

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.

Keywords: motor imagery, motor planning, posture control

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 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 immobilising

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) have 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 and Cordova, 2007).

Following the internal model framework, Figure 1 schematises 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?

Insert Fig. 1 about here

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 be resolved a significant omnibus effect, Bonferroni corrections were applied ($.05/N$, N = number of comparisons).

2.1 Effect of the manual motor imagery task on postural sway

To measure any postural effects of simply performing the manual motor imagery task, we recorded sway from the head and hip segments while participants either stood still (baseline condition) or performed the reaching arm movements. In the latter case, there was no loading of the arm, and the participants had no knowledge of the loading manipulation. ML sway data were analysed using a repeated measures 2 (stance: closed, semi-tandem Romberg) x 2 (task: baseline, imagined reaching) ANOVA.

At the hip segment, ML sway was expectedly greater in the semi-tandem Romberg stance $F(1, 47) = 71.02, p < .0001, \eta_p^2 = .60$. ML sway was also greater during the manual imagery task than in the baseline $F(1, 47) = 13.39, p < .001, \eta_p^2 = .22$. There was no interaction between stance and task condition (Fig. 2A).

At the head segment, ML sway was again greater in the semi-tandem Romberg stance $F(1, 47) = 44.41, p < .0001, \eta_p^2 = .49$. There was also a significant interaction between stance and task condition $F(1, 47) = 8.37, p < .01, \eta_p^2 = .15$. The pattern was the same as for the hip segment in closed stance, but reversed in the semi-tandem Romberg stance (Fig. 2B). Thus, as stance difficulty increased from closed to semi-tandem Romberg, head sway increased less during imagery than in the baseline condition.

Insert Fig. 3 about here

2.2 Baseline measures of stance and arm load

To obtain baseline differences associated with the passive wearing of the arm loads in the two stances, we recorded sway from head and hip segments while participants stood quietly in each of the conditions for 30 s. We analyzed ML sway using a repeated measures 2 (stance: closed, semi-tandem Romberg) x 3 (arm load: 0 kg, 1 kg, 2 kg) ANOVA. Results verified that ML stability was comparatively reduced in the semi-tandem Romberg stance (head segment: $F(1, 47) = 102.00$, $p < .0001$, $\eta_p^2 = .68$, hip segment: $F(1, 47) = 102.75$, $p < .0001$, $\eta_p^2 = .69$. Importantly, neither head, $F(2, 94) = .75$, $p = .47$, nor hip sway was affected by the increasing load of the arm $F(2, 94) = .67$, $p = .51$. There were no other significant effects.

2.3 Timing of Arm Movements

Physical and imagined trials were analyzed separately using a 2 (movement direction: mediolateral (ML), anteroposterior (AP)) x 2 (stance: closed, semi-tandem Romberg) x 3 (load: 0 kg, 1 kg, 2 kg) x 3 (target distance: 15 cm, 30 cm, 45 cm) mixed ANOVA, with repeated measures on all factors except for arm movement direction. Self-reported MT was the dependent variable.

2.3.1 Physical Arm Movements. Self-reported MT increased with target distance, $F(2, 92) = 21.53$, $p < .0001$, $\eta_p^2 = .32$, and arm load, $F(2, 92) = 6.55$, $p < .01$, $\eta_p^2 = .12$ (Fig. 4A). Post hoc tests (Fisher's PLSD) showed that MT significantly increased between all levels of target distance (15 cm and 30 cm $p < .001$, 30 cm and 45 cm $p < .01$, and 15 cm and 45 cm $p < .0001$) and between loads of 0 kg and 1 kg, and 0 kg and 2 kg (both $p < .01$). The significant load x movement direction interaction, $F(2, 92) = 3.26$, $p < .05$, $\eta_p^2 = .07$, showed that the increase in MT between arm loads of 0 kg and 1 kg was exclusive to ML arm movements ($p < .01$). Conversely, the increase in MT

between arm loads of 0 kg and 2 kg occurred only in AP arm movements ($p < .01$). The interaction between target distance, movement direction and stance was marginally significant, $F(2, 92) = 2.98, p = .06, \eta_p^2 = .06$. The timing of ML arm movements increased more sharply with target distance when performed from the closed (18.41 ms/cm) compared to the semi-tandem Romberg stance (11.48 ms/cm). There were no other significant effects.

2.3.2 Imagined Arm Movements. The main effects of target distance, $F(2, 92) = 22.64, p < .0001, \eta_p^2 = .33$, and load, $F(2, 92) = 38.68, p < .0001, \eta_p^2 = .46$, were significant (Fig. 4B). Post hoc tests (Fisher's PLSD) showed that MT significantly increased with each level of target distance and between loads of 0 kg and 1 kg, and 0 kg and 2 kg (all $p < .0001$). The interaction between target distance and load was also significant, $F(4, 184) = 3.13, p < .05, \eta_p^2 = .06$. Imagining wearing the wrist weight increased MT to each target distance (all $p < .0001$), but the difference between 1 kg and 2 kg loads was significant only at the 30 cm target distance ($p < .05$). Therefore, the effect of load on MT was not entirely consistent at each target distance. The interaction between stance, target distance and load was significant, $F(4, 184) = 2.53, p < .05, \eta_p^2 = .05$. Simple comparison tests revealed that the stance x target distance effect was restricted to imagined arm movements in the 0 kg condition, $F(2, 94) = 6.74, p < .01, \eta_p^2 = .13$. Specifically, MTs to the 45 cm target distance were significantly longer in the closed than semi-tandem Romberg stance, $t(47) = 2.52, p = .015$. There were no other significant effects.

Insert Fig. 4 about here

2.4 ML Postural Sway during Arm Movements

Sway measured from the head and hip segments during the performance of physical and imagined arm movements was analyzed separately using a 2 (movement direction: ML, AP) x 2 (stance: closed, semi-tandem Romberg) x 3 (load: 0 kg, 1 kg, 2 kg) mixed ANOVA, with repeated measures on all factors except for movement direction.

2.4.1 Physical Arm Movements. Sway measured from the head segment was significantly greater during AP than ML arm movements, $F(1, 46) = 7.54, p < .01, \eta_p^2 = .14$, and when standing in the semi-tandem Romberg compared to the closed stance, $F(1, 46) = 15.35, p < .001, \eta_p^2 = .25$. The main effect of arm load was also significant, $F(2, 92) = 19.17, p < .0001, \eta_p^2 = .29$ (Fig. 5A). Post hoc tests showed that head sway increased significantly with each level of arm load (0 kg and 1 kg $p < .05$, 1 kg and 2 kg $p < .001$, and 0 kg and 2 kg, $p < .0001$).

Increasing the load of the arm also increased sway at the hip segment, $F(2, 92) = 16.62, p < .0001, \eta_p^2 = .27$. Post hoc tests confirmed that sway increased significantly with each level of arm load (0 kg and 1 kg $p < .01$, 1 kg and 2 kg $p < .01$, and 0 kg and 2 kg $p < .0001$). There were no other significant effects.

2.4.2 Imagined Arm Movements. Sway at the head segment was significantly greater when in the semi-tandem Romberg than the closed stance, $F(1,46) = 72.06, p < .0001, \eta_p^2 = .61$. The main effect of load was not significant, $F(2,92) = .64, p = .53$, but there was a significant load x stance interaction, $F(2,92) = 4.34, p < .05, \eta_p^2 = .09$ (Fig. 5B),

revealed that increasing the load of the arm modulated head sway in the semi-tandem Romberg stance $F(2, 94) = 4.21, p < .05, \eta_p^2 = .08$. Post hoc tests (Fisher's PLSD) showed that sway significantly decreased when imagined load increased from 1 kg to 2kg ($p < .01$).

Sway at the hip segment was significantly greater when in the semi-tandem Romberg than the closed stance, $F(1,46) = 72.76, p < .0001, \eta_p^2 = .61$. The load x stance interaction observed in head sway did not occur in hip sway. There were no other significant effects.

Insert Fig. 5 about here

3. Discussion

In this study, healthy young participants executed as well as imagined reaching movements of the arm while standing in a closed or semi-tandem Romberg stance. Their moving arm was loaded using wrist bands weighing 0 kg, 1 kg or 2 kg during physical arm movements, but not during imagined movements. Participants were asked to imagine making the movements as though they were wearing the corresponding load. We expected that both physical and imagined MTs would increase with distance and load, which would confirm that the load constraint was incorporated into motor planning in both cases. The key point of interest then was whether postural sway recorded at the hip, head, or both segments would show a response to the change in (imagined) loading during imagined arm movements. As there was no aff-P (or indeed aff-A) corresponding to the loading (Fig. 1), measurable

postural adjustments during imagery would suggest that the (imagined) load was centrally factored into P, but P was not successfully inhibited. Thus, the failure to inhibit the postural component of imagined action could not be attributed to afference-influenced processes downstream of central command generation that are not accessible to a central inhibition command (inh-P) (e.g., Boulton and Mitra, 2013; Guillot et al., 2012; Grangeon et al., 2011).

The results showed, first, that scaling of MT to target distance was comparable across task conditions indicating that imagined arm movements were successfully made according to the instructions given. Also, as expected, increased loading of the arm increased the self-reported MTs both the physical and imagined arm movements. In previous work, this slowing effect of load seen in imagined movements has not always been found in physical movements (Cerritelli et al., 2000; Decety et al., 1989). Decety et al. (1989) originally proposed that lengthened MT of loaded imagined movements was representative of the greater muscular force required to move the heavier load. During physical execution this force could readily be applied to maintain a constant movement speed, whereas in imagined task performance it is encoded centrally as a time increase. In the present results, however, load slowed both imagined and physical movements (Fig. 3A, B). As the closed and semi-tandem Romberg stances used here were relatively unstable, participants may have opted for slower movements as load increased in either condition because fast arm movements are more perturbing to stance than movements performed less rapidly (Lee et al., 1987).

Second, analysis of ML postural sway recorded at the head showed that there was indeed a measurable postural adjustment corresponding to the (imagined) loading of the arm in the case of imagined movements (Fig. 4B). ML sway in the less stable

semi-tandem Romberg stance decreased when imagined load increased from 1 kg to 2 kg. This relative restriction of lateral sway when standing in the laterally less stable stance, and imagining arm movements wearing the highest level of imagined load, suggests that centrally modeling a high load resulted in a postural response of stiffening the body when stance stability was lower. It is notable that reduced ML sway under high load and unstable stance was detected by the sensor placed on the head, but not by the one placed at the hip. Thus, the observed sway restriction appears to have been applied selectively to the upper body, as if to counteract the greater moment that would be generated if a higher load were actually placed on the wrist. Note that a tendency towards a specific restriction of head sway during manual motor imagery was also observed relative to the baseline (no imagery) condition.

It is also clear that the postural response to imagined loading was not effectively inhibited. Others (Grangeon et al., 2011; Hamel and Lajoie, 2005) have previously reported similar reductions in postural sway in conjunction with motor imagery, and the type of tightening of positional drift that was observed here is a proven control strategy invoked in response to postural threat (Adkin et al., 2000; Brown and Frank, 1997; Carpenter et al., 1999). Grangeon et al. (2011) have suggested that postural changes during motor imagery could indicate unsuppressed anticipatory postural adjustments (APAs). Previously, arm loading has been shown to influence the feedforward planning of supporting postural adjustments (Bouisset et al., 2000; Bouisset and Zattara, 1987), so the present result could also reflect unsuppressed APAs. However, the exact nature of the postural changes observed here cannot be determined using the current methodology because postural sway was measured across experimental blocks, each consisting of a series of arm movements

to multiple target locations. The present measures could at most reveal systematic changes in sway associated with the variation in experimental conditions.

As we have previously discussed (Boulton and Mitra, 2013), further studies would need to include both kinematic and EMG measures of postural activity taken within the temporal vicinity of individual imagined movements. The muscular activation of the arm would also need to be considered, particularly in the instance of imagined loading, because the discrepancy between ascending afferent signals and the arm's imagined state could have generated some efferent outflow to the arm. It is also possible that the reduction in sway that occurred in the least stable semi-tandem Romberg stance, and under the highest level of (imagined) loading, could be associated with the attentional demands of this particular task combination. The shift in attention due to increasing cognitive demands can result in lower levels of postural sway (e.g., Hunter and Huffman, 2001; Riley et al., 2003; Vuillerne and Teasdale, 2000). It is possible that the imagined movement task was more difficult under the 2 kg than 1 kg load, especially as afferent signals concerning load were not available.

Regardless of the precise origin of the postural effect of imagined arm loading observed here, it is clear (in terms of Fig. 1) that a purely top-down modulation of the postural component of a motor imagery task can escape inhibition. Thus, the 'leakage' of postural adjustment is not attributable to a failure of central inhibition on account of afference-based, execution-time elaborations of postural control further along the efferent pathway. It appears that the central postural command is itself inadequately inhibited during manual motor imagery.

Lemos et al. (2014) have recently offered an alternative proposal for the source of postural changes seen during motor imagery. They suggest that motor

imagery generates sub-threshold excitation of motor pathways (including those involved in postural control), but as the postural synergies are simultaneously active in maintaining balance, a process of signal summing results in supra-threshold postural activation. This is a plausible mechanism for imagery tasks involving the same muscles that are engaged in maintaining upright stance (e.g., imagined jumping while standing upright), but it is not clear how it can explain the present pattern of results. Semi-tandem Romberg stance resulted in a higher level of ML sway in the baseline condition, but the postural adjustment associated with the highly loaded imagined arm movement amounted to a relative reduction in head sway in that particular stance condition. The specific nature of this reversal is difficult to explain by means of signal summation. Also, it is not clear how signal summation could explain the observed confinement of sway reduction to the upper body segment. The simplest explanation of the present data is that, as suggested by the internal model framework, a task-specific P is generated alongside the corresponding A (Fig. 1), but an effective inh-P does not operate during motor imagery to block overt postural motion.

In the present work, we did not control for differences in the participants' MI ability. We assume that the linear scaling of target distance and the low variability of self-reported imagined MT provide evidence of consistent imagery performance. Nevertheless these temporal consistencies do not necessarily correlate with participants' ability to produce richly detailed images (Guillot and Collet, 2005). It is conceivable that postural reactions invoked during motor imagery depend on such image qualities. Further insight could be obtained by the inclusion of introspective measures (for further discussion, see Dickstein and Deutsch, 2007)

Finally, it should be noted that the current findings are based on a sample of young, healthy adults. As both lateral stability (Lord et al., 1999) and motor inhibition (Schlaghecken et al., 2011) decline with age, we would expect the observed effects to be amplified in older individuals. The fact that imagined movements can elicit postural responses has important implications for research on falling and the fear of falling in older adults. Fear of falling is often a psychological consequence of experiencing a fall, and this fear can lead to the restriction of daily living activities, accelerating physical frailty and, consequently, increasing the likelihood of a subsequent fall (Delbraere et al., 2004). Our results suggest that covert rehearsal of challenging movements can induce changes in postural control that may affect balance depending on task conditions. Therefore, simply the thought of some actions could be sufficient to discourage the individual's participation in them. On the other hand, the ability to centrally model the level of loading when parameterizing arm movements is a potentially useful similarity between movement planning in execution and imagery. It may offer opportunities for postural stability to be improved through covert rehearsal of movements (e.g., Hamel and Lajoie, 2005).

Insert Fig. 4 about here

4. Method

4.1 Participants

Participants were all young healthy adults from the University of Warwick community. Forty-eight individuals were recruited for experimental conditions in

which loads were worn during physical practice but not during manual imagery. These participants were: 18-25 years in age ($M=19.73$ yrs., $SD = 1.83$ yrs.), 45-92 kg in weight ($M = 64.24$ kg, $SD = 8.96$ kg), and 155-187.5 cm in height ($M = 171.07$, $SD = 8.96$). Forty-eight individuals participated in conditions contrasting baseline (no imagery) sway with sway during the basic manual motor imagery task (without arm load). They were 18-30 years in age ($M = 20.58$ yrs., $SD = 2.44$ yrs.), 45-92 kg in weight ($M = 62.19$ kg, $SD = 11.82$ kg), and 152-190 cm in height ($M = 168.7$ cm, $SD = 9.7$ cm). All were right handed according to the Edinburgh Handedness Inventory (Oldfield 1971), and none reported any history of neurological or balance impairments. Participants remained naïve to the main objectives of the experiment until data collection was complete. The study was approved by the University of Warwick's Humanities and Social Sciences Research Ethics Committee. All participants gave informed consent in writing, and the experimental protocols complied with the code of ethics in the Declaration of Helsinki.

4.2 Apparatus and Procedure

Participants stood without footwear at the designated location marked on the laboratory floor. They stood with their arms flush to the sides of their body, holding the computer mouse in their left hand. During the practice trials, participants either wore no load (0 kg) or a 1 kg or 2 kg load as a symmetrical band around their right wrist. The practice trials were followed by experimental trials during which participants did not wear the load but performed as though they did.

Polhemus Fastrak motion sensors (Colchester, VT) were attached to the head and hip (sacral region of the back) using Velcro belts (Fig. 2A). Participants' stability in the ML direction was manipulated by varying stance. Depending on experimental

condition, participants stood either in the closed (feet flushed equally together) or the semi-tandem Romberg stance (dominant foot placed partially forwards, Fig. 2B), with the latter offering lower ML stability (see Boulton and Mitra, 2013). Participants were asked to maintain upright stance while they made physical or imagined reaching movements of the right arm. Reaching movements were made to six target locations (1 x 35 cm) displayed on a target surface (100 x 35 cm). The surface was presented at waist level either in the ML or AP direction, with the starting position for each movement (also indicated on the task surface) in line with the participant's right shoulder (Fig. 2C). All targets were well within reach of maximum elbow extension.

The movement sequence of each trial was specified by an auditory stimulus played through two speakers placed at the back of the room. Participants moved their right arm to the start position upon hearing the start signal (Fig. 2D). Following a 2000 ms silence, the name of the target area (e.g., "A", "B", ..., "F") was then heard. Following a further 2000 ms of silence the go-signal was heard, on which participants commenced the arm movement to the stated target location. Participants indicated their arrival at the target location by pressing the left mouse button. Following their response, 3000 ms of silence was observed allowing the participant to return to (or imagine returning to) the arms-by-the-sides position in readiness for the next trial. An E-Prime 2.0 (Psychology Software Tools, Sharpsburg, PA) script delivered these pre-recorded audio signals, randomly sequenced the trials, and collected self-reported movement times. Data collection was conducted in blocks of six trials (each block corresponding to one arm movement to each target). Self-reported MT was measured on a per trial basis and postural sway data was collected over each experimental block (Boulton and Mitra 2013). Thus, posture sway for each combination of load and

stance was estimated over the performance of 12 arm movements (2 movements to each of six targets).

Insert Fig. 2 about here

Participants started each series of trials with four practice blocks in which they stood and made physical reaching movements while wearing the respective load. Two blocks were performed with eyes open and then two with eyes closed. In both instances, one block was completed in each stance. Imagined task performance immediately followed. Participants stood with their eyes closed and imagined making the reaching movements while wearing the respective load. A total of four experimental blocks were performed, with two blocks completed in each stance. Thus, each participant made two imagined arm movements to each target while standing in each stance and imagining wearing each level of load. Thus, during the imagined movement trials, participants did not have afferent signals corresponding to the loads, but were asked to move as if they were wearing the load (see Imagery Instructions). The practice trials (with the loads on) that immediately preceded these imagined trials provided participants fresh memory of operating under the respective loading.

4.3 Imagery Instructions

Participants were instructed to perform all reaching movements as quickly as possible but without sacrificing accuracy. In the imagery trials, participants were instructed to make the reaching movements as if they were still wearing the load. To avoid the explicit biasing of a particular task representation (e.g., visuospatial

representation of the task surface layout vs. kinesthetic representation of the arm), imagery modalities were not contrasted in the instructions. Likewise, which perspective should be used for imagery was not explicitly contrasted. The physical trials always preceded imagined task performance, and formed the task reference, so participants had no reason to not retain a first-person perspective. Importantly, the instructions stressed at several points that participants should imagine *making* the movements, and the instructions ended with the statement “for the experiment to be successful, you must imagine the movements as though you are making them with the wrist weight on.” As the reaching task used in this study is commonly a visuomotor task in daily life, it would be confusing for participants if an explicit contrast was made between kinesthetic and visual imagery, and participants were asked to desist from the latter. Thus, we used the emphasis on imagining making the movements, along with the physical movement practice immediately preceding imagery, to stress the kinesthetic perspective.

4.4 Measures, Design and Data Analysis

Measurements of postural sway were taken from two Polhemus sensors (static accuracy of 0.012 cm RMS with 4 ms latency) attached to the head and the hip segments of the body. The hip-attached sensor provided an estimate of the position of the body’s center of mass. As the experimental task involved (physical and imagined) extensions of the (loaded) upper body mass away from the standing body’s main axis, a postural strategy involving some inter-segmental dynamics was a possibility. For instance, as the arm reached out, the head and hip could move in phase in the opposite direction to counteract the extending arm’s weight. In this case, postural motion would be largely governed by ankle rotation, and head and hip sway would show a similar pattern across conditions, except that head sway would be proportionally

greater (because the head is further away from the point of rotation at the ankle).

Alternatively, participants could invoke hip flexion-extension and move the head and hip segments in an anti-phase pattern (e.g., Bardy et al., 1999), in which case, hip and head sway would not be yoked together across conditions. To retain the ability to detect such differences in the hip and head segments' behavior, we monitored and analyzed sway at both the hip and head segments.

We measured postural sway as the root-mean-square (RMS) drift in mean body position across all (non-overlapping) time windows of 1 s duration in the time series (Boulton and Mitra, 2013; Mitra, 2003). As the stance condition specifically manipulated mediolateral (ML) postural stability, we focused our analysis of sway on the ML component.

To summarize, postural sway analysis followed a 2 x (movement direction: ML, AP) 2 (stance: closed, semi-tandem Romberg) x 3 (arm load: 0 kg, 1 kg, 2 kg) x 3 (target distance: 15 cm, 30 cm, 45 cm) mixed design, with repeated measures on all factors except for movement direction. Half the participants made the movements in the ML direction and the other half in AP. Direction of movement was a between-subjects factor to prevent carry-over effects in imagery (Boulton and Mitra, 2013; Mitra et al., 2013). Manipulations of stance and load were blocked and counterbalanced, and performance on the arm movement task was assessed using mean self-reported MTs to each target distance.

References

- Adkin, A.L., Frank, J.S., Carpenter, M.G., Peysar, G.W., 2000. Postural control is scaled to level of postural threat. *Gait Posture*. 29, 86-90.
- Bardy, B.G., Marin, L., Stoffregen, T.A., Bootsma, R.J., 1999. Postural coordination modes considered as emergent phenomena. *J. Exp. Psychol. Hum. Percept. Perform.* 25, 1284–1301.
- Bonnet, M., Decety, J., Jeannerod, M., Requin, J., 1997. Mental simulation of an action modulates the excitability of spinal reflex pathways in man. *Cogn. Brain Res.* 5, 221-228.
- Bouisset, S., Richardson, J., Zattara, M., 2000. Are amplitude and duration of anticipatory postural adjustments identically scaled to focal movement parameters in humans?. *Neurosci. Lett.* 22, 263-270.
- Bouisset, S., Zattara, M., 1987. Biomechanical study of the programming of anticipatory postural adjustments associated with voluntary movement. *J. Biomech.* 20,735 -742.
- Boulton, H., Mitra, S., 2013. Body posture modulates imagined arm movements and responds to them. *J. Neurophysiol.* 110, 2617-2626.
- Brown, L.A., Frank, J.S., 1997. Postural compensations to the potential consequences of instability: kinematics. *Gait Posture* 6, 89-97.
- Calabrese, P., Messonnier, L., Bijaoui, E., Ebherhard, A., Benchetrit, G., 2004. Cardioventilatory changes induced by mentally imaged rowing. *Eur. J. Appl Physiol.* 91,160-166.

- Carpenter, M.G., Frank, J.S., Silcher, C.P., 1999. Surface height effects on postural control: a hypothesis for a stiffness strategy for stance. *J. Vestib. Res.* 9, 277-286.
- Cerritelli, B., Maruff, P., Wilson, P., Currie, J., 2000. The effect of an external load on the force and timing components of mentally represented actions. *Behav. Brain Res.* 18, 91-96.
- Collet, C., Guillot, A., 2009. Peripheral responses elicited by motor imagery: A window on central and peripheral nervous system relationships related to motor inhibition, in Weingarten, S.P., Penat, H.O. (Eds.), *Cognitive psychology research developments*. Nova Publishers., Hauppauge, NY, pp. 245-259.
- Collet, C., Di Rienzo, F., El Hoyek, N., Guillot, A., 2013. Autonomic nervous system correlated in movement observation and motor imagery. *Front. Hum. Neurosci.* 7, 415.
- Cordova, A., Gabbard, C., 2014. Do older adults perceive postural constraints for reach estimation? *Exp Aging Res.* 40, 578-588.
- Decety, J., Jeannerod, M., 1995. Mentally simulated movements in virtual reality: does Fitt's law hold in motor imagery? *Behav. Brain Res.* 72, 127-134.
- Decety, J., Jeannerod, M., Germain, M., Pastene J., 1991. Vegetative response during imagined movement is proportional to mental effort. *Behav. Brain Res.* 42,1-5.
- Decety, J., Jeannerod, M., Prablanc, C., 1989. The timing of mentally represented actions. *Behav. Brain Res.* 34, 35-42.
- De Lange, F.P., Helmich, R.C., Toni, I., 2006. Posture influences motor imagery: An fMRI study. *NeuroImage* 33, 609-617.

- Delbaere, K., Crombez, G., Vanderstraeten, G., Willems, T., Cambier, D., 2004. Fear-related avoidance of activities, falls and physical frailty. A prospective community-based cohort study. *Age Ageing* 33, 368-373.
- Dickstein, R., Deutsch, J.E., 2007. Motor imagery in physical therapist practice. *Phys. Ther.* 87,942-953.
- Frak, V., Paulignan, Y., Jeannerod, M., 2001. Orientation of the opposition axis in mentally simulated grasping. *Exp. Brain Res.* 136(1), 120-127.
- Gabbard, C., Cordova, A., Lee, S. 2009. Do children perceive postural constraints when estimating reach of action planning? *J Motor Behav.* 41, 100-105.
- Gabbard, C., Cordova, A., Lee, S. 2007. Examining the effects of postural constraints on estimating reach. *J Motor Behav.* 39, 242-246.
- Grangeon, M., Guillot, A., Collet, C., 2011. Postural control during visual and kinesthetic motor imagery. *Appl. Psychophysiol. Biofeedback.* 36, 47-56.
- Grèzes, J., Decety, J., 2001. Functional anatomy of execution, mental simulation, observation and verb generation of actions: a meta-analysis. *Hum. Brain Mapp.* 12:1-19.
- Guillot, A., Collet, C., 2005. Contribution from neurophysiological and psychological methods to the study of motor imagery. *Brain Res. Rev.* 50(2), 387-397.
- Guillot, A., Di Rienzo, F., MacIntyre, T., Moran A., Collet C., 2012. Imagining is not doing but involves specific motor commands: a review of experimental data related to motor inhibition. *Front. Hum. Neurosci.* 6, 247.

- Guillot, A., Lebon, F., Rouffet, D., Champely, S., Doyon, J., Collett, C., 2007. Muscular responses during motor imagery as a function of muscle contraction types. *Int. J. Psychophysiol.* 66, 18-27.
- Hamel, M.F., Lajoie, Y., 2005. Mental imagery: Effects on static balance and attentional demands of the elderly. *Aging Clin. Exp. Res.* 17, 223-228.
- Hunter, M.C., Hoffman, M.A., 2001. Postural control: visual and cognitive manipulations. *Gait Posture.* 13, 41-48.
- Jeannerod, M., 1994. The representing brain: Neural correlates of motor intention and imagery. *Behav. Brain Sci.* 17(2), 187-201.
- Jeannerod, M., 2006. *Motor cognition: What actions tell the self.* Oxford, England: Oxford University Press.
- Johnson, S.H., 2000. Thinking ahead: the case for motor imagery in prospective judgements of prehension. *Cognition.* 74, 33-70.
- Kaneko, F., Murakami, T., Onari, K., Kurumadani, H., & Kawaguchi, K., 2003. Decreased cortical excitability during motor imagery after disuse of an upper limb in humans. *Clinical neurophysiology*, 114(12), 2397-2403.
- Kuo, A.D., 2005. An optimum state estimation model of sensory integration in human postural balance. *J. Neural Eng.* 2, S2350–S249, 2005.
- Lee W.A., Buchanan, T.S., Roger, M.W., 1987. Effects of arm acceleration and behavioral conditions on the organization of postural adjustments during arm flexion. *Exp. Brain Res.* 66, 257-270.

- Lebon, F., Rouffet, D., Collet, D., Guillot, A., 2008. Modulation of EMG power spectrum frequency during motor imagery. *Neurosci. Lett.* 435, 181-185.
- Lemos, T., Rodrigues, E. C., Vargas, C. D., 2014. Motor imagery modulation of postural sway is accompanied by changes in the EMG–COP association. *Neurosci. Lett.* 577, 101-105.
- Lord, S. R., Rogers, M. W., Howland, A., Fitzpatrick, R., 1999. Lateral stability, sensorimotor function and falls in older people. *Journal of the American Geriatrics Society.*
- Mitra, S., 2003. Postural costs of suprapostural task load. *Hum. Movement Sci.* 22(3), 253-270.
- Mitra, S., Knight, A., Munn, A., 2013. Divergent effects of cognitive load on quiet stance and task-linked postural coordination. *J. Exp. Psychol. Hum. Percept. Perform.* 39(2), 323.
- Morasso, P. G., Baratto, L., Capra, R., & Spada, G., 1999. Internal models in the control of posture. *Neural Networks.* 12(7), 1173-1180.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia.* 9, 97–113.
- Orr, E.L., Lacourse, M.G., Cohen, M.J., Cramer, S.C., 2008. Cortical activation during executed, imagined, and observed foot movements. *Neuroreport.* 19, 625-30.
- Papaxanthis, C., Schieppati, M., Gentili, R., Pozzo, T., 2002. Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass. *Exp. Brain Res.* 14, 447-452.

- Riley, M.A., Baker, A.A., Schmit, J.M., 2003. Inverse relation between postural variability and difficulty of a concurrent short-term memory task. *Brain Res. Bull.* 62, 191-195.
- Rodrigues, E.C., Lemos, T., Gouvea, B., Volchan, E., Imbiriba, L.A., Vargas, C.D., 2010. Kinesthetic motor imagery modulates body sway. *Neuroscience* 169: 743-750.
- Schlaghecken, F., Birak, K.S., Maylor, E.A., 2011. Age-related deficits in low-level inhibitory motor control. *Psychol. Aging.* 26, 905-918.
- Sirigu, A., Duhamel, J.R., Cohen, L., Pillon, B., Dubois, B., Agid, Y., 1996. The mental representation of hand movements after parietal cortex damage. *Science.* 273, 1564-1568.
- Stevens, J.A., 2005. Interference effects demonstrate distinct roles for visual and motor imagery during the mental representation of human action. *Cognition.* 95, 329-350
- Stinear, C.M., Byblow, W.D., Steyvers, M., Levin, O., Swinnen, SP., 2006. Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. *Exp. Brain Res.* 168, 157-164.
- Vargas, C.D., Olivier, E., Craighero, L., Fadiga, L., Duhamel, J.R., Sirigu, A., 2004. The influence of hand posture on corticospinal excitability during motor imagery: A transcranial magnetic stimulation study. *Cereb. Cortex.* 14, 1200–1206.
- Verheyden G, van Duijnhoven HJ, Burnett M, Littlewood J, Kunkel D, Ashburn AM. Kinematic analysis of head, trunk, and pelvis movement when people early after

stroke reach sideways. *Neurorehabil Neural Repair* 25: 656-663, 2011.

Vuillerme, N., Nougier, V., Teasdale, N., 2000. Effects of a reaction time task on postural control in humans. *Neurosci. Lett.* 291, 77-80.

Wolpert, D.M., Kawato, M., 1998. Multiple paired forward and inverse models for motor control. *Neural Networks.* 11, 1317-1329.

Footnote

- 1 MT to the three target distances did not statistically differ according to direction (e.g., left/ right movements in the ML condition or front/back movements in the AP condition). Therefore, MTs were analyzed as a function of target distance (15 cm, 30 cm, 45 cm) opposed to specific location (e.g., A, B,... F).

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Figure Captions

Figure 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.

Figure 2. Experimental setup, task conditions, and measurement conventions. A: postural sway was recorded using Polhemus Fastrak sensors placed on the head and the sacral region of the back, B: participants stood in closed or semi-tandem Romberg stance, C: they performed imagined reaching movements from the starting position, as shown, to each of the targets, and D: sequence of events during each arm movement trial (Boulton and Mitra, 2013).

Figure 3. Hip (A) and head (B) sway in baseline and motor imagery task conditions. Error bars indicate standard error.

Figure 4. Effects of task conditions on self-reported movement time during physical (A) and imagined arm movements (B). Error bars indicate standard error.

Figure 5. Effects of task conditions on ML head sway during physical (A) and imagined arm movements (B). Error bars indicate standard error. ** $p < .01$.

Figure 1

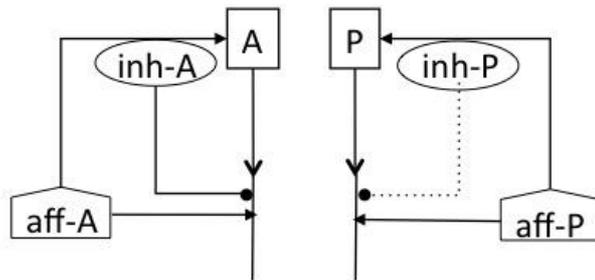


Figure 2

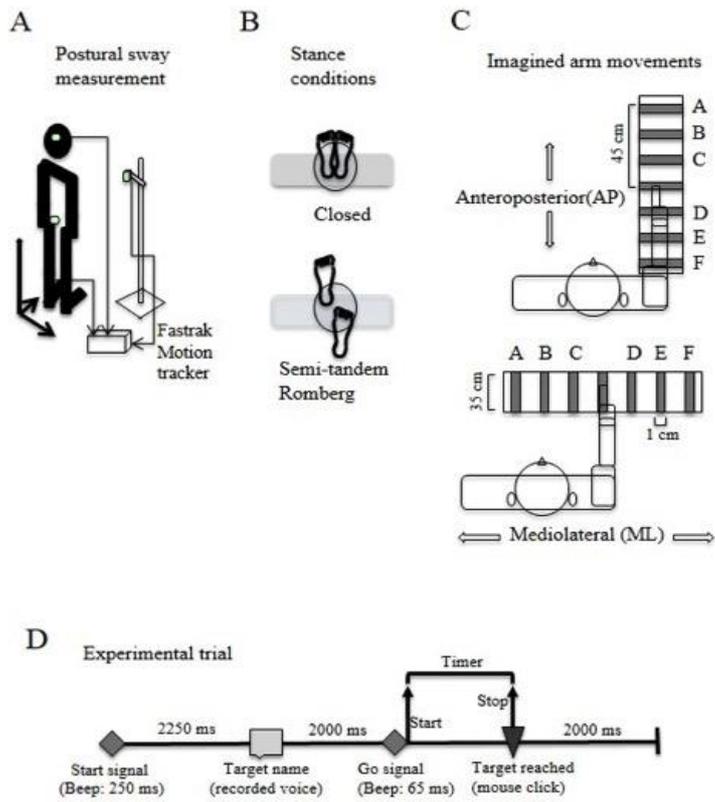


Figure 3

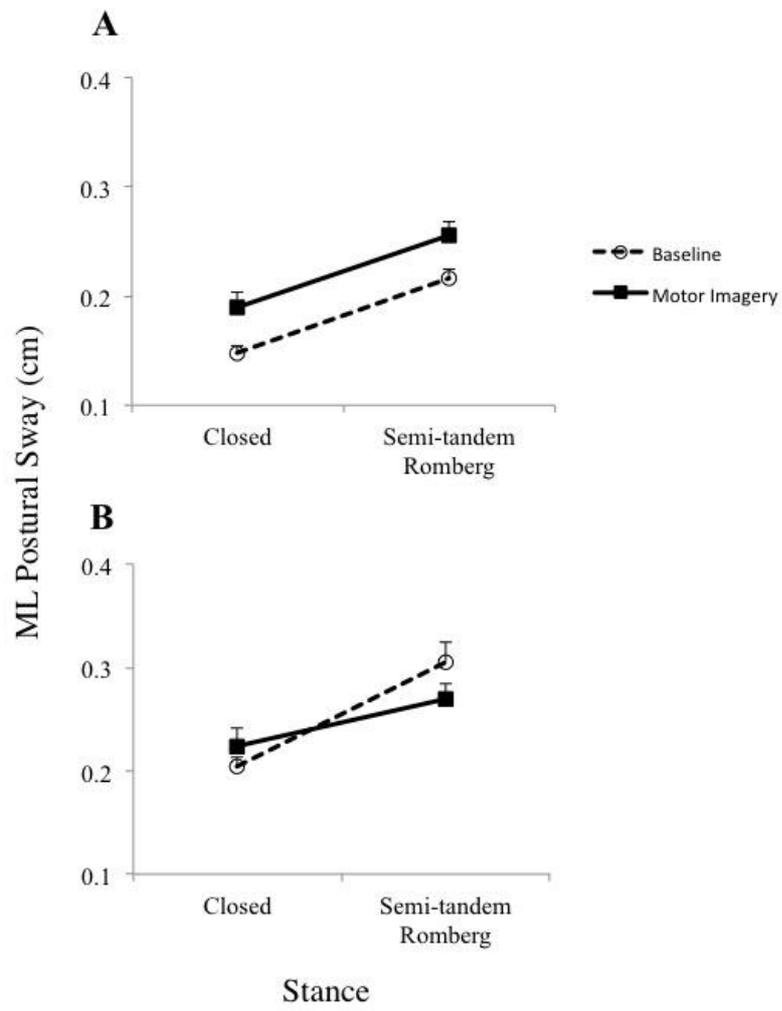


Figure 4

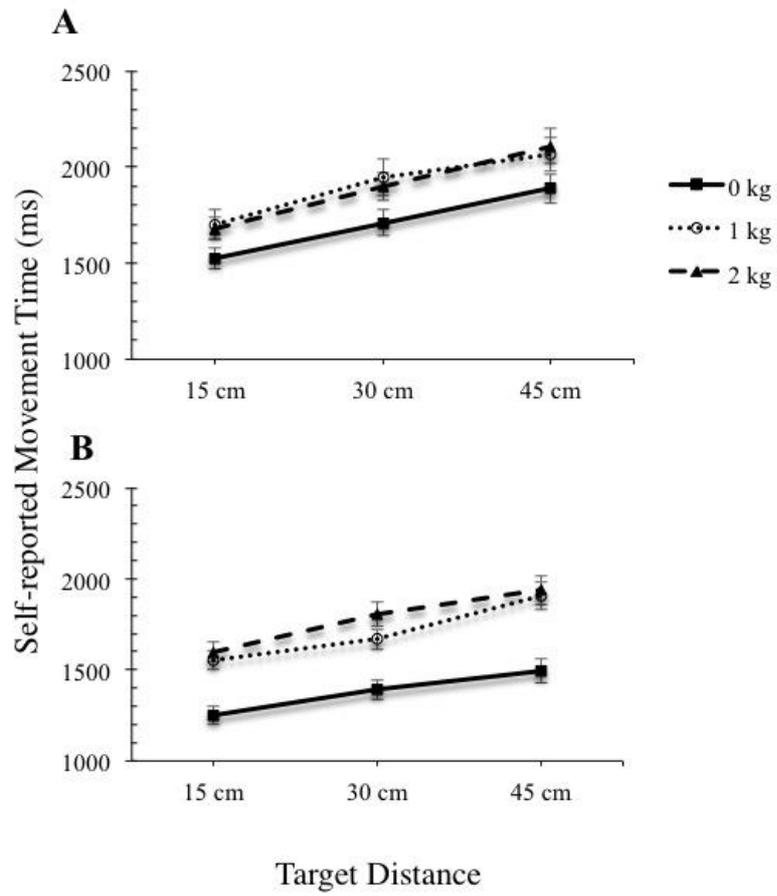


Figure 5

