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The effector independent nature of motor imagery: Evidence from rTMS induced inhibition to the primary motor cortices

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ABSTRACT

Motor imagery (MI), the mental rehearsal of movement, facilitates learning by driving brain activation similar to that of physical practice (PP). However, a growing body of evidence suggests that learning via MI relies more on effector independent as opposed to effector dependent encoding. One approach to probing the nature of MI based learning is to study the primary motor cortex (MC), a brain region known to be critical to effector dependent encoding, but whose involvement in MI is debatable. The current study sought to inform on the nature of MI-based learning by examining the extent to which participants could learn via MI following inhibition of the MC using repetitive transcranial magnetic stimulation (TMS). Forty-seven participants completed an MI-based implicit sequence learning paradigm after receiving inhibitory TMS to the contralateral or ipsilateral MC (TMS groups), or with the coil angled away from the scalp (Sham). The extent to which participants learned was assessed via reaction time differences (dRT) and effect sizes between repeated and random sequences. Similar dRT values and moderate effect sizes were observed across all groups, providing evidence that inhibition of the MC did not disrupt MI-based learning. As the MC is critical to effector dependent encoding, the current findings suggest that MI-based learning does not rely on effector dependent encoding and unlike PP, is more effector independent in nature. Ultimately, these results inform on the nature of MI-based learning.

1. Introduction

Motor imagery (MI), the mental rehearsal of a motor task, is a useful adjunct to physical practice (PP) for aiding learning in numerous domains (Newell, 1991; Wulf et al., 2010). Repetitive activation of brain regions underlying task performance via MI results in structural and functional changes necessary for learning to occur, and learning via MI is thus thought to occur in a manner similar to that of PP (Jeannerod, 2001; Sharma and Baron, 2013). Indeed, MI has been shown to facilitate learning in the absence of prior PP, suggesting its ability to independently generate and update a motor representation (Frank et al., 2014; Kraeutner et al., 2016a). While brain regions activated during MI overlap with those activated during PP (Burianová et al., 2013; Hétu et al., 2013; Kraeutner et al., 2014; Solodkin, 2004), greater recruitment of left hemisphere parietal regions, regions in the hemisphere ipsilateral to the imagined movement, as well as increased involvement of parietal regions that underlie visuospatial processes is observed during MI (Burianová et al., 2013; Hétu et al., 2013; Ingram et al., 2016; Kraeutner et al., 2014), suggesting that the learning achieved through MI requires fundamentally different processes than PP (Ingram et al., 2016).

Generally, it is thought that relative to PP, MI facilitates the perceptual component of learning to a greater extent than the motor component. In sequence learning, stimuli and features of the movement are thought to be processed to create a perceptual representation of the movement, followed by integration of this perceptual representation with the motor program to create a motor representation; processes termed perceptual and executive control processing respectively. Finally, an effector-specific movement generated from the motor representation is executed in a motor processing stage (for a review see Verwey et al. (2015)). Given evidence to date, it appears that MI facilitates the generation of the perceptual representation and its integration into the motor program, but not the actual execution component (i.e., the effector-specific movement). For instance, a study

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conducted by Amemiya et al. (2010) supports this proposition, as their work using an explicit sequence learning task demonstrated that MI led to greater intermanual transfer than PP, leading the authors to conclude that MI is more heavily involved in the perceptual (also referred to as cognitive) aspect of motor learning. Support for the perceptual nature of MI is also evidenced in our previous work (Ingram et al., 2016), in which a perceptual transfer task was employed following MI- or PP-based implicit sequence learning (ISL). Briefly, our prior results showed that following training on an ISL task, a perceptual manipulation used to assess learning impacted performance in the group undergoing MI-based practice to a greater extent than following PP, providing evidence that learning via MI is more perceptual in nature compared to PP. Taken together, these results indicate that learning via MI may rely more on mapping perceptual cues to movement goals, or more generally the encoding of effector independent vs. effector dependent (i.e., the encoding of a specific movement of an effector) information (Ingram et al., 2016; Land et al., 2016).

Accordingly, inhibition of the inferior parietal lobe (IPL), a brain region critical to effector independent learning (Bapi et al., 2006; Cooke et al., 2003), has been shown to disrupt MI-based learning (Kraeutner et al., 2016b). In this work, MI performance was assessed by the extent of learning resulting from MI-based practice, with an impairment in learning attributable to the inability to perform MI following inhibition of the IPL via repetitive transcranial magnetic stimulation (rTMS), whereby a train of pulses is delivered to a targeted brain region to induce transient inhibition (Kraeutner et al., 2016b). Additionally, lesion-based studies investigating the impact of brain damage on MI ability demonstrate that parietal damage impairs MI performance, further supporting its role in MI (McInnes, et al., 2016; Oostra et al., 2016). Taken together, the evidence suggests that the IPL is a brain region key to MI performance in that it encodes the perceptual information necessary for learning via MI to occur, and that damage to this area therefore disrupts this encoding, impairing MI-based learning.

While the notion that MI relies on encoding effector independent information is indeed supported by the aforementioned behavioural and lesion-based studies, the role of effector dependent encoding in MI performance and learning is less clear. One approach to studying effector dependent encoding in MI is through the contribution of the primary motor cortex (referred to throughout as MC) to MI performance and learning, as MC is an area critical to effector dependent learning (Bapi et al., 2006; Grafton et al., 1998). The involvement of MC in MI is inconsistent in the literature (Hétu et al., 2013); for instance, an activation likelihood estimation analysis conducted by Hétu et al. (2013) found consistent MC activation in only 22 of 122 experiments that investigated MI-related brain activity via neuroimaging. Studies showing MC activation during MI generally report a decreased magnitude of the MI-based activation relative to that observed during PP (Lacourse et al., 2005; Porro et al., 1996; Sharma et al., 2008). As an alternative to neuroimaging, the contribution of MC to MI would ideally be investigated directly by probing the role that MC plays in MI performance and learning, in-turn illuminating the dependence of MI-based learning on effector independent encoding. As in our previous work, the use of repetitive TMS to induce transient inhibition of a specific brain region is an ideal approach, whereby interpretation of the resultant behavioural outcome informs on the effectiveness of MI-based training for learning.

Although studies have employed single-pulse TMS to measure changes in cortical excitability of MC during MI (Facchini et al., 2002; Grosprêtre et al., 2015; Lebon et al., 2012; Stinear et al., 2006), as well as to demonstrate plasticity in the MC representation over five days of mental (piano) practice (Pascual-Leone et al., 1995), few have employed inhibitory rTMS protocols to directly examine the contribution of MC to MI (Debarnot et al., 2011; Pelgrims et al., 2011). For instance, previous single-pulse studies examining resting motor threshold (RMT) and motor evoked potential (MEP) amplitude during imagery of simple finger/thumb abduction or tapping tasks have demonstrated a reduction in RMT and increased MEP amplitude during imagery vs. rest, suggesting that MI modulates MC excitability (Facchini et al., 2002; Lebon et al., 2012; Stinear et al., 2006). However, as this work examined imagery in the context of simple finger movements, no behavioural measure of MI performance (i.e., an objective assessment of MI) that captures or quantifies the contribution of MC to MI was included. Importantly, MC involvement in offline improvements in performance (i.e. consolidation processes) has been demonstrated by employing inhibitory rTMS during a resting period following skill acquisition via MI in a test/re-test paradigm (Debarnot et al., 2011), yet it remains unclear whether or not MC is involved in the ‘online’ or early stages of learning via MI. However, a study employing an online inhibitory rTMS protocol (Pelgrims et al., 2011), whereby disruption of activity in either right or left MC was induced at the onset of stimulus presentation, reported impaired performance of a mental rotation task (i.e., a task involving judgments about hand laterality). While accurate determination of hand laterality requires implicit MI, hand laterality judgment tasks are thought to rely on different neural networks compared to conscious performance of kinaesthetic MI (Hétu et al., 2013). Thus, due to methodological limitations that may impact the conclusions drawn regarding the direct contribution of MC to MI, further evidence is needed to investigate whether MC is critical to MI performance, and in turn the importance of encoding effector dependent information to MI-based learning.

The current study seeks to provide further insight on the role of MC in MI and the nature of learning that results through MI by determining whether or not encoding effector dependent information is critical to MI-based learning. To address this objective, we directly probe the contribution of MC to MI performance and learning through the use of continuous theta burst stimulation (cTBS), an offline TMS protocol that permits the creation of a transient virtual lesion prior to MI-based practice of a novel skill (Kraeutner et al., 2016b). The use of cTBS to effectively probe the causal contribution of a brain region to MI has been demonstrated in our previous work using an MI-based ISL task whereby faster reaction times (RTs) to a repeated (implicit) sequence indicates successful learning via MI (Kraeutner et al., 2016a). The degree to which one learns following the ISL task quantifies MI-based learning and thus MI performance. In the context of the present study, if MC is not critical for MI performance and thus MI-based learning, inhibition of MC via non-invasive brain stimulation should not impair MI-based learning. As such, we hypothesize that MI will facilitate learning following inhibition of either contralateral or ipsilateral MC, as demonstrated by decreased RTs of the repeated compared to the random sequences. While it is possible that inhibition of the contralateral MC only would be necessary to address our research question, the presence of bilateral activation observed during MI (Hétu et al., 2013) led us to include a separate group in which inhibition of the ipsilateral MC was performed. We further hypothesized that learning will occur similarly to those receiving sham stimulation, as evidenced by similar effect sizes between RTs to the repeated (implicit) vs. random sequences. Establishing that inhibition of MC does not hinder MI-based learning will provide support for the more effector independent nature of MI and MI-based learning.

2. Method

2.1. Participants

Forty-seven participants (12 male; aged 20.5 ± 3.0 years) were recruited for the study. All were right-handed (Oldfield, 1971), healthy and free of neurological disorder, and each provided written, informed consent. All participants self-reported to have normal hearing and verbally confirmed they understood the instructions prior to the study onset, and each was free of contraindications to TMS (Rossial et al.,