

Body posture modulates imagined arm movements and responds to them

Hayley Boulton and Suvabrata Mitra

Department of Psychology, University of Warwick, Coventry, United Kingdom

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Boulton H, Mitra S. Body posture modulates imagined arm movements and responds to them. *J Neurophysiol* 110: 2617–2626, 2013. First published September 18, 2013; doi:10.1152/jn.00488.2013.—Imagined movements are thought to simulate physical ones, with similar behavioral constraints and neurophysiological activation patterns and with an inhibition mechanism that suppresses movement execution. When upper body movements such as reaching with the arm are made from an upright stance, lower body and trunk muscles are also activated to maintain body posture. It is not clear to what extent parameters of imagined manual movements are sensitive to the postural adjustments their execution would necessitate, nor whether such postural responses are as effectively inhibited as the imagined movements themselves. We asked healthy young participants to imagine reaching movements of the arm while in upright stance, and we measured their self-reported movement times and postural sway during imagined movements. We manipulated mediolateral stance stability and the direction of arm movement (mediolateral or anteroposterior). Imagined arm movements were reportedly slower when subjects were standing in a mediolaterally less stable stance, and the body swayed more when arm movements were imagined in the direction of postural vulnerability. The results suggest that the postural state of the whole body, not just the involved limbs, informs trajectory planning during motor imagery and that measurable adjustments to body posture accompany imagined manual actions. It has been suggested that movement is suppressed during motor imagery by a premotor inhibitory mechanism operating at brain stem or spinal level. Any such inhibition must be incomplete because, for example, it does not eliminate autonomic arousal. Our results suggest that it also does not effectively suppress postural adjustments planned in support of imagined movements.

motor imagery; motor planning; posture control

ACTIVITIES OF DAILY LIVING are frequently accompanied by thoughts about past, present, and future actions. Such imagined movements retain so many characteristics of their physical counterparts that they have been described as simulations of physical actions (Jeannerod 2006). They exhibit temporal scaling of movement duration to distance (e.g., Decety et al. 1989; Papaxanthis et al. 2002; Sirigu et al. 1996), the same speed-accuracy trade-off as expressed in Fitts' law (e.g., Decety and Jeannerod 1996; Stevens 2004), the same adherence to biomechanical constraints (e.g., Frak et al. 2001; Johnson 2000), and the same pattern of simulated effort (e.g., Cerritelli et al. 2000). Neurophysiological evidence suggests a unitary mechanism for movement representation and execution (Bonnet et al. 1997; Clark et al. 2004), and brain imaging points to common patterns of cortical activation between movement imagery and execution (De Lange et al. 2005; Grèzes and Jecety 2001; Orr et al. 2008). The similarities are not limited to central processes either. Imagined movements generate corticospinal excitation (Stinear et al. 2006) and specific, patterned, but level-attenu-

ated EMG activity in the involved muscles (Guillot et al. 2007; Lebon et al. 2008). Also, corticospinal or cerebral activation during motor imagery can be modulated by changes in afferent signals, for example, by immobilizing a limb (Kaneko et al. 2003), or by a limb posture that is incompatible with the imagined action (De Lange et al. 2006; Vargas et al. 2004).

Voluntary limb movements occur within the context of postural coordinations supporting stance and locomotion. Whether imagery of such movements interacts with posture control has only recently begun to be investigated. Rodrigues et al. (2010) measured participants' body sway while they imagined plantar flexion movements. They found that imagery of this task using the kinesthetic modality (i.e., imagining making the movements from the first-person perspective) resulted in increased anteroposterior body sway. The authors considered that this possibly reflected the error signal corresponding to the mismatch between movement representations evoked by imagery and the absence of actual peripheral activity. It has been suggested that forward models of action (encompassing estimates of body and limb positions and velocities, including those necessary for retaining postural stability), possibly based on efferent copies of motor commands, may also be accessed during action observation or imagery (Davidson and Wolpert 2005; Jeannerod 2006; Kuo 2005). Insufficient or incomplete inhibition of postural commands may constitute an alternative explanation of postural adjustments associated with imagined movements. Grangeon et al. (2011) raised this possibility while interpreting the sway modulation they observed when participants imagined a series of vertical, counter-movement jumps. They found that sway was reduced during imagery in the anteroposterior (AP) and mediolateral (ML) axes but that vertical position varied more while the jumps were imagined. The authors suggested that the reduction in AP and ML sway might have been due to increased postural regulation supporting coordination of the jump sequence, whereas the vertical movements were likely to be the result of incomplete inhibition of motor commands. They also discussed the possibility that postural adjustments may be harder to inhibit during imagery because they are highly automated and involve more subcortical and brain stem-level control (e.g., Collet and Guillot 2009).

Reaching movements of the arm suspend mass away from the main body axis and require specific postural compensation for task accuracy as well as balance retention. The imagery tasks used in the studies by Rodrigues et al. (2010) and Grangeon et al. (2011) involved lower body muscles that were simultaneously active in supporting the body in upright stance. Manual actions can be more subtly related to standing in that they may not directly task the same muscles but require support from postural actions to retain the body's balance. In the present study, we investigated whether the body's current

Address for reprint requests and other correspondence: S. Mitra, Dept. of Psychology, Univ. of Warwick, Coventry, CV4 7AL UK (e-mail: subhobrata.mitra@warwick.ac.uk).

postural state affects parameterization of imagined reaching movements of the arm and also whether the postural adjustments that would accompany the execution of such movements are effectively suppressed during motor imagery. We asked healthy young adults to stand and imagine reaching with the arm in the ML or AP direction, and we manipulated the ML stability of their stance (closed vs. semi-tandem Romberg). If the difference in stance stability is factored into the parameterization of imagined arm movements, we expected self-reported movement durations to be slower in the (mediolaterally less stable) Romberg stance, and particularly so if the imagined arm movements were also in the ML direction. Similarly, if imagined movements generate postural adjustments, we expected to observe greater ML sway during imagined movements in the ML direction, particularly in the Romberg stance.

METHODS

Participants

Participants were 32 young adults from the University of Warwick community [age: 18–21 yr (mean = 18.7 yr, SD = 0.7 yr), weight:

43.5–82.6 kg (mean = 59.9 kg, SD = 11.7 kg), height: 150–185 cm (mean = 165.2 cm, SD = 9.1 cm)]. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield 1971), and none reported any history of neurological or balance impairment. They were naive to the purpose of the experiment and were debriefed only at the end of the session. Additionally, 48 healthy young participants (25 women, mean age: 20.8 yr) from the same pool participated in the baseline measurement of body sway associated with the two stances used in the main experiment. 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.

Apparatus and Procedure

Participants stood barefoot at the designated location marked on the laboratory floor with their arms relaxed by their sides, holding a computer mouse in the left hand. Polhemus Fastrak motion sensors (Colchester, VT) were attached using Velcro belts near the hip (sacral region of the back) and on the head (Fig. 1A). According to the experimental condition, they stood either in closed (feet flush together) or semi-tandem Romberg stance (Fig. 1B). These two stances differed in their ML stability: the latter was less stable as indicated by

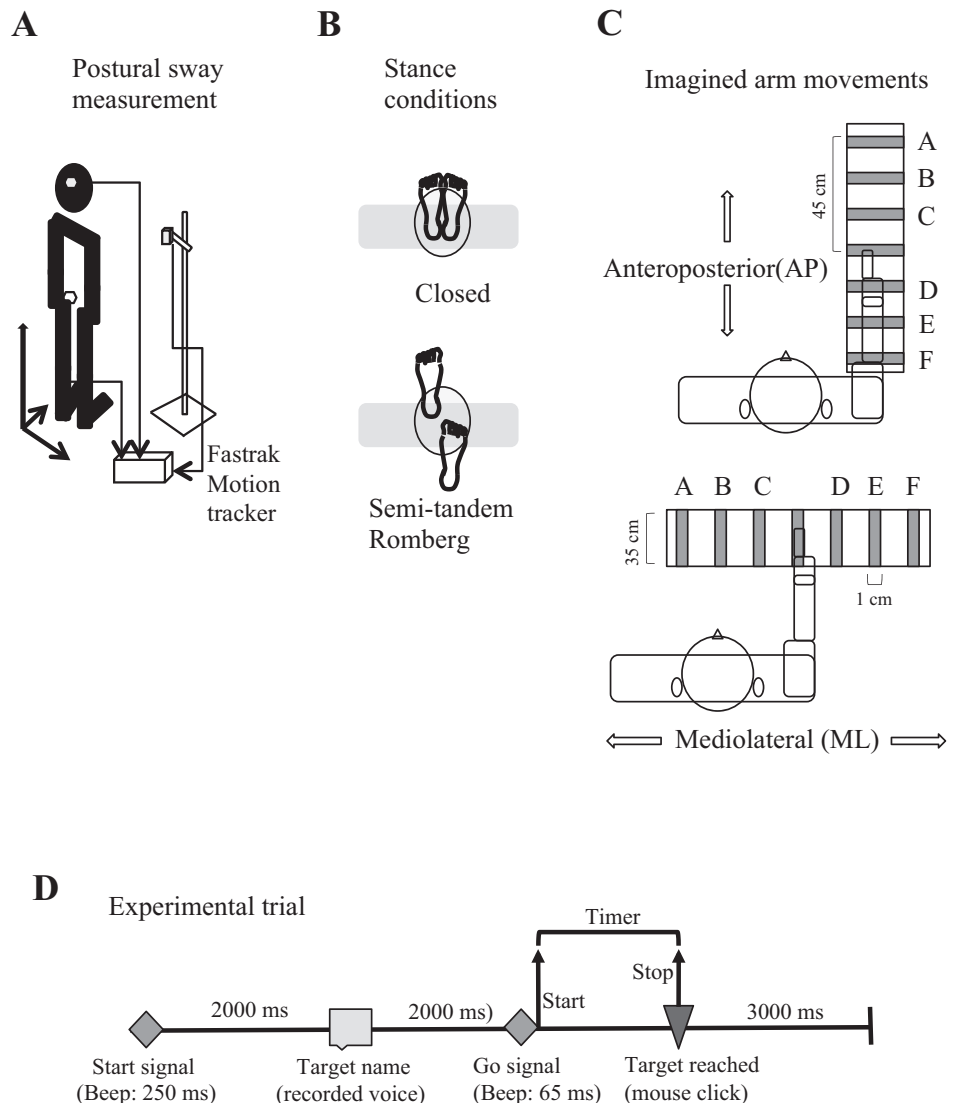


Fig. 1. Experimental setup, task conditions, and measurement conventions. *A*: postural sway was recorded using Polhemus Fastrak sensors placed on the head and the sacral region of the back. *B*: participants stood in closed or semi-tandem Romberg stance. *C*: participants performed imagined reaching movements from the starting position, as shown, in either the anteroposterior (AP) or mediolateral (ML) direction to each of the targets A–F. *D*: sequence of events during each arm movement trial.

greater body sway in baseline measurements during quiet standing (see RESULTS).

The participants' task was to make (practice trials) or imagine (experimental trials) reaching movements of the right arm to each of six target areas (1×35 cm) indicated on a task surface (100×35 cm). The task surface was positioned at waist level and presented in either AP or ML orientation relative to the participants' stance (Fig. 1C). The surface was positioned in line with the participants' right shoulder such that the middle target strip (the starting position for each trial) could be reached by raising the lower right arm to an elbow angle of just over 90° .

Each trial (Fig. 1D) began with a start signal (a 250-ms beep), upon which participants moved (or imagined moving) their right arm to the starting position. After a 2,000-ms silence, participants heard a recorded voice say the name of the target to be reached ("A," "B," . . . , "F"). After a further 2,000 ms of silence, they heard the go signal (a 65-ms beep), upon which they made (or imagined making) the movement to the designated target and clicked the left button of the mouse in their left hand to indicate that they had reached the target. The offset of the go signal set off the timer, and the participants' mouse click stopped it. The next trial began after another 3,000 ms of silence during which participants returned (or imagined returning) to the arms-by-the-sides standing position. An E-Prime script (Psychology Software Tools, Sharpsburg, PA) controlled the sequencing of trial events, including delivery of the prerecorded auditory instructions, timer functions, and random ordering of targets.

The experiment was conducted in blocks of six arm movements (1 each to the 6 targets, in random order). Movement time (MT) was measured on a per movement basis. Postural sway was measured on a per block basis, each time series corresponding to six arm movement trials in a particular orientation (AP or ML), while participants were standing in a given stance (closed or semi-tandem Romberg). At the start of the session, participants were given four practice blocks to become familiar with the required reaching movements. They stood in closed stance and physically made the reaching movements in a self-paced manner. Immediately following these practice blocks, participants performed four experimental blocks in which they imagined making the arm movements. They were instructed simply to imagine moving their index finger to the stated target in the manner instructed (see below). No explicit reference was made in the instructions to visual or kinesthetic imagery modalities. The prospect of third-person imagery (i.e., watching the performance of movements from a different viewpoint) was never raised, so the task context remained throughout in the first-person perspective.

During the imagery trials, participants stood with their eyes open and could see the target board, but the target strips that were visible during the practice trials were no longer available. They were told not to actually make any arm or head movements, the latter also having been reinforced during the practice trials preceding the recorded ones. Participants performed two of the four experimental blocks under instructions to make the imagined movement "as quick as possible" and two blocks under instructions to imagine moving "as straight as possible." These two instruction conditions were included to check that participants carried out the imagery task as instructed (in which case we expected self-reported MT to be longer, and the increase in MT with distance to be greater, in the "as straight as possible" condition). In each instruction condition, one of the two blocks was performed in closed stance and the other in semi-tandem Romberg stance. Block order was counterbalanced. Half of the participants performed the imagined movements in the ML direction and the other half in the AP direction. We included the direction of imagined movement as a between-subjects factor to prevent sporadic carry-over effects in imagery that were reported by some pilot participants (as in Mitra et al. 2013).

Sway Data Analysis

Postural sway measures were collected from the Polhemus sensors attached to both the head and hip segments, and body segment was entered as a factor in the analysis to check that the pattern of sway across experimental conditions did not differ between the segments. In previous research on posture control during motor imagery (e.g., Grangeon et al. 2011; Rodrigues et al. 2010), center-of-pressure measures were obtained from ground reaction forces using a force platform, whereas we measured body sway directly from the hip and head segments using electromagnetic motion trackers. Unlike in the previous studies, the present experiment involved (physical or imagined) extension of upper body mass away from the main axis of the standing body. This raised the possibility of engaging alternative postural strategies to retain balance. For example, to balance the body as the arm reached out in the AP direction, the head and hip could move back in phase, or they could move in anti-phase manner with flexion at the hip (e.g., see Bardy et al. 1999). Given that the arm was unweighted and mostly less than fully extended, we expected the former strategy to be used, but taking separate motion readings from the head and hip segments presented a way of monitoring this; if the head and hip segments showed the same pattern across experimental conditions, with the movement magnitudes proportionally greater at the head than at the hip, the posture control system would likely have approximated an inverted simple pendulum without significant intersegmental articulation. Also, monitoring hip and head motion separately enabled us to scan for any gross head movements during imagery.

AP and ML sway were recorded at 60 Hz and were analyzed as a moving window standard deviation (SD) estimate of short timescale (STS sway) postural activity (<1 -s resolution), and the corresponding root mean square (RMS) mean drift estimate of longer timescale (LTS sway) postural activity at about 1-s resolution (Mitra 2003). We use moving window SD and RMS mean drift to estimate, respectively, a trembling and a rambling aspect of body sway in upright stance (Zatsiorsky and Duarte 2000). The STS sway measure is the average variability of body position within all (nonoverlapping) time windows of 1-s duration in the data series. It gives an indication of the frequency and amplitude of positional adjustments at timescales shorter than 1 s. The LTS sway measure is the average change or drift in body position across all (nonoverlapping) windows of 1-s duration in the time series. Thus a sway time series containing higher frequency or amplitude of microadjustments would yield a greater STS sway magnitude, whereas the LTS sway level would depend more on the absolute distance traversed by body position. The two measures covary, but to varying levels, such as when there is higher frequency of responding but position is confined to a smaller area, or when there are weaker or infrequent adjustments while position drifts over a wider area. They are also complementarily linked in terms of timescale and are well-suited to estimating stable characteristics of non-stationary time series due to the use of moving window statistics (Mitra 2003).

In summary, we manipulated distance (15, 30, or 45 cm), direction (ML or AP), and manner ("as quick as possible" or "as straight as possible") of participants' imagined arm movements, as well as the upright stance (closed or semi-tandem Romberg) in which participants stood as they imagined these movements. Aside from self-reported MT, we also measured STS and LTS sway in both AP and ML directions from the body's hip and head segments. The design used for the different data analyses is indicated in RESULTS.

RESULTS

We analyzed self-reported MT and the LTS and STS measures of AP and ML sway recorded at the hip and head segments using ANOVA with significance level for omnibus effects set to $P < 0.05$. Where multiple post hoc means

Table 1. Baseline measures of postural sway

Body Segment	Stance	LTS Sway, cm		STS Sway, cm	
		ML	AP	ML	AP
Head	Closed	0.204 (0.062)	0.210 (0.059)	0.070 (0.019)	0.072 (0.017)
	Semi-tandem Romberg	0.306 (0.134)	0.211 (0.058)	0.102 (0.031)	0.078 (0.020)
Hip	Closed	0.163 (0.049)	0.151 (0.047)	0.055 (0.015)	0.053 (0.014)
	Semi-tandem Romberg	0.213 (0.056)	0.142 (0.048)	0.073 (0.017)	0.051 (0.014)

Values are means (SD) for baseline measures of long (LTS) and short timescale (STS) sway in the mediolateral (ML) or anteroposterior (AP) direction.

comparisons were needed to resolve a significant omnibus effect, we applied Bonferroni correction using $0.05/N$, where N = number of comparisons.

Baseline Measures of Stance Stability

To obtain baseline differences between the closed and semi-tandem Romberg stances, we asked participants to stand quietly in both stances for 30 s and recorded their hip and head sway using both the measures used in the main experiment (Table 1). On both measures, and for both the hip and head segments, ML sway was greater in the semi-tandem Romberg stance [all $t(47) < -5.8, P < 0.0001$]. AP sway did not differ significantly between the stances even though the support base

along the AP direction was greater in the semi-tandem Romberg stance.

Timing of Physical Arm Movements

We analyzed the physical arm movements made during the practice trials using a 2 (movement direction: ML, AP) × 6 (targets) mixed ANOVA with movement direction as a between-subjects factor and target location as a within-subjects factor. Self-reported MT was the dependent measure. The effect of target location was significant [$F(5,150) = 6.64, P < 0.0001, \eta_p^2 = 0.18$]. MT increased as the distance to the target increased (Fig. 2A). The interaction between movement direction and target location was marginally significant [$F(5,150) = 2.11, P = 0.067, \eta_p^2 = 0.07$]. MTs had a numerical tendency to

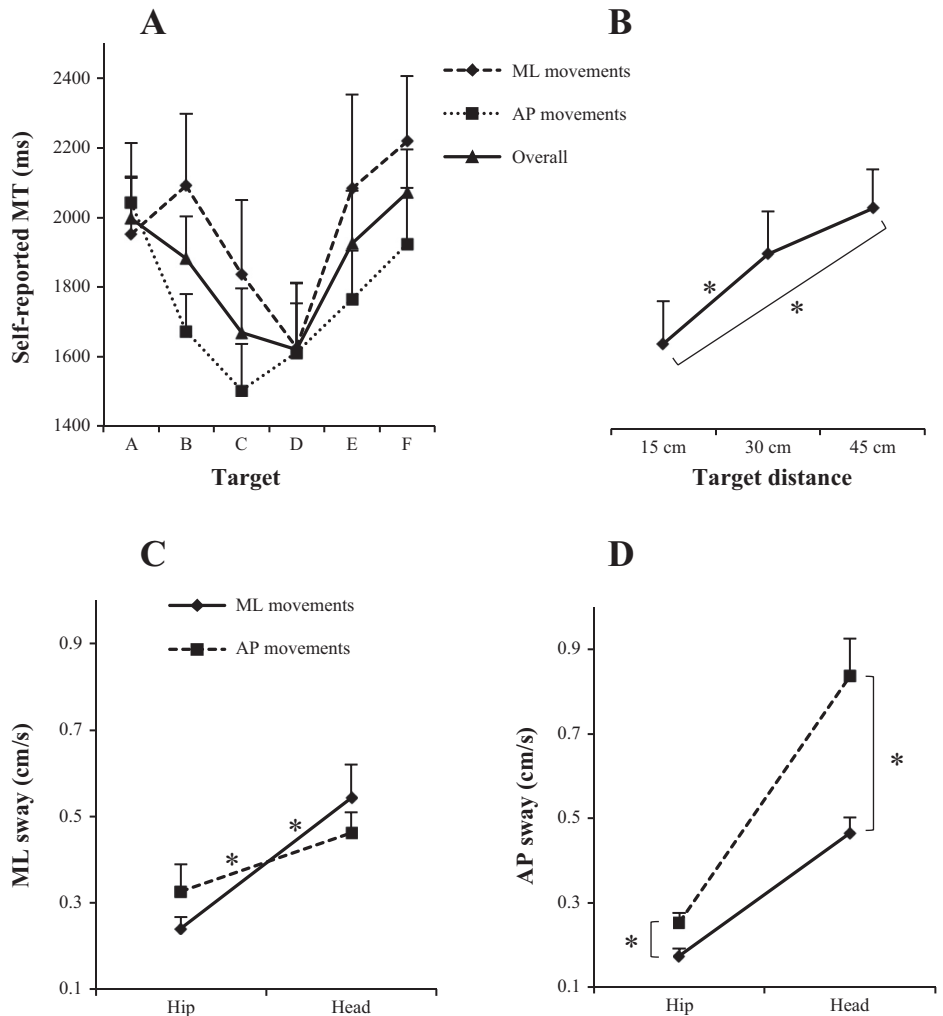


Fig. 2. Effects of task conditions on self-reported movement time (MT; A and B) and ML and AP sway (C and D) during physical arm movements. *Statistically significant differences. Error bars indicate SE.

be longer for movements in the ML direction (Fig. 2A). To form an overall picture of distance scaling during these movements, we also repeated the above analysis with the six targets collapsed into three target distances (Fig. 2, C and D: 15 cm; B and E: 30 cm; A and F: 45 cm). The main effect of target distance was significant [$F(2,60) = 15.82, P < 0.0001, \eta_p^2 = 0.34$]. MT increased almost linearly with target distance (Fig. 2B). Post hoc Fisher's paired least significant difference (PLSD) test showed that MTs increased significantly between target distances of 15 and 30 cm ($P < 0.0001$) and 15 and 45 cm ($P < 0.001$), but not between 30 and 45 cm ($P = 0.07$). No other effects were significant.

Postural Sway During Physical Arm Movements

We analyzed ML and AP components of LTS and STS sway data using a 2 (body segment: head, hip) \times 2 (imagined movement direction: ML, AP) mixed ANOVA with body segment as a within-subjects factor and movement direction as a between-subjects factor.

Mediolateral sway. LTS SWAY MEASURE. ML sway was greater at the head than at the hip segment [$F(1,30) = 34.06, P < 0.0001, \eta_p^2 = 0.53$]. The main effect of movement direction was not significant [$F(1,30) = 0.001, P = 0.98$]. The significant movement direction \times body segment interaction [$F(1,30) = 4.91, P < 0.05, \eta_p^2 = 0.14$] showed that sway measured at the head was greater than that at the hip for arm movements in both ML [$t(15) = 4.30, P < 0.001$] and AP direction [$t(15) = 5.13, P = 0.0001$]. This difference was numerically larger during the former (Fig. 2C). This indicates that the upper body swayed more relative to the hip in the ML direction when arm movements were also along that direction.

STS SWAY MEASURE. The main effect of body segment was significant, with sway measured at the head being greater than that at the hip [$F(1,30) = 93.07, P < 0.0001, \eta_p^2 = 0.76$]. There were no other significant effects.

Anteroposterior sway. LTS SWAY MEASURE. AP sway was greater at the head than at the hip [$F(1,30) = 115.62, P < 0.0001, \eta_p^2 = 0.79$] and greater during AP than during ML arm movements [$F(1,30) = 17.50, P < 0.001, \eta_p^2 = 0.94$]. A significant movement direction \times body segment interaction [$F(1,30) = 12.36, P < 0.01, \eta_p^2 = 0.30$] showed that AP arm movements resulted in both greater head [$t(30) = 4.03, P < 0.001$] and hip sway [$t(30) = 3.15, P < 0.01$]. This difference was numerically greater for head sway (Fig. 2D). Again, this shows that the upper body swayed more relative to the hip in

the AP direction when arm movements were also along the AP direction.

STS SWAY MEASURE. Sway was greater at the head than at the hip [$F(1,30) = 132.67, P < 0.0001, \eta_p^2 = 0.82$] and greater during AP than during ML arm movements [$F(1,30) = 24.69, P < 0.0001, \eta_p^2 = 0.45$]. The significant movement direction \times body segment interaction [$F(1,30) = 11.80, P < 0.01, \eta_p^2 = 0.28$] showed that both head [$t(30) = 4.42, P = 0.0001$] and hip sway [$t(30) = 4.89, P < 0.0001$] were greater during AP than during ML arm movements. This difference was numerically greater in sway at the head.

Timing of Imagined Arm Movements

We analyzed MT data (Table 2) using a 2 (stance: closed, semi-tandem Romberg) \times 2 (instruction: straight, quick) \times 3 (distance: 15, 30, 45 cm) \times 2 (imagined movement direction: ML, AP) mixed ANOVA with all except movement direction as within-subjects factors.¹ MT was longer under instructions to move as straight as possible [$F(1,30) = 41.07, P < 0.0001, \eta_p^2 = 0.58$] and increased linearly with distance [$F(2,60) = 21.69, P < 0.0001, \eta_p^2 = 0.42$]. There was also a significant instruction \times distance interaction [$F(2,60) = 6.61, P < 0.01, \eta_p^2 = 0.18$]; MT increased more sharply with distance under instructions to move as straight as possible (straight: 25.53 ms/cm, quick: 7.86 ms/cm; Fig. 3A). MTs to the 15-cm [$t(31) = 3.64, P < 0.01$], 30-cm [$t(31) = 6.37, P < 0.0001$], and 45-cm target distances [$t(31) = 6.03, P < 0.0001$] were all significantly longer under instructions to move as straight as possible. These results confirmed that participants modulated their imagined movement according to instructions and exhibited the expected temporal scaling of movement duration to distance. Importantly, participants also reported longer MT when standing in semi-tandem Romberg stance [$F(1,30) = 4.91, P < 0.05, \eta_p^2 = 0.15$]. The significant instruction \times stance interaction [$F(1,30) = 8.49, P < 0.01, \eta_p^2 = 0.22$] indicated that this effect of stance was confined to trials in which participants were under instructions to move as quickly as possible (Fig. 3B). There were no other significant effects.

¹ Analysis using the direction of target (left/front: targets A, B, C; right/back: targets D, E, F) as a factor showed that the direction (i.e., whether the imagined movement was to the left or right of the body in the case of ML movements or forward or backward in the case of AP movements) did not have any significant effects. We therefore collapsed (separately for AP and ML movements) the 6 target locations to obtain MTs to 3 target distances of 15, 30, and 45 cm.

Table 2. Self-reported MTs during imagined arm movements

Arm Movement Direction	Target Distance, cm	Movement Time, ms			
		Straight		Quick	
		Closed	Semi-tandem Romberg	Closed	Semi-tandem Romberg
ML	15	2,028.91 (1,352.21)	1,924.13 (1,108.42)	1,055.94 (771.84)	1,260.75 (978.58)
	30	2,292.69 (1,218.44)	2,436.53 (1,331.39)	1,263.75 (727.18)	1,685.84 (1,090.62)
	45	2,856.84 (1,737.66)	2,706.34 (1,547.79)	1,321.81 (730.58)	1,580.03 (1,109.41)
AP	15	1,723.41 (902.13)	1,619.59 (716.74)	988.34 (355.79)	1,585.19 (1,731.51)
	30	2,052.47 (936.97)	2,016.97 (978.90)	1,272.94 (581.05)	1,268.91 (494.93)
	45	2,367.00 (1,082.54)	2,429.59 (899.83)	1,438.44 (716.74)	1,492.59 (649.66)

Values are means (SD) for self-reported movement times (MTs) during imagined arm movements instructed to be as straight or as quick as possible in closed or semi-tandem Romberg stance.

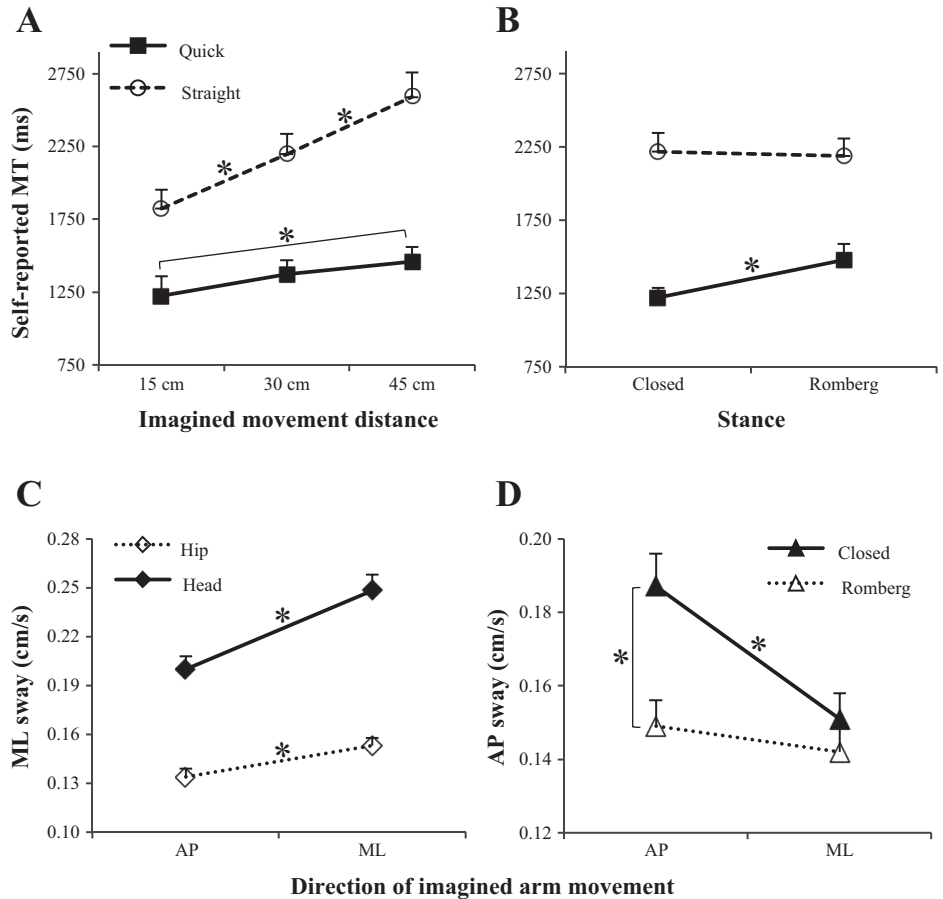


Fig. 3. Effects of task conditions on self-reported MT (A and B) and ML and AP sway (C and D) during imagined arm movements. *Statistically significant differences. Error bars indicate SE.

Postural Sway During Imagined Arm Movements

We analyzed LTS and STS sway data using a 2 (body segment: head, hip) × 2 (stance: closed, semi-tandem Romberg) × 2 (instruction: straight, quick) × 2 (imagined movement direction: ML, AP) mixed ANOVA with all except imagined movement direction as within-subjects factors.

Mediolateral sway. LTS SWAY MEASURE. ML sway (Table 3) was greater in the semi-tandem Romberg stance [$F(1,30) = 11.40, P < 0.01, \eta_p^2 = 0.28$]. Sway measured at the head was greater than that at the hip [$F(1,30) = 126.93, P < 0.0001, \eta_p^2 = 0.81$], and a significant body segment × stance interaction [$F(1,30) = 18.59, P < 0.001, \eta_p^2 = 0.39$] showed that sway was significantly greater in the semi-tandem Romberg stance at the head segment ($P < 0.001$) but only numerically so at the hip segment ($P = 0.08$). These results confirmed baseline measurements showing that participants were less stable in the ML direction while in the semi-tandem Romberg stance and that the sway pattern was similar across the head and hip

segments. Importantly, participants had greater ML sway when they imagined arm movements in the ML direction [$F(1,30) = 5.54, P < 0.05, \eta_p^2 = 0.16$]. The interaction between body segment and imagined movement direction was also marginally significant [$F(1,30) = 4.12, P = 0.051, \eta_p^2 = 0.12$], showing that the effect of imagined movement direction was similar at the hip and head segments but was numerically larger at the latter (Fig. 3C). There were no other significant effects.

STS SWAY MEASURE. Similarly, greater ML sway (Table 4) was measured at the head than at the hip [$F(1,30) = 89.53, P < 0.0001, \eta_p^2 = 0.75$] and during standing in the semi-tandem Romberg stance [$F(1,30) = 27.93, P < 0.05, \eta_p^2 = 0.45$]. There was also a significant body segment × stance interaction [$F(1,30) = 6.82, P < 0.05, \eta_p^2 = 0.19$]; both head and hip sway were greater in semi-tandem Romberg than in closed stance. This effect of stance was larger in head than in hip sway. These results mirror those observed in ML-LTS sway, verifying that ML stability was reduced in the semi-tandem Romberg stance.

Table 3. ML LTS sway during imagined arm movements

Arm Movement Direction	Movement Instruction	Head Sway, cm		Hip Sway, cm	
		Closed	Semi-tandem Romberg	Closed	Semi-tandem Romberg
ML	Straight	0.224 (0.085)	0.265 (0.082)	0.147 (0.048)	0.158 (0.037)
	Quick	0.240 (0.065)	0.263 (0.073)	0.151 (0.041)	0.158 (0.029)
AP	Straight	0.180 (0.051)	0.215 (0.057)	0.127 (0.033)	0.147 (0.040)
	Quick	0.191 (0.059)	0.213 (0.078)	0.132 (0.040)	0.131 (0.044)

Values are means (SD) for ML LTS head or hip sway in closed or semi-tandem Romberg stance.

Table 4. *ML STS sway during imagined arm movements*

Arm Movement Direction	Movement Instruction	Head Sway, cm		Hip Sway, cm	
		Closed	Semi-tandem Romberg	Closed	Semi-tandem Romberg
ML	Straight	0.072 (0.024)	0.088 (0.025)	0.047 (0.014)	0.054 (0.011)
	Quick	0.075 (0.018)	0.086 (0.022)	0.046 (0.010)	0.052 (0.010)
AP	Straight	0.059 (0.017)	0.071 (0.020)	0.045 (0.019)	0.051 (0.018)
	Quick	0.063 (0.017)	0.073 (0.023)	0.043 (0.011)	0.050 (0.026)

Values are means (SD) for ML STS head or hip sway in closed or semi-tandem Romberg stance.

Although the main effect of imagined movement direction was not significant, the significant movement direction \times body segment interaction [$F(1,30) = 4.75$, $P < 0.05$, $\eta_p^2 = 0.13$] showed ML head sway was marginally greater ($P = 0.04$; required corrected level for significance: $P < 0.025$) when imagined arm movements were in the ML direction.

Anteroposterior sway. LTS SWAY MEASURE. AP sway (Table 5) was greater at the head than at the hip [$F(1,30) = 274.12$, $P < 0.0001$, $\eta_p^2 = 0.90$], and it was also greater in closed than in semi-tandem Romberg stance [$F(1,30) = 16.14$, $P < 0.001$, $\eta_p^2 = 0.35$]. Importantly, the stance \times imagined movement direction interaction was significant [$F(1,30) = 6.40$, $P < 0.05$, $\eta_p^2 = 0.17$], showing greater AP sway during imagined arm movements in the AP direction in closed stance but no significant difference between stances during imagined movements in the ML direction (Fig. 3D). Note that the closed stance offers a much smaller support base in the AP direction than does Romberg stance (Fig. 1). There were no other significant effects.

STS SWAY MEASURE. Sway (Table 6) measured at the head was significantly greater than that at the hip [$F(1,30) = 59.37$, $P < 0.0001$, $\eta_p^2 = 0.67$]. Although the main effect of stance was not significant, the significant stance \times movement direction interaction [$F(1,30) = 4.55$, $P < 0.05$, $\eta_p^2 = 0.15$] showed that AP sway during imagined arm movements in the AP direction was greater in the closed than in the semi-tandem Romberg stance. There was no effect of stance on AP sway during imagined arm movements in the ML direction. There were no other significant effects.

DISCUSSION

As in previous studies (e.g., Decety et al. 1989), participants' self-reported MTs scaled with target distance in a similar manner for both physical and imagined movements (Figs. 2B and 3A). In the case of imagined movements, the increase in MT with target distance was also larger when the instruction was to move as straight as possible rather than as quickly as possible. Thus there was clear evidence that participants performed the imagined arm movements as instructed.

The low variability of the imagined MTs also suggests that distance-scaling behavior was quite consistent across participants.

Self-reported MTs of imagined movements in the ML direction were longer in the semi-tandem Romberg stance under instructions to move as quickly as possible. Since this stance is less stable in the ML direction, and ML stability is particularly critical to stance safety (Maki et al. 1994; Swanenburg et al. 2010), slower MT in this stance is consistent with modulation of the imagined movement plan to limit its destabilizing effect on stance. Alternatively, the semi-tandem Romberg stance may have been more demanding because of its relative ML instability (or simply less familiar in this task context given that it did not feature in the practice blocks at the start of the session), reducing the cognitive resources available to guide the arm movements. This could have led to a preference for slower, easier-to-control arm movements. Either way, the observed modulation of imagined MT points to the postural state of the body being incorporated into trajectory planning during motor imagery.

In addition to the above effects, we had also expected to find that during standing in a stance of lower ML stability, movements in the ML direction would be affected more than those in the AP direction. We did not find such a difference in the case of imagined movements. In the physical movement trials, there was a numerical indication of slower MTs in the ML direction (Fig. 2A). However, that interaction between target location and direction of movement was only marginal, and the effect did not retain even marginal significance when the six target locations were resolved into three target distances (Fig. 2B). The physical movements were only performed in closed stance and as practice trials at the start of the session, so we cannot ascertain whether physical movements in the ML direction would have been significantly slower when performed in semi-tandem Romberg stance. Differences in performance characteristics between executed and imagined movement are not always straightforward to compare in any case. For example, Decety et al.'s (1989) study of the effects of load on imagined movements found that imagined, but not physical,

Table 5. *AP LTS sway during imagined arm movements*

Arm Movement Direction	Movement Instruction	Head Sway, cm		Hip Sway, cm	
		Closed	Semi-tandem Romberg	Closed	Semi-tandem Romberg
ML	Straight	0.183 (0.045)	0.179 (0.077)	0.116 (0.038)	0.106 (0.033)
	Quick	0.187 (0.054)	0.177 (0.044)	0.116 (0.033)	0.106 (0.025)
AP	Straight	0.215 (0.044)	0.187 (0.042)	0.147 (0.038)	0.115 (0.040)
	Quick	0.229 (0.093)	0.185 (0.063)	0.157 (0.062)	0.110 (0.039)

Values are means (SD) for AP LTS head or hip sway in closed or semi-tandem Romberg stance.

Table 6. AP STS sway during imagined arm movements

Arm Movement Direction	Movement Instruction	Head Sway, cm		Hip Sway, cm	
		Closed	Semi-tandem Romberg	Closed	Semi-tandem Romberg
ML	Straight	0.061 (0.014)	0.064 (0.023)	0.038 (0.010)	0.055 (0.062)
	Quick	0.061 (0.015)	0.063 (0.013)	0.039 (0.009)	0.037 (0.007)
AP	Straight	0.067 (0.013)	0.063 (0.012)	0.050 (0.020)	0.043 (0.022)
	Quick	0.072 (0.018)	0.065 (0.018)	0.048 (0.014)	0.046 (0.036)

Values are means (SD) for AP STS head or hip sway in closed or semi-tandem Romberg stance.

walking times increased when participants carried an additional load of 25 kg. The authors suggested that the load could be counteracted by increasing effort (to maintain speed) during physical movement, but during imagery this effort may have been encoded centrally and expressed as increased movement time.

Turning to postural sway characteristics during imagined movements, as predicted by the support base sizes of the two stances, participants showed greater ML sway in the semi-tandem Romberg stance and greater AP sway in the closed stance. We also observed greater ML sway during imagined arm movements in the ML direction and greater AP sway during imagined movements in the AP direction (the latter when in closed stance, which has a smaller support base in the AP direction than the Romberg stance). Both these results suggest that participants' postural actions differed depending on the direction (and hence the potential destabilizing effect) of imagined arm movements. Similarly, direction-specific effects on postural sway were also observed during physical arm movements (Fig. 2, C and D). There was no stance manipulation in that case, but the effects emerged in intersegmental dynamics. ML head sway exceeded ML hip sway by a greater margin when arm movements were made in the ML direction. Conversely, AP head sway exceeded AP hip sway by a greater margin during arm movements in the AP direction. In summary, the observed slowing of imagined movements in directions of postural vulnerability supports a strong form of the simulation hypothesis whereby the body's current postural control contingencies are factored to the parameterization of imagined arm movements' trajectories. Greater postural sway in the plane of imagined arm movements, particularly when this corresponds to a direction of postural vulnerability, suggests that manual motor imagery can evoke postural control actions that could have accompanied the execution of imagined movements.

As the first study of potential interactions between manual motor imagery and postural control of upright stance, the focus here was on detecting whether such interactions occur, rather than on resolving their exact nature or the processes that generate them. The limitations of the present study raise several important research questions that require further investigation. First, we did not test whether the observed interactions would be sensitive to specific manipulation of imagery modality (i.e., visual or kinesthetic), imagery perspective (e.g., first or third person), or imagery ability (e.g., Guillot et al. 2009; Solodkin et al. 2004). We asked participants to physically make the movements and then imagine making them immediately thereafter. We did not instruct them specifically to take a first- or third-person perspective, but we also did not raise the prospect of a third-person perspective during the practice

blocks. Relatedly, we gave no clear instructions to adopt a visual or kinesthetic imagery modality. Goal-directed arm movements of the kind performed in this study are likely to involve both visuospatial representations of the limb and target as well as kinesthetic representations of limb articulation (e.g., Prablanc et al. 1986; Wong and Henriques 2009). Notably, kinesthetic imagery specifically requires a focus on feeling the movement, which is not to be confounded with simply visualizing the movement internally. It is possible that explicitly biasing the imagery toward one or the other aspect can modulate the interactions with postural states that were observed here. One possibility is that a strong kinesthetic bias in imagery may result in greater cortical activity in motor areas (Guillot et al. 2009) and lead to a stronger postural correction. In a similar vein, differences in imagery ability, or the vividness of imagery, may have an impact on the postural response. In the present study, we accepted participants' distance-scaling behavior and its modulation by the instructed manner of movement (i.e., "as straight as possible" or "as fast as possible") as evidence that they had planned and mentally executed the arm movements. The two instruction conditions may have differed in difficulty, however, and it remains possible that subjective qualities of the achieved imagery have an impact that future studies classifying participants by imagery ability can document.

Second, the present results do not clarify the exact nature of the postural actions that accompanied the imagined arm movements because we measured postural sway across blocks of several imagined movements in a given direction. Our goal in this first instance was to detect whether any systematic differences in sway accompanied changes to the postural context and spatial orientation of imagined movements. One possibility is that participants made anticipatory postural adjustments (APA) (Krishnan et al. 2012) in the direction opposite to that of imagined arm movements and that these APAs were larger when the imagined movements were expected to have a greater destabilizing effect (e.g., while imagining movements in the ML direction when in the semi-tandem Romberg stance). Another possibility is that participants made postural movements in sympathy with the imagined arm movements. In the physical movement trials, we observed a pattern of proportionally greater upper body sway (relative to hip sway) in the plane of the arm movements. The physical reaching movements may have had a small component of torso motion, either in the direction of the target (i.e., composing the movement out of torso and arm segment motions) or in the direction opposite (to counteract the effects of the arm extending away from the body's vertical axis). A further possibility is that postural adjustments that anticipate or accompany imagined arm movements could also trigger reactive adjustments because imag-

ined movements do not actually deliver the perturbations that would counteract the anticipatory adjustments. Rodrigues et al. (2010) considered a similar possibility (a mismatch between movement representations evoked by imagery and the subsequent absence of actual peripheral activity) in explaining the increase in AP sway they observed when standing participants imagined plantar flexion movements. These considerations suggest that the characteristics of postural actions surrounding imagined movements may be complex and span a longer time period than the duration of the movements per se. We measured postural sway over a block of several imagined movements to enable us to detect differences across experimental conditions in any (or a combination) of these possible components. Further experiments that measure postural actions in the temporal vicinity of individual imagined movements using both kinematic and EMG measures are needed to clarify exactly what actions the postural control system takes during imagined arm movements and why. Also, the present study did not measure whether, or the extent to which, the arm muscles are recruited during imagery, a factor that may affect the postural adjustments that are made. EMG data acquired from the involved arm could help assess the level and effect of motor activation reaching the muscles addressed by imagery.

The execution of postural actions apparently in support of imagined arm movements is worthy of detailed investigation because it may help clarify the mechanisms that allow humans to assemble and simulate motor coordinations without physically executing the corresponding movements. Imagined movements resemble physical ones not only in retaining kinematic and biomechanical constraints but also in incorporating afferent signals regarding the relevant limbs' postural status (as in De Lange et al. 2006) and in generating efferent signals resulting in task-specific but level-attenuated EMG activity in the involved muscles (Guillot et al. 2007; Lebon et al. 2008). Jeannerod (2006) suggested that motor execution is prevented during imagery by an inhibition mechanism that operates at the brain stem or spinal level. Suggested sources of this inhibition include the posterior cerebellum (Lotze et al. 1999) or a pathway descending from the premotor cortex in parallel with corticospinal excitation (Prut and Fetz 1999). It is accepted, however, that any such inhibitory process must be incomplete (Jeannerod 1994, 2006). For instance, autonomic arousal increases during imagined effortful movements despite no actual change in metabolic demand (e.g., Calabrese et al. 2003; Decety et al. 1993), and in addition to such tonic changes, each motor imagery sequence can also elicit specific phasic autonomic activity (e.g., electrodermal responses) (Collet and Guillot 2009; see also Collet et al. 2013). The present results suggest that the incompleteness of inhibition during imagery extends to the supporting postural adjustments that are activated by imagery. This finding has important implications for understanding the mechanisms underlying suppression of movement during imagery. One possibility is that the inhibition mechanism is of relatively central origin and operates upon descending motor commands that directly effect the imagined movement, but cannot access the postural adjustments that are assembled further down the efferent pathway (Grangeon et al. 2011; Guillot et al. 2012).

Regardless of the exact architecture, there is likely to be a life span aspect to this as well, given that postural stability declines with old age, as do inhibitory processes in general (Maylor et al. 2005) and in motor control in particular (Schlaghecken et al. 2011, 2012). Motor imagery is a ubiqui-

tous activity, and it appears reasonable to predict that it elicits a stronger postural response in older, or otherwise balance-impaired, people than we have reported here in young adults. Two aspects of this possibility may be of significant practical interest. First, postural adjustments to nonexistent movements have the potential to destabilize the body in posturally vulnerable individuals and may contribute to their risk of falling or withdrawal from activities of independent living. Conversely, the tendency to produce postural reactions to imagined movements could be harnessed as a means of rehabilitation or exercise. Hamel and Lajoie (2005) showed, for instance, that training older participants to imagine standing in an erect and stable upright stance (while focusing on the kinesthetic sensations associated with the image) led to significant improvements in stance stability and attentional demand. Similar protocols could be developed for a broader range of daily living activities whereby participants are trained to image potentially perturbing voluntary movements (such as those studied here) while focusing on the postural actions that would be required to support them.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

H.B. performed experiments; H.B. and S.M. analyzed data; H.B. and S.M. interpreted results of experiments; H.B. and S.M. prepared figures; H.B. and S.M. drafted manuscript; H.B. and S.M. approved final version of manuscript; S.M. conception and design of research; S.M. edited and revised manuscript.

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