- Thomas AG, Koumellis P, Dineen RA (2011) The fornix in health and disease: an imaging review. *Radiographics* 31:1107–1121.
- Thomas C, Ye FQ, Irfanoglu MO, Modi P, Saleem KS, Leopold DA, Pierpaoli C (2014) Anatomical accuracy of brain connections derived from diffusion MRI tractography is inherently limited. *Proc Natl Acad Sci U S A*

111:16574–16579.

- Thomason ME, Thompson PM (2011) Diffusion Imaging, White Matter, and Psychopathology. *Annual Review of Clinical Psychology* 7:63–85 Available at: <http://dx.doi.org/10.1146/annurev-clinpsy-032210-104507>.
- Tournier J-D, Calamante F, Connelly A (2007) Robust determination of the fibre orientation distribution in diffusion MRI: non-negativity constrained super-resolved spherical deconvolution. *Neuroimage* 35:1459–1472.
- Tournier J-D, Calamante F, Connelly A (2012) MRtrix: Diffusion tractography in crossing fiber regions. *Int J Imaging Syst Technol* 22:53–66.
- Tournier J-D, Yeh C-H, Calamante F, Cho K-H, Connelly A, Lin C-P (2008) Resolving crossing fibres using constrained spherical deconvolution: validation using diffusion-weighted imaging phantom data. *Neuroimage* 42:617–625.
- Türe U, Yaşargil MG, Pait TG (1997) Is There a Superior Occipitofrontal Fasciculus? A Microsurgical Anatomic Study. *Neurosurgery* 40:1226–1232.
- Turken AU, Dronkers NF (2011) The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Front Syst Neurosci* 5:1.
- Tusa RJ, Ungerleider LG (1985) The inferior longitudinal fasciculus: a reexamination in humans and monkeys. *Ann Neurol* 18:583–591.
- Uddin LQ, Supekar K, Amin H, Rykhlevskaia E, Nguyen DA, Greicius MD, Menon V (2010) Dissociable connectivity within human angular gyrus and intraparietal sulcus: evidence from functional and structural connectivity. *Cereb Cortex* 20:2636–2646.
- Ungerleider LG, Galkin TW, Desimone R, Gattass R (2007) Cortical Connections of Area V4 in the Macaque. *Cereb Cortex* 18:477–499.
- Upadhyay J, Maleki N, Potter J, Elman I, Rudrauf D, Knudsen J, Wallin D, Pendse G, McDonald L, Griffin M, Anderson J, Natile L, Renshaw P, Weiss R, Becerra L, Borsook D (2010) Alterations in brain structure and functional connectivity in prescription opioid-dependent patients. *Brain* 133:2098–2114.
- Vandermosten M, Boets B, Poelmans H, Sunaert S, Wouters J, Ghesquière P (2012) A tractography study in dyslexia: neuroanatomic correlates of orthographic, phonological and speech processing. *Brain* 135:935–948.
- Van Essen DC et al. (2012) The Human Connectome Project: a data acquisition perspective. *Neuroimage* 62:2222–2231.
- Vestergaard M, Madsen KS, Baaré WFC, Skimminge A, Ejersbo LR, Ramsøy TZ, Gerlach C, Akeson P, Paulson OB, Jernigan TL (2011) White matter microstructure in superior longitudinal fasciculus associated with spatial working memory performance in children. *J Cogn Neurosci* 23:2135–2146.
- Vinci-Booher S, Caron B, Bullock D, James K, Pestilli F (2021) Development of white matter tracts between and within the dorsal and ventral streams. *bioRxiv:2021.01.27.428423* Available at: <https://www.biorxiv.org/content/10.1101/2021.01.27.428423v1> [Accessed March 30, 2021].
- Von Der Heide RJ, Skipper LM, Klobusicky E, Olson IR (2013) Dissecting the uncinate fasciculus: disorders, controversies and a hypothesis. *Brain* 136:1692–1707.

- Wakana S, Caprihan A, Panzenboeck MM, Fallon JH, Perry M, Gollub RL, Hua K, Zhang J, Jiang H, Dubey P, Blitz A, van Zijl P, Mori S (2007) Reproducibility of quantitative tractography methods applied to cerebral white matter. *Neuroimage* 36:630–644.
- Wandell BA (2011) The neurobiological basis of seeing words. *Ann N Y Acad Sci* 1224:63–80.
- Wandell BA (2016) Clarifying Human White Matter. *Annual Review of Neuroscience* 39:103–128 Available at: <http://dx.doi.org/10.1146/annurev-neuro-070815-013815>.
- Wang F, Sun T, Li X-G, Liu N-J (2008) Diffusion tensor tractography of the temporal stem on the inferior limiting sulcus. *J Neurosurg* 108:775–781.
- Wang H, Akkin T, Magnain C, Wang R, Dubb J, Kostis WJ, Yaseen MA, Cramer A, Sakadžić S, Boas D (2016a) Polarization sensitive optical coherence microscopy for brain imaging. *Opt Lett* 41:2213–2216.
- Wang X, Pathak S, Stefanescu L, Yeh F-C, Li S, Fernandez-Miranda JC (2016b) Subcomponents and connectivity of the superior longitudinal fasciculus in the human brain. *Brain Struct Funct* 221:2075–2092.
- Wang Y, Fernández-Miranda JC, Verstynen T, Pathak S, Schneider W, Yeh F-C (2013) Rethinking the role of the middle longitudinal fascicle in language and auditory pathways. *Cereb Cortex* 23:2347–2356.
- Wassermann D, Makris N, Rath Y, Shenton M, Kikinis R, Kubicki M, Westin C-F (2016) The white matter query language: a novel approach for describing human white matter anatomy. *Brain Structure and Function* 221:4705–4721 Available at: <http://dx.doi.org/10.1007/s00429-015-1179-4>.
- Wasserthal, J., Neher, P., & Maier-Hein, K. H. (2018). TractSeg-Fast and accurate white matter tract segmentation. *NeuroImage*, 183, 239-253.
- Weiner KS, Yeatman JD, Wandell BA (2017) The posterior arcuate fasciculus and the vertical occipital fasciculus. *Cortex* 97:274–276.
- Widge AS, Zorowitz S, Basu I, Paulk AC, Cash SS, Eskandar EN, Deckersbach T, Miller EK, Dougherty DD (2019) Deep brain stimulation of the internal capsule enhances human cognitive control and prefrontal cortex function. *Nat Commun* 10:1536.
- Wouterlood FG, Groenewegen HJ (1991) The Phaseolus vulgaris-leucoagglutinin tracing technique for the study of neuronal connections. *Prog Histochem Cytochem* 22:1–78.
- Wu Y, Sun D, Wang Y, Wang Y (2016a) Subcomponents and Connectivity of the Inferior Fronto-Occipital Fasciculus Revealed by Diffusion Spectrum Imaging Fiber Tracking. *Front Neuroanat* 10:88.
- Wu Y, Sun D, Wang Y, Wang Y, Wang Y (2016b) Tracing short connections of the temporo-parieto-occipital region in the human brain using diffusion spectrum imaging and fiber dissection. *Brain Res* 1646:152–159.
- Yasmin H, Nakata Y, Aoki S, Abe O, Sato N, Nemoto K, Arima K, Furuta N, Uno M, Hirai S, Masutani Y, Ohtomo K (2008) Diffusion abnormalities of the uncinate fasciculus in Alzheimer's disease: diffusion tensor tract-specific analysis using a new method to measure the core of the tract. *Neuroradiology* 50:293–299.
- Yeatman JD, Dougherty RF, Ben-Shachar M, Wandell BA (2012a) Development of white matter and reading skills. *Proc Natl Acad Sci U S A* 109:E3045–E3053.
- Yeatman JD, Dougherty RF, Myall NJ, Wandell BA, Feldman HM (2012b) Tract profiles of white matter

- properties: automating fiber-tract quantification. *PLoS One* 7:e49790.
- Yeatman JD, Dougherty RF, Rykhlevskaia E, Sherbondy AJ, Deutsch GK, Wandell BA, Ben-Shachar M (2011) Anatomical properties of the arcuate fasciculus predict phonological and reading skills in children. *J Cogn Neurosci* 23:3304–3317.
- Yeatman JD, Weiner KS, Pestilli F, Rokem A, Mezer A, Wandell BA (2014) The vertical occipital fasciculus: a century of controversy resolved by in vivo measurements. *Proc Natl Acad Sci U S A* 111:E5214–E5223.
- Yendiki A, Panneck P, Srinivasan P, Stevens A, Zöllei L, Augustinack J, Wang R, Salat D, Ehrlich S, Behrens T, Jbabdi S, Gollub R, Fischl B (2011) Automated probabilistic reconstruction of white-matter pathways in health and disease using an atlas of the underlying anatomy. *Front Neuroinform* 5:23.
- Yeterian EH, Pandya DN (2010) Fiber pathways and cortical connections of preoccipital areas in rhesus monkeys. *J Comp Neurol* 518:3725–3751.
- Yoshida K, Benevento LA (1981) The projection from the dorsal lateral geniculate nucleus of the thalamus to extrastriate visual association cortex in the macaque monkey. *Neurosci Lett* 22:103–108.
- Yoshimine S, Ogawa S, Horiguchi H, Terao M, Miyazaki A, Matsumoto K, Tsuneoka H, Nakano T, Masuda Y, Pestilli F (2018) Age-related macular degeneration affects the optic radiation white matter projecting to locations of retinal damage. *Brain Struct Funct* 223:3889–3900.
- Zaidel D, Sperry RW (1977) Some long-term motor effects of cerebral commissurotomy in man. *Neuropsychologia* 15:193–204.
- Zeki SM (1973) Comparison of the cortical degeneration in the visual regions of the temporal lobe of the monkey following section of the anterior commissure and the splenium. *J Comp Neurol* 148:167–175.