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The role of dorsal premotor cortex in mental rotation: A transcranial magnetic stimulation study

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ABSTRACT

Although activation of dorsal premotor cortex (PMd) has been consistently observed in the neuroimaging studies of mental rotation, the functional meaning of PMd activation is still unclear and multiple alternative explanations have been suggested. The present study used repetitive transcranial magnetic stimulation (rTMS) to investigate the role of PMd in mental rotation. Two tasks were used, involving mental rotation of hands and abstract objects, with either matching (*same* stimuli) or *mirror* stimuli.

Compared to sham stimulation, TMS over right and left PMd regions significantly affected accuracy in the object task, specifically for the *same* stimuli. Furthermore, response times were longer following right PMd stimulation in both the object and the hand tasks, but again, selectively for the *same* stimuli.

The effect of rotational angle on response times and accuracies was greater for the *same* stimuli. Moreover TMS over PMd impaired the performance accuracy selectively in these stimuli, mainly in a task that included abstract objects. For these reasons, the present findings indicate a contribution of PMd to mental rotation.

1. Introduction

In mental rotation tasks, participants typically judge whether two object stimuli presented at different orientations are identical or mirror images of each other. The intriguing finding, first described by Shepard and Metzler (1971) and often observed in these tasks, is that response times (RTs) increase linearly with greater angular disparity between objects. Such pattern of results suggests that individuals manipulate objects in their mind in a similar way as they would physically rotate the objects.

More recent studies have focused on exploring brain regions and networks involved in mental rotation using a variety of human brain research techniques, such as functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS) and event-related potentials (ERPs) (e.g., Bode, Koeneke, & Jäncke, 2007; Cona, Marino, & Semenza, 2016; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Milivojevic, Hamm, & Corballis, 2009a; Tomasino, Borroni, Isaja, & Rumiati, 2005; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002; Wraga, Shephard, Church, Inati, & Kosslyn, 2005; see Zacks, 2008, for a meta-analysis of fMRI studies). Such studies revealed that the posterior parietal regions play a crucial role in mental rotation (e.g., Harris & Miniussi, 2003; Parsons, 2003; Zacks, 2008). The parietal lobe is thought to map the transformation parameters composing the imagined rotation and to use these visuo-motor coordinates to generate a representation that would guide the appropriate movement (Harris & Miniussi, 2003; Snyder, Batista, & Andersen, 2000). As several behavioral studies showed that motor processes support imagery of (covert) movements for mentally rotating objects (e.g., Wexler, Kosslyn, & Berthoz, 1998; Wohlschläger, 2001), great attention has also been directed to the role of primary motor cortex (M1). Yet, the involvement of M1 remains contradictory. While several studies found a substantial contribution of M1 to mental rotation processes (e.g., Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Pelgrims, Michaux, Olivier, & Andres, 2011; Tomasino et al., 2005), others found no involvement of M1 areas (Cona et al., 2016; Sauner, Bestmann, Siebner, & Rothwell, 2006), or considered M1 activation in these tasks as an epiphenomenon and/or a 'spill over' effect of activations from the connected and adjacent brain regions, such as the supplementary motor area (SMA) and the premotor regions (Bode et al., 2007; Eisenegger, Herwig, & Jäncke, 2007). A recent TMS study showed indeed that the SMA is causally involved in mental rotation and supports sequence processing routines required to update and integrate the spatial coordinates of the to-be-rotated stimuli (Cona et al., 2016).

Involvement of premotor regions (BA 6) has also been shown in a

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variety of studies, but the functional meaning of premotor activations during mental rotation tasks is still under debate (e.g., Lamm, Windischberger, Moser, & Bauer, 2007; Wraga et al., 2005; Zacks, 2008), thus multiple hypotheses have been proposed so far. According to the *motor imagery account*, activity in dorsal premotor cortex (PMd) would reflect the imagining of limb movements. For instance, participants would imagine utilizing their hands to rotate the objects, or rotating their own hands if the experimental stimuli were images of hands (Kosslyn, Ganis, & Thompson, 2001; Vingerhoets et al., 2002; Wraga et al., 2005). PMd activation was also interpreted referring to the *affordance theory*, which states that the mere visual presentation of graspable objects can elicit the representation of the actions that can be executed with these objects (Gibson, 1979; Tucker & Ellis, 1998). Based on this theory, PMd activation would be automatically triggered by the presentation of graspable objects (Grèzes & Decety, 2001). Other interpretations attributed PMd activity during mental rotation to preparation and execution of *eye movements* (Carpenter, Just, Keller, Eddy, & Thulborn, 1999), or to the *anticipation of movement consequences* (Wolpert & Kawato, 1998). In this case, PMd activity would underpin aspects of motor control - such as movement planning, preparation and execution - that are similar to those occurring during the actual movement. Finally, most recent studies provided some compelling evidence that PMd activity may not be related to motor processes per se, as previously thought, but may subserve more “cognitive” processes that are specifically related to mental rotation (Lamm et al., 2007; Richter et al., 2000; Sack et al., 2008; Tanaka, Honda, & Sadato, 2005). For example, findings from an fMRI experiment, elegantly designed to assess the functional involvement of the PMd at various stages of mental rotation, revealed that PMd subserves mental rotation processes proper, as the mapping of visuospatial sensory coordinates with the motor acts required to rotate the objects, and the updating of such mapping (Lamm et al., 2007).

Taken together, such views did not lead to a coherent and unitary explanation of the kind of information and computational steps processed in PMd regions during mental rotation. This puzzling inconsistency might be due to heterogeneity of the stimuli and paradigms employed in these studies. Furthermore, all the studies that have focused on investigating the role of PMd regions in mental rotation used fMRI or PET, which are by definition correlational techniques. Therefore, no study so far has clearly tested whether activation of PMd regions has a causal role in mental rotation processes or whether it is merely epiphenomenal to them.

To address this issue, we used repetitive transcranial magnetic stimulation (rTMS) to explore the contribution of PMd regions to mental rotation. TMS is typically used to temporarily and non-invasively disrupt the activity of a restricted cortical area in order to observe the resulting behavioral effects (Walsh & Cowey, 2000, *for a review*).

In our study, short trains of rTMS pulses were applied over left and right PMd while participants were engaged in two distinct tasks involving, respectively, mental rotation of hands and of abstract objects (similar to the classical Shepard-Metzler cubes).

This experiment was designed to investigate: a) whether PMd areas are causally involved in mental rotation; b) whether there is a hemispheric specialization of PMd regions; c) what is the role played by PMd areas, or in other words, which, among the alternative hypotheses, better explains the functional meaning of the PMd regions.

Specifically, to address the last point, we adopted two different categories of stimuli, the hands and the objects, which were suggested to stimulate the use of motor strategies to a different extent. As previously proposed, indeed, abstract stimuli such as Shepard–Metzler objects are more prone to evoke a visual object transformation as compared with hand stimuli, which preferably elicit a motor strategy (Kosslyn et al., 1998; Tomasino, Toraldo, & Rumiati, 2003).

Therefore, we hypothesized that, if PMd areas support motor simulation and imagery in mental rotation, TMS applied over such areas would disrupt performance mainly in the hand task, and to a lesser extent in the task with abstract objects. By contrast, if PMd areas mediate processes related to mental rotation proper, as processing and updating of visuospatial information, TMS would disrupt performance not only in the hand task, but also in the object task.

2. Materials and method

2.1. Participants

Fifteen students of the University of Padua took part in the experiment (10 females; mean age: 25.2; range: 21–31). All participants were right-handed. None of the participants had a history of neurological or psychiatric disorders, or fulfilled exclusion criteria for TMS (Rossi, Hallett, Rossini, Pascual-Leone, & Safety of TMS Consensus Group, 2009). They all had normal or corrected-to-normal vision and no auditory impairment. They gave informed written consent before participating in the study, and were paid 25 euro for their participation. The study was conducted in accordance with the declaration of Helsinki, and was approved by the ethical committee of the Department of General Psychology, University of Padua.

2.2. Stimuli and tasks

The procedure is similar to that used in the study by Cona et al. (2016). The experiment was designed and conducted using E-prime software. Participants seated comfortably in front of a color monitor screen, at a distance of approximately 60 cm.

Two mental rotation tasks, one with pictures of objects and the other with pictures of hands, were administered in counterbalanced order across participants. In each task, pairs of stimuli were presented on a black screen, with the stimulus on the left being the target to which the stimulus on the right was matched. Participants verbally reported whether the stimulus on the right was the same or a mirror version of the stimulus on the left by saying “sì” (yes; *same* stimuli) or “no” (no; mirror stimuli). Verbal responses were recorded using a digital voice recorder.

For the object task, 3-D Shepard and Metzler-like object figures obtained from the dataset by Ganis and Kievit (2014) were used. The objects were white on a black background, and each object was composed of 4 arms, connected end-to-end in a sequence. All objects consisted of 7–11 cubes and had a natural-looking shading effect. For the hand task, 3-D pictures of hands were created using Adobe Photoshop C24 Version 11.0. Like the objects, the hands were white on a black background. The stimulus on the left side was always a left hand whereas the stimulus on the right side was a left hand – in half of the pairs - and a right hand, in the other half the pairs. This was made to avoid visuomotor interference and to minimize a possible left–right confusion (Ganis et al., 2000; Tomasino et al., 2005). The hands were always presented upright. Fig. 1 shows some examples of the stimuli used and the timeline of one experimental trial.

For both tasks, seven different configurations of objects and hands were used to minimize practice effects. In each task, a total of 56 pairs of stimuli were created: seven ‘same’ and seven ‘mirror’ images, appearing at each mental rotation angle (four different angles: 0°, 50°, 100° and 150°). The object stimuli had a size of 26.2° × 13.7° in visual angle, when viewed from a distance of 60 cm. The hand stimuli were created accordingly. All the stimuli were rotated around the vertical axis. The seven hand configurations at 0° were the following: three with the palm facing forward, three with the back of the hand facing forward and one with a lateral view of the hand. The selection of the stimuli was driven by pilot experiments in order to make the object task and the hand task as similar in difficulty to each other as possible. In each trial of both tasks, the sequence of stimuli and events was as follows: A fixation cross appeared on the screen for 500 ms, followed by the target stimuli that remained visible until the response or for a maximum of 3500 ms. If the verbal response occurred before 3500 ms, a blank was