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Q8 Cross-talk connections underlying dorsal and ventral stream integration during hand actions

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ABSTRACT

According to the dual-stream theory, the processing of visual information is divided into a ventral pathway mediating object recognition, and a dorsal pathway supporting visuomotor control. Increasing evidence suggests that these streams are not independent, but where this dorsal-ventral stream integration occurs, in the context of hand actions, remains unknown. We explored the candidate white matter pathways linking dorsal and ventral visual streams in 30 right-handed participants performing hand movements of varying complexity (reaching, grasping and lifting), using advanced diffusion imaging tractography based on the spherical deconvolution and kinematical analysis. We provided for the first time a direct evidence of cross-communication between dorsal and ventral visual streams in humans, through vertical occipital fasciculus and temporo-parietal fibers of the arcuate fasciculus during on-line control of skilled object-oriented hand actions. We showed that individual differences in the microstructure of these cross-talk connections were associated with the variability of arm deceleration, the grip opening phase and the grasp accuracy. This study suggests that hand kinematics, in skilled hand actions where high degree of online control is required, is related to the anatomy of the dorsal-ventral networks, bringing important insights to the dual-stream theory and the sensorimotor organization of hand actions.

Q1 1. Introduction

When we reach, grasp and lift an object, fast integration of sensory information is crucial for performing the movement successfully. According to a dual-stream theory, the processing of visual information is divided into a ventral 'perception' pathway extending to the inferotemporal cortex that mediates object recognition, and a dorsal 'action' pathway projecting to the posterior parietal cortex that supports visuomotor control (Goodale, 2014; Milner & Goodale, 2008; Rizzolatti & Matelli, 2003; Ungerleider & Mishkin, 1982). While a degree of functional specialization and segregation invariably exists

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between the two streams, information processed by the two networks must closely interact in everyday life, especially for more complex behavior such as skilled hand actions (Cloutman, 2013; Milner, 2017; van Polanen & Davare, 2015). Nevertheless, little attention has been payed to how, where, and when the dual streams interact.

Significant insights first emerged from anatomical tract tracing studies in monkeys, describing direct reciprocal interconnections between the two visual streams. For example, ventral inferior temporal area TE has strong bidirectional projections to the inferior parietal lobe (Zhong & Rockland, 2003) and prefrontal cortex (Borra, Ichinohe, Sato, Tanifuji, & Rockland, 2010; Gerbella, Belmalih, Borra, Rozzi, & Luppino, 2010), while the anterior intraparietal sulcus is interconnected to the superior and middle temporal gyri of the ventral stream (Borra et al., 2008). Similarly, diffusion magnetic resonance imaging (MRI) studies in humans reported white matter tracts between superior/middle temporal and inferior parietal regions (Budisavljevic et al., 2015; Catani et al., 2007, 2005) and between dorsal and ventral occipital visual areas (Yeatman, Rauschecker, & Wandell, 2013, 2014). Thus, anatomy points to inter-stream communication that could underlie integration between the two visual pathways. From a functional point of view, studies of the time course and laminar activation profiles in the monkey brain, showed that the two networks engage in a direct cross-talk at multiple stages, at least within the visual domain (Chen et al., 2007; Givre, Schroeder, & Arezzo, 1994; Oram & Perrett, 1996; Schroeder, Mehta, & Givre, 1998). Similarly, functional MRI studies in humans observed that the two streams are not independent, since they exhibit strong functional connectivity during object recognition processes (Freud, Rosenthal, Ganel, & Avidan, 2015; Sim, Helbig, Graf, & Kiefer, 2015) and likely communicate regarding the visual and motor dimensions relevant for the execution of hand actions (Bracci & Peelen, 2013; Fabbri, Stubbs, Cusack, & Culham, 2016; Konen & Kastner, 2008; Mahon, Kumar, & Almeida, 2013; Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010).

Overall, evidence suggests that the integration between the two streams occurs at different levels, including i) shared target brain regions (e.g., prefrontal cortex), ii) feedback loops, and iii) by 'continuous cross-talk' at multiple stages and locations through direct lateral connections between the two streams (Cloutman, 2013). This integration might be especially important for more complex actions, when the dorsal stream needs to retrieve detailed information about object identity stored in the ventral stream areas, while the ventral stream receives up-to-date grasp-related information from dorsal areas to refine the object internal representation (van Polanen & Davare, 2015). Up to date, no study has specifically investigated the 'continuous cross-talk' possibility. Our study aims to fill this gap by exploring the candidate cross-talk connections in humans and their role in skilled actions.

Based on the current neuroanatomical models of dual stream processing (Distler, Boussaoud, Desimone, & Ungerleider, 1993; Felleman & Van Essen, 1991; Ungerleider, Galkin, Desimone, & Gattass, 2008) we hypothesized that the vertical occipital fasciculus (VOF) and the posterior segment of the arcuate fasciculus (pAF), both connecting the lateral surfaces of the ventral and dorsal streams, enable the continuous cross-talk between the two visual streams (Fig. 1A). The VOF is the only major white matter pathway allowing the communication between dorsal and ventral visual maps with full hemifield representations (Takemura et al., 2016; Weiner, Yeatman, & Wandell, 2016; Yeatman et al., 2014, 2013). The VOF likely carries signals from the ventral regions that encode object properties such as form, identity, and color (Cohen et al., 2000; Malach et al., 1995; McKeefry & Zeki, 1997; Wade, Brewer, Rieger, & Wandell, 2002; Zeki et al., 1991) to dorsal regions that map spatial location to action plans (Fischer, Bulthoff, Logothetis, & Bartels, 2012; Merriam, Gardner, Movshon, & Heeger, 2013; Tootell et al., 1997). Parallel and anterior to the VOF, the neighbouring pAF is a temporo-parietal pathway intermingled within the arcuate fasciculus fibers, connecting the inferior parietal lobe with the superior and middle temporal gyri (Budisavljevic et al., 2015; Catani et al., 2007, 2005; Ramayya, Glasser, & Rilling, 2010; Thiebaut de Schotten, Cohen, Amemiya, Braga, & Dehaene, 2014). The pAF connections could represent part of a ventro-dorsal network of the extended dual-stream processing model

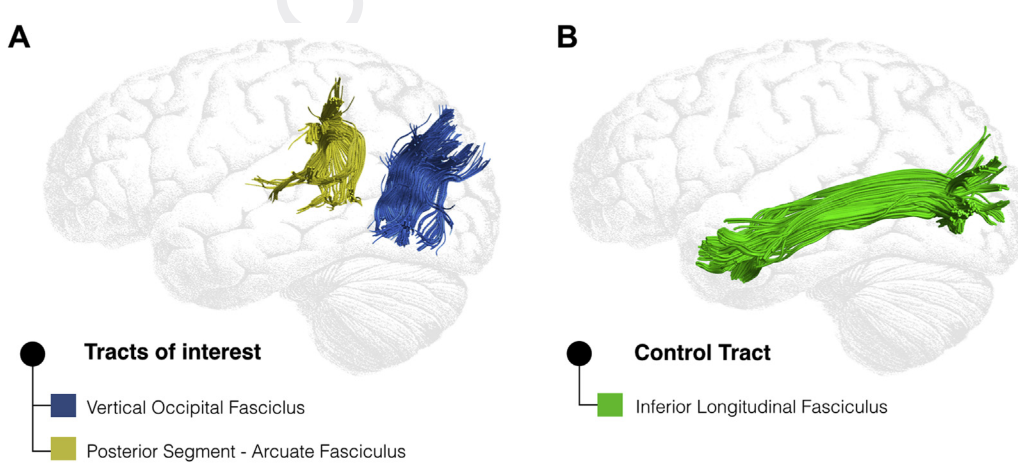

Fig. 1 – Descriptive example of A) the cross-talk connections (tracts of interest) including the VOF (in blue) and the pAF (in yellow); and B) the control tract, ILF in the left hemisphere (in green).

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