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Perspective

Comparative neuroanatomy: Integrating classic and modern methods to understand association fibers connecting dorsal and ventral visual cortex

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ABSTRACT

Comparative neuroanatomy studies improve understanding of brain structure and function and provide insight regarding brain development, evolution, and also what features of the brain are uniquely human. With modern methods such as diffusion MRI (dMRI) and quantitative MRI (qMRI), we are able to measure structural features of the brain with the same methods across human and non-human primates. In this review article, we discuss how recent dMRI measurements of vertical occipital connections in humans and macaques can be compared with previous findings from invasive anatomical studies that examined connectivity, including relatively forgotten classic strychnine neuronography studies. We then review recent progress in understanding the neuroanatomy of vertical connections within the occipitotemporal cortex by combining modern quantitative MRI and classical histological measurements in human and macaque. Finally, we a) discuss current limitations of dMRI and tractography and b) consider potential paths for future investigations using dMRI and tractography for comparative neuroanatomical studies of white matter tracts between species. While we focus on vertical association connections in visual cortex in the present paper, this same approach can be applied to other white matter tracts. Similar efforts are likely to continue to advance our understanding of the neuroanatomical features of the brain that are shared across species, as well as to distinguish the features that are uniquely human.

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1. Introduction

To date, the field of neuroscience has made great progress in understanding the anatomical organization of the networks that support visual processing. Specifically, despite its complexity, the visual system is quite orderly across spatial scales spanning microns to several centimeters - from the retina to subcortical and cortical brain networks. In cortex, insight into how this orderliness gives rise to neural functions contributing to the complexity of perception has been gleaned from comparative studies across species both classically (reviewed in Gross, 1998, pgs. 65–90) and with present methods (Glasser et al., 2014; Lyon, 2009; Tootell et al., 2003; Vanduffel et al., 2014).

For example, whereas classic anatomical and experimental work used lesions in dogs and monkeys to localize a 'visual center' (Gross, 1998), work in humans used case studies in patients to map out relationships between visual deficits and locations of brain damage (Henschen, 1893; Holmes and Lister, 1916; Inouye, 1909). The combination of findings from the two approaches led to an understanding that the occipital cortex contained a systematic representation of features distributed across space in our visual world, which was crucial for visual perception. Of course, now we know that we do not have just one, but instead dozens, of visual areas. Presently, comparative studies have generated systematic criteria for proposing analogous and homologous areas among the visual systems of different species (de Sousa et al., 2010; Felleman and Van Essen, 1991; Kaas, 2013; Leopold et al., 2017; Nieuwenhuys, 1998; Orban et al., 2004; Takahata et al., 2014; Tootell et al., 2003; Zilles, 2005; Zilles and Palomero-Gallagher, 2017).

Perhaps the clearest criteria have been established for comparisons between the structural-functional organization of the macaque, an old-world monkey, and humans, which are evolutionarily separated by about 35 million years (Zilles et al., 2013). Despite the evolutionary separation, the macaque shares many commonalities in brain structure and function with humans. Visual neuroscientists have successfully used the macaque visual system as a comparative model for the human visual system for decades of research spanning rigorous neuroanatomical, electrophysiological, as well as behavioral studies (DeAngelis and Newsome, 1999; De Valois et al., 1974; De Valois and Jacobs, 1968; Felleman and Van Essen, 1991; Fujita et al., 1992; Hubel and Livingstone, 1987; Komatsu and Wurtz, 1988; Kriegeskorte et al., 2008; Livingstone and Hubel, 1988; Luppino et al., 2005; Newsome et al., 1989; Rockland and Pandya, 1979; Tanaka et al., 1986; Tootell et al., 2003; Tsao et al., 2008; Vanduffel et al., 2014; Zeki, 1974; and countless others). In addition to the wide usage of the macaque brain as a model for the structure and function of many human cortical systems, this comparative approach has also been successful using many other mammals - for example, apes (Hecht et al., 2015; Rilling et al., 2008), marmosets (Mitchell and Leopold, 2015; Hung et al., 2015), dolphins (Berns et al., 2015), dogs (Cuaya et al., 2016; Datta et al., 2012), and sheep (Kendrick, 1991; Kendrick et al., 2001). Nevertheless, because of the long, successful history of visual neuroscience research in macaque, this review largely focuses on linking studies of vertical connections within the occipital lobe in human and macaque.

It should be noted that human-macaque comparisons can be challenging largely because very different methods are often used in the two species. For example, while it is possible to collect micron-scale measurements in the living macaque brain, it is very rare to collect similar measurements in living human brains (Rilling, 2014). Non-invasive measurements in humans are often only possible at resolutions ranging from the mm to the cm scale (Logothetis and Wandell, 2004; Shi and Toga, 2017; Wandell, 2016). Indeed, between-species comparisons of the functional organization of visual cortex are commonly made from measurements that differ in a variety of ways. For instance, if we consider electrophysiology and functional magnetic resonance imaging (fMRI), these measurements have vastly different origins (e.g. neuronal vs. hemodynamic) and spatial scales (e.g. microns vs. centimeters). Due to these differences in scale and origin, substantial effort is required to model the relationship between single unit electrophysiology and fMRI measurements (Logothetis et al., 2001; Logothetis and Wandell, 2004). Likewise, there are limitations when attempting to compare anatomical tracer measurements in macaque with MR-based neuroimaging approaches, such as diffusion MRI (dMRI) in humans (Crick and Jones, 1993; Jbabdi and Johansen-Berg, 2011; Rokem et al., 2017; Wandell, 2016). Specifically, tracer studies aim to identify precise details of axon terminals, while dMRI aims to estimate large-scale white matter tracts by measuring orientation of water diffusion in white matter tissue.

A promising approach that ameliorates these differences uses the same non-invasive methodology in both species. The benefit of this approach is that it allows a 'like vs. like' comparison in terms of methodology and signals being measured before delving further into the origins of the organization and signal, but at a cost for resolution. Successful examples of this approach are a number of neuroimaging studies that have examined the large-scale spatial layout of functional maps and functionally-specialized clusters in visual cortex across species using fMRI (Arcaro and Livingstone, 2017; Brewer et al., 2002; Cottereau et al., 2017; Goda et al., 2014; Kolster et al., 2014; Tsao et al., 2008; Vanduffel et al., 2014; Wade et al., 2008). Additional successful examples implement dMRI and compare the organization of major white matter fasciculi, as well as the cortical regions that these fasciculi connect, between species (Catani et al., 2017a; Croxson et al., 2005; Jbabdi et al., 2013; Mars et al., 2016a; Ramnani et al., 2006; Rilling et al., 2008; Schmahmann et al., 2007; Thiebaut de Schotten et al., 2011). However, fewer comparative studies have examined the similarities and differences of association fibers in visual cortex between human and macaque. Due to this gap in knowledge, the measurements of the white matter tracts in visual cortex are the focus of the present review. More specifically, this review focuses on measurements of the recently re-discovered vertical occipital fasciculus (VOF; Takemura et al., 2016b, 2017; Yeatman et al., 2014, 2013), which connects the dorsal and ventral visual streams in the occipital lobe across species.

The remainder of this review can be divided into five main sections: (1) a brief review of methods for analyzing white matter tracts from non-invasive dMRI data, (2) a human-macaque comparison of the macroanatomy of vertical association fibers in visual cortex using present, non-invasive dMRI methods and tractography, (3) a comparison between dMRI findings and invasive anatomical connectivity measurements, including relatively

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forgotten strychnine neuronography findings in macaque, (4) a summary of recent findings supporting microstructural similarities between the VOF and surrounding white matter tracts in human and macaque, and (5) discussion regarding current limitations of dMRI-based tractography as a tool for neuroscience studies, as well as possible solutions.

2. General approach: comparative studies of white matter across species using diffusion MRI and tractography

A primary non-invasive technology to measure white matter tracts is the combination of dMRI and tractography (Assaf et al., 2017; Catani and Thiebaut de Schotten, 2012; Jbabdi and Johansen-Berg, 2011; Mori and Zhang, 2006; Rokem et al., 2017; Shi and Toga, 2017; Thomason and Thompson, 2011; Wandell, 2016). dMRI aims to measure the diffusion of water molecules restricted by white matter tissue organization to estimate the underlying fiber orientation distribution. There is an enormous effort to improve the resolution and quality of the dMRI measurement itself (Jones et al., 2018; McNab et al., 2013; Setsompop et al., 2012; Vu et al., 2015). In standard practice, dMRI measurements are first acquired, then tractography algorithms are used to exploit these measurements to model the trajectory of the long-range neuronal fibers wrapped by myelin sheaths (Behrens et al., 2003; Catani et al., 2002; Conturo et al., 1999; Mori et al., 1999). Over the last two decades, tractography algorithms have improved substantially (Behrens et al., 2003; Conturo et al., 1999; Daducci et al., 2015; Girard et al., 2017; Mangin et al., 2002; Mori et al., 1999; Pestilli et al., 2014; Reisert et al., 2011; Sherbondy et al., 2009, 2008a; Smith et al., 2013; see Wandell, 2016 for a review). Yet, we understand that additional limitations will need to be overcome especially a) to eliminate what are potentially false connections that tractography can generate (Maier-Hein et al., 2017) and perhaps more importantly, b) to identify connections that tractography routinely misses (Jbabdi et al., 2015). Indeed, tractography often faces a difficult trade-off between sensitivity and specificity (Thomas et al., 2014), as we discuss in a later section (see the section titled, "A note on some limitations of dMRI and tractography").

Despite its limitation, dMRI measurements have been beneficial for a variety of studies comparing properties of anatomical connections between human and macaque. Specifically, just as fMRI in awake behaving macaques has been proposed to serve as the 'missing link' between single unit electrophysiology in macaque and fMRI in humans (Orban, 2002), we believe that dMRI has served, and will continue to serve, as the 'missing link' between invasive connectivity methods in macaque and dMRI in humans. Furthermore, dMRI measurements in macaque open avenues to directly compare dMRI-based tractography findings with various types of invasive anatomical connectivity measurements in macaque, as we discuss in the next section.

Comparative dMRI studies typically implement one of two types of approaches: they either compare whole brain cortical parcellations to look at networks of brain connections across species (Azadbakht et al., 2015; Betzel et al., 2018; Calabrese et al., 2015; Donahue et al., 2016; Li et al., 2013; Mars et al., 2016b; Sotiropoulos and Zalesky, 2017; van den Heuvel et al., 2016, 2015; Van Essen et al., 2016) or they perform direct comparisons between individual white matter tracts and the regions that they connect (Croxson et al., 2005; Hecht et al., 2015; Hofer et al., 2008; Jbabdi et al., 2013; Mars et al., 2016a; Oishi et al., 2011; Parker et al., 2002; Ramnani et al., 2006; Rilling et al., 2008; Schmahmann et al., 2007; Takemura et al., 2017; Thiebaut de Schotten et al., 2012, 2011). Both approaches complement one another in that the former affords more theoretical questions about global brain network organization, while the latter is geared toward testing specific anatomical hypotheses. In the sections below, we highlight our recent progress in the latter comparative approach.

3. Vertical association fibers in the occipito-temporal lobe: comparative studies of white matter across species using dMRI and tractography

While there is a growing trend to use dMRI and tractography for comparative studies, a paucity of comparative studies have examined the relatively shorter association fibers within the occipital lobe. Here, we consider how the integration of classical anatomical work in macaque with modern dMRI approaches can improve our understanding of comparative anatomy of vertical association fibers in the occipito-temporal lobe (Takemura et al., 2016b, 2017; Yeatman et al., 2014, 2013).

Vertical white matter fibers connecting ventral portions of the occipital and temporal lobes with dorsal portions of the occipital and parietal lobes have been widely examined and argued for more than a century (Yeatman et al., 2014). Contrary to the 1890s and early 1900s, it is now commonly accepted that vertical white matter fibers (a) exist (Fig. 1A; Güngör et al., 2017; Wu et al., 2016; Yeatman et al., 2014), (b) are located posterior to the arcuate fasciculus (Fig. 1A; Güngör et al., 2017; Panesar et al., 2018; Takemura et al., 2016b; Yeatman et al., 2014), and (c) are important for understanding disease and cognitive skills (Budisavljevic et al., 2018; Duan et al., 2015; Lee Masson et al., 2017; Oishi et al., 2018).

These vertical white matter fibers are often referred to as the vertical occipital fasciculus (VOF). Indeed, recent approaches can identify the VOF using three-dimensional, reproducible dMRI measurements and tractography algorithms (Duan et al., 2015; Lee Masson et al., 2017; Oishi et al., 2018; Panesar et al., 2018; Takemura et al., 2016b, 2017; Weiner et al., 2016; Wu et al., 2016; Yeatman et al., 2014). Importantly, the VOF is not only identifiable with dMRI and tractography, but is also identifiable using different post-mortem dissection techniques (Güngör et al., 2017; Vergani et al., 2014; Wu et al., 2016). While the VOF can be reproducibly identified in living and post-mortem brains using different methods, contentions regarding the structural definition and functional role of the human VOF still remain (Bartsch et al., 2013; Catani et al., 2017b; Martino and Garcia-Porrero, 2013; Panesar et al., 2018; Weiner et al., 2017).

Interestingly, in both post-mortem and living macaque brains, as well as in living human brains, tractography is not even needed to identify the VOF. More specifically, the VOF is visually identifiable from the principal diffusion direction (PDD) map (Pajevic and Pierpaoli, 1999) produced by fitting the diffusion tensor model to dMRI data (Fig. 1A; left panel, in vivo human dMRI; middle panel, ex vivo macaque dMRI; right panel, in vivo macaque dMRI; adapted from Takemura et al., 2017). The three-dimensional trajectory of the VOF is then also consistently reconstructed using tractography methods (Fig. 1B; adapted from Takemura et al., 2017).

The comparison of human and macaque dMRI results reveals some commonalities in gross anatomical organization between the VOF in the two species. Specifically, in both species, the VOF is located within the occipital lobe, adjacent and lateral to the optic radiation (Takemura et al., 2017). The human-macaque commonalities also extend to the visual areas within which the VOF streamlines terminate. For example, the VOF streamlines terminate near V3A dorsally and V4 ventrally across species (Takemura et al., 2017). Thus, while contentions remain regarding homologies of cortical visual field maps (Tootell et al., 2003; Wandell and Winawer, 2011; Winawer et al., 2010), these findings demonstrate a high-degree of VOF homology between humans and macaques.

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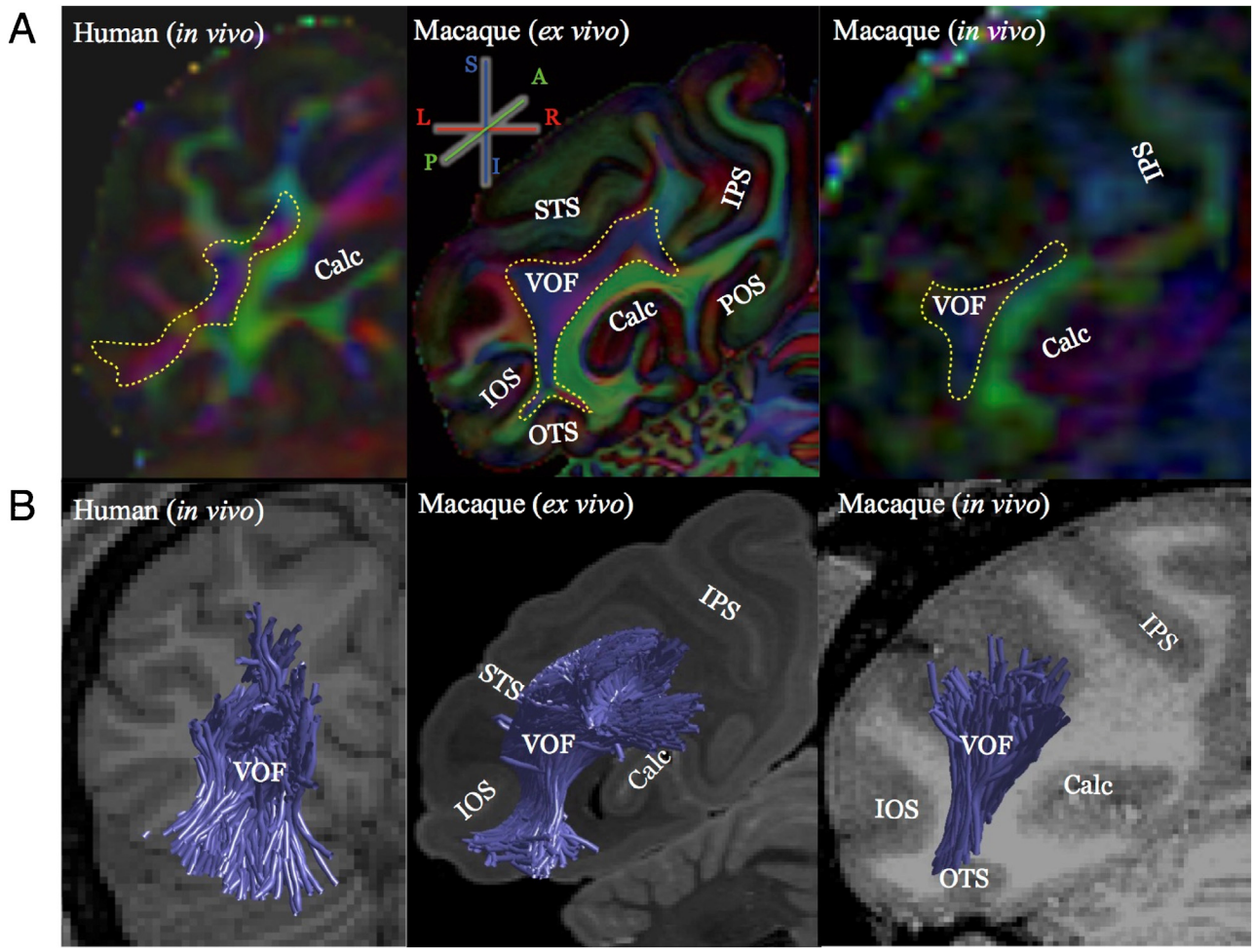

Fig. 1. Evidence supporting the identification of the human and macaque VOF with diffusion MRI. (A) The macaque VOF is visible in PDD map obtained by fitting the diffusion-tensor model to dMRI data. The VOF (dotted yellow outline) depicted using the PDD map in a coronal section, from one representative human and two representative macaque dMRI datasets (left: in vivo human dMRI data at 1.25 mm isotropic resolution, measured by WU-Minn Human Connectome Project; Van Essen et al., 2013; middle: ex vivo macaque dMRI data at 0.25 mm isotropic resolution, measured at National Institute of Health and provided by F. Q. Ye and D. A. Leopold; right: in vivo macaque dMRI data at 0.75 mm isotropic resolution, measured at Max Planck Institute and provided by G. A. Keliris and N. K. Logothetis). The color (see inset, upper left) indicates the principal diffusion direction (red: left-right; green: anterior-posterior; blue: superior-inferior). STS: Superior Temporal Sulcus; IPS: Intraparietal Sulcus, Calc: Calcarine Sulcus, POS: Parieto-occipital sulcus, OTS: Occipitotemporal sulcus; IOS: Inferior Occipital Sulcus. (B) Macaque and human VOF reconstructed using ensemble tractography (Takemura et al., 2016a). VOF reconstructions are shown for in vivo human (left), ex vivo macaque (middle) and in vivo macaque (right) data. Figures are reproduced from Takemura et al. (2017) with permission.

4. Diffusion MRI measurements of the VOF are consistent with invasive connectivity studies in macaque: from classic strychnine neuronography to chemical tracers

In both macaques and humans, dMRI findings of the VOF are consistent with descriptions of the VOF in classic and modern fiber dissection work (Güngör et al., 2017; Martino and Garcia-Porrero, 2013; Takemura et al., 2017; Wernicke, 1881; Wu et al., 2016; Yeatman et al., 2014). When definitions of white matter tracts match between dMRI studies and classical dissection methods, there is an increased sense of confidence for the existence of the fascicles among researchers. However, we note that gross dissection methods may describe anatomy of white matter tracts that are at a scale which may not provide enough detail to resolve particular questions or debates on cortico-cortical connections in systems neuroscience. Instead, additional invasive methods - such as chemical tracers - do enable what could be considered a more fine-grained view of cortico-cortical connections. Here, we summarize a number of different invasive anatomical measurements - from relatively forgotten strychnine neuronography to modern chemical tracers - that are consistent with the dMRI and tractography identification of the VOF.

4.1. Strychnine neuronography

Decades before dMRI was invented, evidence for vertical connections within the occipital lobe were identified using invasive strychnine neuronography methods (Bailey et al., 1944, 1943; McCulloch, 1944; Petr et al., 1949). Strychnine neuronography is a chemical stimulation method used to examine connections of cortical foci. Specifically, applying strychnine (which is a glycine antagonist) to one cortical focus causes electrical activity (e.g. strychnine spikes) to propagate to other cortical foci (de Barenne and McCulloch, 1939). Using these methods, connections can be examined among cortical areas. Bailey, Bonin, and McCulloch conducted a series of studies in the 1940s that identified connections consistent with the VOF in macaque and chimpanzee (Fig. 2A). In the late 40 s, Petr et al. (1949) replicated these findings of vertical connections in the occipital lobe of macaque with strychnine neuronography and further related them to the cytoarchitectonic parcellations of the occipital, temporal, and parietal lobes. Interestingly, while Bonin and Bailey (1947) are commonly credited for differentiating area TEO from TE based on cytoarchitecture, it was actually findings from strychnine neuronography that served as the first evidence to parcellate these areas from one another (Takemura

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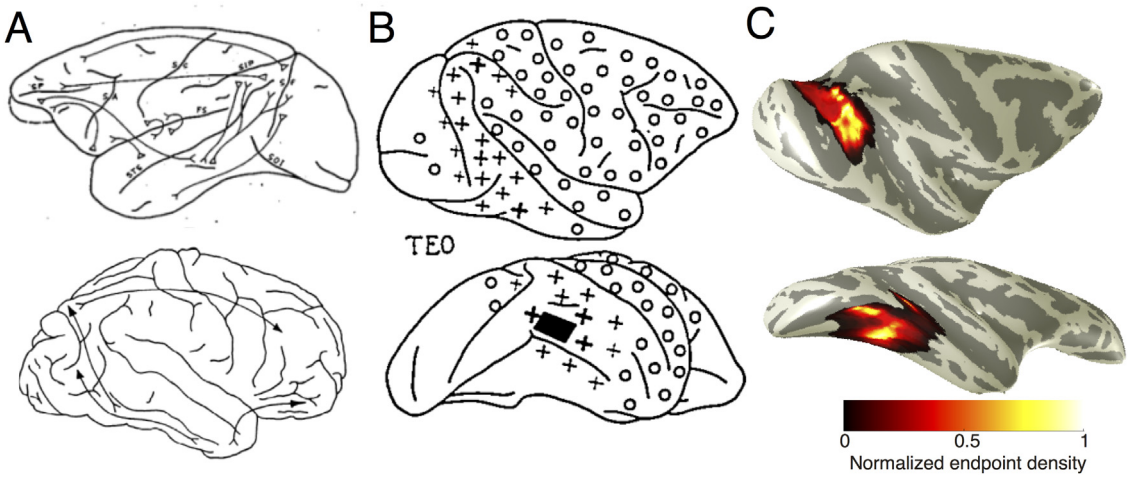

Fig. 2. From strychnine neuronography to dMRI: The identification of vertical connections in macaque visual cortex across methods. (A) *Top*: Fig. 1 from Bailey et al. (1944). Schematic illustration of long fiber tracts of Macaca mulatta identified with strychnine neuronography. Note the vertical connections depicted in the occipital lobe, which Bailey et al. (1944) described as connecting "the posterosuperior part of the inferior parietal lobule (area 39) to the posterior part of the temporal lobe (area 37)" (pg. 414). Figure is reproduced from Bailey et al. (1944) with permission. *Bottom*: Fig. 4 from Bailey et al. (1943). Fiber tracts in chimpanzee as determined by strychnization and electrical recording. Again, note the vertical connections depicted in the occipital lobe, which Bailey et al. describe in the context of the VOF. Figure is reproduced from Bailey et al. (1943) with permission. (B) Fig. 1 from Petr et al. (1949). Efferent connections from the lateral surface of the temporal lobe. +, connections found; o, areas explored, but no connections found. Heaviness of crosses indicates intensity of firing. Note that strychnization ventrally induced intense firing dorsally, which contributed to Petr et al. to differentiate TEO from TE. Figure is reproduced from Petr et al. (1949) with permission. (C) An example inflated cortical surface reconstruction of a right hemisphere in macaque. For comparison, the orientation of lateral (top) and ventral (bottom) views of the brain are similar to those in (B). Dark gray pixels depict sulci, while light gray pixels depict gyri. Estimated VOF streamline endpoints from high-resolution dMRI data acquired from a macaque brain (subject M1 in Fig. 1A and B; *Top*, dorsal VOF endpoint; *Bottom*, ventral VOF endpoint; Takemura et al., 2017). The hot color map indicates the normalized number of VOF streamlines having endpoints close to gray matter voxels.

et al., 2017; Weiner, 2018). Specifically, Petr et al. (1949) parcellated area TEO from TE based on 'characteristic connections' not displayed by TE (Fig. 2B). Part of these characteristic connections were a large dorso-ventral connection (crosses in Fig. 2B) between TEO and the lunate/angular gyrus. The authors wrote:

> *"Strychnine applied to the posterior part of the third temporal gyrus fired more posteriorly. This region is intermediate between the peri-occipital cortex OA and the true temporal cortex TE. Although it could not be recognized by Bonin and Bailey, 1947 as a separate cytoarchitectonic area, it has such characteristic connections that there can be little doubt that this region is the precursor of the separable area called by Economo in man PH. When strychnized it fires the second temporal convolution, the fusiform gyrus, both fore and aft the lunate sulcus (OA and OB) and into the parietal lobe both above and below the intraparietal sulcus (PEp and PG). We could not find any firing along the sulcus principalis but we did find reverse firing into the intermediate region (TEO) from the sulcus principalis and also from the angular gyrus at the junction of the sulcus intraparietalis and the lunate sulcus (Fig. 1 TEO)."*

Nearly 70 years later, we were able to identify vertical connections in the macaque occipito-temporal lobe with dMRI (Fig. 2C) that were similar to those identified by Petr et al. (1949) (Fig. 2B). It should also be clearly stated that a few years prior, Bailey et al. also identified vertical connections in the occipital lobe using strychnine neuronography in both chimpanzees and macaques, but related these connections to the VOF and not cortical parcellations (Bailey et al., 1944, 1943; Fig. 2A). Altogether, historically, vertical connections, and not classic cytoarchitectonic methods, differentiated area TEO from TE (which was later verified behaviorally with ablation studies; Iwai and Mishkin, 1969; Weiner, 2018). Presently, non-invasive dMRI methods and tractography identify the VOF in macaque, which is consistent with these classic results using invasive strychnine neuronography methods.

Although classic strychnine neuronography provided valuable findings regarding association fibers in occipital cortex, later studies demonstrated limitations of this approach (Frankenhaeuser, 1951; Wall and Horwitz, 1951). Specifically, neuronal firings in some parts of the central nervous system were not affected by the presence of strychnine (Dow, 1938; Frankenhaeuser, 1951; Wall and Horwitz, 1951). Following these observations, additional studies showed that the density of glycine receptors significantly varied across brain areas, and was generally very low in areas of the cerebral cortex in both rodents and humans (Frostholm and Rotter, 1985; Probst et al., 1986).

4.2. Nauta method

Dissatisfied with how brain connections were being measured, in the early 1950s, Nauta developed a new type of method that used silver staining to identify terminals of degenerating axons following a cortical lesion (Nauta and Ryan, 1952). This method has since been widely implemented and was integral for unveiling the laminar and columnar distributions of geniculo-cortical fibers in macaque (Hubel and Wiesel, 1972). In direct relation to vertical fibers in the occipital cortex, Clarke (1994) examined cortico-cortical fiber pathways in human occipital cortex (Fig. 3A; Clarke, 1994) using the Nauta method. Specifically, after lesioning a portion of cortex adjacent to V3A in dorsal occipital cortex, they found that axon terminals from this lesion were distributed across many areas including human V4 (hV4) in ventral visual cortex. These findings are consistent with the dMRI and tractography findings described in the previous section explicating that the VOF in living humans also connects hV4 ventrally and V3A dorsally (Fig. 3A; Takemura et al., 2016b).

4.3. Chemical tracers

In addition to the Nauta method, a variety of chemical tracers, such as Biotinylated Dextran Anime (BDA), Horseradish Peroxidase (HRP) and Cholera toxin B subunit (CTB: see Lanciego and Wouterlood, 2011 for a review) were also developed to examine neural connectivity and some of these approaches also identified vertical connections between macaque dorsal and ventral occipital cortex. For instance, Umitsu and Iwai (1980) used HRP to identify fibers connected to posterior inferotemporal cortex (area TEO),

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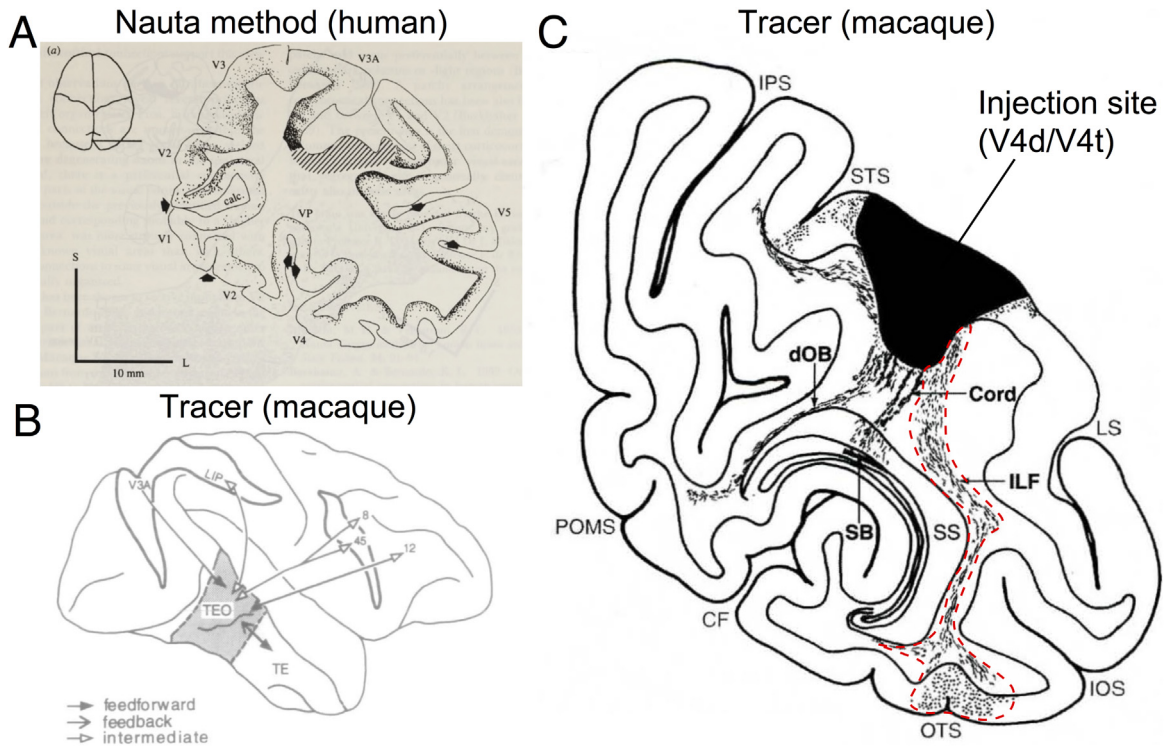

Fig. 3. Anatomical studies of association fibers in visual cortex using the Nauta method or chemical tracers. (A) Clarke (1994) examined the association fibers in human visual cortex using the Nauta method. The figure depicts a coronal slice of a human brain that includes a lesion site in dorsal occipital cortex (hatched area) that is adjacent to area V3A. Arrows indicate the border of visual areas based on cyto- or myeloarchitectonic criteria. Clarke reported a number of connections by inspecting terminals of degenerated axons in other areas. There are a number of axon terminals in area V4, consistent with the dMRI-based observations of the human VOF (Takemura et al., 2016b). Reproduced from Clarke (1994) with permission. (B) After anterograde and retrograde tracer injections to macaque area TEO, Webster et al. (1994) identified connections between V3A dorsally and TEO ventrally. Reproduced from Webster et al. (1994) with permission. (C) Schmahmann and Pandya (2006) injected anterograde tracer with radiolabeled isotope into macaque dorsal occipital cortex (case 19 in Schmahmann and Pandya, 2006). The cortical area marked in black is the injection site (V4 dorsal and V4t) of anterograde tracer. Areas highlighted with dotted red lines in the white and gray matter indicate white matter tracts between the injection site and ventral occipital cortex around the OTS, which is consistent with VOF endpoints identified with dMRI and tractography (Fig. 1). We note that Schmahmann and Pandya (2006) labelled connections as portions of the Inferior Longitudinal Fasciculus (ILF), likely because it is difficult to distinguish the VOF from the ILF in the macaque brain (Takemura et al., 2017). Reproduced from Schmahmann and Pandya (2006).

and reported a series of dorsal connections in the cortical vicinity of those just described (Umitsu and Iwai, 1980; Weiner, 2018). Additionally, connections between dorsal (V3A and V4d) and ventral areas (including TEO) were also reported in later studies using tracers such as Wheat Germ Agglutinin conjugated to HRP (WGA-HRP; Fig. 3B; Distler et al., 1993; Webster et al., 1994). More recent studies that implemented multiple types of tracers also reported connections between V3A dorsally and V4 ventrally in macaques (Ungerleider et al., 2008). And yet, still other studies measured the connectivity of the brain using anterograde tracers labelled with radiolabeled isotope (Schmahmann and Pandya, 2006), which - contrary to the tracer approaches just described - enable the visualization of fiber pathways within white matter. Fig. 3C illustrates one case that implemented this approach (case 19 in Schmahmann and Pandya, 2006). Specifically, they found ventral terminations within and surrounding the OTS after tracer injections within dorsal V4 and adjacent area V4t, which is once again consistent with what we observed with dMRI and tractography in macaques (Takemura et al., 2017).

4.4. *Inconsistencies and moving forward*

Despite these converging results across a wide range of non-invasive and invasive methods that support vertical connections between ventral and dorsal visual cortex, we also stress that anatomical studies have also reported a number of observations that may not necessarily be in line with VOF findings. For example, we note that Schmahmann and Pandya (2006) labelled the identified terminations described at the end of the previous paragraph as a portion of the Inferior Longitudinal Fasciculus (ILF) rather than the VOF. This is likely because it is difficult to distinguish the VOF and ILF in the macaque brain (Takemura et al., 2017). Additionally, it is not yet fully clear how to establish relationships between a large number of connections reported in tracer studies (e.g. Seltzer and Pandya, 1984) with fiber tracts reported in dMRI or Klinger's dissection method (Decramer et al., 2018). Recent development of novel post-mortem imaging methods, such as polarized light imaging (PLI), is very promising to fill this gap between tracers and dMRI especially because PLI provides a data format closer to dMRI, but with micrometer resolution (Axer et al., 2011; Caspers et al., 2015; Zeineh et al., 2017; Zilles et al., 2016).

5. Histological and quantitative MRI measurements elucidate microstructural inter-species similarities of white matter tracts

Classic and modern histological measurements across species have provided precise anatomical descriptions of microarchitectural features such as the structure and organization of cells and myelin across cortical layers (Amunts and Zilles, 2015). However, it is generally challenging to associate these findings that are typically conducted in 2-D brain slices to coarse-scale neuroimaging (such as dMRI or fMRI), which is conducted in 3-D volumes. In order to fill this gap between fine-scale histology and relatively coarse-scale neuroimaging, there is a necessity to use 3-D technology that

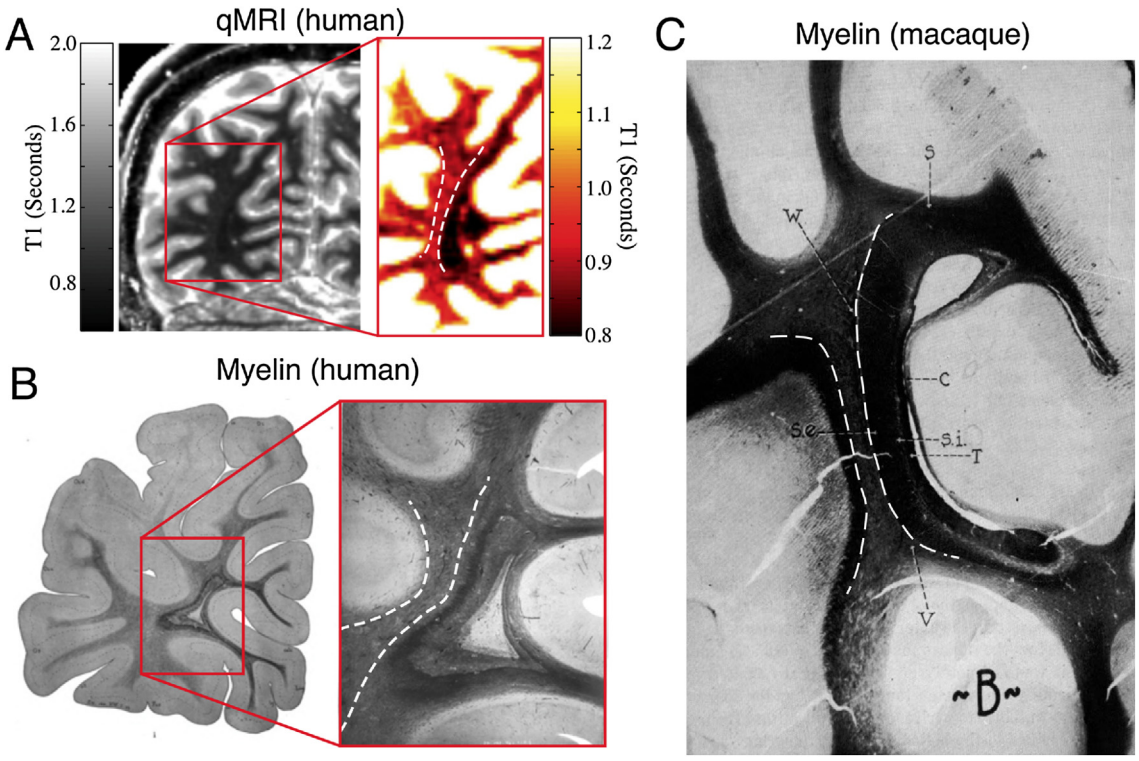

Fig. 4. Modern and classic microstructural tissue properties of the VOF in human and macaque. (A) In vivo quantitative T1 measurements (qMRI) of an example human brain. The expanded T1 scale of the inset shows that T1 in the VOF (dotted white line) is higher than in the adjacent medial tracts. Higher T1 is associated with less myelination. Image reproduced from Yeatman et al. (2014). (B) Postmortem section in human from Vogt (1904) stained for myelin. The VOF stains lighter than nearby occipital lobe tracts, which captures the same differences in occipital lobe white matter tissue properties as the quantitative T1 measures in A. (C) Postmortem section in macaque from Bonin et al. (1942). Original caption for their Fig. 8B reads: "Transverse section through brain of macaque, stained after Weigert. C, stratum calcinarum; S, fasciculus transversus cunei; S. e., stratum sagittale externum; S. i., stratum sagittale internum; T, tapetum; V, fasciculus transversus lingualis; W, vertical occipital fasciculus." The authors refer to the latter two tracts with a V and W to reflect the anatomists (Vialet and Wernicke, respectively) whose names are most often associated with those tracts throughout history. Dotted white lines have been added to the Vogt and Bonin images to highlight the location of the VOF across images included in A–C. These data suggest that microstructural differences between the VOF and nearby white matter tracts in macaque are likely measurable with qMRI.

provides reasonable estimates of microstructural information measured in histology such as myelination.

Recent studies have progressed in achieving this goal through developments of quantitative MRI (qMRI; Mezer et al., 2013; Tofts, 2003; Weiskopf et al., 2015). In essence, qMRI combines several different parameter settings of the MR scanning sequence, which removes measurement biases and results in multiple measurements of anatomy that are linked to microstructural features (Mezer et al., 2013; Weiskopf et al., 2015). Specifically, this approach enables users to quantify and compare the voxelwise image intensity of anatomical images across brain areas or individuals. Importantly, a series of studies show that one such parameter of qMRI, T1 (R1) relaxation time, is highly correlated with myelin volume fraction (Lutti et al., 2014; Stüber et al., 2014; Waehnert et al., 2016). Such a correspondence offers the opportunity to quantify microstructural changes linked to myelin in-vivo, as well as to compare 3-D anatomical images acquired with MR to 2-D histological sections stained for myelin (Stikov et al., 2015).

Fig. 4 shows the application of this approach to the VOF in humans and non-human primates. As illustrated in Fig. 4A and B, the VOF (dotted white outline) can be distinguished from adjacent white matter based on differences in T1 relaxation rates (Fig. 4A), much as differences in the density of myelination staining identifies the VOF in postmortem human tissue (Fig. 4B; Vogt, 1904). Specifically, the VOF is much brighter compared to adjacent tracts that are much darker and thus, more heavily myelinated. The difference in tissue properties between the VOF and adjacent white matter can be appreciated in each individual brain, and likely influences the nature of the signals carried by the pathway (Yeatman et al., 2014).

For the first time, we also compare the human organization of the VOF and surrounding tracts with macaque using classic histology data (Fig. 4C; Bonin et al., 1942). Specifically, we uncovered an image of a myelin-stained section from a macaque that depicted a similar relationship between the VOF and surrounding white matter tracts buried in a conference proceeding from the early 1940s. In particular, Bonin et al. identify the VOF ('W' in the image) as a light band of white matter compared to surrounding tracts, which is similar to the criteria used by Vogt (Fig. 4B) in human. Because this qualitative difference in myelin content illustrated in the histological section (Fig. 4B) is quantitatively measurable with qMRI in humans (Fig. 4A), it is likely that this difference is also quantifiable with qMRI in macaque, which can be tested in future studies. More generally, this approach linking classic histological measurements with modern qMRI measurements reveals similarities in the microstructural tissue composition of the VOF compared to surrounding tracts across species.

6. A note on some limitations of diffusion MRI and tractography

As we have discussed here, vertical connections in occipital cortex can be identified using both invasive and non-invasive methods in humans and macaques. Nevertheless, we are also at a time in the field when many researchers are pointing out situations in which tractography fails if it is not accurately supervised by anatomical knowledge (Maier-Hein et al., 2017; Thomas et al., 2014). Recent studies have demonstrated limitations of dMRI-based tractography in (1) the ability to solve crossing fibers (Maier-Hein et al., 2017;

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Roebroeck et al., 2008), (2) its dependency on tractography algorithms or parameter settings (Bastiani et al., 2012; Chamberland et al., 2014; Domin et al., 2014; Kunimatsu et al., 2004; Parizel et al., 2007; Taoka et al., 2009; Thomas et al., 2014), and (3) its accuracy for estimating fiber projections into cortical gray matter (Reveley et al., 2015). Importantly, Thomas et al. (2014) pointed out that one significant challenge of tractography is a trade-off between specificity and sensitivity: methods with higher sensitivity are more susceptible to false positives, while methods with higher specificity are more susceptible to false negatives. We fully acknowledge that tractography has limitations and should be used with great care in order to draw accurate and reproducible neuroanatomical conclusions. After all, no method is perfect and we remain optimistic when considering the many potential paths forward for reducing these limitations.

For example, several methodical approaches are currently being developed to solve these established problems. The first - and perhaps the most intuitive approach - is to incorporate prior anatomical knowledge when identifying specific white matter tracts with tractography that are known to exist from invasive methods (Catani et al., 2002; Conturo et al., 1999; Wakana et al., 2004). For instance, anatomical knowledge regarding the optic radiation was often used to improve the accuracy of the algorithms used to identify this pathway using tractography (Benjamin et al., 2014; Chamberland et al., 2017; Kammen et al., 2016; Sherbondy et al., 2008b). This approach (1) substantially reduced the problem of false positives in tractography, (2) is now widely implemented in several different types of tractography software (Wassermann et al., 2016; Yeatman et al., 2018, 2012; Yendiki et al., 2011), and (3) effectively identifies reproducible connections using dMRI (and tractography), as well as tracers (Jbabdi et al., 2013; Schmahmann et al., 2007; Takemura et al., 2017; Thiebaut de Schotten et al., 2011). However, this approach is only applicable when identifying major white matter tracts that are known to exist and are established as accepted fascicles in the wide neuroanatomical literature.

The second approach is to statistically evaluate tractography by estimating how well a set of streamline trajectories predicts the measured dMRI signal (Caiafa and Pestilli, 2017; Daducci et al., 2015; Pestilli et al., 2014; Sherbondy et al., 2009, 2008a; Smith et al., 2013). For example, Linear Fascicle Evaluation (LiFE; Caiafa and Pestilli, 2017; Pestilli et al., 2014) is a method that first predicts dMRI signals from connections (streamlines) that are generated by tractography algorithms, and then removes streamlines that do not explain dMRI signals. This approach increases the specificity of tract estimates (Schurr et al., 2018). Furthermore, by also testing how much the removal of a specific tract reduces the prediction accuracy of dMRI signals, this approach has provided methods to evaluate the degree of statistical evidence supporting the identification of novel white matter tracts identified in living brains (Caiafa and Pestilli, 2017; Gomez et al., 2015; Leong et al., 2016; Pestilli et al., 2014; Takemura et al., 2016a; Uesaki et al., 2018). Of course, we also acknowledge that a statistically significant model only means that the model can explain data, but does not fully guarantee that the model is anatomically correct (Daducci et al., 2016).

In our view, these two approaches are complementary. Macaque dMRI is an ideal case for integrating the strength of these two approaches to draw careful conclusions in tractography studies. For example, as described in the first approach (and as we reviewed in this paper), we collected established anatomical evidence of the macaque VOF from classical and modern studies using various anatomical methods. As described in the second approach, we used LiFE to statistically evaluate the evidence of macaque VOF in relation to dMRI signals (Takemura et al., 2017).

Finally, we note that a comparison between anatomical studies and tractography itself still has significant challenges. Studies comparing tractography and anatomical tracers often draw completely different conclusions regarding the degree of correlation between the two measurements (Aydogan et al., 2018; Azadbakht et al., 2015; Donahue et al., 2016; Thomas et al., 2014; van den Heuvel et al., 2015). We believe that these apparently conflicting conclusions are largely derived from the fact that different groups are testing different tractography methods, while also using different types of tracer data with respect to (a) tracer types, (b) selections of injection sites, and (c) quantification methods. We stress that data sharing and open science will continue to enable independent laboratories to test different methods and the scientific community can carefully evaluate problems arising from method selections as we have done with the VOF and the connections with visual field maps in our previous work (Takemura et al., 2017).

7. Concluding remarks

In this paper, we have reviewed how recent advanced neuroimaging methods of white matter and classical neuroanatomical studies of connectivity can be incorporated together to provide insights regarding the comparative anatomy of the VOF. While we focus on the human-macaque comparison of the VOF, the same approach can be applied to other white matter tracts across species. In this comparative approach, we also stress the importance of the classical literature in providing additional support for similarities and differences in microstructural and macroanatomical features of white matter across species. Additionally, despite the fact that dMRI and tractography may have some limitations, comparative dMRI studies with the combination of (a) careful understanding of the historical and modern literature of invasive anatomical methods in humans and macaques, (b) novel statistical evaluation methods, and (c) open sharing of data and methods (Glasser et al., 2016; Majka et al., 2016; Milham et al., 2018; Reveley et al., 2017; Woodward et al., 2018) has the potential to help overcome these limitations. We believe this combination will continue to advance dMRI-comparative approaches moving forward beyond vertical association connections in visual cortex. Future studies implementing a comparative dMRI approach as we review here will continue to advance our knowledge regarding what neuroanatomical features of the brain are shared with other species, as well as what features are uniquely human.

Competing financial interests

The authors declare no competing financial interests associated with this article.

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