Contralateral Coding of Imagined Body Parts in the Superior Parietal Lobe

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In monkeys, neurons in the superior parietal lobe (area 5) code for spatial position of contralateral body parts by combining visual and somatosensory signals. Using a modified version of the classical mental rotation task, we were able to demonstrate that in humans activation in the contralateral superior parietal lobe could be evoked when mental rotation was combined with motor imagery of hands. These findings show that even in the absence of visual and somatosensory input, information provided by motor imagery suffices to induce contralateral superior parietal lobe monitoring of the imagined limb configuration. This constitutes an important prerequisite for effective imagined motor practice that can be used to improve actual motor performance.

Introduction

Mental imagery is an important tool for many cognitive tasks such as perspective changes, problem solving and motor learning. One of the best studied imagery tasks is mental rotation of three-dimensional (3-D) objects as originally described by Shepard and Metzler (Shepard and Metzler, 1971). In this study the authors found that when people compared two similar objects in different orientations, an increment of time is required for each degree of angular disparity between the objects, which has been interpreted as showing that people perform such tasks by mentally rotating the objects along the same trajectories as would occur if the objects were physically rotated (Kosslyn, 1994; Kosslyn *et al.*, 2001a). With the advent of neuroimaging methods, converging evidence has been found for the involvement of area V5/human MT in mental rotation, presumably reflecting the imagination of the virtual object movement (Cohen *et al.*, 1996; Barnes *et al.*, 2000). Moreover, the role of inferior and posterior parietal regions is commonly acknowledged (Cohen *et al.*, 1996; Tagaris *et al.*, 1997; Barnes *et al.*, 2000; Harris *et al.*, 2000; Jordan *et al.*, 2001). Subdivisions of the intraparietal sulcus (IPS) are known to process 3-D visual information in ego-, allo- and object-centered reference frames (Andersen *et al.*, 1997; Mesulam, 1999; Nakamura *et al.*, 2001; Shikata *et al.*, 2001) and to be involved in visuo-spatial attention (Coull and Nobre, 1998), both of which are necessary requirements for successful performance of mental rotation tasks. Additionally, neurons in IPS have been shown to engage in controlling saccadic eye movements (Andersen *et al.*, 1997; Gregoriou and Savaki, 2001), which are likely to occur when subjects are required to compare two simultaneously presented objects.

Compared to the relatively consistent results on the neural bases of the visual transformation processes, the involvement of motor and somatosensory areas remains controversial. While some studies on mental rotation of objects found activation in primary and secondary sensorimotor areas (Cohen *et al.*, 1996; Carpenter *et al.*, 1999; Richter *et al.*, 2000; Lamm *et al.*, 2001), others did not show consistent activation within the sensorimotor system (Barnes *et al.*, 2000; Harris *et al.*, 2000; Jordan *et al.*, 2001). A possible explanation for these conflicting results could lie in the fact that neither possible eye movements nor the subjects' rotation strategy were controlled. The latter is especially important as it is possible that different subjects use different rotation strategies that may or may not involve motor imagery, thereby accounting at least in part for the contradictory findings.

A possible rotation strategy could consist of imagining object grasping and turning with one's own hand (Kosslyn *et al.*, 2001b), thus combining visual and motor imagery. These processes are dissociable and seem to be subserved by different cortical areas (Sirigu and Duhamel, 2001). Similar to movement execution motor imagery is controlled predominantly by the contralateral hemisphere, which has been shown in Parkinson's disease (Dominey *et al.*, 1995), in callosotomy patients (Parsons *et al.*, 1998) and in patients with parietal lesions (Sirigu *et al.*, 1996). Moreover, imagination of movement seems to underlie the same physical constraints as does its execution (Decety *et al.*, 1989; Decety and Jeannerod, 1995; Crammond, 1997). Although imagining simple or complex hand movements involves many cortical areas that also subserve motor execution (Stephan *et al.*, 1995; Porro *et al.*, 1996; Lotze *et al.*, 1999; Thobois *et al.*, 2000), the systems responsible for both functions do not overlap completely (Deiber *et al.*, 1998; Jeannerod and Frak, 1999). Several studies have indicated that primary motor cortex is not necessary to accurately imagine hand movements (Parsons *et al.*, 1995; Sirigu *et al.*, 1996); but see elsewhere (Kosslyn *et al.*, 1998; Ganis *et al.*, 2000). Rather, a role for the parietal cortex in these tasks has been established (Crammond, 1997). Using a variety of motor imagery tasks, Sirigu and colleagues (Sirigu *et al.*, 1996; Sirigu and Duhamel, 2001) found that posterior and superior parietal lesions lead to a dissociation between execution and imagination of contralateral hand and finger movements, with imagination being primarily affected. This dissociation was not found in normal subjects. Consequently, the parietal cortex has been hypothesized to evaluate imagined motor performance by comparing reafferent signals with stored internal representations of motor plans (Crammond, 1997). In addition, in tasks requiring a combination of visual and motor imagery (e.g. imagining acting upon objects), parietal regions might fulfil a coupling function between visual and motor processes (Sirigu and Duhamel, 2001).

The successful performance of mental rotation of body parts requires constant monitoring of the spatial position and orientation of the respective limb. In non-human primates neurons in superior parietal cortex (area 5) code for spatial position of the contralateral arm in body-centered coordinates (Scott *et al.*, 1997). This finding was recently extended by another study examining the integration of somatosensory and visual information in macaques (Graziano *et al.*, 2000). The authors compared the neural responses in superior parietal area

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5 to a felt real arm versus a fake seen arm and their results revealed that neurons contralateral to either arm were sensitive to both the seen and the felt positions. These neurons did not respond to the seen position of other objects and were able to discriminate between the right and the left arm. As neurons in S1 behaved differently, the authors concluded that area 5 is the first stage at which visual information about contralateral arm position is integrated with somatosensory information.

Considering the results described so far, the goal of the present study was to examine the processes underlying mental rotation of 3-D objects in combination with motor imagery. We therefore manipulated rotation strategies by training subjects to imagine themselves grasping and rotating objects with their own hand (which will be referred to as 'active rotation'). In the control conditions the subjects' task was to imagine objects rotating without the influence of external forces (which will be referred to as 'passive rotation'). Based on the findings of previous studies, we formulated the following hypothesis.

Active rotation requires a combination of motor imagery of rotational hand movements and of imagined object rotation. As these combined processes do not provide somatosensory feedback, activation differences between active and passive rotation should be confined to contralateral superior parietal regions without the involvement of S1. These differences would reflect the coding of spatial position and orientation of the imagined hand, using information arising from mental imagery.

In order to test this hypothesis we developed a paradigm (see Fig. 1) that was derived from the original mental rotation task used in previous studies. However, this paradigm differed in several important aspects in order to overcome problems associated with the original task. First of all, subjects were intensely trained to employ two different rotation strategies, thus allowing for a better control of the strategy used. Secondly, the rotation axis was indicated to prevent subjects from trying out false rotation directions, which would make it difficult to collapse results over subjects. Thirdly, only one stimulus was presented at a time to minimize the influence of eye movements. Although this introduced a working memory component, it was identical for both active and passive rotation. And finally, the appearance of the stimuli was modified in order to prevent subjects from using alternative strategies to solve the task.

Materials and Methods

Subjects

Fifteen healthy, right-handed volunteers (nine female) with normal or corrected-to-normal vision gave written informed consent to participate in this study. The study was approved by the local ethics committee. All subjects understood the instructions without difficulty and none were aware of the hypotheses at the time of testing. However, due to radio frequency contaminations of the MR images, two subjects had to be excluded from further analysis, leaving a total of 13 subjects entering the final data set.

Cognitive Task

The experimental paradigm is shown in Figure 1. All stimuli used in the experiment were created using Matlab 5.3.1 (The MathWorks, Inc.). Four different trial types (experimental conditions, active_right, active_left; control conditions, passive_right, passive_left) were tested in a modified version of the original mental rotation task (Shepard and Metzler, 1971). The 3-D stimuli used in most studies of mental rotation (Shepard and Metzler, 1971; Cohen *et al.*, 1996; Tagaris *et al.*, 1997; Kosslyn *et al.*, 1998; Barnes *et al.*, 2000; Richter *et al.*, 2000; Kosslyn *et al.*, 2001b) were constructed by arranging cubes along the three major axes. As this opens the possibility of solving the task at least partly by counting the number of cubes and then imagining how many cubes have to be in a specific position to match the reference stimulus, we deconstructed the stimuli as can be seen in Figure 1. Furthermore, in the standard version of this task the subject is required to determine whether or not two simultaneously presented stimuli are identical. This procedure introduces a substantial amount of eye movements due to repeated comparisons between the two stimuli. It has also been shown that with increasing angular disparity it cannot be assumed that different subjects rotate the stimuli along the same trajectories (Metzler and Shepard, 1974), thus leading to interindividual differences in task performance. To overcome these problems we changed the task in the following ways: each trial began with a single stimulus being presented statically for 350 ms; during the following 800 ms the stimulus performed a rotation of 10° (at 12.5°/s) along a specific axis before flipping back into the original position; the stimulus then remained on the screen for an additional 500 ms before it disappeared. Subjects had to memorize the appearance of the stimulus and the rotation direction in both the experimental and the control conditions. In order to manipulate the rotation strategies, the two experimental sessions required participants to imagine themselves grasping the object with their right (active_right) or left (active_left) hand. Following the disappearance of the figure, a blank screen was shown for 2000 ms, then a different stimulus was presented. The subject was now required mentally to rotate the first stimulus along the indicated axis to determine whether or not both were identical. In half of the trials, the second stimulus was a rotated version of the first one, with rotation angles ranging from 20 to 180° in 20° increments. Rotation was either in the picture plane or in depth around the vertical or horizontal axis. The remaining figures were mirror-reversed figures that had been rotated in the same way. The second figure was presented until the subject responded with a button press; no time limit was set. However, subjects were instructed to rotate the stimuli as fast as possible and to press the appropriate button (left button, identical; right button, not identical) as soon as they had made their decision. The subjects' task in the

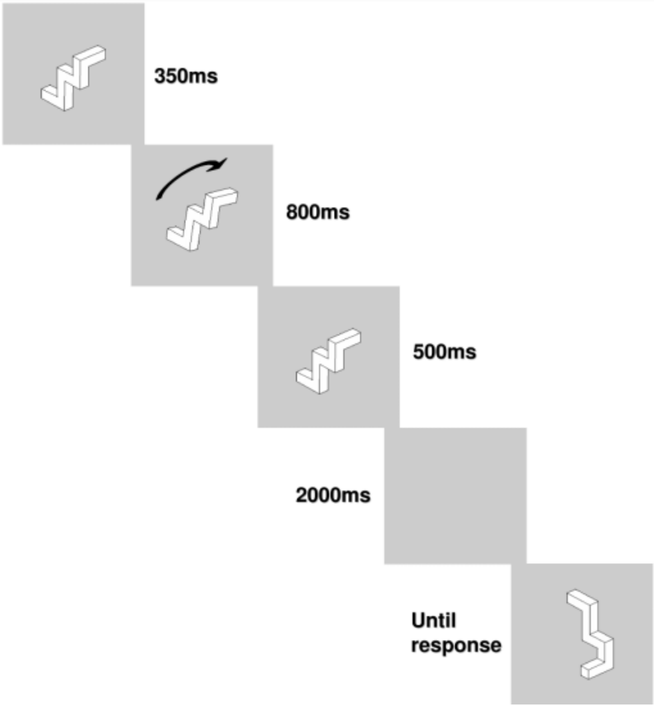

Figure 1. Paradigm of the rotation conditions. The first stimulus was presented statically for 350 ms, followed by a 10° rotation (48 frames) along a specific axis before flipping back into the original position. Subjects had to memorize both the appearance and the rotation direction of the first stimulus in all four conditions. When the second stimulus appeared, mental rotation of the first stimulus along the indicated axis was to be performed. The second stimulus was presented until the subject decided by a button press whether or not both stimuli were identical. In the example shown here, both stimuli were the same, with the second one having been rotated 180° along the *x*-axis.

experimental sessions consisted of imagining object rotation by rotation of the imagined right (active_right) or left (active_left) hand. To avoid interference with preparatory motor processes, subjects had to respond with the hand contralateral to the imagined hand (active_right — button press with the left hand; active_left — button press with the right hand). In the passive_right (button press with the right hand) and passive_left (button press with the left hand) control conditions, subjects were instructed to imagine the stimulus rotating by itself without the influence of external forces. Following the subject's response, there was an inter-trial interval with a randomized duration of 8–12 s.

In summary, we ensured that visual stimulation did not differ between control and experimental conditions. As the only difference between active and passive mental rotation consisted of the additional motor imagery component, control conditions were carefully matched for working memory load and visuo-spatial attention. Moreover, we defined the appropriate contrasts to only compare conditions with the response hand being identical. Therefore, all activation differences observed between active and passive rotation could be reliably attributed to the additional motor imagery component. We are confident of having minimized the influence of eye movements as far as possible although we were not able to measure eye movements on line.

All subjects were scanned during the two experimental and the two control sessions in a pseudo-randomized order. Prior to each session the subject was informed about the rotation strategy to be applied. Each session contained 50 stimulus pairs and lasted between 10 and 15 min (depending on the individual rotation speed). To identify regions involved in somatosensory and motor processing, we included an additional session requiring subjects to perform rotational hand movements with their right and left hands, respectively. This session always took place after two of the four mental rotation conditions had been completed and subjects were instructed to perform one rotational movement with the respective hand whenever the word 'right' or 'left' appeared on the screen. Using a block design, 24 rotations with each hand had to be performed, with the hand being changed after every eighth run. Participants were neither able to see their hands in this session nor in the mental rotation sessions.

In order to ensure adequate performance all subjects were trained one or two days prior to fMRI scanning. In this training session participants performed both the two experimental and the two control sessions with an equal number of stimuli as compared to the fMRI scanning sessions (50 stimulus pairs per condition). To avoid subjects solving the task during scanning by means of processes other than mental rotation (e.g. recognition memory), different sets of stimuli were used in the training sessions. The training procedure proved successful, as the percentage of correct responses in the fMRI scanning sessions was relatively high compared to other studies on mental rotation (see Results).

MRI Acquisition

MR scanning was performed on a 1.5 T MRI Scanner (Siemens Vision), a standard headcoil was used. Thirty-two contiguous axial slices (without gap) were acquired using a gradient echo echo planar (EPI) T_2*-sensitive sequence (T_R = 2.6 s, T_E = 40 ms, flip angle 90°, matrix 64 × 64, field of view 210 × 210 mm). A high resolution (1 × 1 × 1 mm voxel size) T_1-weighted structural MRI was acquired for each volunteer using a 3-D Flash sequence.

A liquid crystal display video-projector back-projected the stimuli on a screen positioned on top of the head coil. Subjects lay on their backs within the bore of the magnet and viewed the stimuli comfortably via a 45° mirror that reflected the images displayed on the screen (10 ×15° field of view). To minimize head movements, all subjects were stabilized with tightly packed foam padding surrounding the head. The task sequence was controlled by a PC running the 'Presentations' package (Neurobehavioral Systems, www.neurobehavioralsystems.com). Stimulus presentation was tightly synchronized with image acquisition.

Image Processing and Statistical Analysis

Image processing and statistical analysis were carried out using SPM99 (www.fil.ion.ucl.ac.uk/spm). All volumes were realigned to the first volume, spatially normalized (Friston *et al.*, 1995) to a standard EPI template (Evans *et al.*, 1993) and finally smoothed using a 12 mm full-width at half-maximum isotropic Gaussian kernel. Data analysis was performed by modeling the onsets of every first and second stimulus as trains of delta functions convolved with a hemodynamic response function (HRF). To ensure that only trials when subjects actually did perform mental rotation were analyzed data were trimmed before analysis by eliminating all trials with response times greater than two standard deviations from the mean of the rotation time in that cell (defined by condition and angle) for that subject. Furthermore, only trials with correct responses were considered for further analysis.

An event-related approach was used since the stimulus onset asynchrony was randomized and not constant. The same procedure was applied to session three (rotational hand movements) with the onsets of every movement being modeled. Regression coefficients for all regressors were estimated using least squares within SPM99. Specific effects were tested with appropriate linear contrasts of the parameter estimates for the HRF regressor of all trial types, resulting in a *t*-statistic for each voxel. These *t*-statistics constitute a statistical parametric map (SPM). SPMs are interpreted by referring to the probabilistic behavior of Gaussian random fields. Data were analyzed for each subject individually (first-level analysis) and for the group. At the group level, a random effects approach (Friston *et al.*, 1999) was applied to obtain results that could be generalized beyond the subjects taking part in this study. This was done by entering the results of the first-level analysis into a one-sample *t*-test, thus reducing the degrees of freedom to 'number of subjects – 1'. The threshold was set to $P < 0.05$ corrected for multiple comparisons. In regions of interest as determined by our hypotheses, correction was based on these regions (left and right superior parietal lobe, spherical search volume = 2145 mm^3). For display purposes, the structural volume of one individual was co-registered to the functional scans by normalizing it to a T_1 template in the same space as the template used to normalize the functional data sets. After co-registration with the functional data the brain surface was triangularized to display activations of the group on the individual 3-D-rendered brain.

Results

Behavioral Results

We analyzed response times and error rates to ensure that subjects did, in fact, perform the task. In the passive_right and passive_left control conditions, the percentages of correct responses averaged across all participants were 80.35 and 76.85%, respectively. As can be seen in Figure 2, response times showed a constant increase depending on angular disparity. In the experimental conditions active_right and active_left, the average numbers of correct trials were at similar levels (79.69 and 75.27%). Apart from that, response times also showed similar increases (see Fig. 2), no significant differences between regression coefficients of experimental and control conditions were found (active_right versus passive left, $z = -1.1$, $P < 0.14$; active_left > passive_right, $z = 0.3$, $P < 0.39$). We also compared error rates between experimental and control conditions using paired *t*-tests; neither the comparison passive_right versus active_left ($t = 0.02$, $P < 0.5$) nor passive_left versus active_right ($t = 0.16$, $P < 0.45$) revealed significant differences.

Based on previous studies on mental rotation (Shepard and Metzler, 1971; Cooper, 1976; Alivisatos and Petrides, 1997; Kosslyn *et al.*, 1998; Ganis *et al.*, 2000; Jordan *et al.*, 2001) we assumed that increasing response times with increasing angular disparities indicate that subjects solve the task by mentally rotating the stimuli. Therefore, we subjected response times to a two-way analysis of variance (ANOVA) with angular disparity and rotation strategy as the respective factors. The linear trend observable in Figure 2 was confirmed by the two-way ANOVA, revealing a significant main effect of angular disparity across conditions ($F = 4.82$, $P < 0.001$). In contrast, we did not obtain a significant main effect of condition ($F = 1.37$, $P < 0.25$). Interaction effects between condition and angular disparity were not observed ($F = 0.5$, $P < 0.97$). Taken together the behavioral data

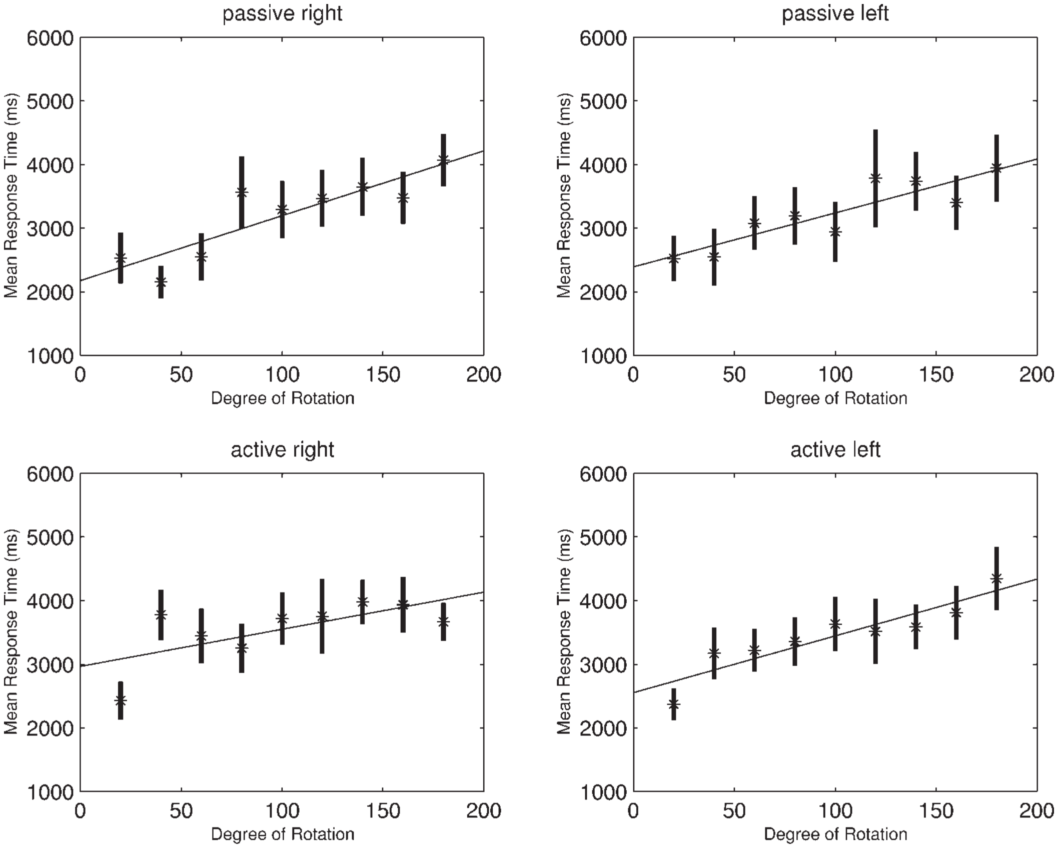

Figure 2. Behavioral results. Response times averaged across subjects ($n = 13$) and respective standard errors of means are presented for all angular disparities. Regardless of rotation condition, increases in response time with increasing angular disparities were observed, which is indicated by the least-squares fit.

indicate that (i) subjects did perform the tasks by carrying out mental rotation and (ii) task difficulty did not vary between conditions.

fMRI Results

To check for specific activation when mental rotation was combined with imagery of rotational hand movements, we defined contrasts comparing active versus passive conditions. As it was important that only activation differences due to differences in mental rotation strategy would be observed, all processes involved in performing the motor response had to be identical. We therefore defined the appropriate contrasts as follows: active_right > passive_left (motor response with the left hand in both conditions) and active_left > passive_right (motor response with the right hand in both conditions). Figure 3*a* displays the group results obtained from these contrasts; Table 1 shows the locations of the activation maxima according to Montreal Neurological Institute space (Evans *et al.*, 1993), the t-statistic and the corresponding P-values. The active_right > passive_left comparison revealed significant activation in the left superior parietal lobe. Most importantly, this activation was located contralaterally to the imagined hand. It was centered in the depth of the postcentral sulcus, ranging from the caudal part of area 2 to the most rostral part of area 7. The activation did not extend into the anterior part of the intraparietal sulcus (area AIP) which has been described to be located more laterally and in the intraparietal sulcus (Shikata *et al.*, 2001; Simon *et al.*, 2002). Similar activation patterns were seen in the right hemisphere when comparing the active_left versus passive_right conditions. Neural responses were centered in the postcentral sulcus stretching again from the posterior bank of area 2 to the most anterior part of area 7. However, the activation extended more medially, involving a small part of ipsilateral medial superior parietal lobe as well.

To illustrate the activation during imagined and executed movements Figure 3*b* shows the results of the relevant contrasts. The neuronal responses elicited by executed movements were located predominantly in contralateral primary motor cortex, supplementary motor area and in ipsilateral cerebellum. The activation observed in primary motor cortex extended posteriorly into postcentral regions, thus leading to an overlap in the postcentral sulcus with activation evoked by active rotation.

Discussion

In the present study we were able to demonstrate that cortical activation observed during mental rotation could be manipulated by different rotation strategies. In particular, our results indicate that mental rotation *per se* mainly requires visuo-spatial transformation processes, whereas additional activation in the somatosensory system can be evoked by combining mental rotation with motor imagery. This activation was contralateral to the imagined hand and, considering the fact that mental rotation does not provide somatosensory feedback, we interpret our findings as showing that in humans, information provided by mental imagery is used in the contralateral superior parietal lobe to monitor the imagined configuration of the limbs.

According to congruent results in the literature on mental rotation, there is an increase in response time with increasing angular disparity (Shepard and Metzler, 1971; Cooper, 1976; Alivisatos and Petrides, 1997; Kosslyn *et al.*, 1998; Ganis *et al.*,

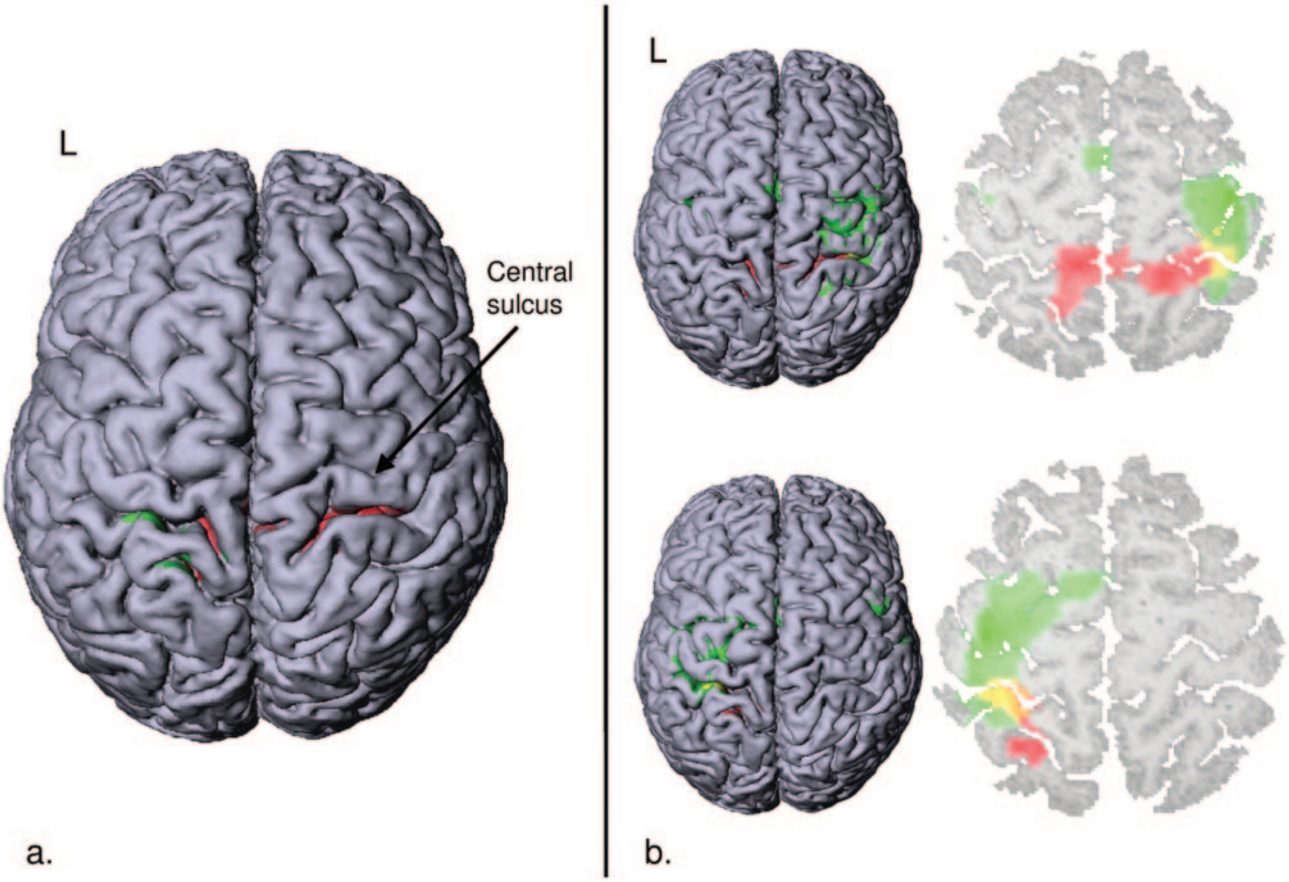

Figure 3. (*a*) Group results for active versus passive rotation. Cortical regions significantly activated for the comparison active mental rotation versus control. Results of the random effects analysis are rendered on an individual brain surface with a threshold of $P < 0.05$, corrected for multiple comparisons. Red: active_left > passive_right (motor response with the right hand in both conditions). Activation was centered in the right superior parietal lobe, thus being contralateral to the imagined hand. Activation extended into medial regions, involving a small part of ipsilateral medial superior parietal lobe as well. Green: active_right > passive_left (motor response with the left hand in both conditions). Activation was focused in the left superior parietal lobe, which was contralateral to the imagined hand. (*b*) Group results for movement execution and imagined rotation. Upper panel: movement execution and imagined rotation with the left hand. Neuronal responses elicited by executing rotational hand movements ($P < 0.001$, uncorrected) were located predominantly in contralateral primary motor cortex, supplementary motor area and in ipsilateral cerebellum. The activation observed in primary motor cortex extended posteriorly into the postcentral sulcus, thus leading to an overlap with the activation evoked when subjects rotated the stimuli with the imagined left hand (active_left). Green: execution of rotational movements with the left hand. Red: Imagining object rotation with the left hand versus control (contrast active_left > passive_right). Yellow: areas activated by both conditions. Transverse section at $z = 63$. Lower panel: movement execution and imagined rotation with the right hand. Neuronal responses evoked by executed movements ($P < 0.001$, uncorrected) were focused on contralateral primary motor cortex, supplementary motor area and ipsilateral cerebellum. Again, the activation observed during movement execution and imagined rotation with the right hand (active_right) overlapped in the contralateral postcentral sulcus. Green: execution of rotational movements with the right hand. Red: Imagining object rotation with the right hand versus control (contrast active_right > passive_left). Yellow: areas activated by both conditions. Transverse section at $z = 66$.

2000; Jordan *et al.*, 2001). This is commonly interpreted as showing that participants solve the task by performing mental rotation instead of doing simple visual discrimination. The behavioral performance of our subjects was in line with these findings, which we interpret as good evidence that participants did in fact rotate the stimuli along the axis indicated by the first stimulus. Despite our relatively demanding paradigm, overall performance was comparable to that found in other studies of mental rotation. Furthermore, the difficulty of the task did not differ between experimental and control conditions regarding both error rates and response times, which replicates the findings reported by Kosslyn and colleagues (Kosslyn *et al.*, 2001b). In conclusion, any differences observed in BOLD-responses could be reliably attributed to differences in rotation strategy between active and passive rotation.

In monkeys neurons in superior parietal area 5 have been shown to be involved in hand reaching and grasping (Scott *et al.*, 1997; Nakamura *et al.*, 2001). These neurons, as well as those in the medial intraparietal region (MIP), receive visual inputs from parieto-occipital areas and send visual information and motor-related commands to dorsal premotor area 6 (Matelli *et al.*, 1998; Shipp *et al.*, 1998; Caminiti *et al.*, 1999). However, the results by Graziano and colleagues (Graziano *et al.*, 2000) indicate that area 5 is not merely concerned with the spatial position of a visual stimulus but also with its identity. Furthermore, apart from being sensitive to visual signals, area 5 neurons also process somatosensory information from contralateral limbs. Along the ascending somatosensory pathway from the periphery to area S1 and to area 5, area 5 seems to be the first stage at which visual information about contralateral arm position is integrated with somatosensory information. This bimodal integration could form the basis for the complex body schema needed to adjust posture and to guide movement (Graziano *et al.*, 2000). Taken together, these findings suggest a possible role for the superior parietal lobe in the integration of somatosensory and visual inputs about location and identity of

Table 1
Spatial coordinates of the local maxima in the group analysis

Region	Coordinates [x, y, z (mm)]		Voxel-level (t-score)
	Right hemisphere	Left hemisphere	
Local activation maxima for the contrast active_left > passive_right			
Contralateral superior parietal lobe	21, –42, 63		5.68*
	33, –33, 54		4.65*
	33, –39, 63		4.43*
Ipsilateral superior parietal lobe		–9, –36, 60	6.68*
Local activation maxima for the contrast active_right > passive_left			
Contralateral superior parietal lobe		–27, –39, 66	3.32*
		–21, –54, 69	3.76*
Local activation maxima for movement execution with the left hand			
Primary motor cortex	42, –15, 63		7.62*
Supplementary motor area	3, –6, 51		5.16*
Cerebellum		–24, –51, –27	5.72*
Local activation maxima for movement execution with the right hand			
Primary motor cortex		–36, –21, 63	13.13*
Supplementary motor area		–6, –3, 51	10.75*
Cerebellum	24, –48, –27		8.09*

*$P < 0.05$, corrected.

contralateral limbs. This information is transferred to premotor areas involved in planning of motor acts.

Our results contribute new information to the current understanding of superior parietal lobe functions by demonstrating that it is also sensitive to signals arising from mental imagery in the absence of somatosensory input. The observed superior parietal activation was contralateral to the imagined hand, which is in accordance with several studies demonstrating lateralization in motor imagery (Dominey *et al.*, 1995; Sirigu *et al.*, 1996; Parsons *et al.*, 1998). This activation presumably reflects a coupling between visual imagery of object rotation and motor imagery and is supported by findings from neurological patients (Sirigu and Duhamel, 2001). The motor imagery component (imagining hand movement), which seems to be based primarily on motor resources under instructions to perform imagery in the first person, as opposed to third person (Sirigu and Duhamel, 2001), can be conceptualized as a comparison between reafferent sensory signals and a stored representation of the motor plan as it normally unfolds. When we imagine movements of body parts this constant monitoring of the spatial position and orientation of the imagined body part is required to achieve a convergence between imagined and physically executable movements. More importantly, these processes are likely to be involved in imagined motor practice as the ensuing improvements in motor performance (Murphy, 1994; Roure *et al.*, 1999; Peynircioglu *et al.*, 2000) indicate a tight congruency between imagined and executed motion sequences.

Comparing activation during executed rotational hand movements and imagined movements revealed a substantial overlap of neuronal responses in the superior parietal lobe. This is in accordance with the findings by Graziano and colleagues (Graziano *et al.*, 2000) showing that the superior parietal lobe is sensitive to both visual and somatosensory input. In the session requiring movement execution, only somatosensory feedback was provided, whereas in the mental rotation sessions only information elicited by mental imagery was available. Further studies are needed to investigate whether the results presented here can be replicated and generalized across other body parts as well.

We can only speculate about the activation extending into medial and ipsilateral parts of the superior parietal lobe when considering the active_left > passive_right contrast. In this active condition subjects were required to imagine themselves grasping and rotating the object with their left, non-dominant hand, as all participants were right-handed. Performing the task with the non-dominant hand might have increased the need for cognitive processing resources, thus leading to a broader activation. This assumption is supported by studies showing that performance asymmetries between dominant and non-dominant limbs exist for both executed and imagined movements (Decety and Lindgren, 1991; Parsons, 1994; Maruff *et al.*, 1999). Moreover, the sensation of effort seems to be more pronounced when motor imagery tasks involve the non-dominant limb compared to the dominant one (Decety and Lindgren, 1991). In the present study we did not observe activation in primary motor cortex when contrasting active and passive mental rotation. This finding is not in line with a recent study suggesting that activity in M1 during mental rotation of 3-D objects could be evoked by rotation strategy (Kosslyn *et al.*, 2001b). However, in that study the effect was only evident when comparing active with passive mental rotation, but not when comparing active mental rotation to a perceptual control task. Furthermore, it might be possible that activity observed in M1 when imagining this movement was due to rehearsal of the motor representation as subjects turned real objects with their hands prior to positron emission tomography (PET) scanning in that study, thus leading to subtle increases in muscle tone. This view would be consistent with data indicating a greater sensitivity of M1 neurons to 'intrinsic' motor components such as muscle tone, joint angle etc. (Scott *et al.*, 1997). Additionally, the lack of primary motor cortex activation during motor imagery in many neuroimaging studies (Parsons *et al.*, 1995; Jeannerod and Frak, 1999) and the prominent role of the parietal cortex for motor imagery as demonstrated in neurological patients (Sirigu *et al.*, 1996; Sirigu and Duhamel, 2001) indicate that primary motor cortex is not absolutely necessary to imagine motor acts. Activation differences between experimental and control conditions in premotor and supplementary motor areas were also not observed, although both regions have consistently been involved in motor imagery (Parsons *et al.*, 1995; Stephan *et al.*, 1995; Lotze *et al.*, 1999; Thobois *et al.*, 2000). This could be explained by the fact that passive mental rotation also might require abstract motor processes as indicated by behavioral studies (Wexler *et al.*, 1998). However, it is also possible that this lack of activation may be in part due to inter-individual variability. We checked this possibility by analyzing the individual results of all 13 subjects, leading to the result of two subjects showing premotor activation and one subject exhibiting activation in the supplementary motor area. This variability might reflect individual differences in motor imagery that have been suggested to explain subjective reports of neurological patients (Sirigu and Duhamel, 2001).

In the light of our findings, we believe the actual rotation strategy employed by each individual subject to be the crucial parameter for the conflicting results of previous studies on mental rotation of 3-D objects. As long as the task only consists of determining by mental rotation whether or not two simultaneously presented stimuli are identical, subjects are free to choose their preferential rotation strategy. These could consist of either imagining the object rotating by itself, by imagined hand movements, or even of applying verbal strategies. By training and giving specific instructions and by deconstructing the appearance of the stimuli, we are confident of having minimized individual variations in rotation strategy, leading to results that could be reliably attributed to controlled differences in mental imagery.

In summary, the results obtained in the present study support and extend the functions of the superior parietal lobe as proposed by several groups (Crammond, 1997; Graziano *et al.*, 2000; Sirigu and Duhamel, 2001). In order to monitor location and identity of contralateral body parts needed for adjusting posture or guiding motor acts this region is likely to integrate somatosensory and visual information. Our data extend this view by showing that information provided by motor imagery also is processed in the superior parietal lobe to code for the configuration of the imagined contralateral limb. This coding presumably consists of monitoring spatial position and orientation of the imagined body part by comparing reafferent signals with stored representations of the motor plan as it normally unfolds. These processes might constitute an important prerequisite for effective imagined motor practice that has been shown to improve motor performance. In sport psychology, for example, athletes' performance can be substantially enhanced by use of mental imagery techniques.

Notes

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