

Posture influences motor imagery: An fMRI study

Floris P. de Lange,^{a,*}¹ Rick C. Helmich,^{a,b,1} and Ivan Toni,^{a,c}

^a*FC. Donders Centre for Cognitive Neuroimaging, Radboud University Nijmegen, Kapittelweg 29, 6500 HB Nijmegen, The Netherlands*

^b*Department of Neurology, Radboud University Medical Centre Nijmegen, The Netherlands*

^c*Nijmegen Institute for Cognition and Information, Radboud University Nijmegen, The Netherlands*

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Motor imagery is widely used to study cognitive aspects of the neural control of action. However, what is exactly simulated during motor imagery is still a matter of debate. On the one hand, it is conceivable that motor imagery is an embodied cognitive process, involving a simulation of movements of one's own body. The alternative possibility is that, although motor imagery relies on knowledge of the motor processes, it does not entail an actual motor simulation that is influenced by the physical configuration of one's own body. Here we discriminate between these two hypotheses, in the context of an established motor imagery task: laterality judgments of rotated hand drawings.

We found that reaction times of hand laterality judgments followed the biomechanical constraints of left or right hand movements. Crucially, the position of subjects' own left and right arm influenced laterality judgments of left and right hands. In neural terms, hand laterality judgments activated a parieto-frontal network. The activity within this network increased with increasing biomechanical complexity of the imagined hand movements, even when the amount of stimulus rotation was identical. Moreover, activity in the intraparietal sulcus was modulated by subjects' own hand position: a larger incongruence in orientation between the subjects' hand and the stimulus hand led to a selective increase in intraparietal activity.

Our results indicate that motor imagery generates motor plans that depend on the current configuration of the limbs. This motor plan is calculated by a parieto-frontal network. Within this network, the posterior parietal cortex appears to incorporate proprioceptive information related to the current position of the body into the motor plan.

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Introduction

It is widely held that imagining performing an action and actually performing the action rely on partly overlapping mechanisms. However, the exact nature of the relationship between

imagined and executed movements remains controversial. In particular, it is not well understood *what* is simulated during motor imagery. Is it a simulation of a movement of one's own body (Jeannerod, 1994) or is it a more abstract implementation of general kinematic rules of biological motion (Viviani and Schneider, 1991; Fitts and Peterson, 1964)? If motor imagery entails a simulation of one's own body movements, then this simulation should depend not only on the action requirements but also on the configuration of one's own body in space. This would be an instance of embodied cognition (Gallese, 2003). Conversely, if motor imagery entails a simulation of a third person's body movement, or merely the selection of an action's goal, then this simulation would require knowledge of the motor processes involved, but no actual motor simulation. This would be an instance of a cognitive process that is independent from the contingent physical characteristics of the agent.

The issue whether motor imagery is embodied remains controversial. Some studies observed an influence of hand posture on motor imagery (Nico et al., 2004; Shenton et al., 2004; Parsons, 1987; Sirigu and Duhamel, 2001; Vargas et al., 2004). Other studies, using hemiplegic patients, showed that motor simulations can be successfully carried out in absence of the ability to produce these actions (Johnson et al., 2002b; Johnson, 2000). The issue goes well beyond the boundaries of motor imagery: movement simulation is a process at the basis of several models of motor planning (Wolpert and Ghahramani, 2000), action observation (Jeannerod, 2001), and social cognition (Gallese et al., 2004; Jacob and Jeannerod, 2005), and it is therefore relevant to precisely define the characteristics of this process. In this study we test these contrasting predictions, both at the behavioral and at the neural level, in the context of a well-established imagery task: the hand laterality judgment task.

Psychophysical studies suggest that, when subjects observe a hand in a certain orientation and have to decide whether it is a left or a right hand, they solve this task by imagining their own hand moving into the stimulus orientation for comparison (Parsons, 1987, 1994; Sekiyama, 1982). These studies found that the time required for a hand laterality judgment is similar to the time taken to execute a corresponding movement. Crucially, the trajectory imagined during laterality judgments of left and right hands is

* Corresponding author. Fax: +31 24 36 10652.

E-mail address: floris.delange@fcdonders.ru.nl (F.P. de Lange).

¹ These authors contributed equally to this work.

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strongly influenced by the biomechanical constraints of actual left-hand and right-hand movements. A series of neuroimaging experiments also suggests a large cognitive and neural overlap between the hand laterality judgment task and execution of actions (de Lange et al., 2005; Rumiati et al., 2001; Sekiyama, 1982; Parsons, 1994; Parsons et al., 1998; Tomasino et al., 2003). On the basis of these findings, the hand laterality task is taken as an instance of motor imagery rather than a purely visual mental rotation task, and it has been extensively used to study cognitive aspects of the action system in a range of motor-related neuropathologies (Schwoebel et al., 2001; Fiorio et al., 2006; Tomasino et al., 2003; Johnson, 2000; de Lange et al., 2004).

In this study, we test for the embodied nature of movement simulation, as operationalized by the hand laterality task, both at the behavioral and at the neural level. First, we used fMRI to identify which regions increase their neural activity with increasing biomechanical complexity of the imagined movement, even when the amount of stimulus rotation is identical. Our approach exploits the fact that rotating right hands in clockwise orientations requires biomechanically more complex movements than counterclockwise rotations, whereas the opposite holds true for left hands (Parsons, 1994). This novel approach (in the context of neuroimaging) allows to identify the network that is specifically involved in imagined hand movements, while avoiding the interpretational and methodological problems that arise when using a secondary task to control for visuospatial processes only loosely related to movement simulation (de Lange et al., 2005; Kosslyn et al., 1998). Second, we assessed to what extent the hand laterality judgment task entails motor simulations of *one's own* body, by probing the influence of posture on performance of this task. For this, we manipulated the posture of subjects left and right hand, independently. If motor imagery evokes motor simulations of one's own body, then the current position of the left and right hand should have an effector-specific effect on behavioral performance. Moreover, this should influence the activity of the neural architecture subserving the integration of postural information in the motor plan.

Methods

Subjects

Seventeen healthy male participants (age 24 ± 3 years, mean \pm SD) took part in the study after giving written informed consent according to institutional guidelines of the local ethics committee (CMO region Arnhem-Nijmegen, the Netherlands). All participants were consistent right-handers (Edinburgh Handedness Inventory (Oldfield, 1971) score $88 \pm 14\%$, mean \pm SD).

Stimuli

We used line drawings of left and right hands, viewed from the palm and from the back. As illustrated in Fig. 1A, four drawings of left hands and right hands at different orientations (upright: 0° ; counterclockwise (CCW): -45° , -90° , -135° ; clockwise (CW): $+45^\circ$, $+90^\circ$, $+135^\circ$; or upside-down: 180°) were used, giving rise to a set of 64 stimuli. These stimuli were presented through a PC running Presentation software (Neurobehavioral systems, Albany, USA). They were projected onto a screen at the back of the scanner and seen through a mirror above the subjects' heads. The stimuli subtended a visual angle of $\sim 10^\circ$.

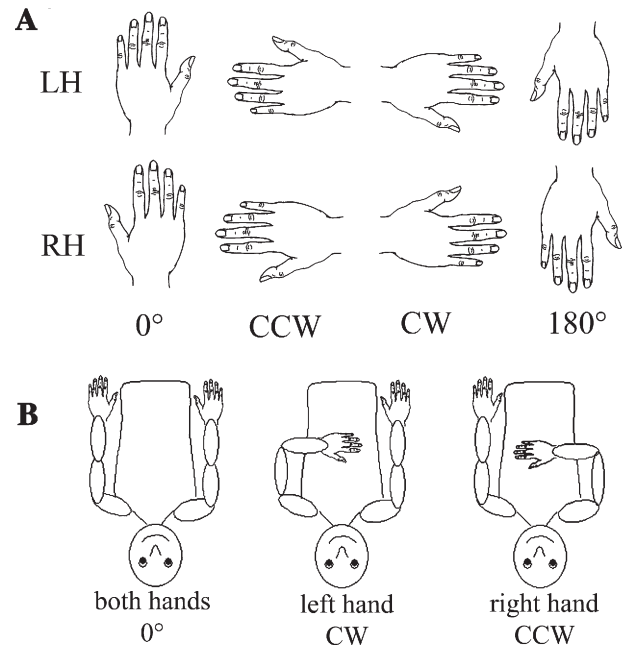


Fig. 1. Task setup. (A) Example of stimuli used. Subjects had to judge whether the stimulus was a left or right hand, irrespective of its orientation, which could be upright (0°), rotated clockwise (CW), counterclockwise (CCW), or upside down (180°). (B) Postural manipulation. Prior to each block of trials, subjects were instructed to adopt one of three postures: both arms extended (0°), the left arm flexed in a CW orientation, or the right arm flexed in a CCW orientation. Subjects lay supine in the scanner and responded by pressing one of two buttons attached to their left and right big toe.

Experimental time course and procedures

The subjects' task was to report whether the hand drawing on display represented a left hand or a right hand (regardless of its orientation) by pressing one of two buttons attached to their left or right big toe. The stimuli were serially presented to the subjects in a random order. During scanning, the subjects' left and right feet were firmly attached to an MR-compatible button box, and reaction times and error rates were measured for subsequent behavioral analysis. Before the start of the scanning session, participants were trained to perform the task adequately, both outside the scanner (64 trials) and inside the scanner (48 trials).

The imaging session consisted of 30 task blocks intermixed with 30 baseline periods. At the beginning of each block, a cartoon (Fig. 1B) instructed the subjects to position their arms in one of three postures: (1) both arms extended [i.e., in a 0° orientation]; (2) the left forearm flexed [i.e., in a CW orientation]; (3) the right forearm flexed [i.e., in a CCW orientation]. To facilitate the positioning of the left and right forearms and to ensure that they were consistently placed in the same position, we placed a marker on the chest of the subjects, such that the arm flexion stopped when the hand reached the marker. The period during which the cartoon was displayed and the postural adjustment took place (6 s) was followed by a baseline period (10 s) during which a fixation cross was displayed on the screen. Then, the subject carried out a block of 16 consecutive trials. Each trial started with a fixation cross, displayed for a variable interval

(1.5–2.5 s), followed by the presentation of a hand drawing. After the subject responded by pressing either the right or left big toe, the visual stimulus was replaced by the baseline fixation cross till presentation of the next hand drawing. Orientation and laterality of the hand drawings was randomized from trial to trial. On the basis of pilot data, the reaction time cut-off was set at 3 s. In total, each subject performed 480 trials (3 postures \times 2 hands \times 8 orientations \times 10 replications), with a total scanning time of \sim 35 min. During the whole experiment, the subjects were lying supine in the scanner, facing the bore of the magnet, unable to see their hands. After the experiment, the subjects filled out a questionnaire concerning awareness of task strategy and effects of the postural manipulation on task performance.

Behavioral analysis

We investigated the influence of stimulus laterality, stimulus orientation, and arm posture on reaction time (RT). We focused our analysis on trials with CCW and CW stimulus orientations, since these orientations are identical in terms of the amount of stimulus rotation but differ in biomechanical complexity. We formalized our behavioral analysis in a $2 \times 2 \times 3$ repeated-measures ANOVA with RT as a dependent variable. LATERALITY (2 levels: left vs. right), stimulus ORIENTATION (2 levels: CCW vs. CW) and POSTURE (3 levels: arms extended, left arm in CW orientation, right arm in CCW orientation) were the independent factors. When interactions were significant, the simple main effects were investigated by post-hoc simple *t*-tests. The alpha-level of all behavioral analyses was set at $p < 0.05$, univariate approach.

Image acquisition

Functional images were acquired on a Siemens TRIO 3.0 T MRI system (Siemens, Erlangen, Germany) equipped with echo planar imaging (EPI) capabilities, using the standard head coil for radio frequency transmission and signal reception. Blood oxygenation level-dependent (BOLD) sensitive functional images were acquired using a single shot gradient EPI-sequence (TE/TR=30/2200 ms; 32 axial slices, voxel size=5.5 \times 3.5 \times 3.5 mm; FOV=224 mm). High-resolution anatomical images were acquired using a MP-RAGE sequence (TE/TR=4.43/1960 ms; voxel size=1.0 \times 1.0 \times 1.0 mm, 176 sagittal slices; FOV=256 mm).

Image analysis

Functional data were pre-processed and analyzed with SPM2 (Statistical Parametric Mapping, www.fil.ion.ucl.ac.uk/spm). First, functional images were spatially realigned using a sinc interpolation algorithm that estimates rigid body transformations (translations, rotations) by minimizing head-movements between each image and the reference image (Friston et al., 1995). Subsequently, the time-series for each voxel was realigned temporally to acquisition of the middle slice. Images were normalized to a standard EPI template centered in Talairach space (Ashburner and Friston, 1999) by using 12 linear parameters (translation, rotation, zoom, and shear) and resampled at an isotropic voxel size of 2 mm. The normalized images were smoothed with an isotropic 10 mm full-width-at-half-maximum Gaussian kernel. Anatomical images were spatially coregistered to the mean of the functional images (Ashburner and Friston, 1997) and spatially normalized by using the same transformation matrix applied to the functional

images. The ensuing pre-processed fMRI time series were analyzed on a subject-by-subject basis using an event-related approach in the context of the General Linear Model. For each trial, square-wave functions were constructed with a duration that corresponded to the mean reaction time of the subject. The haemodynamic responses generated by each explanatory variable were modeled by convolving these square-wave functions with a canonical haemodynamic response function (Friston et al., 1995). Finally, the statistical model included separate regressors of no interest, modeling the period in which the subject changed posture, incorrect and missed responses, residual head movement-related effects, and low-frequency signal drifts over time. Parameter estimates for all regressors were obtained by maximum-likelihood estimation, using a temporal high-pass filter (cut-off 60 s), and modeling temporal autocorrelation as an AR(1) process. Linear contrasts pertaining to the main effects of the factorial design were calculated. Contrasts of the parameter estimates for the 24 main effects (3 POSTURES \times 2 HAND LATERALITIES \times 4 ORIENTATIONS) constituted the data for the second-stage analyses, which treated participants as a random effect (Friston et al., 1999).

The analysis of biomechanical complexity on neural activity considered the LATERALITY of the stimulus (2 levels: left hand, right hand) and the stimulus ORIENTATION (4 levels: 0°, CCW, CW, 180°) as independent explanatory variables. To assess which neural structures were implicated in the behaviorally observed effect of posture, we performed a 2×2 factorial analysis, with the factors POSTURE (2 levels: “arms stretched” vs. “left/right arm flexed in medial orientation”) and stimulus ORIENTATION (2 levels: medial vs. lateral). Medial orientations are orientations of the hand towards the midline of the body (CW for the left hand, CCW for the right hand), whereas lateral orientations are orientations away from the midline of the body (CCW for the left hand, CW for the right hand).

Statistical inference

First, we isolated regions that were showing increases in neural activity with increasing biomechanical complexity of imagined movements for both the left and the right hand. To this end, we created separate Statistical Parametric Maps (SPMs) of the *t* statistics (*t*-contrasts) for each hand. More specifically, we tested for BOLD changes that followed the biomechanical constraints of the right hand [$0^\circ < \text{CCW} < \text{CW} < 180^\circ$], as indicated by the corresponding behavioral data (Fig. 2A, red squares); and for BOLD changes that followed the biomechanical constraints of the left hand [$0^\circ < \text{CW} < \text{CCW} < 180^\circ$] indicated by the corresponding behavioral data (Fig. 2A, blue diamonds). We then tested the conjunction null hypothesis that there was no effect in any of the two SPMs (Nichols et al., 2005), using a voxel-level family-wise error (FWE) threshold of $p < 0.05$ corrected for multiple comparisons across the whole brain. The ensuing SPM identified regions in which there was a significant increase in BOLD signal as a function of orientation for both left and right hands, according to their specific biomechanical constraints. We investigated effects of stimulus LATERALITY and ORIENTATION by a 2×2 repeated measures ANOVA following the same approach described above for the analysis of behavioral data within the four regions that were isolated by this contrast.

Second, we assessed whether there were modulations of neural activity as a function of the subject’s own arm posture. More

specifically, we tested which regions showed significantly higher activity during motor imagery of stimuli in a lateral orientation, when the subjects' arm posture was flexed in a medial position, compared to when the subjects' arm posture was in a neutral position. Since the behavioral effect of posture was very similar across the left and the right hand, for this analysis we collapsed across the left and the right hand. Furthermore, *a priori* anatomical information from previous studies (de Lange et al., 2005; Johnson et al., 2002a) as well as the (orthogonal) contrast in this dataset showed that the intraparietal sulcus and dorsal precentral sulcus are implicated in imagined actions. Therefore, we could use this prior information to constrain our search space (Friston et al., 2006). Accordingly, we defined a search volume comprising spheres of 10 mm around these regions and corrected our results for multiple comparisons using a FWE threshold of $p < 0.05$ within this search volume (Worsley et al., 1996). We also performed a whole-brain analysis to assess for modulations of neural activity outside of our search volume.

Finally, we investigated the influence of *response execution* (flexion of either the left or right big toe) on cerebral activity. Under the assumption that regions involved in controlling the execution of big toe movements are not involved in controlling imagined hand actions, this contrast provides us with a further internal control to test for the anatomical and functional specificity of the orientation and postural effects on cerebral activity identified in the previous two analyses. This analysis was implemented by creating an SPM of the F statistics coding for differential effects of LATERALITY (i.e., following presentations of left and right hands drawings), irrespectively of ORIENTATION and POSTURE.

Anatomical inference

Anatomical details of significant signal changes were obtained by superimposing the SPMs on the structural images of the subjects. The atlas of Duvernoy et al. (1991) was used to identify relevant anatomical landmarks. When applicable, Brodmann Areas were assigned on the basis of the SPM Anatomy Toolbox (Eickhoff et al., 2005), i.e., the anatomical position of our significant clusters and local maxima was formally tested against published three-dimensional probabilistic cytoarchitectonic maps.

Results

Behavioral performance—HAND LATERALITY and ORIENTATION effects

Subjects accurately engaged in the hand laterality judgment task (mean error rate $2 \pm 1\%$). As illustrated in Fig. 2A, RTs increased with increasing rotation of the hand drawings. Identification of right hands was significantly faster than identification of left hands (main effect of HAND LATERALITY: $F_{(1,16)} = 26.8$; $p < 0.001$). Furthermore, the RT profile was qualitatively different for left and right hand stimuli: left hand stimuli were easier to judge in CW than in CCW orientations, whereas the reverse was true for right hand stimuli (HAND LATERALITY \times ORIENTATION interaction: $F_{(1,16)} = 11.9$; $p = 0.003$). This observation suggests that biomechanical constraints also apply to imagined hand movements, and corroborates previous research showing that mental rotation of hands involves the act of imagining one's own hand from its current position to the stimulus orientation for comparison (Parsons, 1994).

Behavioral performance—POSTURE effects

Fig. 2B shows RTs for CCW and CW orientation for left and right hand stimuli separately, and for the different postures of the left and right arms. As stated before, CCW orientations were more difficult than CW orientations for left hands ($F_{(1,16)} = 7.12$; $p = 0.017$) whereas CW orientations were more difficult than CCW orientations for right hands ($F_{(1,16)} = 14.0$; $p = 0.002$). Crucially, these effects were modulated by subjects' posture. When subjects put their own left hand in a CW orientation (Fig. 2B, open blue diamonds/dashed blue line), solving imagined actions for left hands in CCW (opposite) orientations became more difficult (POSTURE \times ORIENTATION interaction: $F_{(1,16)} = 5.97$; $p = 0.027$; post-hoc test for CCW: $F_{(1,16)} = 6.02$; $p = 0.026$). Analogously, when subjects put their own right hand in a CCW orientation (Fig. 2B, open red squares/dashed red line), solving imagined actions for right hands in CW orientations became more difficult (POSTURE \times ORIENTATION interaction: $F_{(3,48)} = 6.49$; $p = 0.022$; post-hoc test for CW: $F_{(1,16)} = 4.78$; $p = 0.044$).

Post-scanning interviews showed that subjects either failed to notice (60% of the subjects) or to explain (40% of the subjects) how posture influenced performance in either task, emphasizing

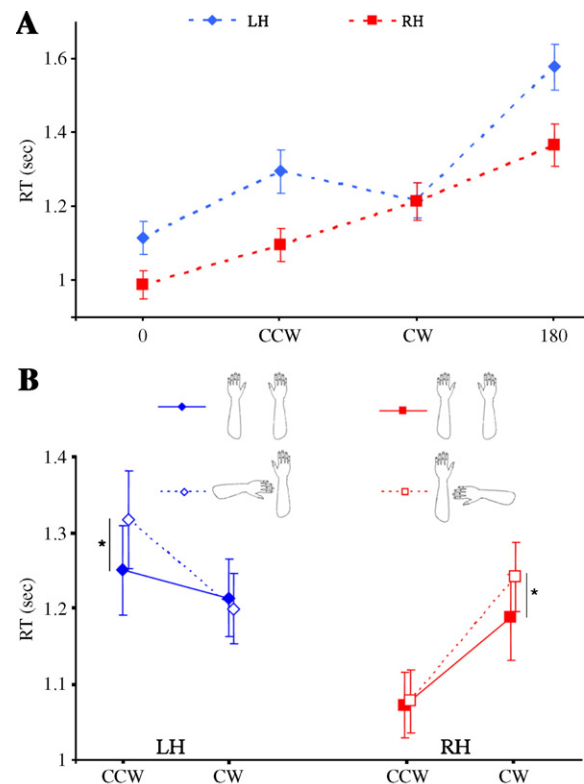


Fig. 2. Behavioral performance. (A) Reaction times (mean \pm SEM) for laterality judgments of left hands (LH, in blue) and right hands (RH, in red) in upright (0°), counterclockwise (CCW), clockwise (CW) and upside down (180°) orientations, collapsed over the different arm postures. (B) Reaction times for LH and RH in CW and CCW orientations, for the different postures separately. Putting the left hand in a CW orientation (open blue diamonds/blue dashed line) impaired laterality judgments of left hands in CCW orientations. Analogously, putting the right hand in a CCW orientation (open red squares/red dashed line) impaired laterality judgments of right hands in CW orientations.

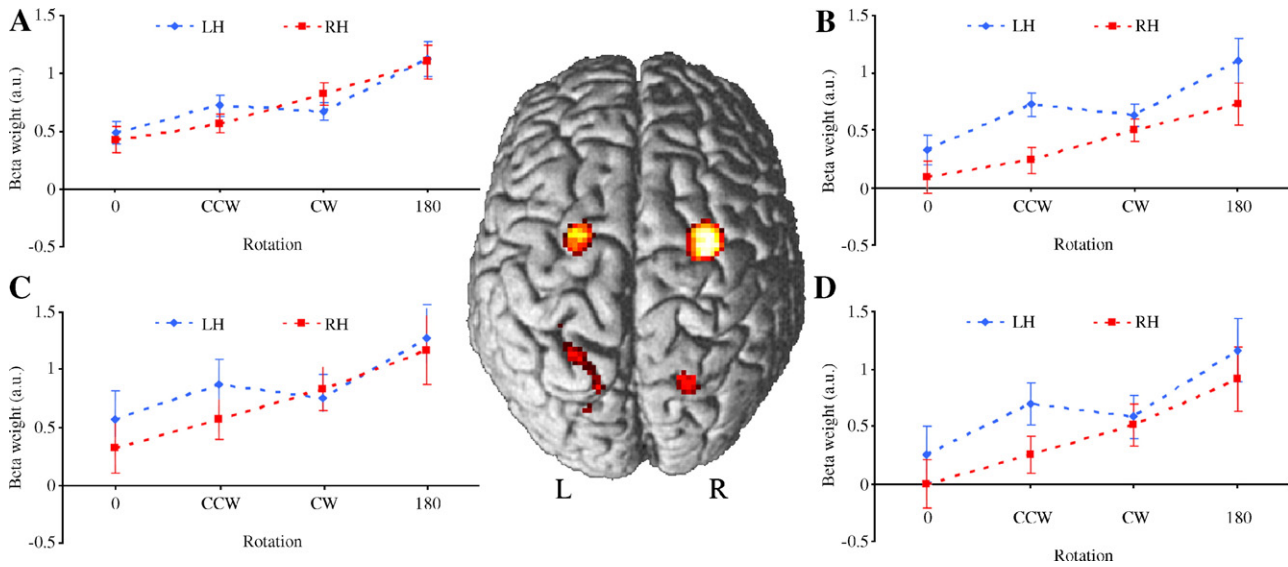


Fig. 3. Neural activity modulated by biomechanical complexity. Plotted are the parameter estimates of the BOLD response (\pm SEM) of the four regions showing significant orientation-related effects following the arms' biomechanical constraints. For graphical purposes map is thresholded at $T > 4.6$. (A) Left PMd. (B) Right PMd. (C) Left IPS. (D) Right IPS.

the implicit nature of the imagined actions and the influence of the posture of one's own body on this process.

Cerebral activity—HAND LATERALITY and ORIENTATION effects

We tested for significant changes in BOLD signal as a function of stimulus orientation for both left and right hands, according to their specific biomechanical constraints. In line with previous results (de Lange et al., 2004, 2005; Johnson et al., 2002a), this effect occurred in a restricted cerebral network (Fig. 3), centered around the intraparietal sulcus (IPS) and the dorsal precentral sulcus of both hemispheres (Table 1). The precentral clusters fall rostral to the probability range of BA4a, and within the probability range (20–40%) of BA6 (Eickhoff et al., 2005). Therefore, they can be labeled as dorsal premotor cortex (PMd). The intraparietal clusters fall caudal to the probability range of BA2.

Right PMd (Fig. 3B) showed significantly stronger responses when a left hand picture was presented, as compared to when a right hand picture was presented ($F_{(1,16)}=67.4$; $p < 0.001$). Furthermore, the activity of this region varied according to the arms' biomechanical constraints, showing different orientation effects for left and right hands (HAND LATERALITY \times ROTATION interaction: $F_{(1,16)}=20.3$; $p < 0.001$). A significant effect of biomechanical constraints was also found in the left PMd (Fig. 3A; HAND LATERALITY \times ORIENTATION interaction: $F_{(1,16)}=9.22$; $p = 0.008$). However, in contrast to the response pattern of the right PMd, the left PMd cluster was not influenced by the LATERALITY of the hand drawings ($F_{(1,16)}=0.48$; $p = 0.50$), but instead showed a comparable level of activity during trials involving left and right hands (Fig. 3A). Right IPS (Fig. 3D) showed a response profile similar to that of right PMd, with significantly higher activity following the presentation of left hand drawings ($F_{(1,16)}=7.37$; $p = 0.015$) and a significant HAND LATERALITY \times ORIENTATION interaction ($F_{(1,16)}=28.0$; $p < 0.001$). Left IPS (Fig. 3C) showed a similar response as left PMd, with no significant effect of HAND LATERALITY ($F_{(1,16)}=2.39$; $p = 0.142$) but a

significant HAND LATERALITY \times ORIENTATION interaction ($F_{(3,48)}=20.9$; $p < 0.001$).

Cerebral activity—POSTURE effects

A 2×2 factorial analysis with the factors POSTURE (2 levels: "arms stretched" vs. "left/right arm flexed in medial orientation") and stimulus ORIENTATION (2 levels: medial vs. lateral) showed increased neural activity in the left IPS ($[-24, -56, 56]$; $T=3.56$, $p=0.032$ corrected for search volume) for stimuli in lateral orientations when the subjects' own hand was flexed in a medial position, compared to when the subjects' own hand was in a neutral position (Fig. 4). This finding is in close correspondence with the behaviorally observed effect of posture, i.e. longer RTs for hand stimuli in a lateral orientation (CCW for left hands, CW for right hands) when the subjects' own hand is in a medial position (CW for left hands, CCW for right hands).

Cerebral activity—execution-related effects

Finally, we assessed the activation profiles and anatomical localization of brain regions related to response execution (Figs.

Table 1
Regions showing a modulation of biomechanical complexity

Anatomical region	Hemisphere	T-value	p-value	Stereotactic coordinates
Dorsal intraparietal sulcus	L	4.8	0.024	-18 -66 48
	R	5.1	0.014	20 -66 52
Dorsal precentral sulcus	L	6.3	<0.001	-24 -8 54
	R	6.9	<0.001	30 -8 56

Spatial coordinates of the local maxima of regions showing a parametric increase in activity with increasing biomechanical complexity for both left hands and right hands. All results are corrected for multiple comparisons across the whole brain using a FWE-correction method with a threshold of $p < 0.05$.

Table 2
Regions showing general task-related activity

Contrast	Anatomical region	Hemisphere	T-value	p-value	Stereotactic coordinates		
LH > RH	Central sulcus	R	14.2	<0.001	12	-32	74
	Parietal operculum	R	7.6	<0.001	34	-20	14
	Cerebellum (lobus centralis)	L	10.7	<0.001	-14	-38	-32
RH > LH	Central sulcus	L	15.8	<0.001	-8	-34	72
	Parietal operculum	L	7.5	<0.001	-32	-24	16
	Cerebellum (lobus centralis)	R	6.7	<0.001	20	-32	-34

Spatial coordinates of the local maxima of regions showing general task-related differences between motor imagery of left hands and motor imagery of right hands. These areas did *not* show a parametric increase with increasing biomechanical complexity. All results are corrected for multiple comparisons across the whole brain using a FWE-correction method with a threshold of $p < 0.05$.

5A–B), i.e. the flexion/extension of the big toes used to report the laterality judgment required by the task. When subjects responded by moving the right or left foot, we observed activity in the contralateral primary motor cortex (medial wall, around the leg area) and secondary somatosensory cortex (parietal operculum PO1 and PO2; 70–90% probability range), as well as in ipsilateral cerebellum (all p -values < 0.001). A complete list of activated regions is given in Table 2. Notably, there was neither an effect of ORIENTATION nor a HAND LATERALITY \times ORIENTATION interaction in these regions (all p -values > 0.10; see Figs. 5A–B).

Discussion

This study investigated the neural mechanisms of simulated movements, and assessed the embodied nature of this process.

Behavioral data supported the hypothesis that postural information influenced the motor imagery process. In neural terms, two regions increased their activity with increasing complexity of the imagined movement, even when the amount of stimulus rotation was identical: the intraparietal sulcus and the dorsal premotor cortex. This confirms that both parietal and frontal regions are involved in the transformation of motor variables from external to internal coordinate systems (Sergio and Kalaska, 2003; Scott et al., 1997; Scott and Kalaska, 1997). Within this network, only the intraparietal sulcus changed its imagery-related activity as a function of subjects' own arm posture. This result suggests that, even within the largely recurrent computational architecture of the parieto-frontal network (Burnod et al., 1999; Johnson et al., 1996), the posterior parietal cortex might have a privileged role for incorporating somatosensory information on the current body's position into a motor plan (Andersen et al., 1997). In the following sections, we discuss our behavioral and imaging results, elaborating on the implications of these findings for current models of action simulation (Gallese and Goldman, 1998; Oztog et al., 2005).

Behavioral effects

Reaction times were a function of the biomechanical complexity of the imagined movements induced by the hand-laterality judgment task, rather than a monotonic function of the rotation of the hand drawings. Right hands that were rotated in a CW direction were more difficult than when they were rotated in a CCW direction. For left hands, the pattern was the opposite (Fig. 2). Since subjects' performance revealed a preferred direction of rotation that was tuned to the laterality of the hand drawing on display, we can exclude that subjects solved the task by mentally rotating (i) the same hand across trials (e.g. their dominant hand), or (ii) either hand at random. These alternative ways of solving the task would have resulted in (i) a systematic preference for one of the rotation directions, or (ii) no preference whatsoever. Overall, our results corroborate previous findings (Parsons, 1987, 1994; Sekiyama, 1982) and indicate that subjects were simulating a hand movement, rather than performing a visual mental rotation of the hand drawing.

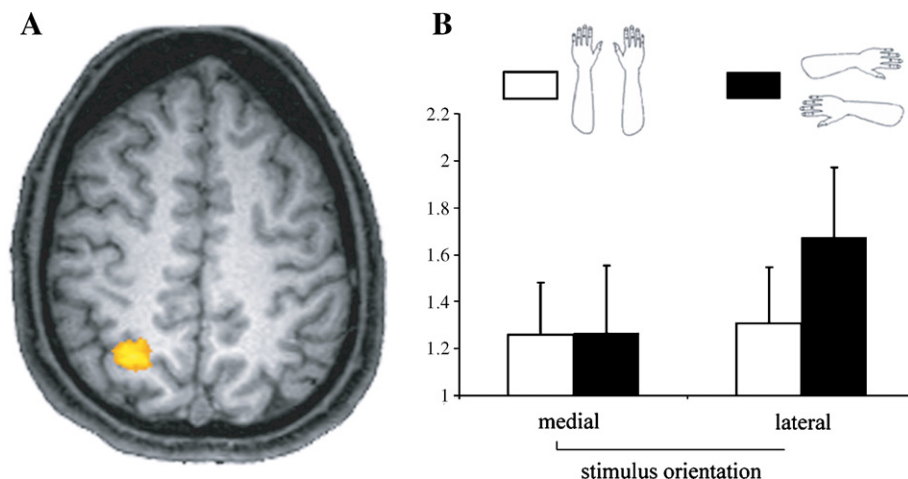


Fig. 4. Postural modulation of neural activity. (A) Anatomical localization of the postural effect on neural activity. For graphical purposes, the map is thresholded at $T > 2.5$. (B) Activity profile of the left intraparietal sulcus. During laterality judgments of stimuli in a medial orientation there was similar neural activity, irrespective of whether the subjects put their own arms in a neutral position (white bar) or a medial position (black bar). During laterality judgments of stimuli in a lateral orientation, there was increased activity when subjects put their own hand in the opposite medial orientation (black bar), compared to the neutral position (white bar).

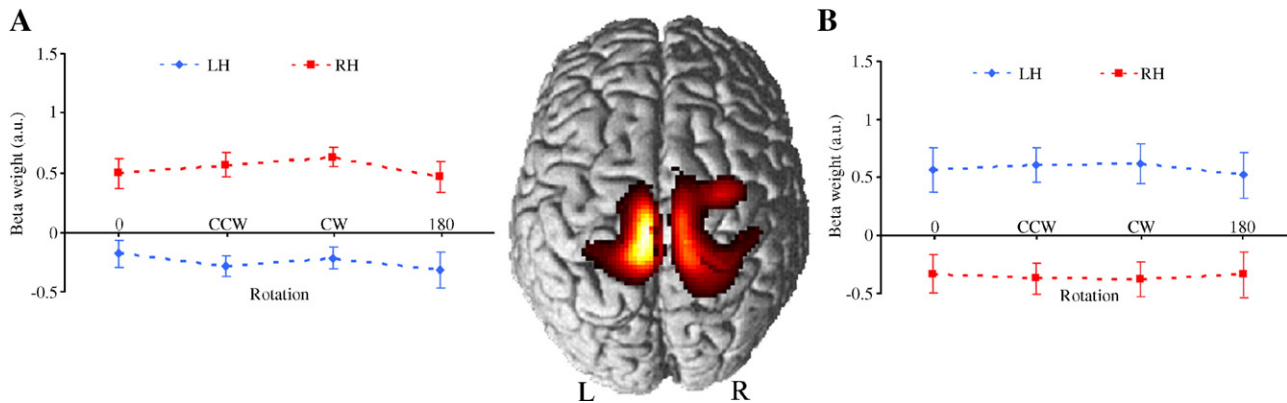


Fig. 5. Neural activity related to movement execution. Plotted is the parameter estimate of the BOLD response (\pm SEM) of two regions showing activity differences due to movement execution. For graphical purposes map is thresholded at $T > 4.6$. (A) left sensorimotor cortex, leg area. (B) Right sensorimotor cortex, leg area.

Notably, the position of the subjects' forearms influenced their performance in an effector-specific manner, and the direction of the effect was consistent with the position of the forearms. When subjects put their left or right arm in the biomechanically easier orientation (CW for left hands, CCW for right hands), the identification of the left or right hand in opposite, biomechanically complex orientations was more difficult (Fig. 2B). This postural effect was not related to direct visual information of the subjects' own hands, given that the subjects were unable to see their own hands. The effect was not driven by sensory feedback during ongoing movements, as subjects did not move their arms during the imagery task. Also, the postural effect cannot be a generic by-product of posture (i.e. subjects' comfort or limb's position awareness), since the effect was an *interaction* between the posture of the subject's own hand, the laterality of the hand shown on the screen, and the orientation of the hand shown on the screen. These behavioral results extend and detail the effects of posture on behavioral performance observed in earlier reports that manipulated the posture of both limbs simultaneously (Parsons, 1994; Sirigu and Duhamel, 2001).

Cerebral effects

Biomechanical complexity of the imagined movements significantly modulated cerebral activity in dorsal intraparietal and premotor regions. These regions showed stronger responses following presentation of left hands drawings in CCW orientations (w.r.t. to CW orientations), while the opposite pattern emerged following presentation of right hands drawings. This effect was restricted to the parieto-frontal motor planning network: contiguous primary somatomotor regions responded to actual movements of the big toes, but not to the orientation and laterality of the hand drawings (Fig. 5). The cerebral effect showed a degree of lateralization: right intraparietal and premotor activity showed higher activity for motor imagery of the contralateral left hand, while the corresponding regions on the left hemisphere showed equal levels of activity for imagined movements of left and right hands. The cerebral effect could not be driven by attentional or oculomotor factors, since these factors were not related to hand biomechanical constraints and laterality. Taken together, our imaging results confirm that mental simulation of hand movements depend on motor processes (Gerardin et al., 2000), and show a degree of lateralization. This

finding extends the left-hemispheric dominance found for selecting and preparing actual motor responses (Schluter et al., 1998, 2001; Verstynen et al., 2005) to imagined hand movements.

Within the parieto-frontal motor planning network, only the intraparietal sulcus was sensitive to the manipulation of posture: when there was a larger incongruence between arm posture and the stimulus orientation, there was increased activity in this region, but not in the premotor cortex. The larger computational load to merge the proprioceptive arm-related information with the motor plan thus seems to be calculated in the parietal cortex. This finding supports the notion that the posterior parietal cortex integrates both sensory signals from many modalities (e.g. visual, proprioceptive, auditory and vestibular) and efferent copy signals from motor structures (Andersen et al., 1997) during the generation of a motor plan, in order to generate an estimate of the movement end-point (Desmurget et al., 1999). This simulation may then be forwarded to the dorsal premotor cortex for selection of the appropriate motor plan, as suggested by the Prospective Action Model (Johnson et al., 2002a).

Implications and predictions

We have shown that body posture *obligatorily* influences simulated actions; although the postural manipulation was irrelevant to correctly solving the task, it could impair performance (Fig. 2). This finding appears relevant for motor theories of perception that rely on tight links between planning and observation of actions (Calvo-Merino et al., 2005; Oztop et al., 2005). If observation of actions were to amount to the retrieval of a motor program that can reproduce them, and tap into the same processes as imagery of actions, we would expect that action observation should be influenced by the body configuration of the observer. Alternatively, if action observation depends on extracting action goals (Wohlschlagler et al., 2003; Fogassi et al., 2005) and thus relies on different functional mechanisms than action simulation, then action observation should not be necessarily bound to the posture of the observer.

Conclusions

Mental rotation of left and right hands followed the biomechanical constraints of the left and right hand, and showed increases obeying

these constraints in a specific bilateral parieto-frontal circuit. Within this circuit, the right hemisphere was preferentially activated for left hand movements, whereas the left hemisphere was active for both left and right hands. Moreover, behavioral performance and activity in the intraparietal sulcus was influenced by subjects' own arm posture. These findings illustrate the embodied nature of imagined movements and point to a specific cerebral site for integrating different sources of information during movement simulation.

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