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One tract, two tract, old tract, new tract: A pilot study of the structural and functional differentiation of the inferior fronto-occipital fasciculus

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ABSTRACT

The inferior fronto-occipital fasciculus (IFOF), a major ventral white matter pathway, has been shown to be a crucial component of semantic (Moritz-Gasser, Herbet & Duffau, 2013) and lexical/orthographic (Vandermosten, Boets, Polemans, Sunaert, Wouters & Ghesquière, 2012) processing. However, recent anatomical studies of the brain have revealed at least two differentiable components of the IFOF: a dorsal component projecting from the frontal lobe to the superior parietal lobule and a ventral component connecting the frontal lobe with the inferior occipital gyrus and posterior temporal lobe (Martino, Brogna, Robles, Vergani & Duffau, 2010). We have replicated this anatomical division using a deterministic tractography protocol in DTI Studio with high inter-rater reliability (ICC $>$ 0.9). Furthermore, we provide the first evidence of a functional distinction between these two components. We compared diffusion measures (fractional anisotropy [FA], as well as MD, AD, RD) with reaction times on five different reading tasks: basic naming of pure exception words, regular words, and mixed exception/regular words, and go/no-go tasks involving either pseudohomophone or nonword foils. We found a functional divide in the left IFOF, whereby dorsal FA was correlated with performance on tasks that required higher levels of visual attention and response selection (go/no-go and mixed naming tasks), while ventral FA was more broadly correlated with naming performance. This suggests that the anatomical distinction described by Martino et al. (2010) is indeed mirrored by a functional distinction, and indicates that future investigations of neuroanatomical models of reading and speech production should consider the dorsal and ventral IFOF as separate entities.

1. Introduction

Detailed parsing of white matter tracts is becoming increasingly common. For example, the arcuate fasciculus (AF) is now frequently characterized as consisting of at least three major sub-components (Catani & Schotten, 2008, Catani, Jones, & Ffytche, 2005; Makris et al., 2005). These distinctions have proven fruitful, as recent studies have found the different AF components to be associated with separate behavioural functions (Makris et al., 2005; Vandermosten et al., 2012). Thus, detailed tract breakdown can contribute to more specific and accurate predictive modeling of how damage or poor development of each segment may impact functional capacity (Fridriksson, Guo, Fillmore, Holland, & Rorden, 2013; Gullick & Booth, 2015; Ramsey et al., 2017). For example,

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while it is known that damage to the AF after stroke leads to language deficits, a recent large lesion study indicated that posterior AF damage is specifically predictive of poor language outcomes (Ramsey et al., 2017). In the future, this knowledge may be used to better plan surgical treatments and predict individual outcomes, particularly in the field of neuro-oncology (Voets, Bartsch, & Plaha, 2017). Such tract decomposition has recently been applied to the inferior fronto-occipital fasciculus (IFOF; Martino et al., 2010) and the findings indicate that distinguishing between a dorsal and ventral IFOF is not only feasible, but may similarly allow for greater functional specificity in studies of white matter and language.

1.1. Anatomy of the IFOF

Multiple post-mortem studies have been able to clearly delineate the IFOF, which directly connects occipito-temporal (and parietal) areas to the frontal lobe through the external/extreme capsule region (Curran, 1909; Davis, 1921; Hultkrantz, 1929; Crosby, Humphrey, & Lauer, 1962; Ebeling & von Cramon, 1992; Kier, Staib, Davis, & Bronen, 2004). Catani, Howard, Pajevic, and Jones (2002) performed the first comprehensive in vivo study of human white matter tracts, to compare to previous post-mortem results. Using diffusion tensor magnetic resonance tractography, they were able to clearly delineate the IFOF, projecting from the inferior-lateral and dorsal-lateral frontal cortex to the posterior temporal cortex and the occipital lobe. These results were widely replicated in other diffusion tensor tractography studies, showing very similar anterior and posterior terminations (Catani & de Schotten, 2008; Lawes et al., 2008; Mori et al., 2002; Wakana, Jiang, Nagae-Poetscher, Van Zijl, & Mori, 2004). More recent anatomical studies have demonstrated not only diverse connectivity in the IFOF, but also several discernible components (Caverzasi, Papinutto, Amirbekian, Berger, & Henry, 2014; Martino et al., 2010; Sarubbo, De Benedictis, Maldonado, Basso, & Duffau, 2013), which have raised questions about the separability of the IFOF into multiple sections.

Martino et al. (2010) were the first to suggest a differentiation between a dorsal and ventral IFOF. In their post-mortem study, they discovered that the IFOF could be separated into two easily distinguishable components at the ventral portion of the external capsule. The dorsal (superficial) component projected from the frontal operculum to the superior parietal lobule and superior/middle occipital gyri, while the ventral (deep) component projected to the posterior/basal temporal region (inferior temporal gyrus, temporal-occipital sulcus) and the inferior occipital gyrus.

Most recently, Caverzasi et al. (2014), Hau et al. (2016), and Wu, Sun, Wang, and Wang (2016) have conducted larger scale in vivo studies of this white matter tract. Using Q-ball reconstruction of High-Angular Resolution Diffusion Imaging, Caverzasi et al. (2014) not only revealed much more complex anterior connectivity than had previously been described, but they found that a dorsal component of the IFOF did appear to project into the superior parietal lobule in all participants. Hau et al. (2016) was not able to delineate superior parietal lobe projections in all participants, possibly due to the fact that the long streamlines did not always reach their posterior site of termination, but they did find projections to this region in the majority (57%) of participants. Wu et al. (2016) similarly found significant inter-subject variability in the connectivity of the IFOF, with a maximum overlap of 40% in the central portion of the tract running from the orbito-frontal, frontal polar, superior and inferior frontal cortices to the occipital, fusiform, and pericalcarine regions. As with Hau et al. (2016), they were only able to distinguish superior parietal terminations in 50% of the studied hemispheres. While these studies reveal the individual variability in cortical terminations of the IFOF, they also provide strong evidence for the validity of the findings in Martino et al. (2010) and demonstrate the feasibility of delineating a dorsal and ventral IFOF in vivo.

1.2. IFOF and language

Current neurophysiological models of language distinguish between a dorsal (occipital-parietal-frontal) pathway and a ventral (occipital-temporal) pathway (Cohen, Dehaene, Vinckier, Jobert, & Montavont, 2008; Hickok & Poeppel, 2004; Indefrey & Levelt, 2004; Saur et al., 2008). Although the most recent versions of this framework currently describe parallel processing streams in speech and auditory language comprehension, the original theories of dorsal/ventral processing originated in visual-based models with primates (Mishkin & Ungerleider, 1983) and individuals with brain damage (Milner & Goodale, 1993). This dorsal/ventral visual processing theory attributed the ventral visual pathway to object identification and the dorsal visual pathway to spatial/action based processes. Researchers using fMRI methodologies have supported this distinction with the ventral pathway being linked to tasks that include processing highly familiar stimuli, for example, high frequency words (Cohen et al., 2008; Jobard, Crivello, & Tzourio-Mazoyer, 2003) or to the completion of tasks that require semantic information, for example, text comprehension (e.g., Saur et al., 2008; see also Dick & Tremblay, 2012). In contrast, these same fMRI studies provide evidence that the dorsal pathway forms a parallel stream that is particularly sensitive to higher-order linguistic tasks, such as processing of unfamiliar stimuli (e.g., rotated words; Cohen et al., 2008), and/or tasks that are highly reliant on phonological decoding/sequencing (e.g., overt pronunciation of nonwords [letter strings that do not spell or sound like a real word]; Jobard et al., 2003). In other words, while the ventral system is ideal for quickly recognizing and extracting meaning from text under regular circumstances, the dorsal stream supplements the ventral stream by allowing for the break down and processing unusual or unfamiliar text.

To date, the IFOF has been generally thought to be the major direct pathway underlying the ventral stream described above (Duffau, Herbet, & Moritz-Gasser, 2013). In line with this hypothesis, dysfunction in this region can have a significant negative effect on reading and semantic processes. For example, electrostimulation of this tract causes severe semantic paraphasias (Duffau, 2008; Duffau et al., 2005; Gil-Robles et al., 2013; Mandonnet, Nouet, Gatignol, Capelle, & Duffau, 2007) as well as impairments in semantic tasks, such as picture naming (Moritz-Gasser et al., 2013). Lesions to this region similarly cause impairments in both semantic fluency (Almairac, Herbet, Moritz-Gasser, de Champfleur, & Duffau, 2014) and object naming/association tasks (Han et al., 2013).