

Lateral Somatotopic Organization During Imagined and Prepared Movements

Pascale Michelon, Jean M. Vettel and Jeffrey M. Zacks

JN 95:811-822, 2006. First published Oct 5, 2005; doi:10.1152/jn.00488.2005

You might find this additional information useful...

This article cites 78 articles, 23 of which you can access free at:

<http://jn.physiology.org/cgi/content/full/95/2/811#BIBL>

Updated information and services including high-resolution figures, can be found at:

<http://jn.physiology.org/cgi/content/full/95/2/811>

Additional material and information about *Journal of Neurophysiology* can be found at:

<http://www.the-aps.org/publications/jn>

This information is current as of February 16, 2006 .

Lateral Somatotopic Organization During Imagined and Prepared Movements

Pascale Michelon,¹ Jean M. Vettel,² and Jeffrey M. Zacks¹

¹ Psychology Department, Washington University, St. Louis, Missouri; and ² Department of Cognitive and Linguistics Sciences, Brown University, Providence, Rhode Island

Submitted 11 May 2005; accepted in final form 1 October 2005

Michelon, Pascale, Jean M. Vettel, and Jeffrey M. Zacks. Lateral somatotopic organization during imagined and prepared movements. *J Neurophysiol* 95: 811–822, 2006. First published October 5, 2005; doi:10.1152/jn.00488.2005. Motor imagery is a complex cognitive operation that requires memory retrieval, spatial attention, and possibly computations that are analogs of the physical movements being imagined. Likewise, motor preparation may or may not involve computations that are analogs of actual movements. To test whether motor imagery or motor preparation activate representations that are specific to the body part whose movement is imagined or prepared, participants performed, imagined, and prepared hand movements while undergoing functional MRI scanning. Actual hand movements activated components of the motor system including primary motor and somatosensory cortex, the supplementary motor area, the thalamus, and the cerebellum. All of these areas showed strong lateral organization, such that moving a given hand activated the contralateral cortex and ipsilateral cerebellum most strongly. During motor imagery and motor preparation, activity throughout the motor system was much reduced relative to overt movement. However, significant lateral organization was observed during both motor imagery and motor preparation in primary motor cortex, the supplementary motor area, and the thalamus. These results support the view that the subjective experience of imagined movement is accompanied by computations that are analogs of the physical movement that is imagined. They also suggest that in this regard motor imagery and motor preparation are similar.

INTRODUCTION

Motor imagery is the ability to imagine performing a movement without executing it. Motor imagery and motor execution overlap in their computational features and in their neural substrates (for a review, see Jeannerod 1995). However, the term “motor imagery” encompasses a range of computational processes, which can be arranged hierarchically (Jeannerod 1994). High-level processes include memory for targets of movement and attention to spatial locations. Low-level processes may include mapping the effector-specific sequence of commands necessary to make a desired movement. This requires solving two difficult inverse problems: The *inverse kinematics* problem is the mapping of a desired movement path to the sequence of joint angles that will produce it. The *inverse dynamics* problem is the mapping from those joint angles to a sequence of muscle torques. We will refer to the performance of these computations without overt movement as *motor simulation*. The subjective experience of motor imagery may require one to perform a motor simulation. However, another possibility is that it only involves high-level processes. The question of whether motor imagery involves motor simulation

is important because motor simulation processes have a different computational form than high-level memory and attention processes: Unlike those processes, motor simulation stands in an analog relationship to the imagined action. The primary goal of the present study was to test whether neural correlates of motor simulation could be identified during motor imagery. To what extent motor imagery can be differentiated from motor preparation, the readiness to perform an action, was also assessed.

Just as the computations supporting motor imagery can be arranged hierarchically, so to can the brain regions supporting motor function (Dum and Strick 2002). Critical components implementing motor functions include the primary motor cortex (M1), the supplementary motor area (SMA), the premotor cortex (PM), the cingulate motor zones (CZ), and the cerebellum. During actual movements, many of these areas show somatotopic organization. Two types of somatotopy can be distinguished: *lateral organization* occurs when one-half of the body is represented in a brain area predominantly in the corresponding hemisphere (*ipsilateral*) or in the opposite hemisphere (*contralateral*). *Homuncular organization* occurs when nearby body parts within one-half of the body (e.g., the right hand and right elbow) are represented in nearby brain locations. Lateral and homuncular organization have been observed in M1, first during direct cortical stimulation in awake patients (Penfield and Rasmussen 1950) and recently in neuroimaging studies of motor activity (e.g., Alkadhi et al. 2002; Grafton et al. 1991; Overduin and Servos 2004). Both types of somatotopic organization in SMA and PM have been revealed by work with nonhuman primates (Godschalk et al. 1995; Kurata 1989; Mitz and Wise 1987). A few recent studies using either electrical stimulation in epileptic patients (Fried et al. 1991; Yazawa et al. 1998) or neuroimaging during actual movements (Colebatch et al. 1991; Fox et al. 1985; Maccotta et al. 2001; Mayer et al. 2001) have provided evidence for both lateral and homuncular organization in SMA.

The role of these regions in motor imagery has been studied in a number of positron emission tomography (PET) and functional MRI (fMRI) studies. Most of the initial PET studies reported that M1 is not activated by motor imagery, and some more recent fMRI studies are consistent with this finding (Binkofski et al. 2000; Decety et al. 1988, 1994; Gerardin et al. 2000; Stephan et al. 1995). However, a growing number of studies using fMRI have reported activity in M1 while subjects imagined making a movement with their left or right hand (Dechent et al. 2004; Leonardo et al. 1995; Lotze et al. 1999; Luft et al. 1998; Porro et al. 1996; Roth et al. 1996). Activity

Address for reprint requests and other correspondence: P. Michelon, Dept. of Psychology, Washington Univ., St. Louis, MO 63130 (E-mail: pmichelo@artsci.wustl.edu).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

in SMA and PM has been consistently reported during motor imagery. Results for the CZ, thalamus, and cerebellum have been mixed (for reviews, see Decety et al. 2002; Picard and Strick 2001).

In summary, several of the regions activated during actual movement are activated during motor imagery. However, it is not known what computations these areas are performing during motor imagery. Brain activity during a motor imagery task could result from high-level processes such as memory and attention or from motor simulation. Somatotopic organization provides one means to distinguish between the two. High-level representations of plans for actions or targets of movement do not have to be somatotopically organized. However, the processes required by motor simulation should be organized in such a way, if they have the same format as the computations supporting actual movement. Thus if a motor imagery task leads to motor simulation, activity during that task should be somatotopically organized.

The evidence regarding somatotopic organization during motor imagery is surprisingly sparse. Indirect evidence comes from electroencephalographic studies, which have measured the surface electrical activity during imagined left and right hand movements, and found evidence for lateral organization (Galdo-Alvarez and Carrillo-de-la-Peña 2004; Pfurtscheller and Neuper 1997; Pfurtscheller et al. 1999). Until recently, there was little direct evidence for either lateral or homuncular somatotopic organization during motor imagery. Two neuroimaging studies that reported tests for contralateral organization did not find it (Lotze et al. 1999; Roth et al. 1996). Both studies also failed to detect lateral somatotopic organization in SMA during actual movements, suggesting that this null result has been caused by lack of power or to particulars of the task design. Another neuroimaging study reported significant homuncular organization in M1 during motor imagery, but this brief report included no direct tests of such organization (Stippich et al. 2002). A recent study that showed clear homuncular and lateral organization in M1 and PMC during actual movements found no evidence of homuncular organization in these areas during motor imagery and only weak evidence of lateral organization in the hand area or PMC (Hanakawa et al. 2005). Finally, two studies using reasoning tasks likely to involve motor simulation did report lateral organization in the intraparietal sulcus and superior parietal lobe, but not in motor cortex (Johnson et al. 2002; Wolbers et al. 2003). In fact, only one study has reported clear evidence of homuncular organization of evoked brain activity during motor imagery (Ehrsson et al. 2003). In this experiment, participants performed and imagined bilateral hand, toe, or tongue movements, and the resulting activity was directly compared across tasks, revealing a clear superior/medial to inferior/lateral progression in M1 during both execution and imagery. The results also provided some evidence for homuncular organization in SMA and PM during imagery, but the data were less clear. Thus more data are clearly needed regarding both lateral and homuncular somatotopic organization during motor imagery. The absence of evidence is surprising, given that such data are crucial to understanding the processes underlying motor imagery.

Closely related to motor imagery is motor preparation. Motor preparation can be defined as readiness to perform an action. It may differ from motor imagery in at least two

substantive ways. First, it is possible that the typical subjective experience of motor imagery does not require that one perform a motor simulation, only to retrieve a stored high-level representation of an action, whereas motor preparation requires motor simulation to be ready to perform the action on command. Second, the opposite could be the case: Retrieval of a high-level action plan may be sufficient to prepare a movement, whereas motor simulation may be required to create the subjective experience of motor imagery.

Existing evidence suggests that motor imagery and motor preparation do not in fact differ substantially. The neural substrates of motor preparation have been extensively studied in monkeys using paradigms in which the animal is given preparatory information and has to withhold the behavior during a delay before receiving a go cue. Brain activity during the delay period has been observed mainly in the prefrontal cortex, PM, SMA, M1, and the parietal cortex (Alexander and Crutcher 1990; Romo et al. 1992; Wise and Mauritz 1985). fMRI studies of motor preparation in humans in which similar delayed response paradigms were used also suggest that M1, SMA, PM, the cingulate cortex, and the cerebellum are involved in motor preparation (Cui et al. 2000; Lee et al. 1999; Ramnani and Miall 2003; Richter et al. 1997; Toni et al. 2002; Watanabe et al. 2002; Zang et al. 2003).

There is little neuroimaging evidence for or against somatotopic organization during motor preparation. Most of the studies mentioned above involved preparing an action with only one limb, which did not permit one to assess the degree to which activity related to motor preparation is somatotopically organized. One study asked participants to prepare a unimanual movement of the left or right hand, but did not test for lateral organization (Lee et al. 1999). However, ample indirect evidence comes from electrophysiological studies in which the "Bereitschaftspotential" or readiness potential (BP) was observed. The BP is a slow negative wave that develops before the onset of the movement (Deecke et al. 1969). After a symmetrical onset (reaching a maximum amplitude above the SMA), BP amplitude becomes larger over the hemisphere contralateral to the movement side (above the precentral region) (Barrett et al. 1986; Cui and Deecke 1999; McAdam and Seales 1969). Cortical recording studies with patients also suggest that SMA may show homuncular organization during motor preparation (Ikeda et al. 1992; Yazawa et al. 1998, 2000). These electrophysiological results suggest that motor preparation involves simulation.

The study reported here was designed to answer two questions about the role of simulation processes in motor imagery and motor preparation. First, which components of the motor system, if any, show lateral somatotopic organization during motor imagery? Answering this question is crucial to distinguish between motor simulation processes and higher-level processes that may underlie the motor activity observed during motor imagery. Whereas Ehrsson et al. (2003) examined homuncular somatotopic organization, these experiments focused on lateral organization. Second, does the distribution of lateral somatotopic organization during motor preparation differ from that during motor imagery?

Lateral somatotopic organization was measured during movement, motor imagery, and motor preparation. Participants were asked to execute, imagine, or prepare lateral rotational

hand movements with either their left or their right hand, while brain activity was measured with fMRI. For the preparation task, the movements were countermanded on most trials (no-go trials), but occasionally the movement was executed immediately after the preparation interval (go trials).

Three features of the experimental design were optimized to maximize power to detect lateral somatotopic organization. First, a large number of MRI measurements were collected for each participant. Second, components of the motor system were anatomically identified in each participant. Third, the task designs were constructed to dissociate brain activity caused by motor tasks from that caused by processing of instructional cues. Specifically, the motor preparation task was designed to distinguish between activity related to motor preparation *per se* and activity related to processing the preparation cue. Such a distinction could not be drawn in most of the previous fMRI studies of motor preparation (Cui et al. 2000; Lee et al. 1999; Richter et al. 1997; Watanabe et al. 2002; Zang et al. 2003), with a few exceptions (Ramnani and Miall 2003; Toni et al. 1999, 2002). To separate motor preparation from cue processing, the motor preparation task included both go trials and no-go trials and baseline trials on which no movement was prepared.

METHODS

Participants

Twelve participants (4 females; mean age, 23.6 yr) were recruited from the Washington University community. All participants had normal or corrected-to-normal vision, were native English speakers, were right-handed as measured by the Edinburgh Handedness Inventory (Raczkowski et al. 1974), and reported no history of significant neurological problems. Participants were paid and provided informed consent in accordance with guidelines set by the Washington University Humans Studies Committee.

Imaging procedures

Imaging was conducted on a Siemens 3 T Vision System (Erlangen, Germany). Noise cancellation headphones and ear plugs were used to dampen scanner noise. Visual stimuli were generated on an Apple Power Macintosh G3 computer using PsyScope (Cohen et al. 1993) and were projected onto a screen positioned at the head of the magnet bore by a LCD projector. Participants viewed the stimuli by way of a mirror mounted on the scanner's head coil. Padding around the head and a piece of tape positioned across the forehead were used to minimize head movement.

Structural imaging included a high resolution ($1 \times 1 \times 1.25$ mm) sagittal T1-weighted MP-RAGE (TR = 2,100 ms, TE = 3.9 ms, flip angle = 7° , TI = 1,000 ms) and a T2-weighted fast turbo-spin echo (TSE) scan. Functional data were acquired using a T2-weighted asymmetric spin-echo echoplanar sequence sensitive to blood oxygenation level-dependent (BOLD) contrast (TR = 2,048 ms, TE = 25 ms, 4.0×4.0 mm in-plane resolution). Whole brain coverage was achieved with 32 contiguous 4-mm slices. Slice tilts and offsets were prescribed in relation to the AC-PC plane on the basis of fast automatic atlas registration of a low resolution (2-mm cubic voxel) MP-RAGE scan. The complete imaging session lasted ~ 2 h.

Stimuli and tasks

Participants performed three tasks during the functional runs. In the *perform* task, they were instructed to perform a rotational movement of the left or right hand at 1 Hz for ~ 4 s (4.15 s). In the

imagine task, they were asked to imagine performing such a movement but to refrain from making any movement. In both tasks, on each trial, an L, R, or X cue was presented. When the cue was L or R, participants were instructed to begin moving or imagining moving immediately and to continue for the duration of the cue (4.15 s). If the cue was an X, they were to rest (*baseline* trials). At the end of the trial, the L, R, or X was replaced after 4.15 s by a red octagon, which was their cue to stop. The octagon remained on the screen for 2 s. The total trial duration (6.14 s) corresponded to three scanner acquisition frames. In both tasks, one-third of the trials were left hand trials, one-third were right hand trials, and one-third were baseline (rest) trials. In the *prepare* task, the same L, R, and X cues were used. Participants were instructed that when an L or R was presented they should prepare a movement of their left or right hand. They were asked to continue to prepare throughout the 4.15-s duration of the cue. If the cue was an X, they were instructed to rest. L or R cues were replaced either by a red octagon, signaling that they were not to move on that trial (no-go), or by a green circle, which cued them to perform the movement (go). X cues were always followed by a red octagon. The octagon or circle remained on screen for 2 s, for a total trial duration of 6.14 s. In the *prepare* task, one-half of the trials were no-go trials (one-half left hand, one-half right hand), one-quarter were go trials (one-half left hand, one-half right hand), and one-quarter were baseline trials.

In the three tasks, all stimuli were shown centrally. They were presented according to a rapid presentation randomized event-related design (Burock et al. 1998), in which each trial type (left, right, or baseline) appeared with equal probability on each trial.

Procedure

Participants practiced the tasks before beginning the scanning session. First, they learned the unilateral hand rotational movement and its pace (1 rotation/s) using a metronome. In a mock scanner environment, they practiced the three tasks as many times as needed. Second, they practiced the tasks on a computer and completed 36 trials of the *perform* task, 36 trials of the *imagine* task, and 48 trials of the *prepare* task. Finally, they practiced the tasks during the high-resolution structural scan and completed 24 trials each of the *perform* and *imagine* tasks and 32 trials of the *prepare* task. This extensive practice session was conducted to minimize body movements and errors during the scans.

Once participants completed the initial training and were made comfortable in the scanner, structural images were acquired, and the slice prescription for the functional data acquisition was computed. The final practice session was conducted during the longest structural scan, the high-resolution MP-RAGE scan. Participants then completed nine BOLD runs, three of each task. Performance of the *perform*, *imagine*, and *prepare* tasks was blocked by scanner run. The order of the three tasks was counterbalanced across participants. Each BOLD run for the *perform* and *imagine* tasks lasted 359 s (60 3-frame trials plus 4 initial fixation frames) and each run for the *prepare* task lasted 477 s (80 3-frame trials plus 4 initial fixation frames). The first four frames during which a fixation cross was presented were later dropped from the analysis to permit stabilization of the longitudinal magnetic field.

Each scanning session was videotaped to monitor for inappropriate movements during the tasks.

fMRI data analysis

Preprocessing included 1) compensation for slice-dependent time shifts, 2) elimination of odd/even slice intensity differences caused by interpolated acquisition, 3) realignment of all data acquired in each subject within and across runs to compensate for rigid body motion (Ojemann et al. 1997), and 4) intensity normalization to a whole brain

mode value of 1,000. The functional data were transformed into the stereotaxic atlas space of Talairach and Tournoux (1988) by computing a sequence of affine transforms (1st frame EPI to T2-weighted TSE to MP-RAGE to atlas representative target), which were combined by matrix multiplication. Reslicing the functional data in conformity with the atlas involved only one interpolation. For cross-modal (e.g., functional to structural) image registration, a locally developed algorithm was used.

Ten motor regions were identified in each brain hemisphere, based on anatomic landmarks (Fig. 1). The regions were traced based on a parcellation of the motor areas proposed earlier (Crespo-Facorro et al. 1999, 2000; Picard and Strick 1996, 2001). The borders for each of the regions are listed in Table 1, and descriptive statistics for the regions' locations are given in Table 2.

For each participant, the fMRI signal was averaged over each anatomically defined region and submitted to statistical analyses based on the general linear model. The model included effects corresponding to left hand, right hand, and baseline trials. For the perform and imagine tasks, for each effect, a predictor variable was constructed by creating a variable whose value was 1 during the 4-s actual or imagined periods, and zero otherwise, and convolving that variable with a model hemodynamic response function (Boynton et al. 1996). To measure the overall activation in a given region, we estimated the fMRI signal change for both left and right hand trials, relative to rest trials. To measure lateral organization, we compared the fMRI signal change in the hemisphere contralateral to the hand that moved or was imagined to move to fMRI signal change in the ipsilateral hemisphere. For each effect of interest, the magnitude for each participant for each region was averaged across the two hemispheres. Group-level activity was characterized with random-effects *t*-test.

For the prepare task, separate predictor variables were created to model the hemodynamic response to brain activity during the 4-s preparation intervals and brain activity during the 2-s response intervals. By combining separate predictors to model the preparation and response intervals with catch trials on which no movement was prepared, this approach provides an estimate of activity during the preparation interval uncontaminated by the actual movements during the response period of the go trials (Ollinger et al. 2001a,b). The analyses reported here focus on the preparation intervals, excluding

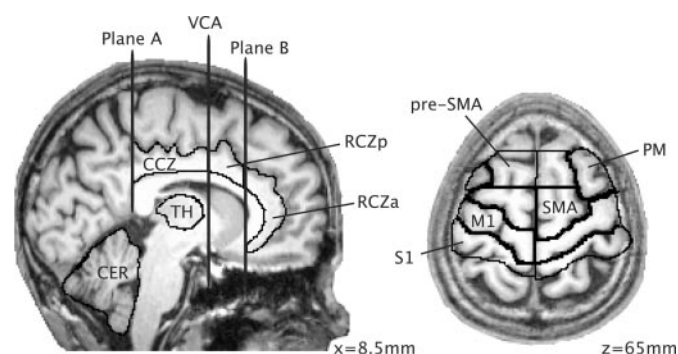


FIG. 1. A representative example of the parcellation of the 10 motor regions identified anatomically for each individual. Sagittal slice shows the cerebellum (CER), thalamus (TH), caudal cingulate zone (CCZ), posterior rostral cingulate zone (RCZp), and anterior rostral cingulate zone (RCZa). Three reference planes are also depicted, which were defined based on tracing a line between the anterior and posterior commissures (AC-PC line): plane A (vertical line drawn through where the central sulcus intersects the medial wall and perpendicular to the AC-PC line), VCA (vertical line drawn through the anterior commissure and perpendicular to the AC-PC line), and plane B (vertical line drawn from the most anterior point of the internal genu of the corpus callosum and perpendicular to the AC-PC line). Axial slice shows the primary somatosensory cortex (S1), primary motor cortex (M1), supplementary motor area (SMA), presupplementary motor area (pre-SMA), and premotor cortex (PM). For a precise anatomic description of each region, see Table 1.

the go and no-go intervals, as the processes involved in countermanding or executing a motor plan once it is formed were not the focus of the study. *t*-tests were conducted to characterize the response of each motor region during the preparation intervals. One set of *t*-tests assessed overall changes in activity in each region, and a second set assessed the degree of lateral organization.

RESULTS

For all fMRI analyses, we adopted an alpha level of 0.05, using the Bonferroni procedure to correct for multiple comparisons across the 10 motor regions. As this is a quite conservative procedure, we will also discuss effects of interest that approached but did not reach statistical significance after correcting for multiple comparisons.

Task-related increases in activity

Activity caused by actual movement or motor imagery was calculated by comparing activity during the left and right trials in each task to baseline trials in the same task. During the perform task, increases in BOLD activity were strongest in the primary somatosensory cortex (S1), M1, SMA, the thalamus, and the cerebellum (Fig. 2). For S1, 10 of the 12 participants showed increases in BOLD activity during task performance; for the other four regions, 11 of 12 participants showed increases. At the group level, all five of these regions showed significant increases. PM, anterior rostral cingulate zone (RCZa), and posterior rostral cingulate zone (RCZp) showed trends toward changes in activity during the perform task, which were significant at the single-region level but did not survive correction for multiple comparisons. RCZp increased in activity, whereas PM and RCZa decreased.

During the imagine task, robust increases were found only in SMA (Fig. 2). All of the 12 participants showed increased activity in SMA in this task, and activity in SMA was significant at the group level. M1 increased consistently in activity (11 of 12 participants), but this trend was significant only at the single-region level and failed to survive correction for multiple comparisons. PM, caudal cingulate zone (CCZ), RCZa, RCZp, and the thalamus all showed less consistent changes in activity, which were significant at the single-region level but did not survive corrections for multiple comparisons. In RCZp, the trend was toward increasing during the imagine task (7 of 12 participants); in the other regions, the trend was toward decreasing (8 of 12 participants for CCZ, 9 of 12 for PM and RCZa).

Activity caused by motor preparation was calculated by comparing activity during left and right preparation intervals to the baseline, including both go and no-go trials. Overall activity during the preparation period of the prepare task showed a pattern that was similar to that for the imagine task, but weaker and more variable across participants (Fig. 2.) In SMA, the most consistently activated region, 9 of 12 participants showed increases. This led to a group-level trend that was significant at the single-region level but failed to survive correction for multiple comparisons. S1, PM, and RCZa showed trends toward decreases in activity that were significant at the single-region level but did not survive correction for multiple comparisons (9 of 12 participants for S1 and RCZa, 10 of 12 for PM).

TABLE 1. Six borders used to trace each motor region and the plane in which the region was traced

	Superior	Inferior	Posterior	Anterior	Lateral	Medial	Trace in Plane
S1	Dorsal surface	Superior portion: cingulate sulcus; inferior portion: termination of sulcus	Postcentral sulcus	Central sulcus	Lateral edge	Superior to cingulate: medial wall; inferior to cingulate: fundus of sulcus	Axial
M1	Dorsal surface	Superior portion: cingulate sulcus; inferior portion: termination of sulcus	Central sulcus	Precentral sulcus	Lateral edge	Superior to cingulate: medial wall; inferior to cingulate: fundus of sulcus	Axial
SMA	Dorsal surface	Cingulate sulcus	M1	VCA*	Superior Frontal Sulcus	Medial wall	Coronal
Pre-SMA	Dorsal surface	Cingulate sulcus	VCA*	Plane B†	Superior Frontal Sulcus	Medial wall	Coronal
PM	Dorsal surface	Extension of the cingulate sulcus to lateral edge	M1	Plane B†	Lateral edge	Superior frontal sulcus	Coronal
CCZ	Cingulate sulcus	Corpus callosum	Plane A‡	VCA*	Lateral edge of cingulate sulcus	Medial wall	Coronal
RCZp	Cingulate sulcus	Corpus callosum	VCA*	Plane B†	Lateral edge of cingulate sulcus	Medial wall	Coronal
RCZa	Superior cingulate sulcus	Inferior cingulate sulcus	Plane B†	Anterior edge of cingulate sulcus	Lateral edge of cingulate sulcus	Medial wall	Coronal
Thalamus	Edges determined based on contrast properties of the structure in T1 image						Axial
Cerebellum	Edges determined based on contrast properties of the structure in T1 image						Sagittal

*VCA: vertical line drawn through the Anterior Commissure and perpendicular to the AC-PC line. †Plane B: vertical line drawn through the most anterior point of the internal genu of the Corpus Callosum and perpendicular to the AC-PC line. ‡Plane A: vertical line drawn through where the central sulcus intersects the medial wall and perpendicular to the AC-PC line. S1, primary somatosensory cortex; M1, primary motor cortex; SMA, supplementary motor area; PM, premotor cortex; CCZ, caudal cingulate zone; RCZp, posterior rostral cingulate zone; RCZa, anterior rostral cingulate zone.

Activity during motor imagery and motor preparation was directly compared at the individual and group levels, using a *t*-test of the same form as those for the analyses of the single tasks. These provided weak evidence for differences between motor preparation and motor imagery. In three regions, the group-level analyses indicated trends that were significant at the single-region level but failed to survive correction for multiple comparisons. In M1, the increase observed during motor imagery was smaller during motor preparation. In CCZ, the decrease observed during motor imagery was smaller during motor preparation. In the thalamus, the decrease observed during motor imagery switched to a very small increase in the motor preparation condition.

Lateral organization

Lateral organization in each task was calculated by comparing trials on which the cued movement (e.g., right hand) was contralateral to a given region (e.g., in the left hemisphere) to trials on which the cued movement (e.g., right hand) was ipsilateral to the given region (e.g., in the right hemisphere). For the prepare task, only the preparation interval was analyzed. In the perform task, every region that showed significant overall increases in activity also showed significant lateral organization (Fig. 3). This reflected contralateral organization in the cortex and ipsilateral organization in the cerebellum, as expected. Comparing Figs. 2 and 3 indicates that lateral orga-

TABLE 2. Location of the centers of mass of the motor region

	Left Hemisphere			Right Hemisphere		
	X	Y	Z	X	Y	Z
S1	-33.9 (1.8)	-31.4 (2.6)	54.3 (1.9)	35.0 (2.9)	-29.3 (3.3)	55.2 (2.1)
M1	-31.4 (2.0)	-18.1 (2.4)	54.1 (2.1)	31.5 (1.9)	-16.8 (2.7)	55.7 (1.5)
SMA	-13.1 (1.6)	-10.8 (2.3)	62.6 (1.7)	13.5 (1.4)	-10.4 (2.3)	63.2 (2.4)
Pre-SMA	-13.4 (1.4)	7.8 (0.9)	58.4 (1.7)	13.6 (1.5)	7.8 (0.6)	60.0 (2.3)
Premotor	-36.2 (1.9)	5.8 (0.9)	47.2 (2.6)	36.9 (2.2)	7.0 (1.3)	50.3 (2.1)
CCZ	-6.7 (0.5)	-23.6 (3.7)	37.0 (2.5)	7.8 (0.6)	-22.1 (3.3)	37.6 (2.2)
RCZp	-6.8 (0.8)	7.5 (0.9)	34.5 (1.9)	7.8 (0.7)	7.5 (1.0)	35.8 (2.3)
RCZa	-7.9 (0.7)	28.2 (1.7)	9.6 (1.7)	9.0 (0.7)	28.1 (1.8)	10.0 (2.6)
Thalamus	-8.1 (1.1)	-19.9 (1.7)	7.0 (1.7)	9.8 (1.2)	-18.8 (1.6)	6.8 (1.6)
Cerebellum	-23.1 (1.6)	-62.8 (1.1)	-41.2 (1.6)	26.6 (2.0)	-62.9 (0.8)	-39.8 (1.5)

Locations are given as the mean x , y , and z coordinates in the atlas of Talairach and Tournoux (1988), with SD in parentheses. Note that several of these regions are quite concave, in which case the center of mass is only an approximate description of the location of the region.

nization was generally more consistent across participants than the overall level of activity. In S1, M1, SMA, and the thalamus, all 12 participants showed greater activity in contralateral cortex during movement, and in the cerebellum, all 12 participants showed greater activity in the ipsilateral hemisphere. In CCZ, 11 of 12 participants had greater activity in contralateral cortex. Lateral organization was significant at the group level in S1, M1, SMA, CCZ, the thalamus, and the cerebellum. RCZp showed a trend toward contralateral organization (10 of 12 participants) that was significant at the single-region level but failed to survive correction for multiple comparisons.

Lateral organization during motor imagery is shown in the middle panel of Fig. 3. Activity was greater in contralateral than ipsilateral M1 for all 12 participants, and greater in contralateral SMA for 11 participants. Both effects were statistically significant at the group level. In S1 and the thalamus, 10 of 12 participants showed greater activity in the contralateral hemisphere during imagined movement. This led to a significant group-level effect in the thalamus, whereas this trend in S1 was statistically significant only at the single-region level.

Lateral organization during motor preparation showed a pattern similar to that for motor imagery (Fig. 3). However, unlike overall activity, lateral organization was stronger and

more consistent across participants during preparation than during imagery. All 12 participants showed greater contralateral activity during motor preparation in both M1 and SMA, and 11 of 12 showed greater contralateral activity in S1 and the thalamus. At the group level, lateral organization was statistically significant in all four regions. There was a trend toward group-level ipsilateral organization in the cerebellum (10 of 12 participants), which was significant at the single-region level but did not survive correcting for multiple comparisons.

Lateral organization during motor imagery and motor preparation were directly compared at the individual and group levels, using t -test of the same form as those for the analyses of the single tasks. These provided no evidence for differences in lateral organization between the two tasks.

Movement during the scanning sessions

The videotapes made during the scanning session were viewed by a trained observer who coded for movement errors during each trial. Hand movements while imagining or preparing a movement were extremely rare: one participant moved a hand during one imagery trial and two participants moved a hand during one trial each of the preparation task. Hand movements during rest trials were minimal [mean = 0.73 ±

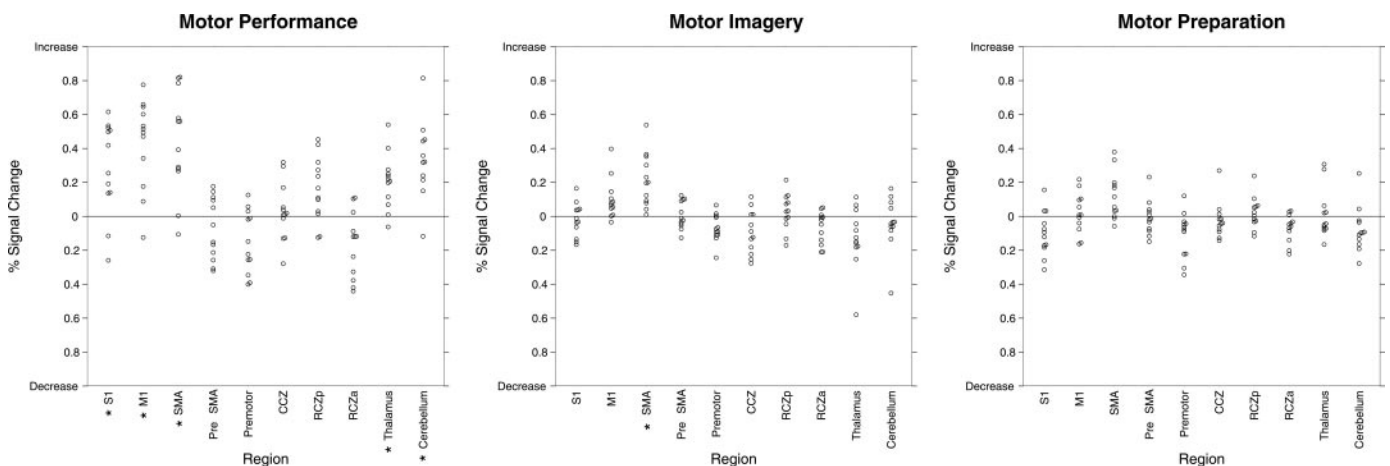


FIG. 2. Overall changes in activity during motor performance, motor imagery, and motor preparation. Overall activation was calculated by comparing activity during the left and right trials in each task to baseline trials in the same task. Each participant is represented by a single point for each region. Horizontal locations of nearby points have been jittered for visibility. Asterisks in red indicate regions that differed significantly from 0, corrected for multiple comparisons across regions.

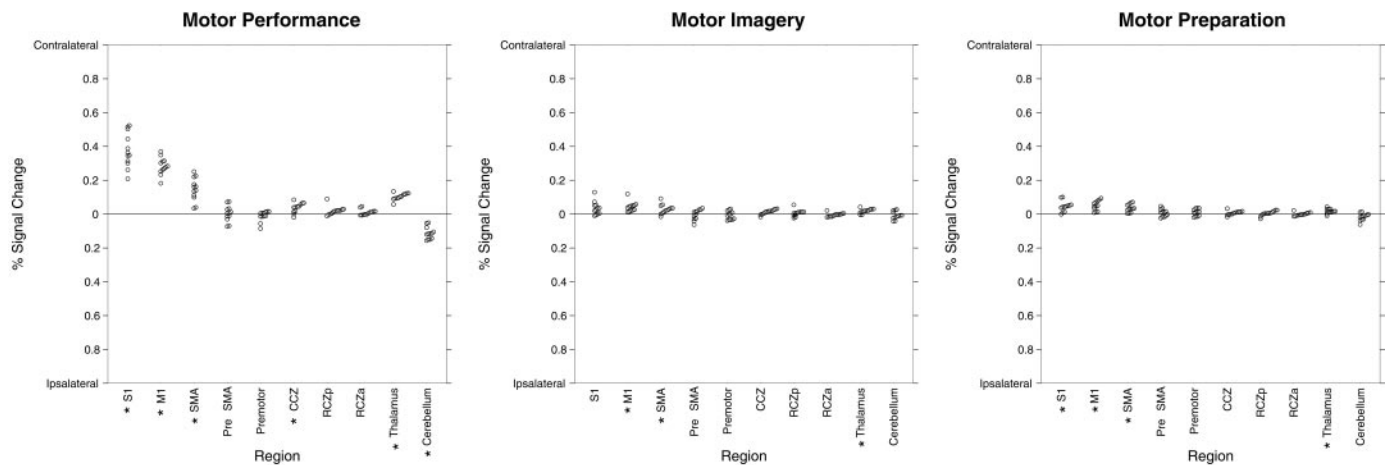


FIG. 3. Lateral organization during motor performance, motor imagery, and motor preparation. Lateral organization was measured by comparing the signal change in the hemisphere contralateral to the hand that executed the task to the signal change in the ipsilateral hemisphere. Format of the figure follows that of Fig. 2, except that y-axis values describe degree of lateral organization rather than of overall activity.

0.99% (SD)] as were hand movements after the no-go cue (mean = $1.67 \pm 2.22\%$) or foot or leg movements in general (mean = $0.96 \pm 1.10\%$). A movement of the uncued hand was occasionally observed during the actual movements task (mean = $2.71 \pm 3.20\%$) or during the go trials in the prepare task (after the go cue; mean = $2.36 \pm 2.30\%$).

Electromyographic experiments

Despite the fact that virtually no movement was observed during the imagine task and during the preparation interval of the prepare task, it is possible that small movements, not detectable on the video image, could lead to detectable BOLD signal in motor areas. To assess this possibility, two separate EMG studies were conducted. A Grass polygraph (Model 7E) was used. The EMG signal was sampled and integrated five times per second (time constant of 0.2), and 60-Hz noise was filtered out. The polygraph was calibrated so that each pen deflection covered $50 \mu\text{V}$. The EMG was recorded from the biceps muscles of both arms.

The goal of the first EMG study was to ensure that subjects could perform the imagine task without actually moving. Participants executed both the imagine and the perform tasks. The goal of the second study was to test whether subjects could perform the prepare task without actually moving during the preparation period. Participants executed the prepare task, which include a motor preparation component as well as a performance component (go trials). For all three tasks, the task design followed the one used during the fMRI study.

EMG experiment 1: imagine and perform tasks

Eight participants (6 females; mean age, 22.1 yr) were tested who had not participated in the fMRI study. The perform and imagine tasks used were the same as those used during the fMRI study. First, after the movement was learned, participants performed four blocks of 30 trials each (2 blocks of the imagine task and 2 blocks of the perform task). This corresponded to the practice session of the fMRI study. Second, they performed two blocks of 39 trials each (1 of each task). This corresponded to the second practice session of the fMRI study.

Finally, they performed two blocks of 60 trials each (1 of each task). This corresponded to two BOLD runs of the fMRI study.

For each participant, the muscle response in each arm on each trial of the perform and imagine tasks was estimated by the difference between the minimum and maximum EMG values during the trial. One set of analyses examined individual participants' performance. For each participant, within-subject *t*-tests were conducted comparing muscle responses during trials on which the participant imagined moving their hand to rest trials, separately for the left and right hands. Across all participants, no statistically significant differences were found between imagined movement trials and rest trials [largest $t(52) = 1.6$, $P = 0.10$]. In contrast, for every participant, the difference between actual movements of each hand and rest trials was statistically significant [smallest $t(52) = 4.61$, $P < 0.0001$].

A second set of analyses characterized performance of the group as a whole with random effects *t*-test. The average muscle response was computed for each participant, for each trial type (left hand, right hand, and rest) in each task. The results are presented in Table 3. There was no evidence that EMG activity in the left or right bicep was greater during imagined right movements than during rest [left: $t(7) = -1.47$, $P = 0.18$; right: $t(7) = 0.98$, $P = 0.36$]. Similarly, activity in the left bicep was not greater during imagined left movements than during rest [$t(7) = -.83$, $P = 0.43$] and tended to be lower in the right bicep during imagined left movements than during rest [$t(7) = -2.11$, $P = 0.07$]. In contrast, EMG activity was higher than rest in the left bicep for actual left movement and

TABLE 3. Mean evoked EMG activity (μV) in the left and right biceps muscles while imagining a rotation of the left or hand or while resting

	Imagine Left	Imagine Right	Rest
Left bicep	0.22 (0.23)	0.10 (0.14)	0.32 (0.52)
Right bicep	0.19 (0.16)	0.43 (0.50)	0.29 (0.26)

These values represent mean differences between maximum and minimum values for each trial (SD across participants in parentheses). Data are from EMG experiment 1.

in the right bicep for actual right movement [left: $t(7) = 7.19$, $P < .001$; right: $t(7) = 9.97$, $P < 0.001$]. Activity in the left bicep during right movements and in the right bicep during left movement did not differ significantly from activity during rest [left: $t(7) = 1.73$, $P = 0.13$; right: $t(7) = 1.71$, $P = 0.13$]. In summary, these data provided evidence that participants did not covertly move an arm when they imagined moving it.

EMG experiment 2: prepare task

Eight participants who had not participated in the fMRI study or in the first EMG study were tested (8 females; mean age, 20.4 yr). The preparation task used in the fMRI study was used. First, after the task was learned, participants performed one block of 48 trials. This corresponded to the practice session of the fMRI study. Second, they performed one block of 32 trials (2nd practice session of the fMRI study). Finally, they performed two blocks of 80 trials each. This corresponded to two BOLD runs of the fMRI study.

Recall that participants occasionally were cued to perform the prepared movement (go trials). The EMG signal evoked by the movement on those trials sometimes failed to return to baseline before the next trial started. To avoid artifacts caused by this carryover, all trials that followed a go trial were excluded from the analyses. (In the neuroimaging analyses, such carryover effects are controlled for by the trial counterbalancing and statistical modeling of the carryover.) As before, the muscle response in each arm on each trial was estimated by computing the difference between the minimum and maximum EMG values during the trial. To target the preparation period, the interval examined began with the onset of the letter cue and ended with the onset of the octagon or circle.

One set of analyses examined individual participants' performance. For each participant, within-subject t -tests were conducted comparing muscle responses caused by prepared movements to rest. Analyses were conducted separately for each arm (e.g., comparing muscle responses in the right arm during prepared right-handed movements to muscle responses in the right arm during rest trials). Muscle responses during preparing to move an arm were never significantly greater in that arm than during rest trials. The only statistically significant comparisons indicated *lower* EMG activity during preparation than during rest [largest $t(43) = 2.58$, $P < 0.02$].

A second set of analyses characterized performance of the group as a whole with random effects t -test. The average muscle response was computed for each participant for each trial type (left hand, right hand, and rest). The results are shown in Table 4. Activity in the left or right bicep was not greater during preparation of left-handed movements than during rest

TABLE 4. Mean evoked EMG activity (μV) in the left and right biceps muscles while preparing a movement of the left or right hand

	Prepare Left	Prepare Right	Rest
Left bicep	7.57 (5.12)	7.61 (5.04)	7.94 (5.69)
Right bicep	10.17 (5.75)	9.43 (5.57)	9.93 (5.48)

These values represent mean differences between maximum and minimum values for each trial (SD across participants in parentheses). Data are from EMG experiment 2.

[left: $t(7) = -1.09$, $P = 0.31$; right: $t(7) = 0.86$, $P = 0.41$]. Similarly, activity in the left bicep was not greater during the preparation of right-handed movements than during rest [$t(7) = -1.23$, $P = 0.26$] and was *lower* in the right bicep during preparation of right-handed movement than during rest [$t(7) = -3.39$, $P < 0.02$]. In summary, these data provided no evidence that participants covertly moved an arm when they prepared to move it.

DISCUSSION

These data provide conclusive evidence for lateral organization in the motor system during both motor imagery and motor preparation. Together with evidence for homuncular organization during motor imagery (Ehrsson et al. 2003), they indicate that when people imagine performing a movement or prepare to perform that movement, they activate somatotopically mapped representations of the effectors involved. This finding makes an important step beyond previous reports that various components of the motor system show increased BOLD activity during motor imagery by providing insight into the nature of some of the computations underlying motor imagery. In particular, this finding supports the view that both motor imagery and motor preparation involve not just higher-level memory retrieval and spatial attention processes, but also motor simulation. One possibility is that somatotopically organized activity during motor imagery and motor preparation reflects the computation of the inverse kinematics or inverse dynamics of the imagined or prepared movement.

Lateral somatotopic organization

Across the motor system, lateral organization was strongest during actual movement and somewhat weaker during imagined and prepared movement. Replicating previous studies (Colebatch et al. 1991; Fox et al. 1985; Grafton et al. 1991; Mayer et al. 2001), statistically significant contralateral organization during actual movement was observed in S1, M1, SMA, CCZ, and the thalamus, and significant ipsilateral organization was found in the cerebellum. Of special interest here, significant lateral organization was observed during both motor imagery and motor preparation in M1, SMA, and the thalamus, and also in S1 during the motor preparation task.

The finding of lateral organization during motor preparation is consistent with electrophysiological studies of neural activity before the onset of a planned movement, known as BPs or readiness potentials (Barrett et al. 1986; Cui and Deecke 1999; McAdam and Seales 1969). Results from previous EEG recordings from the skull surface suggest that BPs have two components: an early one (BP1) that is not lateralized and originates from SMA and a later one (BP2) that is contralateral to the prepared movement and originates from M1 (Barrett et al. 1986; Cui and Deecke 1999; McAdam and Seales 1969). Our data suggest that the neural generators of both BP1 and BP2 are lateralized. Given the low spatial resolution of electrophysiological studies, left and right SMA cannot usually be dissociated. This may explain why lateralization of potentials originating in this area had not been observed earlier. In fact, a recording study on patients with implanted electrodes suggest that BPs are lateralized even in SMA (Ikeda et al. 1992).

Overall magnitude of evoked responses

As was the case for lateral organization, the overall evoked response was also stronger throughout the motor system during actual movement than during motor imagery or motor preparation. Statistically significant increases during actual movement were observed in M1, S1, SMA, the thalamus, and the cerebellum. During motor imagery and motor preparation, the overall level of activity throughout the motor system was substantially reduced, remaining statistically significant only in SMA during motor imagery. Overall changes activity in M1 during motor imagery did not differ significantly from baseline activity, replicating previous results (Binkofski et al. 2000; Decety et al. 1988, 1994; Gerardin et al. 2000; Stephan et al. 1995). There were no instances in which evoked responses to motor imagery or motor preparation were larger in magnitude than evoked responses to actual movements. This pattern is consistent with previous studies of motor imagery (e.g., Porro et al. 1996). Weaker activity in M1 during imagery than during motor execution may come from inhibition originating in SMA during motor imagery (Solodkin et al. 2004).

It is also possible that weakness of overall activity during motor imagery and motor preparation was the result of the repetitive movement used in this study. Indeed previous research has shown that the amplitude of activity varies with task complexity, in particular in SMA (Gordon et al. 1998; Shibasaki et al. 1993). Moreover, with repetition of the task, participants may rely less on motor simulation than on memory retrieval, which would reduce the lateralization pattern. It would be interesting to replicate our results using more complex motor tasks, such as finger-to-thumb opposition sequences. Regarding the relation between lateral organization and overall activity in SMA, there are two possible outcomes. First, it is possible that the greater the activity in SMA, the greater the lateral organization. This would suggest that the same neurons in SMA represent the limb to be moved and the sequence of movement to be performed. Second, it is possible that the lateral organization is independent of the overall level of activity in SMA. This would suggest that different neurons represent the limbs to be moved and the sequence of action to be performed.

Importantly, an EMG study of performance of the three tasks used found no evidence for micromovements during the motor imagery task. This is consistent with previous reports of similar tasks (Binkofski et al. 2000; Luft et al. 1998; Roth et al. 1996), although EMG activity has been shown during motor imagery in other studies (Bonnet et al. 1997; Livesay and Samaras 1998; Stephan et al. 1995). The present EMG data indicate that the observed BOLD changes during motor imagery in this paradigm cannot be attributed to actual movements. The same conclusions apply to the motor preparation period of the preparation task because no EMG activity was observed during this interval.

Functional role of anterior cortical motor areas

Minimal overall changes in activity and minimal lateral organization were observed in pre-SMA, PM, RCZa, and RCZp. These findings support the view that these regions have more in common with prefrontal cortex than lower levels of the motor hierarchy. This interpretation is consistent with a num-

ber of previous findings. Although SMA has been associated with motor execution per se in previous studies, pre-SMA has not (Picard and Strick 1996). These results also are consistent with the proposed dissociation between CCZ and the rostral cingulate zones (RCZa and RCZp) (Picard and Strick 2001), with RCZa implicated in conflict monitoring rather than motor function per se (Braver et al. 2001). However, these results provide no evidence for activity in RCZp during actual, imagined, or prepared movement. One possibility is that the movements studied here were too simple to evoke RCZp activity. The relative absence of activity in PM during these tasks is somewhat surprising, given its known role in motor planning and execution (Dum and Strick 2002; Gerardin et al. 2000). However, as with RCZp, it is possible that the movements studied here were too simple to evoke responses in PM. Another possibility is that previous studies, which used looser anatomic criteria and/or spatial smoothing, conflated M1 activity with activity in PM. Also of note, no evidence was found for lateral organization in PM. This would seem to be at odds with the finding of somatotopic organization in PM in nonhuman primates; however, microstimulation recordings indicate that the hand area of monkey premotor cortex is fairly superior and medial (Godschalk et al. 1995), which could place its homolog in the human SMA.

Functional role of the cerebellum

Large portions of the cerebellum have been shown to play a major role in motor control and coordination and have significant reciprocal connections with motor and somatosensory cortex (Thach et al. 1992). These connections are relayed in part through somatotopically mapped connections in the thalamus (Vitek et al. 1996). The cerebellum increased in activity during motor performance but not during motor imagery or motor preparation. Reductions in cerebellar activity during motor imagery compared with motor execution had been observed in previous studies (Decety et al. 1994; Lotze et al. 1999). Lotze et al. (1999) suggested that such reduced activity may reflect inhibitory processes to block the execution of the imagined movement. The neural generator(s) of such inhibitory signals have not yet been identified. These signals may be generated within the cerebellum itself (Lotze et al. 1999) or may originate in the cortex. Potential candidate areas in the cortex are the middle frontal gyrus and the inferior frontal gyrus, which have been shown to be involved in the inhibition of inappropriate responses (e.g., Brass et al. 2001; Watanabe et al. 2002).

Interactions between excitation and inhibition

The thalamus was robustly activated during motor performance, but showed essentially no overall change in activity during motor imagery and motor preparation. (The largest change in the thalamus during imagery or preparation was a nonsignificant *decrease*.) However, statistically significant lateral organization was observed in the thalamus during both imagery and preparation. A similar pattern was observed in S1. Regarding S1, one possibility is that nonspecific inhibitory signals, which are not somatotopically organized, are integrated with somatotopically organized excitatory signals in regions projecting to S1, allowing motor simulation processes

to proceed without the production of frank movements. Consistent with this interpretation is the report of a patient with bilateral parietal lesions (Schwoebel et al. 2002). When asked to imagine performing movements, he frequently carried them out, without awareness of doing so. Regarding the thalamus, the processes involved may be different. The thalamus is thought to select potential action plans via excitatory reciprocal connections with the cortex and inhibitory connections coming from basal ganglia (Mink 1996). The inhibitory output of the basal ganglia is believed to act as a selective brake on motor generator in the cortex to inhibit unwanted movements. Thus decreased activity in the thalamus during motor imagery and preparation compared with motor execution may reflect identical levels of inhibition during execution and imagery/preparation, but reduced excitatory activity coming from the cortex (i.e., less amplification of correct movement plans).

Relationship between motor imagery and motor preparation

As noted in the Introduction, it is possible that motor simulation could be selectively involved only in motor imagery, or, alternatively, motor simulation could be selectively involved only in motor preparation. The level of activity and the pattern of lateralization elicited across motor regions during motor preparation were quite similar to the level of activity and the pattern of lateralization elicited by motor imagery. This result suggests that motor simulation is involved in a similar way during motor imagery and preparation. Such results support Jeannerod (1994)'s proposition that the difference between motor imagery and motor preparation is one of degree rather than kind. Motor imagery is necessarily conscious, whereas motor preparation may not give rise to a conscious sensation. Jeannerod argued that when motor preparation is prolonged, the intention to act becomes a motor image of the action.

In addition to motor simulation, preparing a manual response also may depend on attention to the planned response, analogous to the role of visual attention in preparing to process visual stimuli or move the eyes. Lesion and neuroimaging studies suggest that such motor attention depends on areas in the left parietal cortex (Rushworth et al. 1997, 2001). The functional relationship between motor attention and motor preparation is not yet clear. One possibility is that the parietal attention system is necessary for performing a motor simulation during motor preparation. It would be of interest to test whether patients with compromised attentional systems show reduced somatotopic mapping in frontal cortex during motor preparation tasks.

There was weak evidence that the overall changes in activity during motor imagery in M1 and CCZ were reduced in magnitude during motor preparation. These trends, though suggestive and consistent with previous results (Stephan et al. 1995), should be interpreted with some caution. Difference such as these could reflect specifics of the task design rather than general processing differences between motor imagery and motor preparation. For example, the presence of a variable go or no-go cue after the preparation interval during the motor preparation task may have encouraged participants to stop motor preparation processes immediately, whereas the constant stop cue during the motor imagery task may have exerted a weaker stopping effect on motor imagery processes. Or, the

relative rarity of go trials may have reduced motivation to prepare during the preparation interval. This leaves open the question of whether activity during motor preparation reflects reduced excitatory activity throughout the motor network, or active inhibition at some stage. This question should be addressed in future studies focusing on inhibitory processes per se.

In conclusion, the results reported here support the hypothesis that motor imagery is a mental analog of motor execution. In the same way that visual mental imagery may preserve specific visual properties of visual percepts, motor imagery seems to include motor simulation processes closely related to the form and timing of actual movements. In the domain of visual imagery, studies of the degree to which mental imagery preserves the spatiotopic mapping of visual experience have been both contentious and informative (Klein et al. 2004; Kosslyn 1994). It is our hope that these findings may productively constrain theories of motor imagery; in particular, we believe these data render less tenable theories that posit that motor imagery involves only the early stages of the motor hierarchy.

The finding that motor imagery seems to engage motor simulation has implications for neurorehabilitation, training, and problem-solving. Measurement of somatotopically organized activity during motor performance and motor imagery may provide a means to more accurately diagnose the nature of processing deficits in patients with apraxia or other movement disorders. The observation of motor simulation during mental imagery provides a mechanism for the well-documented benefits of mental practice of physical activities (e.g., Feltz and Landers 1983). Finally, motor simulation during mental imagery may interact with other forms of imagery to allow people to simulate the consequences of actions they might take before committing to the performance of a movement sequence.

ACKNOWLEDGMENTS

We thank R. Larsen for the loan of the electrical recording equipment and E. Akbudak, M. McAvoy, R. Buckner, and A. Snyder for technical assistance with functional MRI data collection and analysis methods.

GRANTS

This research was supported in part by the Mallinckrodt Institute of Radiology.

REFERENCES

- Alexander GE and Crutcher MD.** Preparation for movement: neural representations of intended direction in three motor areas of the monkey. *J Neurophysiol* 64: 133–150, 1990.
- Alkadhi H, Crelier GR, Boendermaker SH, Golay X, Hepp-Reymond MC, and Kollias SS.** Reproducibility of primary motor cortex somatotopy under controlled conditions. *Am J Neuroradiol* 23: 1524–1532, 2002.
- Barrett G, Shibasaki H, and Neshige R.** Cortical potentials preceding voluntary movement: evidence for three periods of preparation in man. *Electroencephalogr Clin Neurophysiol* 63: 327–339, 1986.
- Binkofski F, Amunts K, Stephan KM, Posse S, Schormann T, Freund HJ, Zilles K, and Seitz RJ.** Broca's region subserves imagery of motion: a combined cytoarchitectonic and fMRI study. *Hum Brain Map* 11: 273–285, 2000.
- Bonnet M, Decety J, Jeannerod M, and Requin J.** Mental simulation of an action modulates the excitability of spinal reflex pathways in man. *Brain Res Cogn Brain Res* 5: 221–228, 1997.
- Boynton GM, Engel SA, Glover GH, and Heeger DJ.** Linear systems analysis of functional magnetic resonance imaging in human V1. *J Neurosci* 16: 4207–4221, 1996.
- Brass M, Zysset S, and von Cramon DY.** The inhibition of imitative response tendencies. *Neuroimage* 14: 1416–1423, 2001.

- Braver TS, Barch DM, Gray JR, Molfese DL, and Snyder A. Anterior cingulate cortex and response conflict: effects of frequency, inhibition and errors. *Cereb Cortex* 11: 825–836, 2001.
- Burock MA, Buckner RL, Woldorff MG, Rosen BR, and Dale AM. Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *Neuroreport* 9: 3735–3739, 1998.
- Cohen JD, MacWhinney B, Flatt M, and Provost J. Psyscope: an interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers. *Behav Res Method Instrum Comput* 25: 257–271, 1993.
- Colebatch JG, Deiber MP, Passingham RE, Friston KJ, and Frackowiak RS. Regional cerebral blood flow during voluntary arm and hand movements in human subjects. *J Neurophysiol* 65: 1392–1401, 1991.
- Crespo-Facorro B, Kim JJ, Andreasen NC, O'Leary DS, Wisner AK, Bailey JM, Harris G, and Magnotta VA. Human frontal cortex: an MRI-based parcellation method. *Neuroimage* 10: 500–519, 1999.
- Crespo-Facorro B, Kim JJ, Andreasen NC, Spinks R, O'Leary DS, Bockholt HJ, Harris G, and Magnotta VA. Cerebral cortex: a topographic segmentation method using magnetic resonance imaging. *Psychiatr Res* 100: 97–126, 2000.
- Cui RQ and Deecke L. High resolution DC-EEG analysis of the Bereitschaftspotential and post movement onset potentials accompanying uni- or bilateral voluntary finger movements. *Brain Topogr* 11: 233–249, 1999.
- Cui SZ, Li EZ, Zang YF, Weng XC, Ivry R, and Wang JJ. Both sides of human cerebellum involved in preparation and execution of sequential movements. *Neuroreport* 11: 3849–3853, 2000.
- Decety J, Chaminade T, Gràzes J, and Meltzoff AN. A PET exploration of the neural mechanisms involved in reciprocal imitation. *Neuroimage* 15: 265–272, 2002.
- Decety J, Perani D, Jeannerod M, Bettinardi V, Tadary B, Woods R, Mazziotta JC, and Fazio F. Mapping motor representations with positron emission tomography. *Nature* 371: 600–602, 1994.
- Decety J, Philippon B, and Ingvar DH. rCBF landscapes during motor performance and motor ideation of a graphic gesture. *Euro Arch Psychiatry Neurol Sci* 238: 33–38, 1988.
- Dechent P, Merboldt KD, and Frahm J. Is the human primary motor cortex involved in motor imagery? *Brain Res Cogn Brain Res* 19: 138–144, 2004.
- Deecke L, Scheid P, and Kornhuber HH. Distribution of readiness potential, pre-motion positivity, and motor potential of the human cerebral cortex preceding voluntary finger movements. *Exp Brain Res* 7: 158–168, 1969.
- Dum RP and Strick PL. Motor areas in the frontal lobe of the primate. *Physiol Behav* 77: 677–682, 2002.
- Ehrsson HH, Geyer S, and Naito E. Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *J Neurophysiol* 90: 3304–3316, 2003.
- Feltz DL and Landers DM. The effects of mental practice on motor skill learning and performance: a meta-analysis. *J Sports Psychol* 5: 25–57, 1983.
- Fox PT, Fox JM, Raichle ME, and Burde RM. The role of cerebral cortex in the generation of voluntary saccades: a positron emission tomographic study. *J Neurophysiol* 54: 348–369, 1985.
- Fried I, Katz A, McCarthy G, Sass KJ, Williamson P, Spencer SS, and Spencer DD. Functional organization of human supplementary motor cortex studied by electrical stimulation. *J Neurosci* 11: 3656–3666, 1991.
- Galdo-Alvarez S and Carrillo-de-la-Peña MT. ERP evidence of MI activation without motor response execution. *Neuroreport* 15: 2067–2070, 2004.
- Gerardin E, Sirigu A, Lehéricy S, Poline JB, Gaymard B, Marsault C, Agid Y, and Le Bihan D. Partially overlapping neural networks for real and imagined hand movements. *Cereb Cortex* 10: 1093–1104, 2000.
- Godtschalk M, Mitz AR, van Duin B, and van der Burg H. Somatotopy of monkey premotor cortex examined with microstimulation. *Neurosci Res* 23: 269–279, 1995.
- Gordon AM, Lee JH, Flament D, Ugurbil K, and Ebner TJ. Functional magnetic resonance imaging of motor, sensory, and posterior parietal cortical areas during performance of sequential typing movements. *Exp Brain Res* 121: 153–166, 1998.
- Grafton ST, Woods RP, Mazziotta JC, and Phelps ME. Somatotopic mapping of the primary motor cortex in humans: activation studies with cerebral blood flow and positron emission tomography. *J Neurophysiol* 66: 735–743, 1991.
- Hanakawa T, Parikh S, Bruno MK, and Hallett M. Finger and face representations in the ipsilateral precentral motor areas in humans. *J Neurophysiol* 93: 2950–2958, 2005.
- Ikeda A, Lèuders HO, Burgess RC, and Shibasaki H. Movement-related potentials recorded from supplementary motor area and primary motor area. Role of supplementary motor area in voluntary movements. *Brain* 115: 1017–1043, 1992.
- Jeannerod M. The representing brain: neural correlates of motor intention and imagery. *Behav Brain Sci* 17: 187–245, 1994.
- Jeannerod M. Mental imagery in the motor context. *Neuropsychologia* 33: 1419–1432, 1995.
- Johnson SH, Rotte M, Grafton ST, Hinrichs H, Gazzaniga MS, and Heinze HJ. Selective activation of a parietofrontal circuit during implicit imagined prehension. *Neuroimage* 17: 1693–1704, 2002.
- Klein I, Dubois J, Mangin JF, Kherif F, Flandin G, Poline JB, Denis M, Kosslyn SM, and Le Bihan D. Retinotopic organization of visual mental images as revealed by functional magnetic resonance imaging. *Brain Res Cogn Brain Res* 22: 26–31, 2004.
- Kosslyn SM. *Image and Brain: The Resolution of the Imagery Debate*. Cambridge, MA: MIT Press, 1994.
- Kurata K. Distribution of neurons with set- and movement-related activity before hand and foot movements in the premotor cortex of rhesus monkeys. *Exp Brain Res* 77: 245–256, 1989.
- Lee KM, Chang KH, and Roh JK. Subregions within the supplementary motor area activated at different stages of movement preparation and execution. *Neuroimage* 9: 117–123, 1999.
- Leonardo M, Fieldman J, Sadato N, Campbell G, Ibanez V, Cohen L, Deiber M-P, Jezzard P, Pons T, Turner R, Le Bihan D, and Hallett M. A functional magnetic resonance imaging study of cortical regions associated with motor task execution and motor ideation in humans. *Hum Brain Map* 3: 83–92, 1995.
- Livesay JR and Samaras MR. Covert neuromuscular activity of the dominant forearm during visualization of a motor task. *Percept Mot Skills* 86: 371–374, 1998.
- Lotze M, Montoya P, Erb M, Hèulsmann E, Flor H, Klose U, Birbaumer N, and Grodd W. Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *J Cogn Neurosci* 11: 491–501, 1999.
- Luft AR, Skalej M, Stefanou A, Klose U, and Voigt K. Comparing motion- and imagery-related activation in the human cerebellum: a functional MRI study. *Hum Brain Map* 6: 105–113, 1998.
- Maccotta L, Zacks JM, and Buckner RL. Rapid self-paced event-related functional MRI: feasibility and implications of stimulus- versus response-locked timing. *Neuroimage* 14: 1105–1121, 2001.
- Mayer AR, Zimbelman JL, Watanabe Y, and Rao SM. Somatotopic organization of the medial wall of the cerebral hemispheres: a 3 Tesla fMRI study. *Neuroreport* 12: 3811–3814, 2001.
- McAdam DW and Seales DM. Bereitschaftspotential enhancement with increased level of motivation. *Electroencephalogr Clin Neurophysiol* 27: 73–75, 1969.
- Mink J. The basal ganglia: focused selection and inhibition of competing motor programs. *Prog Neurobiol* 50: 381–425, 1996.
- Mitz AR and Wise SP. The somatotopic organization of the supplementary motor area: intracortical microstimulation mapping. *J Neurosci* 7: 1010–1021, 1987.
- Ojemann JG, Akbudak E, Snyder AZ, McKinstry RC, Raichle ME, and Conturo TE. Anatomic localization and quantitative analysis of gradient refocused echo-planar fMRI susceptibility artifacts. *Neuroimage* 6: 156–167, 1997.
- Ollinger JM, Corbetta M, and Shulman GL. Separating processes within a trial in event-related fMRI II: analysis. *Neuroimage* 13: 218–229, 2001a.
- Ollinger JM, Shulman GL, and Corbetta M. Separating processes within a trial in event-related fMRI I: the method. *Neuroimage* 13: 210–217, 2001b.
- Overduin SA and Servos P. Distributed digit somatotopy in primary somatosensory cortex. *Neuroimage* 23: 462–472, 2004.
- Penfield W and Rasmussen T. *The Cerebral Cortex of Man*. New York: Macmillan, 1950.
- Pfurtscheller G and Neuper C. Motor imagery activates primary sensorimotor area in humans. *Neurosci Lett* 239: 65–68, 1997.
- Pfurtscheller G, Neuper C, Ramoser H, and Müllner-Gerking J. Visually guided motor imagery activates sensorimotor areas in humans. *Neurosci Lett* 269: 153–156, 1999.
- Picard N and Strick PL. Motor areas of the medial wall: a review of their location and functional activation. *Cereb Cortex* 6: 342–353, 1996.
- Picard N and Strick PL. Imaging the premotor areas. *Curr Opin Neurobiol* 11: 663–672, 2001.

- Porro CA, Franciscato MP, Cettolo V, Diamond ME, Baraldi P, Zuiani C, Bazzocchi M, and di Prampero PE.** Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *J Neurosci* 16: 7688–7698, 1996.
- Raczkowski D, Kalat JW, and Nebes R.** Reliability and validity of some handedness questionnaire items. *Neuropsychologia* 12: 43–47, 1974.
- Ramrani N and Miall RC.** Instructed delay activity in the human prefrontal cortex is modulated by monetary reward expectation. *Cereb Cortex* 13: 318–327, 2003.
- Richter W, Andersen PM, Georgopoulos AP, and Kim SG.** Sequential activity in human motor areas during a delayed cued finger movement task studied by time-resolved fMRI. *Neuroreport* 8: 1257–1261, 1997.
- Romo R, Scarnati E, and Schultz W.** Role of primate basal ganglia and frontal cortex in the internal generation of movements. II. Movement-related activity in the anterior striatum. *Exp Brain Res* 91: 385–395, 1992.
- Roth M, Decety J, Raybaudi M, Massarelli R, Delon-Martin C, Segebarth C, Morand S, Gemignani A, Däcorps M, and Jeannerod M.** Possible involvement of primary motor cortex in mentally simulated movement: a functional magnetic resonance imaging study. *Neuroreport* 7: 1280–1284, 1996.
- Rushworth FS, Krams M, and Passingham RE.** The attentional role of the left parietal cortex: the distinct lateralization and localization of motor attention in the human brain. *J Cogn Neurosci* 13: 698–710, 2001.
- Rushworth MF, Nixon PD, Renowden S, Wade DT, and Passingham RE.** The left parietal cortex and motor attention. *Neuropsychologia* 35: 1261–1273, 1997.
- Schwoebel J, Boronat CB, and Coslett HB.** The man who executed “imagined” movements: evidence for dissociable components of the body schema. *Brain Cogn* 50: 1–16, 2002.
- Shibasaki H, Sadato N, Lyshkow H, Yonekura Y, Honda M, Nagamine T, Suwazono S, Magata Y, Ikeda A, Miyazaki M, Fukuyama H, Asato R, and Konishi J.** Both primary motor cortex and supplementary motor area play an important role in finger movement. *Brain* 116: 1387–1398, 1993.
- Solodkin A, Hlustik P, Chen EE, and Small SL.** Fine modulation in network activation during motor execution and motor imagery. *Cereb Cortex* 14: 1246–1255, 2004.
- Stephan M, Fink GR, Passingham RE, Silbersweig D, Ceballos-Baumann AO, Frith CD, and Frackowiak RS.** Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J Neurophysiol* 73: 373–386, 1995.
- Stippich C, Ochmann H, and Sartor K.** Somatotopic mapping of the human primary sensorimotor cortex during motor imagery and motor execution by functional magnetic resonance imaging. *Neurosci Lett* 331: 50–54, 2002.
- Talairach J and Tournoux P.** *Co-Planar Stereotaxic Atlas of the Human Brain*. New York: Thieme, 1988.
- Thach WT, Goodkin HP, and Keating JG.** The cerebellum and the adaptive coordination of movement. *Annu Rev Neurosci* 15: 403–442, 1992.
- Toni I, Schluter ND, Josephs O, Friston K, and Passingham RE.** Signal-, set- and movement-related activity in the human brain: an event-related fMRI study. *Cereb Cortex* 9: 35–49, 1999.
- Toni I, Shah NJ, Fink GR, Thoenissen D, Passingham RE, and Zilles K.** Multiple movement representations in the human brain: an event-related fMRI study. *J Cogn Neurosci* 14: 769–784, 2002.
- Vitek JL, Ashe J, DeLong MR, and Kaneoke Y.** Microstimulation of primate motor thalamus: somatotopic organization and differential distribution of evoked motor responses among subnuclei. *J Neurophysiol* 75: 2486–2495, 1996.
- Watanabe J, Sugiura M, Sato K, Sato Y, Maeda Y, Matsue Y, Fukuda H, and Kawashima R.** The human prefrontal and parietal association cortices are involved in NO-GO performances: an event-related fMRI study. *Neuroimage* 17: 1207–1216, 2002.
- Wise SP and Mauritz KH.** Set-related neuronal activity in the premotor cortex of rhesus monkeys: effects of changes in motor set. *Proc R Soc Lond B Biol Sci* 223: 331–354, 1985.
- Wolbers T, Weiller C, and Büchel C.** Contralateral coding of imagined body parts in the superior parietal lobe. *Cereb Cortex* 13: 392–399, 2003.
- Yazawa S, Ikeda A, Kunieda T, Mima T, Nagamine T, Ohara S, Terada K, Taki W, Kimura J, and Shibasaki H.** Human supplementary motor area is active in preparation for both voluntary muscle relaxation and contraction: subdural recording of Bereitschaftspotential. *Neurosci Lett* 244: 145–148, 1998.
- Yazawa S, Ikeda A, Kunieda T, Ohara S, Mima T, Nagamine T, Taki W, Kimura J, Hori T, and Shibasaki H.** Human presupplementary motor area is active before voluntary movement: subdural recording of Bereitschaftspotential from medial frontal cortex. *Exp Brain Res* 131: 165–177, 2000.
- Zang Y, Jia F, Weng X, Li E, Cui S, Wang Y, Hazeltine E, and Ivry R.** Functional organization of the primary motor cortex characterized by event-related fMRI during movement preparation and execution. *Neurosci Lett* 337: 69–72, 2003.