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Research Report

Incomplete inhibition of central postural commands during manual motor imagery

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ABSTRACT

Imagined movements exhibit many of the behavioral and neurophysiological characteristics of executed actions. As a result, they are considered simulations of physical actions with an inhibition mechanism that suppresses overt movement. This inhibition is incomplete, as it does not block autonomic preparation, and it also does not effectively suppress postural adjustments planned in support of imagined movements. It has been suggested that a central inhibition command may fail to suppress postural adjustments because it may not have access to afference-based elaborations of the postural response that occur downstream of central motor planning. Here, we measured changes in the postural response associated with imagining manual reaching movements under varying levels of imagined loading of the arm. We also manipulated stance stability, and found that postural sway reduced with increased (imagined) arm loading when imagining reaching movements from the less stable stance. As there were no afferent signals associated with the loading constraint, these results suggest that postural adjustments can leak during motor imagery because the postural component of the central motor plan is itself not inhibited effectively.

1. Introduction

The ability to covertly plan an action in a way that enhances preparedness and potential success of the action has obvious advantages in survival-critical domains such as predation or social interaction. To be undetectable, such planning must avoid overt motion, but to be effective, it must be rich in execution-relevant detail. Indeed, the generation of covert movements, commonly termed motor imagery, appears to be largely similar to programming overt movements for execution. For instance, motor imagery exhibits similar speed–accuracy tradeoff (Decety and Jeannerod, 1995; Stevens, 2005) and temporal scaling of movement time with distance (Decety et al., 1989; Papaxanthis et al., 2002; Sirigu et al.,1996), adheres to similar biomechanical constraints (Frak et al., 2001; Johnson, 2000), and generates similar patterns of effort (Cerritelli et al., 2000), cortical activation (De Lange et al., 2006; Grèzes and Decety, 2001; Orr et al., 2008), and corticospinal excitation (Stinear et al., 2006). According to the simulation hypothesis, these similarities suggest that motor imagery involves a sequence of neural events similar to motor execution, except that an inhibition mechanism operates downstream along the efferent pathway, possibly at the brainstem or spinal level, to suppress overt movement (Bonnet et al., 1997; Jeannerod, 2006). If such an inhibition mechanism exists, it must be incomplete (Jeannerod, 1994), because motor imagery has been shown to produce subliminal EMG activity in the involved

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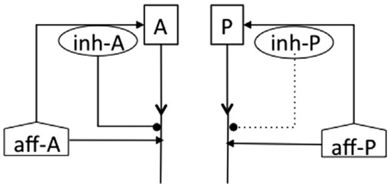

Fig. 1 – Schematic representation of commands and inhibition during motor imagery. A and P signify the action and postural components of the motor command associated with an imagined action. Afferent signals and motor inhibition relevant to A and P are shown as aff-A and aff-P, and inh-A and inh-P, respectively. See text for details.

muscles (Guillot et al., 2007; Lebon et al., 2008), as well as tonic and phasic autonomic responses preparing the body for action (Calabrese et al., 2004; Collet et al. 2013; Collet and Guillot, 2009; Decety et al. 1991).

Recent work has also shown that motor imagery can result in task-linked adjustments to the body's posture and balance. For example, Rodrigues et al. (2010) found that imagining plantar flexions of the foot amplified anteroposterior sway, whereas Grangeon et al. (2011) reported that postural sway decreased when imagining a series of counter-movement vertical jumps. Boulton and Mitra (2013) investigated imagery of manual reaching movements while standing, and found that postural sway increased when participants imagined arm movements in the direction of postural instability. It is not clear why such postural adjustments are executed (i.e., escape inhibition) when the focal movement is effectively suppressed. One possibility is that postural adjustments are not as easily inhibited because they are largely automated and generated sub-cortically. This autonomy of response may arise in the way posture control encapsulates the use of efferent and afferent signals to balance the body while supporting the descending motor commands. The suggestion is that the inhibition command, if it is of a more central origin, may not have access to the postural synergies assembled further down the efferent pathway (Boulton and Mitra, 2013; Guillot et al., 2012; Grangeon et al., 2011).

The most influential theories of motor control posit that movement planning (including postural control) uses an internal model of the action system (Wolpert and Kawato 1998; Kuo, 2005; Morasso et al., 1999). The intended action generates a set of motor commands through the application of an inverse model. A forward model then uses an efference copy of the generated commands to predict the feedback that the action ought to generate. In the case of overt action, feedback may help guide the movement, and by comparison against predicted feedback, provide the basis for learning or refining the skill involved. In the case of motor imagery, action planning must depend solely on estimates of the required motor commands. This estimation is not exclusively a central, top-down process, however, as there is evidence of afferent signals regarding the state of the motor periphery affecting imagery. For instance, cerebral or corticospinal activation during imagery can be modulated by immobilizing a limb (Kaneko et al., 2003), or by a limb posture that is incompatible with the imaged action (De Lange et al., 2006; Vargas et al., 2004). Also, the level of postural demand (e.g., sitting versus standing) has been found to modulate errors in manual reach estimation in young and older adults—greater postural demand in standing posture reverses the tendency to overestimate reaching ability, demonstrating the incorporation of postural constraints into the trajectory planning involved in manual motor imagery (Cordova and Gabbard, 2014; Gabbard et al., 2007).

Following the internal model framework, Fig. 1 schematizes possible routes of information flow during motor imagery. Whether for execution or imagery, it is assumed that motor commands are generated centrally for the action itself (A) as well as the necessary postural adjustments (P). Afference-based modulation of A and P can occur along the efferent pathway. Afference relevant to A and P (aff-A and aff-P) may influence the central generation of A and P, respectively, or their elaboration along the descending pathway. In the case of motor imagery, centrally generated inhibition is postulated for both the A (inh-A) and P (inh-P) components, but based on previous work, inh-A is assumed capable of blocking execution of A, whereas the status of inh-P is unclear. Are postural adjustments executed during motor imagery because P itself fails to be inhibited by inh-P, or because P and aff-P combine to produce postural synergies to which inh-P might not have access?

To test the extent to which afference-based mechanisms downstream of central command generation contribute to postural adjustments during motor imagery, the present study investigated a motor imagery task in which a key determinant of movement parameterization (as well as postural adjustment) was provided in a purely top-down manner. As in Boulton and Mitra (2013), we asked participants to stand upright in stances of varying stability and imagine making reaching movements of the arm to targets at varying distances. In the physical practice trials, participants wore wristbands of varying loads around their wrist. In the imagined movement trials that immediately followed, however, they did not wear the loads, but were asked to imagine making the movements as though they were wearing the load. As the load in question was not present on the arm during motor imagery, that is, there was no aff-A or aff-P corresponding to the load, A and P would need to incorporate its effect on the sole basis of a central estimate. We asked participants to provide self-reports of imagined movement time to ascertain whether A incorporated the (imagined) load constraint, for example, by increasing movement time as load increased. The key question then was whether P reflected the top-down load constraint as well. If there was a measurable postural response consistent with this imagined loading, it would indicate both that P corresponding to the load was centrally programmed, and that inh-P did not effectively block its execution.

2. Results

Self-reported movement time (MT) and mediolateral (ML) head and hip sway data were analyzed using ANOVA with significance level for omnibus effects set to $p < .05$. Where multiple post-hoc means comparisons were needed to