Neuropsychologia 51 (2013) 410–417

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Human parietal and primary motor cortical interactions are selectively modulated during the transport and grip formation of goal-directed hand actions

Michael Vesia [a,b,*], David A. Bolton [a,b], George Mochizuki [a,c], W.R. Staines [a,b]

[a] Heart and Stroke Foundation Centre for Stroke Recovery, Sunnybrook Health Sciences Centre, Toronto, ON, Canada
[b] Department of Kinesiology and Faculty of Applied Health Sciences, University of Waterloo, Waterloo, ON, Canada
[c] Department of Physical Therapy, University of Toronto, Toronto, ON, Canada

ARTICLE INFO

Article history:
Received 3 July 2012
Received in revised form
29 September 2012
Accepted 19 November 2012
Available online 1 December 2012

Keywords:
Transcranial magnetic stimulation
Frontal cortex
Parietal cortex
Reaching
Grasping
Visuomotor transformations
Sensorimotor control

ABSTRACT

Posterior parietal cortex (PPC) constitutes a critical cortical node in the sensorimotor system in which goal-directed actions are computed. This information then must be transferred into commands suitable for hand movements to the primary motor cortex (M1). Complexity arises because reach-to-grasp actions not only require directing the hand towards the object (transport component), but also preshaping the hand according to the features of the object (grip component). Yet, the functional influence that specific PPC regions exert over ipsilateral M1 during the planning of different hand movements remains unclear in humans. Here we manipulated transport and grip components of goal-directed hand movements and exploited paired-pulse transcranial magnetic stimulation ($_{pp}$TMS) to probe the functional interactions between M1 and two different PPC regions, namely superior parieto-occipital cortex (SPOC) and the anterior region of the intraparietal sulcus (aIPS), in the left hemisphere. We show that when the extension of the arm is required to contact a target object, SPOC selectively facilitates motor evoked potentials, suggesting that SPOC-M1 interactions are functionally specific to arm transport. In contrast, a different pathway, linking the aIPS and ipsilateral M1, shows enhanced functional connections during the sensorimotor planning of grip. These results support recent human neuroimaging findings arguing for specialized human parietal regions for the planning of arm transport and hand grip during goal-directed actions. Importantly, they provide new insight into the causal influences these different parietal regions exert over ipsilateral motor cortex for specific types of planned hand movements.

1. Introduction

Reaching out to grasp an object is an effortless process that engages complex control systems in the parietofrontal network of the brain. This network is composed of cortical interconnected circuits including the posterior parietal cortex (PPC), premotor cortex (PM), and primary motor cortex (M1) (Andersen & Cui, 2009; Davare, Kraskov, Rothwell, & Lemon, 2011; Filimon, 2010). Frontal and parietal areas are strongly interconnected and function together for many aspects of action planning. M1 is a source of motor commands (Evarts & Thach, 1969), whereas PPC is involved in many higher-level aspects of action planning, intention, and decision making (Andersen & Cui, 2009). It is currently unclear, however, how these interconnected brain areas functionally interact in the healthy human, and whether different PPC regions have distinct roles in computing action plans that influence motor output from the ipsilateral M1.

To plan a goal-directed hand action, not only must the brain compute the location of the target relative to the hand, but also the posture of the hand and fingers to anticipate the size, shape, and orientation of the object well before contact is achieved (Grafton, 2010). This goal-directed behaviour is driven by sensory information and depends on behavioural context of the internal motor-goal (Gail & Andersen, 2006). A highly influential theory of visuomotor planning, the two-channel hypothesis (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), proposes that areas located in the posteromedial portion of the intraparietal sulcus (IPS) are involved in the planning of reaching movements, whereas a more anterolateral region of IPS integrates grasp-related information about an object. Specifically, in monkeys the medial intraparietal area (MIP) and area V6A encode a particular direction of reach (Andersen & Buneo, 2002; Fattori, Gamberini, Kutz, & Galletti, 2001; Fattori, Kutz, Breveglieri,

* Corresponding author at: Sunnybrook Health Sciences Centre and University of Waterloo Brain Sciences Research Program 2075 Bayview Avenue Rm. A408 Toronto, ON, Canada M4N 3M5. Tel.: +1 416 480 6100x7289; fax: +1 416 480 5775.
E-mail address: mvesia@mac.com (M. Vesia).

0028-3932/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neuropsychologia.2012.11.022

Marzocchi, & Galletti, 2005), while the anterior intraparietal area (AIP) encodes a particular type of grasp (Baumann, Fluet, & Scherberger, 2009; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Sakata, Taira, Murata, & Mine, 1995). In humans, supporting evidence for this proposed division of labour comes from a recent neuroimaging study (Cavina-Pratesi, Monaco, et al., 2010) that found differences between arm transport and grip formation in distinct parietal regions, namely the superior parieto-occipital cortex (SPOC) and anterior intraparietal sulcus (aIPS), respectively. Similarly, perturbation approaches using transcranial magnetic stimulation (TMS) have causally implicated SPOC in reaching (Busan, Barbera, et al., 2009; Busan, Monti, Semenic, Pizzolato, & Battaglini, 2009; Vesia, Prime, Yan, Sergio, & Crawford, 2010) and aIPS for grasping (Davare, Andres, Clerget, Thonnard, & Olivier, 2007; Tunik, Frey, & Grafton, 2005; Rice, Tunik, & Grafton, 2006), but did not probe their 'connectivity' with other regions within the circuit. In spite of this, there is also evidence that challenges the independence of the two components (Fattori et al., 2009; Fattori et al., 2010; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011).

These findings, however, offer little insight into whether these parietal regions exert a pivotal or merely subsidiary influence over other nodes of the cortical reach-to-grasp network (Vesia & Davare, 2011). Recent advances in TMS techniques, using paired-pulse TMS protocols ($_{pp}$TMS), have shown it is possible to study cortico-cortical interactions with millisecond resolution in a 'two-node' neural circuit using two coils (Koch & Rothwell, 2009; Rothwell, 2011). For instance, $_{pp}$TMS has been used to probe causal connectivity between PPC, PM, and M1 (Baumer et al., 2006; Civardi, Cantello, Asselman, & Rothwell, 2001; Koch et al., 2007; Mochizuki, Huang, & Rothwell, 2004). Importantly, it can also be exploited to test whether or not these connections can be modulated by task demands (Buch, Mars, Boorman, & Rushworth, 2010; Davare, Montague, Olivier, Rothwell, & Lemon, 2009; Davare, Lemon, & Olivier, 2008; Davare, Rothwell, & Lemon, 2010; Koch et al., 2008, 2010; O'Shea, Sebastian, Boorman, Johansen-Berg, & Rushworth, 2007; Ziluk, Premji, & Nelson, 2010).

Here, we combined $_{pp}$TMS with two tasks: touching or grasping a peripheral object placed near or far from the starting hand location. With this task manipulation we aimed to isolate PPC-M1 interactions before movement onset that are functionally specific to processes associated with either transport or grip components of object-directed hand actions. We predicted that interactions between SPOC-M1 are selectively modulated during the planning of arm transport, whereas aIPS-M1 connections are specialized for hand grip. The present experiment tested this for the first time in humans, examining how such connections at rest might vary with motor context.

2. Materials and methods

2.1. Subjects

Seven right-handed (Oldfield, 1971) volunteers (four females and three males; aged 22–38 years) participated in all experiments after providing written informed consent. All participants were in good health with normal or corrected-to-normal visual acuity and, according to self-report, without any known contraindications to TMS (Keel, Smith, & Wassermann, 2001). All experimental procedures received ethical approval by the Office of Research Ethics at the University of Waterloo and conformed to the Declaration of Helsinki.

2.2. Experimental procedures

Although the transport component of reach movements depends on the activity of muscles acting at the shoulder joint, both arm transport (Koch et al., 2008) and precision grip (Davare et al., 2009, 2010; Koch et al., 2010) movements selectively activate the first dorsal interosseous (FDI) muscle and motor evoked potentials (MEPs) can be measured reliably from this muscle compared to proximal shoulder muscles; thus, we recorded surface electromyographic (EMG) muscle activity from the right hand of FDI using 9 mm diameter, Ag–AgCl surface-cup electrodes. The active electrode was placed over the muscle belly and the reference electrode over the metacarpophalangeal joint of the index finger. EMG was amplified 1000×, band-pass filtered between 2 Hz and 2.5 kHz (Intronix Technologies Corporation Model 2024F, Canada), digitized at 5 kHz by an analogue-to-digital interface (Micro1401, Cambridge Electronics Design, Cambridge, UK), and then recorded by a computer using SIGNAL software (Cambridge Electronic Devices, Cambridge, UK) and stored for off-line analysis.

2.3. Transcranial magnetic stimulation

To investigate PPC-M1 interactions in the left hemisphere, we used a paired-pulse stimulation technique (Rothwell, 2011) using two custom-made figure-of-eight branding coils (inner diameter, 50 mm) connected to two Magstim 200^2 stimulators and held in position on the scalp surface by articulated coil stands (Magstim, Whitland, UK). The magnetic stimulus had a nearly monophasic pulse configuration with a rise time of ~100 μs, decaying back to zero over ~0.8 ms. The test stimulus (TS) was delivered over M1 through a coil placed tangentially to the scalp at a 45° angle to the mid-sagittal line to induce a posterior–anterior current flow across the central sulcus (Fig. 1**A**). The conditioning stimulus (CS) was delivered over each PPC site (SPOC or aIPS) in the left hemisphere through another coil held tangential to the scalp surface along a parasagittal line and slightly medial (~15°) to induce a posterior–anterior-directed current in the underlying cortical tissue (Fig. 1**A**). This orientation was chosen to allow positioning of both coils over the same hemisphere. The CS and TS stimuli were set at 90% and 120% of the resting motor threshold (rMT), respectively (Koch et al., 2007). Interstimulus intervals (ISI) between CS and TS were 4, 6, 8, or 10 ms. TS alone was delivered in one out of five trials, and MEP amplitudes measured in this condition were used as baseline values. We defined rMT as the lowest intensity that evoked five small responses ($\geq$50 μV peak-to-peak) in the contralateral FDI muscle in a series of 10 stimuli when the subject kept FDI muscles relaxed in both hands (Rossini et al., 1994). The average rMT was 41.4% ± 3.9 of maximal stimulator output across sessions. The frequency, intensity, and duration of the TMS pulses were well within safe limits (Machii, Cohen, Ramosestebanez, & Pascual-Leone, 2006; Rossi, Hallett, Rossini, & Pascual-Leone, 2009; Wassermann, 1998).

2.4. Localization of brain sites

To identify loci of interest and monitor the TMS coil position, we used frameless stereotaxic neuronavigation (Brainsight; Rogue Research, Canada). Before testing in the behavioural sessions, we acquired a T1-weighted, high-resolution MRI from each participant using a 3 T scanner (General Electric Healthcare, Waukesha, WI, USA). First, we defined the hand motor area of the left M1 as the point where stimulation evoked the largest MEP from the contralateral FDI muscle. The coregistration confirmed that the M1 site overlapped the hand knob (Yousry et al., 1997). Next, we selected two different parietal stimulation sites in the left hemisphere: superior parieto-occipital cortex (SPOC) and a region over the anterior intraparietal sulcus (aIPS). Both parietal sites were localized according to individually determined anatomical landmarks. In particular, SPOC (Fig. 1**B**) was defined as a region situated along the medial surface of the

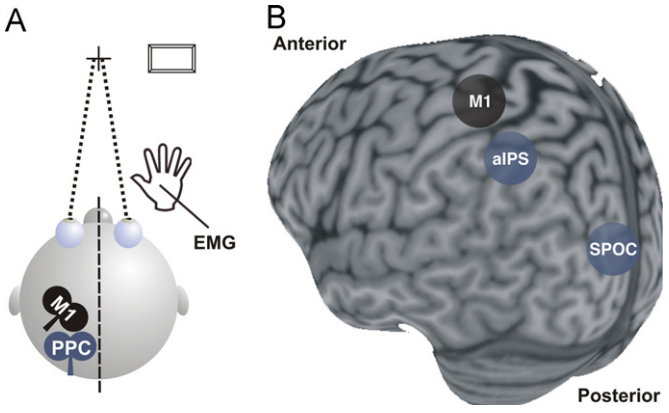

Fig. 1. A, Schematic representation of the paired-pulse TMS protocol used to probe functional interactions between PPC and M1. A conditioning pulse (90% rMT) is applied to PPC to examine its effect on a subsequent suprathreshold (120% rMT) test pulse to M1 during task-specific demands. Any possible change in the amplitude of the right hand muscle response to TMS is measured with electromyography (EMG). **B**, Location of stimulation points over M1 (black ellipse) and PPC sites (blue ellipses), namely SPOC and aIPS, in the left hemisphere. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)