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Research report

Human dorsomedial parieto-motor circuit specifies grasp during the planning of goal-directed hand actions

Michael Vesia [a,*], *Michael Barnett-Cowan* [b,c], *Behzad Elahi* [a], *Gaayathiri Jegatheeswaran* [a], *Reina Isayama* [a], *Jason L. Neva* [c], *Marco Davare* [d,e], *W. Richard Staines* [c], *Jody C. Culham* [b] and *Robert Chen* [a]

[a] *Krembil Research Institute, University Health Network and Division of Neurology, University of Toronto, Toronto, ON, Canada*
[b] *Department of Psychology, Brain and Mind Institute, University of Western Ontario, London, ON, Canada*
[c] *Department of Kinesiology, University of Waterloo, Waterloo, ON, Canada*
[d] *Sobel Department of Motor Neurosciences and Motor Disorders, Institute of Neurology, University College London, Queen Square, London WC1N 3BG, United Kingdom*
[e] *Movement Control and Neuroplasticity Research Group, Department of Kinesiology, Biomedical Sciences Group, Katholieke Universiteit Leuven, 3001 Leuven, Belgium*

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ABSTRACT

According to one influential view, two specialized parieto-frontal circuits control prehension: a dorsomedial stream for hand transport during reaching and a dorsolateral stream for preshaping the fingers during grasping. However, recent evidence argues that an area within the dorsomedial stream—macaque area V6A and, its putative human homolog, superior parietal occipital cortex (SPOC) – encodes both hand transport and grip formation. We tested whether planning varied hand actions modulates functional connectivity between left SPOC and ipsilateral primary motor cortex (M1) using a dual-site, paired-pulse transcranial magnetic stimulation paradigm with two coils ($_{ds}$TMS). Participants performed three different hand actions to a target object comprising a small cylinder atop a larger cylinder. These actions were: reaching-to-grasp the top (GT) using a precision grip, reaching-to-grasp the bottom (GB) using a whole-hand grip, or reaching-to-touch (Touch) the side of the target object without forming a grip. Motor-evoked potentials (MEPs) from TMS to M1, with or without preceding TMS to SPOC, were recorded from first dorsal interosseous (FDI) and abductor digiti minimi (ADM) hand muscles in two experiments that varied timing parameters (the stimulus onset asynchrony, SOA, between the 'GO' cue and stimulation and interpulse interval, IPI, between SPOC and M1 stimulation). We found that preparatory response amplitudes in the SPOC-M1 circuit of different hand muscles were selectively modulated early in the motor plan for different types of grasps. First, based on

* *Corresponding author*. 12MC-421, Krembil Research Institute, 399 Bathurst Street, Toronto, ON M5T 2S8, Canada.
E-mail address: mvesia@mac.com (M. Vesia).
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SPOC-M1 interactions, across two experiments, the role of the ADM was facilitated during a whole-hand grasp of a large object (GB) relative to other conditions under certain timing parameters (SOA = 150 msec; IPI = 6 msec). Second, the role of the FDI was facilitated during hand action planning compared to rest. These findings suggest that the human dorsomedial parieto-motor stream plays a causal role in planning grip formation for object-directed actions.

1. Introduction

Object-directed hand actions require the brain to compute the location of the target relative to the hand (transport component) and the posture of the hand and fingers to anticipate the size, shape, and orientation of the object (grip component) well before contact is achieved (Jeannerod, 1981). These different motoric functions are thought to depend on two distinct parieto-frontal circuits (Caminiti, Ferraina, & Mayer, 1998; Culham & Valyear, 2006; Davare, Kraskov, Rothwell, & Lemon, 2011; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Vesia & Crawford, 2012), both of which send output to primary motor cortex (M1) for action execution. The dorsomedial stream, which includes superior parieto-occipital cortex (SPOC), the medial part of the intraparietal sulcus (mIPS), and dorsal premotor cortex (PMd), has been implicated in programming arm transport during reaching (Davare, Zenon, Pourtois, Desmurget, & Olivier, 2011; Vesia, Prime, Yan, Sergio, & Crawford, 2010), selection of wrist posture (Fattori et al., 2009; Monaco et al., 2011), and online control of actions (Grol et al., 2007; Rizzolatti & Matelli, 2003). The dorsolateral stream, which includes a circuit from the caudal intraparietal sulcus (cIPS) to the anterior intraparietal sulcus (aIPS) to ventral premotor cortex (PMv), has been implicated in programming hand grip during grasping (Cavina-Pratesi et al., 2010; Vesia, Bolton, Mochizuki, & Staines, 2013), object awareness and action understanding (Rizzolatti & Matelli, 2003), or actions that require precision (Grol et al., 2007). However, experimental data do not always support this strict functional dichotomy between reaching and grasping organized along dorsomedial and dorsolateral streams.

An alternative view proposes that dorsomedial stream integrates reaching requirements with a goal-directed grasp (Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003; Grafton, 2010). There is growing neurophysiological and neuroimaging evidence indicating that parietal activity within the dorsomedial stream encodes both reaching and grasping movements [*for review see*, (Turella & Lingnau, 2014)]. For example, neural activity in macaque area V6A, a key node within the dorsomedial circuit, is sensitive to reach direction and grasp (Fattori, Breveglieri, Amoroso, & Galletti, 2004; Fattori, Kutz, Breveglieri, Marzocchi, & Galletti, 2005; Fattori et al., 2010). A recent neuroimaging study in humans has also shown that preparatory signals in superior parieto-occipital cortex (SPOC), the putative human homolog of area V6A (Cavina-Pratesi et al., 2010; Pitzalis et al., 2013), encode planned reach-to-touch and reach-to-grasp movements differently (Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011). The functional importance of such activity, however, can be difficult to interpret because these methods cannot determine whether this parietal activation reflects neural processing that is critical for grasp planning or whether it is indirect. An alternative is to use transcranial magnetic stimulation (TMS) in a dual-site paired-pulse paradigm to examine the causal relations of parieto-motor interactions with millisecond resolution using two coils [$_{ds}$TMS; (Koch & Rothwell, 2009; Rothwell, 2010)]. This allows characterization of the flexibility of these connections to change with task demands and examination of the degree to which these cognitive demands influence parietal preparatory signals that shape motor output (Bestmann & Duque, 2015; Vesia & Davare, 2011).

An important, yet unresolved, question is whether processing in human parietal regions within the dorsomedial stream plays a causal role in determining grasping motor parameters before movement onset. We previously showed using paired-pulse $_{ds}$TMS that the dorsomedial SPOC-M1 circuit selectively encodes the transport component (Vesia et al., 2013). However, our experimental design did not vary grip type or examine the time course of prehension-related interactions for different hand muscles in the early motor plan. This is important for several reasons. First, reach-to-grasp actions likely involve dynamic interactions between the transport and grip components (Haggard & Wing, 1995). Second, tasks that are more complex and demanding appear to require greater inter-regional interactions within the dorsomedial circuit (Verhagen, Dijkerman, Grol, & Toni, 2008). Third, parieto-frontal interactions during grasp preparation are muscle-specific (Davare, Lemon, & Olivier, 2008; Davare, Montague, Olivier, Rothwell, & Lemon, 2009; Davare, Rothwell, & Lemon, 2010; Koch et al., 2010). Fourth, given that the dorsomedial stream specifies motor parameters controlling arm, wrist, and finger movements just before movement onset (Fabbri, Strnad, Caramazza, & Lingnau, 2014; Fattori et al., 2010, 2009; Galletti et al., 2003; Gallivan et al., 2011; Monaco et al., 2014, 2011; Verhagen, Dijkerman, Medendorp, & Toni, 2013) and may use feedback to monitor and correct them (Fattori, Breveglieri, Bosco, Gamberini, & Galletti, 2015), we may have simply missed the relative timing of these sensorimotor computations.

Here we address these concerns by using a paired-pulse $_{ds}$TMS approach and task manipulations requiring different hand–object interactions. We manipulated the timing and functional specificity of grasp-related physiological interactions between left SPOC and ipsilateral M1 during the