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Using *in vivo* probabilistic tractography to reveal two segregated dorsal 'language-cognitive' pathways in the human brain ☆

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ABSTRACT

Primate studies have recently identified the dorsal stream as constituting multiple dissociable pathways associated with a range of specialized cognitive functions. To elucidate the nature and number of dorsal pathways in the human brain, the current study utilized *in vivo* probabilistic tractography to map the structural connectivity associated with subdivisions of the left supramarginal gyrus (SMG). The left SMG is a prominent region within the dorsal stream, which has recently been parcellated into five structurally-distinct regions which possess a dorsal–ventral (and rostral-caudal) organisation, postulated to reflect areas of functional specialisation. The connectivity patterns reveal a dissociation of the arcuate fasciculus into at least two segregated pathways connecting frontal-parietal-temporal regions. Specifically, the connectivity of the inferior SMG, implicated as an acoustic-motor speech interface, is carried by an inner/ventro-dorsal arc of fibres, whilst the pathways of the posterior superior SMG, implicated in object use and cognitive control, forms a parallel outer/dorso-dorsal crescent.

1. Introduction

Although traditionally conceptualized as a single processing stream, recent evidence from studies of both humans and non-human primates has identified dissociable parallel components in the dorsal pathway, each associated with a different cognitive and language function (Binkofski & Buxbaum, 2012; Catani, Jones, & ffytche, 2005; Catani et al., 2007; Isenberg, Vaden, Saberi, Muftuler, & Hickok, 2012; Kravitz, Saleem, Baker, & Mishkin, 2011; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006). Within the visuo-motor domain, at least three separate dorsal pathways have been postulated in the non-human primate brain, including a parieto-prefrontal pathway involved in visuospatial processing, a parieto-premotor pathway involved in the visual guidance of action, and a parieto-temporal pathway involved in spatial navigation (Kravitz et al., 2011). Within the human brain, there is also evidence of a division of the dorsal pathway into two subdivisions, one involving the superior parietal lobe, specialised for online actions directed at a visual stimulus based on its structural properties (i.e., reaching and grasping), and one involving the inferior parietal lobe, specialised for actions related to an object's functional properties (Binkofski & Buxbaum, 2012). However, there is evidence that further dissociations of the dorsal stream, specifically that involving the inferior parietal lobe, may be present, particularly in the linguistic domain (Catani et al., 2005; Catani et al., 2007; Friederici, 2009; Friederici, 2011; Glasser & Rilling, 2008). Studies have found the arcuate fasciculus (AF), a major dorsal language tract, to be composed of two parallel pathways, including a 'direct' connection between Broca's and Wernicke's areas (corresponding to classical conceptualizations of the AF), and an 'indirect' connection between the two regions mediated via the inferior parietal cortex (Catani et al., 2005; Catani et al., 2007). Catani et al. (2005), Catani et al. (2007) postulated that the dissociable AF pathways were associated with separable linguistic functions, with the direct pathway underlying phonological processing and sound-to-motor mapping, and the indirect pathway supporting higher level lexical-semantic language processes.

However, there is some evidence that the anatomical divisions of the AF, specifically the 'indirect' frontal-parietal-temporal segment, may be more complex. A dorso-dorsal/ventro-dorsal division of connectivity has been identified in the monkey inferior parietal cortex, with rostral regions connecting via ventro-dorsal pathways and caudal regions via more dorso-dorsal routes (Gregoriou, Borra, Matelli, & Luppino, 2006; Schmahmann & Pandya, 2006). There is some initial evidence that such an organization may also be

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present in the human brain. A recent study which examined human inferior parietal connectivity via cortico-cortical evoked potentials revealing connections from dorsal and ventral parietal regions to corresponding dorsal and ventral premotor and inferior frontal regions (Matsumoto et al., 2012). This dorso-dorsal/ventro-dorsal organization is also mirrored in functional dissociations, with divisions observed within the left supramarginal gyrus (SMG) associated with cognitive control (dorsal) and phonological encoding-recoding (ventral) (Ravizza, Delgado, Chein, Becker, & Fiez, 2004).

The left SMG is a prominent region within the dorsal stream and is an important relay between frontal and temporal brain regions via fibre tracts including the AF (Catani et al., 2005; Catani et al., 2007; Frey, Campbell, Pike, & Petrides, 2008; Parker et al., 2005). Structurally, the SMG has been found to possess a complex cytoarchitecture, and has recently been parcellated using modern techniques into five structurally-distinct regions, roughly organized into a dorsal row of three areas (PFt, PF, PFm) and a ventral group of two entering into the Sylvian fissure (PFop, PFcm; Caspers et al., 2006; Caspers et al., 2008; see Fig. 1). Functional imaging and lesion studies have identified the left SMG to be equally functionally complex, associated with a wide range of cognitive tasks including spatial perception, mental imagery, visuomotor control, motor skill learning and cognitive control (Cabeza & Nyberg, 2000; Nickel & Seitz, 2005; Table 1). An inspection of the functions ascribed to the different cytoarchitectural regions presented in Table 1 reveals a complicated picture, and the mapping between the structural divisions and areas of functional specialisation is by no means one-to-one. Many functional similarities can be indentified across the five SMG sub-regions, however, close examination reveals some potentially informative differences. For example, all subregions appear to be heavily implicated in motor functioning. However, while the dorsal cytoarchitectonic regions are associated with motor planning and execution more generally, the ventral regions appear to be more strongly associated with orofacial movement more specifically.

Both classical and contemporary studies have implicated the left SMG in a variety of language functions, including naming (De-Leon et al., 2007; Pei. et al., 2011), reading (Cloutman, Newhart, Davis, Heidler-Gary, & Hillis, 2011; Hillis et al., 2001), spelling (Cloutman et al., 2009), repetition (Fridriksson et al., 2010), and verbal working memory (Cabeza & Nyberg, 2000). However, the left SMG's roles in language are unclear. Some studies have suggested a role in multimodal sensory integration and semantic processing (Binder, Desai, Graves, & Conant, 2009), others have implicated the SMG in auditory-motor controlled mappings and phonological processing (Rauschecker & Scott, 2009), while others have argued that the left SMG may be only minimally involved in language, if at all (Glasser & Rilling, 2008). Our working hypothesis for this study was that, rather than being mutually exclusive and rival interpretations of left SMG function, this variation probably reflects the existence of dissociated dorsal pathways between different subregions of the left SMG. However, the underlying neural connectivity of the SMG in humans, and its potential structural–functional subdivisions remain poorly understood.

The current study utilized probabilistic tractography to explore the neural connectivity of the human left SMG, comparing seed regions within the dorsal and ventral SMG. Seed regions for tracking were defined based on the SMG's underlying cytoarchitecture. The dorsal–ventral nature of the recently defined cytoarchitectural divisions makes these regions useful boundaries in the definition of seed regions for tracking. In addition, both cellular microstructure and neural connectivity are heavily implicated in determining the functional specialization of a region. Cytoarchitecture determines a region's local processing capabilities whilst its connectivity governs the nature and flow of information to and from an area (Behrens & Johansen-Berg, 2005). Primate studies have observed that functionally and cytoarchitectonically distinct brain regions appear to be associated with distinct cortico-cortical connection patterns, suggesting a strong relationship between brain connectivity and cellular microstructure (Passingham, Stephan, & Kotter, 2002; Rozzi et al., 2006). Importantly, a recent study which utilized tractography to map the underlying anatomical connectivity of the superior (dorsal) SMG (and angular gyrus), found differing patterns of connectivity across the different cytoarchitectural regions explored (Caspers et al., 2011). As such, exploring the connectivity profiles of the five SMG cytoarchitectural regions may help to reveal important differences in its underlying neuroanatomical connectivity, and the existence of separable dorsal stream pathways within the human brain.

2. Materials and methods

2.1. Participants and image acquisition

Thirteen participants (4 females; mean age = 23.3, range = 19–37) gave written informed consent to participate in the study,

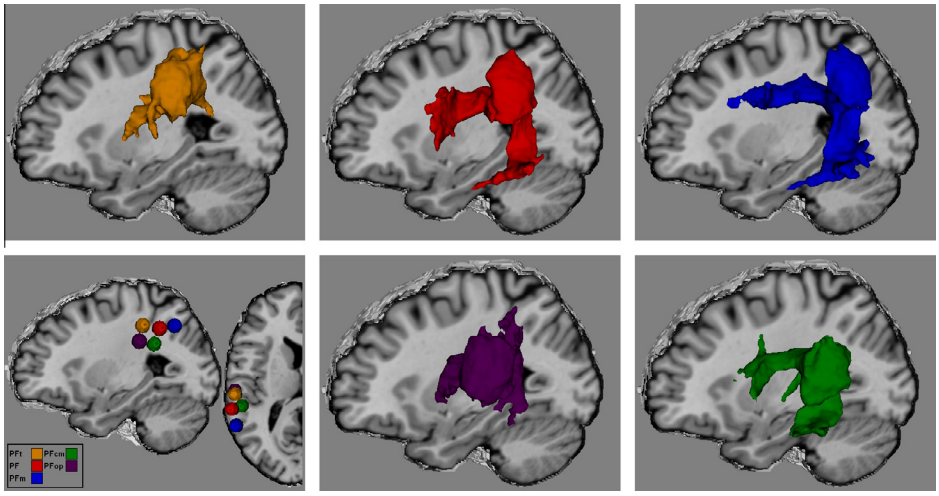

Fig. 1. Location of the five left SMG cytoarchitectonic areas used as seed regions for probabilistic tracking (bottom left), depicting the three dorsal SMG regions PFt (orange), PF (red), and PFm (blue), and the two ventral SMG regions PFcm (green) and PFop (purple). Fibre pathways found for each tractographic region are presented. The tracts depicted represent the combined group tracking results (including only those pathways that passed the first-level, i.e., individual subject-level, threshold), transformed into standard MNI space.