Functional Neuroanatomy of Mental Rotation

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Abstract

■ Brain regions involved in mental rotation were determined by assessing increases in fMRI activation associated with increases in stimulus rotation during a mirror-normal parity-judgment task with letters and digits. A letter–digit category judgment task was used as a control for orientation-dependent neural processing unrelated to mental rotation per se. Compared to the category judgments, the parity judgments elicited increases in activation in both the dorsal and the ventral visual streams, as well as higher-order premotor areas, inferior frontal gyrus, and anterior insula. Only a subset of these areas, namely, the posterior part of the dorsal intraparietal sulcus, higher-order premotor regions, and the anterior insula showed increased activation as a function of stimulus orientation. Parity judgments elicited greater activation in the right than in the left ventral intraparietal sulcus, but there were no hemispheric differences in orientation-dependent activation, suggesting that neither hemisphere is dominant for mental rotation per se. Hemispheric asymmetries associated with parity-judgment tasks may reflect visuospatial processing other than mental rotation itself, which is subserved by a bilateral fronto-parietal network, rather than regions restricted to the posterior parietal. ■

INTRODUCTION

Mental rotation refers to the imagined rotation of a visual image from one orientation to another, and seems to be required when information about the handedness, or parity, of an object needs to be accessed. For example, deciding whether a misoriented letter is printed in its normal form or whether it has been mirror-reversed requires mental rotation to the upright before this parity decision can be made (Cooper & Shepard, 1973). Parity-judgment tasks are frequently used to investigate neural mechanisms underlying mental rotation. Neuroimaging studies have identified a network of regions including parietal regions (e.g., Koshino, Carpenter, Keller, & Just, 2005; Seurinck, Vingerhoets, Vandemaele, Deblaere, & Achtenb, 2005; Podzebenko, Egan, & Watson, 2002; Harris et al., 2000; Alivisatos & Petrides, 1997; Richter, Ugurbil, Georgopoulos, & Kim, 1997; Cohen et al., 1996); ventral stream regions such as the inferior temporal gyrus (Koshino et al., 2005), the lateral occipital cortex (Podzebenko et al., 2002), and area MT (Cohen et al., 1996); and higher-order premotor regions (Podzebenko et al., 2002; Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Richter et al., 2000) that have been associated with parity-discrimination tasks. However, it remains unclear which of these areas reflect the mental-rotation process per se, and which subserve other cognitive processes associated with parity judgments.

It has often been suggested that mental rotation per se is predominantly subserved by the right parietal cortex.

The involvement of the posterior parietal cortex (PPC) in parity tasks has been supported by a number of other neuroimaging studies (Koshino et al., 2005; Jordan, Schadow, Wuestenberg, Heinze, & Jäncke, 2004; Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002; Podzebenko et al., 2002; Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001; Lamm et al., 2001; Harris et al., 2000; Tagaris et al., 1996, 1997, 1998; Richter et al., 1997; Cohen et al., 1996), as well as by neuropsychological (Mehta & Newcombe, 1991; Ditunno & Mann, 1990; Farah & Hammond, 1988), TMS stimulation (Feredoes & Sachdev, 2006; Harris & Miniussi, 2003), and direct cortical stimulation (Zacks, Gilliam, & Ojemann, 2003) studies. Alivisatos and Petrides (1997) also found that the inferior parietal lobule, a portion of the PPC, showed larger activation levels for parity judgments about rotated characters compared with upright characters, leading them to propose that these areas are involved in mental rotation per se, as opposed to other cognitive processes associated with parity discriminations.

However, activation in areas other than the parietal cortex are frequently found in response to parity judgments, most notably in higher-order prefrontal regions (Koshino et al., 2005; Jordan et al., 2001, 2002, 2004; Podzebenko et al., 2002; Lamm et al., 2001; Richter et al., 2000; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Alivisatos & Petrides, 1997; Cohen et al., 1996), as well as in subcortical regions within the basal ganglia (Crucian et al., 2003; Harris, Harris, & Caine, 2002; Alivisatos & Petrides, 1997). Therefore, it seems difficult to argue that mental rotation depends on processing only within the PPC if parity judgments consistently elicit activation within other cortical regions.

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Prefrontal activation is commonly attributed to working memory or attentional demands (Podzebenko et al., 2002; Carpenter et al., 1999; Cohen et al., 1996). There is also evidence for involvement of the primary motor cortex. Eisenegger, Herwig, and Jäncke (2007) found that transcortical magnetic stimulation applied over the left primary motor cortex increased motor cortex activation during mental rotation of Shepard–Metzler figures, suggesting involvement of the right hand in mental rotation processes. They suggest, though, that this activation is most likely to be spillover from neighboring prefrontal areas involved in mental rotation. Consistent with this interpretation, Bode, Koeneke, and Jäncke (2007) found that the effect was independent of the strategy used to mentally rotate, or of the stimuli used; for example, it was no more prevalent when the stimuli were pictures of hands than when they were pictures of external objects. Prefrontal involvement, in turn, may be linked to parietal involvement. The temporal characteristics of the BOLD signal are comparable between the higher-order premotor areas and the PPC. For example, Richter et al. (2000) have shown that the duration of the BOLD signal increases within higher-order premotor regions is correlated with RTs, comparable to the effects observed within the PPC (Richter et al., 1997). Furthermore, Lamm et al. (2001) have shown that parietal and premotor activation follow similar time courses.

Further, although the majority of studies support right-hemispheric dominance for mental rotation (Heil, 2002; Harris et al., 2000; Yoshino, Inoue, & Suzuki, 2000; Bajric, Rosler, Heil, & Hennighausen, 1999; Heil, Rauch, & Hennighausen, 1998; Pegna, Khateb, Spinelli, Landis, & Michel, 1997; Mehta & Newcombe, 1991; Corballis & Sergent, 1988; Farah & Hammond, 1988), some studies have supported left-hemispheric dominance (e.g., Alivisatos & Petrides, 1997; Mehta & Newcombe, 1991), and others suggest bilateral activation (Podzebenko et al., 2002; Jordan et al., 2001; Just, Carpenter, Maguire, Diwadkar, & McMains, 2001; Carpenter et al., 1999; Cohen et al., 1996). One suggestion is that rotation of simple stimuli may be holistic, favoring the right hemisphere, whereas rotation of complex stimuli, such as the torus shapes used by Shepard and Metzler (1971), may induce part-wise rotation, favoring the left hemisphere (Bethell-Fox & Shepard, 1988; Just & Carpenter, 1985). This, in turn, may depend on the degree of mental rotation. Feredoes and Sachdev (2006) found that TMS of both the left and the right intraparietal sulcus (IPS) affected accuracy, but not RTs, for parity judgments with 3-D torus shapes. The effects on accuracy depended on the degree of rotation required, with impaired performance for rotations up to 120° following right parietal stimulation, and impairment at 180° rotations following left parietal stimulation. Feredoes and Sachdev (2006) suggested that rotation through smaller angles may have been holistic, whereas rotations through larger angles may have been piecemeal.

In the present study, following Cooper and Shepard (1973), we used alphanumeric characters, with the aim of encouraging holistic mental rotation. To elicit mental rotation, participants performed parity judgments—that is, they judged whether each character was normal or backward. Even this task, though, has failed to yield consistent results in neuroimaging studies. Harris et al. (2000) did find right parietal activation, but Alivisatos and Petrides (1997) found activation in the left inferior and posterio-superior parietal cortices, and Podzebenko et al. (2002) found bilateral activation of parietal areas. Thus, the issue of whether mental-rotation processes are lateralized to one hemisphere or the other has not yet been clearly resolved.

One difficulty with previous investigations is that hemispheric asymmetry is generally assessed in terms of whether activation is present in one or other hemisphere, or bilaterally, but this overlooks the possibility that activation may be present in one hemisphere without reaching statistical threshold, or that there is significant activation in both hemispheres but activation is more pronounced in one than in the other. For example, activation may be elicited primarily in one hemisphere, but commissural fibers carry weaker activation to the other. In the present study, activation in the two hemispheres was compared statistically. Although interhemispheric comparisons may be distorted due to structural asymmetries, this technique should still provide a more secure basis for detecting functional asymmetries. We attempted to alleviate the effect of structural asymmetries by using a relatively coarse smoothing kernel rather than individual voxels in comparing activation between hemispheres.

We varied the degree to which stimuli were rotated away from the upright in separate blocks of trials. This enabled us to separate out activation that depended linearly on angular orientation, likely to reflect mental rotation, from activation related nonlinearly to orientation, which is likely to be due to sources other than mental rotation. Carpenter et al. (1999) used a similar technique in their study involving mental rotation of Shepard–Metzler figures. Other studies have varied the proportion of trials requiring mental rotation between blocks. Using this technique, Harris et al. (2000) found correlated activation in the right inferior parietal sulcus, whereas Podzebenko et al. (2002) reported bilateral parietal activation, but with right-hemispheric dominance.

The stimuli in the present study were presented at three equidistant stimulus orientations—30°, 100°, and 170° from upright—with equal numbers rotated clockwise and counterclockwise. Orientation was held constant within blocks. In order to control for processes not uniquely related to the parity-judgment task itself, such as pattern and object recognition, decision making, motor planning, and motor output, we included a simple letter–digit category-judgment task that would also involve these processes. Thus, the design of the present

study is a 2 × 3 factorial design with task and orientation as factors. Because we were also interested in hemispheric asymmetries, we also included hemisphere as a factor in the analysis.

METHODS

Participants

Fourteen neurologically normal volunteers (6 women), ranging in age from 22 to 32 years (mean age = 26.21 years), participated. All had normal or corrected-to-normal vision and were right-handed as assessed by Edinburgh Handedness Inventory (Oldfield, 1971), with laterality quotients (LQ) ranging from 60 to 100 (mean LQ = 90.82). The procedures were approved by the University of Auckland Human Participants Ethics Committee, and all participants gave their informed consent to participate in the experiment.

Stimuli

Four letters (P L R F) and four digits (2 4 5 7) printed in bold Arial 72-point font were used as stimuli. They were presented in their normal and mirror-reversed form at three clockwise and counterclockwise rotations from upright: 30°, 100°, and 170°. The amount of rotation (30°, 100°, or 170°) was used as a between-block factor; that is, in each block, the characters were only rotated by a single amount, either clockwise or counterclockwise. Each block of trials consisted of eight stimuli, which were controlled for character type (letter or number), character version (normal or backward), and rotational direction (clockwise or anticlockwise). The character identity was randomly selected.

Tasks

The participants performed two tasks, a mirror-normal discrimination (parity task) and a letter–digit discrimination (category task). The participants responded by clicking the mouse with the right hand. In the parity task, the participants were required to press the left mouse button if they judged the character to be normal, and the right mouse button if they judged it to be mirrored. In the category task, the participants pressed the left mouse button if they judged the character to be a letter, and the right mouse button if they judged the character to be a digit. In both the cases, they were instructed to respond as quickly as possible without sacrificing accuracy.

Procedure

Each block of trials was preceded by a 9-sec rest block which consisted of a fixation screen for 5 sec, followed by an instruction screen for 3 sec, and ended by another fixation of 1 sec. The instruction screen informed the participants which task they were to perform next, and reminded them which mouse buttons corresponded to which decision. The last block of trials in each run was followed by a 6-sec fixation-only rest block to allow for temporal delay in the BOLD signal.

The stimuli were presented for 2 sec and followed by a 250-msec interstimulus interval, during which a small fixation cross was presented centrally. Thus, the duration of each experimental block was 18 sec. The participants were instructed to make a response while the stimulus was on the screen, and if they failed to make a response during that period, to wait for the next stimulus and respond to that. RTs and accuracy were recorded.

Thus, the experimental design followed a 2 × 3 factorial model, with two tasks and three stimulus orientations. Each block of trials corresponded to one of the conditions, and each condition was repeated twice during a scanning session.

Two sequences of experimental blocks were designed. In both sequences, parity and category tasks alternated until both tasks were completed with stimuli presented at all three orientations, and then the sequence was run in reverse order. One of the sequences began with the parity task, with stimuli presented at the smallest orientation (30°) and the stimulus rotation increased every two blocks. The other sequence began with the category task, with stimuli presented at the largest orientation (170°), and degree of stimulus rotation decreased every two blocks. This method was employed to offset the effects of linear drifts in signal intensity which are inherent to fMRI acquisition.

Each participant performed at least two practice blocks, one for each of the two sequences, before going into the scanner to ensure that they were able to perform the task with high accuracy under the speed limitations. During scanning, each participant performed both of the sequences twice, resulting in four scanning sessions. The order in which these sequences were administered was counterbalanced between subjects.

Image Acquisition

Images were acquired using a 1.5-T Siemens Avanto scanner (Erlangen, Germany). Each session started with an acquisition of at least two T1-weighted structural volumes using 3-D MP-RAGE sequence (TR = 11 msec; TE = 4.94 msec; flip angle: 15°; FOV: 25.6 × 20.8 cm; matrix size: 256 × 208; 170 to 176 axial slices, ensuring whole brain coverage, parallel to AC–PC line; slice thickness: 1 mm; interslice gap: 0 mm; resulting in 1 × 1 × 1 mm voxels). Following this, a total of 113 volumes, in addition to two "dummy" scans which were not recorded and were designed to control for T1 saturation, were acquired during each of the four functional scanning sessions, resulting in 452 T2*-weighted volumes

per subject, corresponding to 48 volumes per condition per subject. The EPI acquisition sequence parameters were as follows: TR = 3000 msec; TE = 50 msec; flip angle = 90°; FOV = 19.2 cm; matrix size: 64 × 64; with interleaved slice acquisition, starting at the bottom; 30 slices parallel to AC–PC line; slice thickness: 4 mm; 25% gap: resulting in 3 × 3 × 5 mm voxels; whole brain coverage of 150 mm.

Image Preprocessing

SPM5 software (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk) was used for image processing and analysis. The first three image volumes were discarded to allow for T1 equilibration, and the first volume of the first session was used as a target for coregistration of the first volume of each of the three subsequent sessions. The remaining volumes within each session were then realigned to the first volume of that session and the mean of all volumes across the four sessions was created. The realigned volumes were corrected for slice-timing differences and referenced to the middle slice. For each participant, the available T1 volumes were coregistered and averaged. The average T1-weighted structural image was then coregistered to the mean of the functional volumes. Normalization parameters were estimated using the unified segmentation procedure (Ashburner & Friston, 2005), and were used to normalize the structural and functional images to the stereotactic coordinate system defined by the MNI. Finally, the functional volumes were spatially smoothed using an anisotropic Gaussian filter of 9 × 9 × 15 mm (thrice the voxel size) at full-width at half-maximum (FWHM).

RESULTS

Behavioral Results

In order to maintain a parallel between analysis of behavioral and fMRI data, RTs and accuracy, as percent correct, were analyzed with a 2 × 3 repeated-measures ANOVA, with task and orientation as factors. Huynh–Feldt ε value correction (Huynh & Feldt, 1976) was used to correct for sphericity violations associated with repeated-measures effects. Due to problems with data acquisition, the accuracy measures for two of the participants were excluded from the analysis. The remaining participants had miss rates ranging from 0 to 1.56%. Correct and incorrect responses were used to calculate the mean RTs for each of the six experimental conditions. Again, to maintain consistency between the analyses of behavioral measures and fMRI data, RTs and accuracy were calculated within each session separately and then averaged across the four sessions. Figure 1 shows RTs and accuracy as a function of stimulus orientation for the two tasks.
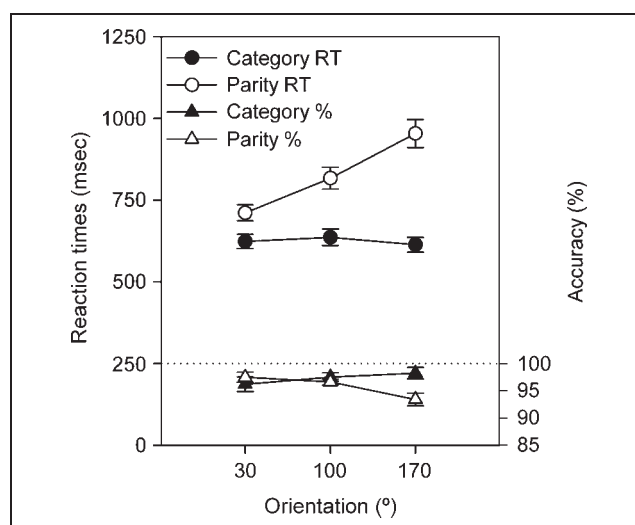

Figure 1. Reaction times (in milliseconds) and accuracy (as % correct) for parity and category tasks as a function of stimulus orientation. Reaction times are plotted as circles, accuracies as triangles.

Analysis of RTs showed significant main effects of task [$F(1, 13) = 59.52, p < .001$] and orientation [$F(2, 26) = 71.93, p < .001, \varepsilon = 0.751$], as well as a significant interaction between them [$F(2, 26) = 61.12, p < .001, \varepsilon = 0.965$]. Significant differences between tasks were observed at all orientations ($p \leq .002$) and ranged between 87.6 msec at 30° and 340.0 msec at 170°. Simple effects analysis showed a significant effect of orientation on the parity task [$F(2, 26) = 77.85, p < .001, \varepsilon = 0.700$], and consisted predominantly of a significant linear trend [$F(1, 13) = 90.41, p < .001, 99.47\%$ variance explained]. The quadratic trend was not significant [$F(1, 13) = 2.83, p = .117$]. The effect of orientation on the category task just failed to reach significance [$F(2, 26) = 3.474, p = .055, \varepsilon = 0.857$]; this near-significant result cannot be attributed to mental rotation because mean RT was slightly lower at 170° than at 30°, as Figure 1 shows.

In terms of accuracy, the main effects of task [$F(1, 11) = 2.00, p = .185$] and stimulus orientation [$F(2, 22) = 1.26, p = .303, \varepsilon = 0.988$] were not significant, but there was a significant interaction between them [$F(2, 22) = 7.98, p = .006, \varepsilon = 0.751$]. Significant differences between tasks were observed for 170° orientation only ($p = .002$). Simple effects analysis showed a significant effect of orientation on the parity task [$F(2, 22) = 4.69, p = .026, \varepsilon = 0.866$], attributable to a linear decrease in response accuracy with increasing angular disparity [$F(1, 13) = 5.45, p = .040, 90.18\%$ of variance explained]. The quadratic trend did not reach significance [$F(1, 11) = 2.83, p = .177$]. The effect of stimulus orientation again just failed to reach significance for the category task [$F(2, 22) = 3.43, p = .052, \varepsilon = 0.973$], with accuracy, if anything, increasing with orientation, which is again inconsistent with mental rotation.

In summary, the data support the notion that the parity task elicited mental rotation, as indicated by the prevalent linear trend apparent in the RTs. The category task provided no evidence for mental rotation. Although the parity task took longer to execute than the category task, the task difficulty—as indicated by performance accuracy—was similar.

Imaging Results

Functional data analysis was performed using a two-step procedure consisting of a within-subjects general linear model (GLM) time-series regression, and random-effects factorial ANOVA, with the resulting parameter estimates as the dependent measure. Firstly, for each subject, the time-series analysis was performed with a GLM (Friston et al., 1995) with the six experimental conditions (2 tasks × 3 orientations) and six movement parameters, three for position and three for rotation, as explanatory variables. The movement parameters were included in the design matrix as potentially confounding nuisance covariates. Each experimental block was modeled as a series of events, and each event was convolved with the canonical hemodynamic response function. The implicit baseline condition, consisting of a fixation and instruction period, was not included in the model. Before estimation, low-frequency noise was removed using a high-pass filter with a cutoff period of 128 sec, and serial correlations among scans were removed with an autoregressive moving average first-order model (AR(1)) implemented in SPM5.

Model estimates (or beta coefficients) generated by this first-level GLM analysis were then used for random-effects group analysis. In order to obtain a single voxelwise beta estimate per subject, each of the six experimental conditions was collapsed across the four sessions.

Hemispheric Asymmetries

In order to examine whether there are hemispheric asymmetries associated with either the parity task or mental rotation itself, hemisphere was introduced as a factor. As described above, six voxelwise beta estimates were generated from the first-level GLM analysis. Two versions of these images were then created: the original, ''nonflipped'' version, and a mirror-reversed, ''flipped'' version. The flipping is performed by changing the sign of the x-coordinates. Following the sign reversal, the voxels on the left side (negative values) of the nonflipped image are interpreted as now ''located'' on the right of the ''flipped'' image (positive values). A similar method was used by Podzebenko et al. (2002) to assess hemispheric asymmetries associated with mental rotation.

Because both flipped and nonflipped images contain all the same voxels, the analysis was restricted to the nominal right hemisphere by creating a mask that only contains voxels with positive x-coordinates. Therefore, the nonflipped images contain voxels from the original right hemisphere, whereas the flipped images contain voxels from the left hemisphere. This was then used as a hemisphere factor in a random-effects ANOVA, which also included task and orientation as factors.

Therefore, 12 contrast images (2 tasks, 3 orientations, and 2 hemispheres) per subject were analyzed using factorial-design random-effects ANOVA for each voxel, as implemented in SPM5. It may be of note that comparing voxels with identical coordinates in the left and the right hemispheres may result in structural asymmetries influencing the functional results. In order to minimize these effects, as well as the effects of structural differences between subjects, we used a relatively large smoothing kernel of three times the voxel size (i.e., $9 \times 9 \times 15$ mm^3).

Violations of sphericity resulting from repeated measures and possible nonhomogeneity of variance were corrected using algorithms as implemented by SPM5. Model estimation was initially performed with all the available voxels, which numbered 33,625. Anatomical labels and Brodmann's area (BA) labels were derived through Anatomy, an SPM-extension toolbox (Eickhoff, S.; www.fz-juelich.de/ime/spm_anatomy_toolbox). Because the IPS was considered to be of particular importance for this study, the nomenclature for the anatomical labels for this area were based on the article by Orban et al. (2006).

Descriptive Statistics

To visualize which areas showed increased activation in response to any of our six experimental conditions, contrasts showing increases in activation relative to the implicit baseline were calculated. Figure 2 illustrates areas of significant [false discovery rate (FDR) corrected $p < .05$] increases in activation elicited by the parity task or the category task in comparison with the implicit baseline. It is evident that the distribution of left-hemispheric responses is similar between the tasks, and include ventral stream regions, the dorsal intraparietal sulcus (dIPS), the sensorimotor cortex, the inferior frontal gyrus (IFG), as well as lateral and medial supplementary premotor areas (pre-SMA). Increases in activation in the ventral intraparietal sulcus (vIPS) were apparent only in response to the parity task.

The picture is considerably different over the right hemisphere. The parity task produced a more symmetrical pattern of activations between the hemispheres, whereas the categorization task failed to elicit the corresponding changes in the right hemisphere. Specifically, there was a lack of activation in the right lateral pre-SMA, the dIPS, and the IFG in response to the category task. Additionally, the category task elicited right-hemispheric activation in the anterior portion of the ventral stream, with no corresponding activation in the left hemisphere. The parity task elicited bilateral

Figure 2. Cortical rendering of significant increases (FDR corrected $p < .05$) in response to category and parity tasks, compared to the implicit baseline.

Category task | Parity task
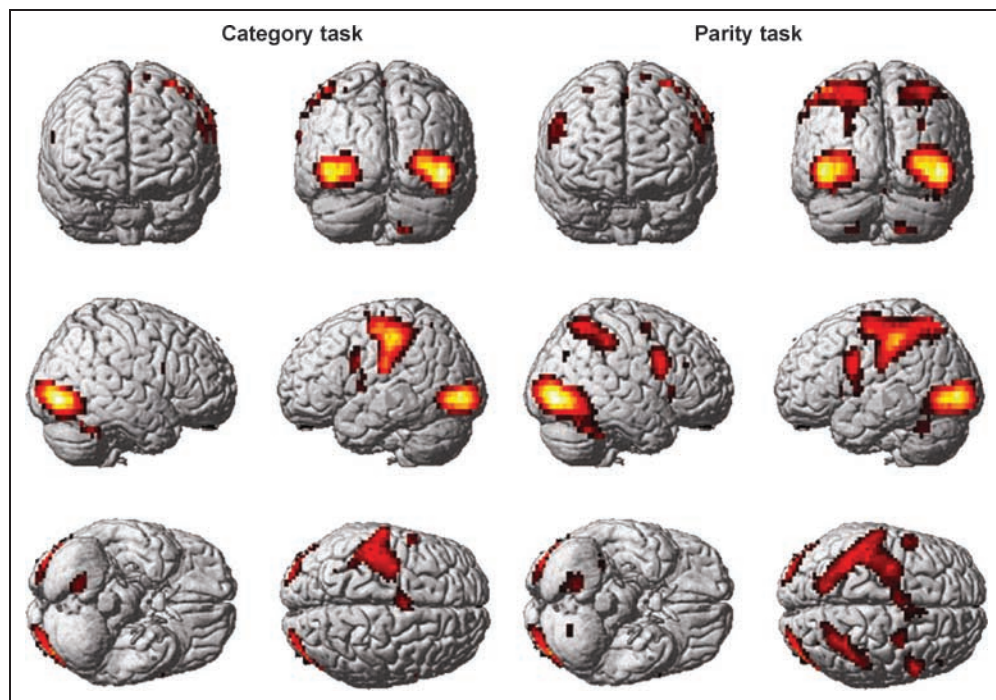
ventral stream activation in the corresponding anterior area.

Masking

Because no prior hypotheses were made regarding deactivation relative to the implicit baseline, any voxels that showed negative estimates were excluded from further analysis. Thus, a mask was created which contained only the voxels which, on average, showed positive estimates within either task, within either hemisphere, collapsed across the three orientations. Furthermore, because both flipped and nonflipped contrasts were included in the analysis, the search was restricted to the "right" hemisphere which now contained both the right (nonflipped) and left (flipped) model estimates. Activation threshold was set at $p < .05$, corrected for multiple comparisons using the family-wise error (FWE) correction on the basis of the random-field theorem (Worsley, Poline, Vandal, & Friston, 1995) with 92.1 of resolution elements and smoothness of statistical volume with dimensions of $10.6 \times 10.6 \times 17.3$ mm at FWHM.

Effects of Interest

The aim of this study was to determine which cortical regions were involved in mental rotation per se and whether there were any hemispheric asymmetries for this process. As we were primarily interested in the effects of task demands on hemispheric asymmetries as well as orientation processing, and interaction between all three factors, the analysis was focused on task effects, and interactions between task and the other two factors. Therefore, main effects of orientation and hemisphere, as well as the two-way interaction between these two factors, were omitted from the analysis.

Task-related Effects

We hypothesized that both parity and category tasks would involve processes associated with object recognition, response selection and execution, and that the parity task would additionally require mental rotation and associated processes such as recognition of character orientation, increased visuospatial working memory and attentional demands, and parity discrimination itself.

The parity task elicited greater activation than the category task in the posterior portion of the inferior temporal gyrus, the middle occipital gyrus, and throughout the IPS, extending from the traverse-occipital sulcus to the postcentral sulcus, including the vIPS, and middle and anterior portions of the dIPS (dIPSm and dIPSa; see Table 1 for summary statistics, MNI coordinates, and anatomical labels at peak activation voxels; see Figure 3 for cortical surface rendering and glass-brain statistical parametric maps [SPMs] with numerical labels corresponding to Table 1). Additionally, greater activation in response to the parity task was observed in the anterior insula, the IFG, and the medial and lateral pre-SMA. A single voxel showing the reverse pattern was observed in the mid-orbital gyrus, where amplitude of parameter estimates was more positive for the category task. Only a portion of the vIPS was also involved in Task-by-Hemisphere interaction (examined in the following

Table 1. Results for Main Effect of Task, Task-by-Hemisphere Interaction, Linear Component of the Task-by-Orientation Interaction, and Linear Trend for the Parity Task

Label	Location	Brodmann's Areas	Cluster Extent (mm³)	x y z (mm)	F
Task-related Effects					
Parity > Category					
3	dIPSa	BA 7	26,370	15 −69 55	119.87***
4	dIPSm	BA 7		33 −51 55	87***
5	dIPSa/m	BA 7		27 −57 55	85.89***
1	ITG	BA 37	10,710	48 −63 −5	61.43***
2	MOG/MT	BA 19		39 −81 10	46.12***
8	anterior insula	BA 13	1755	30 24 5	47.54***
6	IFG	BA 44	2790	54 9 25	39.72***
9	lateral pre-SMA	BA 6	1530	27 0 55	33.26***
7	IFG	BA 46	90	51 30 25	23.58*
10	medial pre-SMA	BA 6	90	3 15 50	21.51*
Category > Parity					
11	mid-orbital gyrus	BA 11	45	6 27 −10	22.71*
Task-by-Hemisphere Interaction					
1	poIPS/vIPS	BA 39	2520	39 −63 25	34.12***
2	poIPS/vIPS	BA 39		36 −69 35	32.99***
3	MFG	BA 6	225	48 9 50	26.03**
4	medial pre-SMA	BA 32	90	9 24 45	23.43*
5	lateral pre-SMA	BA 8	45	30 12 40	21.59*
Task-by-Orientation Interaction—Linear Component					
6	SMG	BA 40	360	60 −24 20	25.35**
5	lateral pre-SMA	BA 6	45	30 0 60	22.03*
2	dIPSm	BA 7	90	30 −54 55	21.78*
3	vIPS	BA 7	45	27 −63 35	21.53*
4	medial pre-SMA	BA 6	45	3 15 50	21.26*
1	poIPS/dIPSm	BA 7	90	15 −66 55	20.92*
Linear Trend for the Parity Task					
Increase (170° > 30°)					
1	dIPSm	BA 7	2835	27 −54 65	37.28***
2	poIPS/dIPSm	BA 7		15 −66 55	32.91***
3	medial pre-SMA	BA 6	225	3 15 50	31.1**
4	lateral pre-SMA	BA 6	585	27 0 65	29.05**
5	Anterior insula	BA 47	45	33 18 0	22.96*
Decrease (30° > 170°)					
6	medial SMA	BA 6	45	3 −9 70	22.15*

Up to three local maxima more than 8 mm apart are shown for the larger clusters. Direction of differences is also indicated. Note that a single voxel extent is 45 mm³.

dIPSa = anterior portion of the dorsal intraparietal sulcus; dIPSm = middle portion of the dorsal intraparietal sulcus; ITG = inferior temporal gyrus; MOG/MT = middle occipital gyrus/middle temporal; IFG = inferior frontal gyrus; pre-SMA = presupplementary motor area; poIPS = parieto-occipital; vIPS = ventral intraparietal sulcus; MFG = middle frontal gyrus; SMG = supramarginal gyrus; SMA = supplementary motor area.

*p < .05, FWE corrected.

**p < .01, FWE corrected.
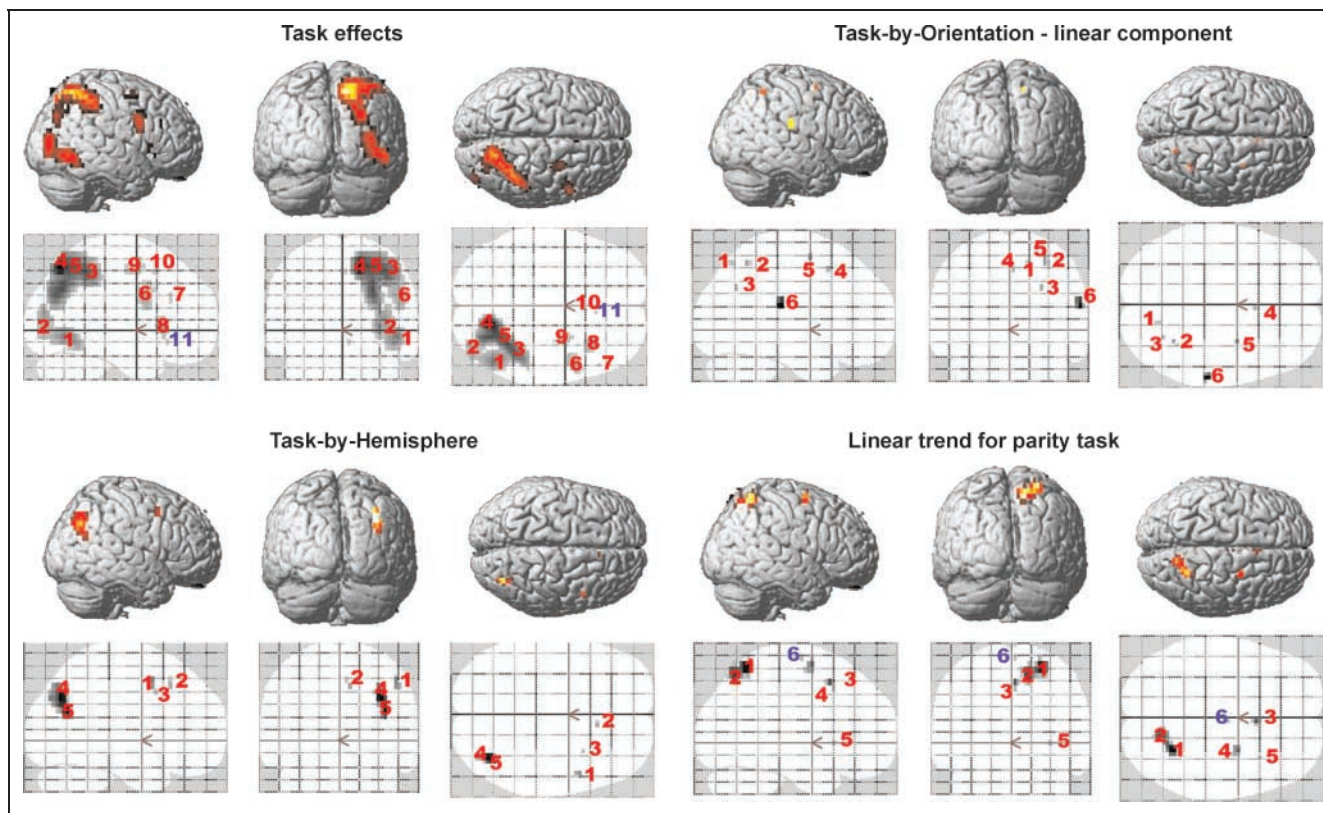
***p < .001, FWE corrected.

Figure 3. Cortical surface rendering of significant voxels showing main effect of task (red: parity > category; blue: category > parity), Task-by-Hemisphere interaction, linear component of the Task-by-Orientation interaction, and linear trend for the parity task (red: $170° > 30°$; blue $30° > 170°$) hypothesized to reflect mental rotation displayed on cortical surface rendering. Glass-brain SPMs are also presented with numerical labels for peak activation voxels (see Table 1 for anatomical labels and summary statistics corresponding to peak activation voxels). Activation is shown only on the nominal right hemisphere.

section), whereas other areas identified in comparison between tasks were not involved in this, or any other, interaction.

Task-by-Hemisphere Interaction

The second question of interest was whether there were any task-related hemispheric differences. A significant Task-by-Hemisphere interaction was observed in the vIPS, as well as in the lateral and medial pre-SMA, and a portion of the middle frontal gyrus corresponding to the dorsolateral prefrontal cortex. Significant activation clusters for the Task-by-Hemisphere interaction and associated parameter estimates at peak activation voxels are represented on a glass-brain SPM and cortical surface rendering in Figure 3, and summary statistics for peak activation voxels are represented in Table 1. The parameter estimates for this interaction at five local maxima are plotted in Figure 4 and can be used to characterize the Task-by-Hemisphere interaction in distinct cortical regions. In all of the clusters of interest, parity task elicited larger activation than the category task on the right, but not on the left. Furthermore, larger right than left hemisphere activation was observed for the parity task only.

Task-by-Orientation Interaction

The next question of interest was whether there were cortical regions that responded to stimulus orientation differently according to the task. With three stimulus orientation conditions, effects of orientation can be examined using linear and quadratic polynomial contrasts. Significant Task-by-Linear-trend interaction was observed in lateral and medial pre-SMA, vIPS, dIPSm, and supramarginal gyrus. Summary statistics with MNI coordinates and anatomical labels are displayed in Table 1, whereas cortical surface rendering and glass-brain SPMs with numerical labels are presented in Figure 3. Significant linear increases in the BOLD signal with increase in stimulus orientation were observed in the pre-SMA, vIPS, and dIPSm, whereas significant *decreases* in BOLD signal were observed within the supramarginal gyrus. No significant Task-by-Quadratic-trend interaction was observed.

Simple Effects

To investigate whether these interaction effects were due to increases in the parity task, linear increases for each task were investigated separately. Only the parity task elicited significant increase in activation associated

with increases in stimulus orientation, and no reliable effects were observed for the category task. Significant activation clusters for linear trends in the parity task are represented on cortical surface rendering, and peak activation voxels are numerically labeled on the corresponding glass-brain SPM in Figure 3. The linear trend in the parity task was observed in six discrete clusters: with increases in activation observed in the dIPSm, midline and lateral pre-SMA, and anterior insular region; and decreases in activation were observed in the midline SMA (see Table 1 for summary statistics, anatomical labels, and MNI coordinates). The parameter estimates plotted in Figure 5 illustrate that linear increases in BOLD signal are only observed for the parity task, with no comparable effects for the category task.

## Task-by-Orientation-by-Hemisphere Interaction

The next question was whether mental rotation–related increases in activation with increases in stimulus orientation differed between the hemispheres. No significant voxels were observed for this comparison. These results provide no evidence for hemispheric dominance for mental rotation.

DISCUSSION

The aim of the study was to further investigate functional neuroanatomy and hemispheric asymmetries associated with mental rotation. We used the Cooper and Shepard (1973) task because this was thought to be a good measure of pure mental rotation uncontaminated with piecemeal processing, and thus, more likely to elicit right-hemispheric processing. We also used a letter–digit categorization task that did not elicit mental rotation, but served as a control task designed to account for effects related to object recognition and decision-making processes. Thus, increases in activation for the parity task, compared with the category task, should reflect effects related to mental rotation as well as additional processes such as recognition of character orientation, increased visuospatial working memory and attentional demands, and parity discrimination itself. Because mental rotation is associated with linear increases in RTs as a

Figure 4. Parameter estimates as a function of task and hemisphere for the five peak activation voxels showing Task-by-Hemisphere interaction. MNI coordinates and anatomical labels are indicated above each graph, and numerical labels corresponding to the information in Table 1 and Figure 3 are also included. Error bars indicate 95% confidence interval of the mean.
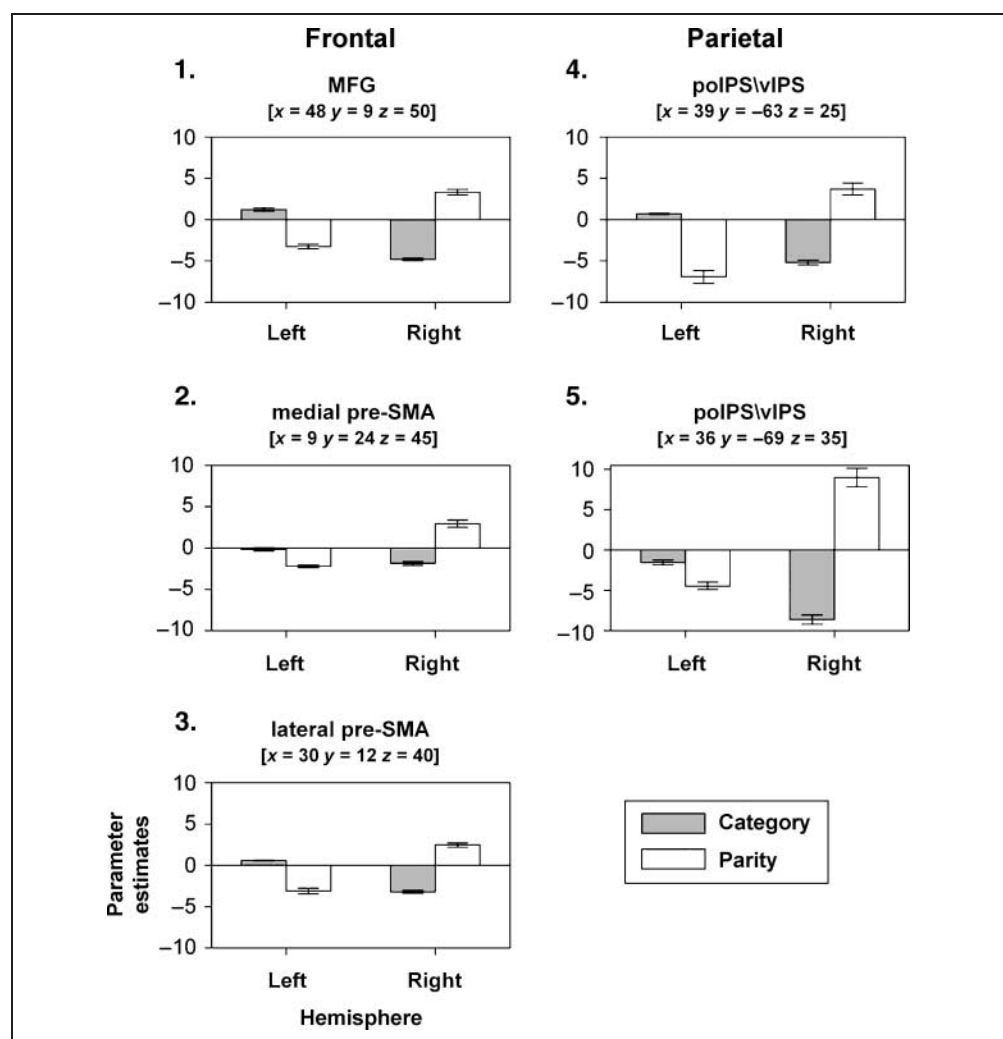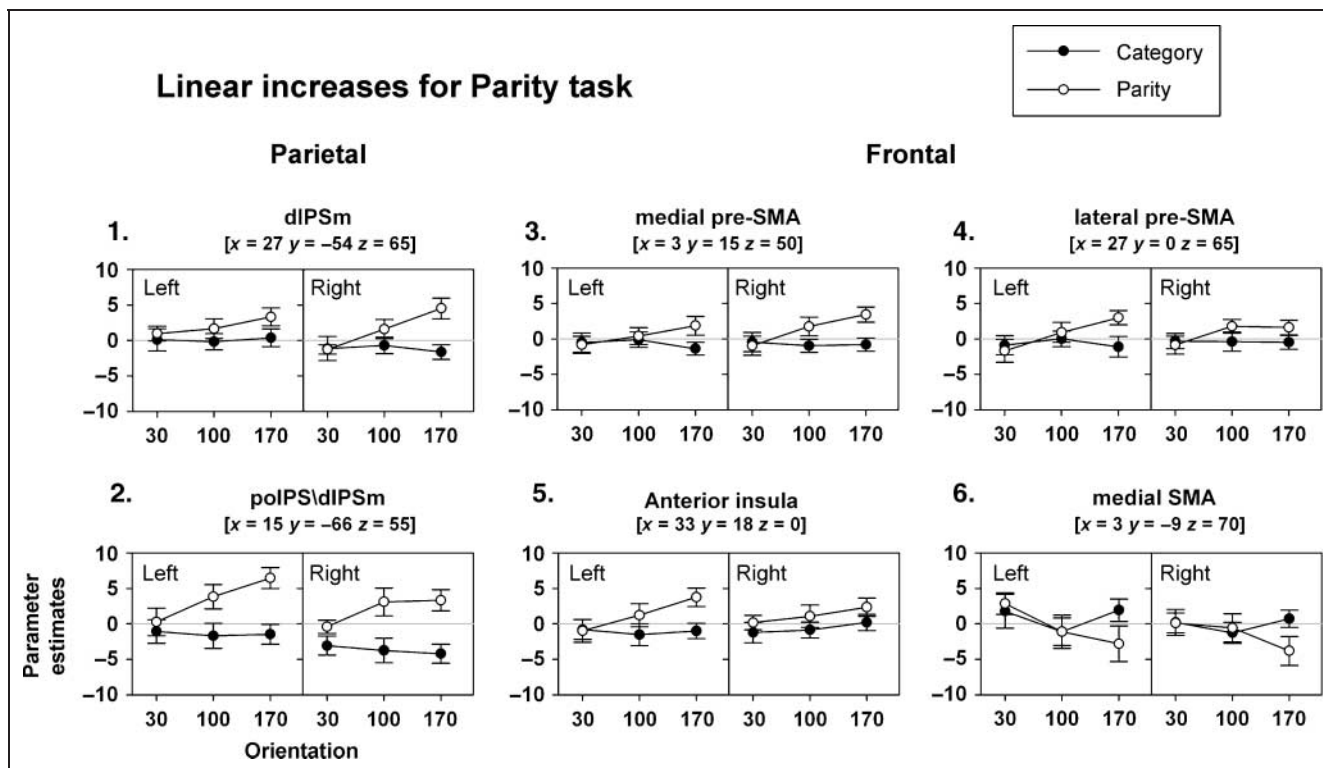
Figure 5. Parameter estimates as a function of task, orientation, and hemisphere for the six peak activation voxels showing linear increases as a function of stimulus for the parity task. MNI coordinates and anatomical labels are indicated above each graph, and numerical labels corresponding to the information in Table 1 and Figure 3 are also included. Error bars indicate 95% confidence interval of the mean.

function of stimulus orientation, we hypothesized that a similar relationship between angular departure from upright and the BOLD signal should be observed in areas that are involved in mental rotation per se.

Hemispheric Asymmetries

As evident from Figure 2, in terms of hemispheric lateralization, both tasks activated comparable regions in the left hemisphere, but the parity task differed from the category task in that activity tended to be bilateral and symmetrical. Both tasks elicited activation within response-related sensory–motor regions, which can be related to right-handed responses. The preferential involvement of the left hemisphere in the category task may also reflect the fact that the stimuli were alphanumeric characters (Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; James, James, Jobard, Wong, & Gauthier, 2005; Pernet, Celsis, & Démonet, 2005; Pernet et al., 2004; Garrett et al., 2000; Polk & Farah, 1998).

Because the left-hemispheric involvement within these regions was present for both tasks, and right hemisphere activation was only elicited by the parity task, these overall effects reflect bilateral involvement in the parity task and left hemisphere involvement in the category task. These areas also show greater overall activation in response to the parity task than to the category task. Task-specific hemispheric asymmetries, as indicated

by the interaction between task and hemisphere, suggest that the right hemisphere might show dominance for cognitive processes involved in the parity task, but not in mental rotation per se. The Task-by-Hemisphere interaction also indicates that the extent of activation elicited by the parity task is larger, compared to the category judgment, on the right, although the specific differences between the hemispheres in terms of the degree of activation within a task are restricted to the parity task. Hemispheric asymmetries can therefore be interpreted as left-hemispheric dominance for perception, recognition, and categorization of alphanumeric characters (e.g., Joseph et al., 2006; James et al., 2005), as well as for response generation due to right-handed responses in this study, and additional recruitment of the right hemisphere associated with visuospatial processing demands imposed by the parity task.

Parity Discrimination

The parity task elicited increases in BOLD signal activation bilaterally within the ventral stream, IFG, dIPS, vIPS, anterior insula, as well as the lateral and medial pre-SMA. Unilateral activation was also observed within the left somatosensory cortex and in the right cerebellum. The distribution of the activation in response to the parity task was similar to the pattern of activation in response to the category task on the left, with the exception of the

vIPS, which was only active in response to the parity task. The parity task also elicited increases in activation on the right in comparable regions. However, the magnitude of the activation on both the left and the right was significantly greater in all of these regions for the parity task, with the exception of the sensorimotor and cerebellar activation.

Therefore, parity-task-related increases in activation were observed in the ventral stream, vIPS and dIPS, IFG, anterior insula, and lateral and medial pre-SMA. In some respect, at least, this pattern of results is not unexpected. The parity task probably involves all the perceptual, cognitive, and response-related processing stages involved in category judgments. In addition to the shared processing steps, parity judgments are also likely to require additional spatial processing of the stimuli, such as determining the orientation of the object, deciding which way to rotate it to upright, generating a mental image, mental rotation to upright, and finally, parity discrimination. Thus, it is not surprising that the parity judgment task elicited a greater degree of activation than the category task.

Ventral Stream

In addition to the regions that showed linear increases in activation, which we attributed to mental rotation per se, increases in activation for the parity task, relative to the category task, were observed in the ventral stream, throughout the IPS, and in the dorsolateral prefrontal regions. These areas, however, did not show linear increases with angular orientation. Alivisatos and Petrides (1997) also reported increases in these areas in a PET study for parity judgments relative to category judgments, although the category task was performed only with upright nonmirrored characters. They suggested that the increases in the ventral stream were associated with increased difficulty in processing of mirror-reversed and misoriented stimuli, rather than task-related demands. This conclusion is not supported by the current data because the stimuli were identical for the two tasks. The results from the present study, therefore, suggest that the parity task required more perceptual processing than the category task. This extra processing may have involved the identification of orientation itself, which is necessary for mental rotation but not for categorization.

It is also possible that categorization does not require that individual letters and digits be identified; experiments on visual search show, for example, that search for individual digits among letters is accomplished in parallel, whereas searching for letters among letters requires serial search (Schneider & Shiffrin, 1977). Parity judgments may, therefore, require that the characters be individually identified, whereas category can be accomplished without this further step. Given that mental image formation recruits similar cortical regions as perception (e.g., Kosslyn, Ganis, & Thompson, 2001), an-

other possible reason for greater involvement of ventral stream areas in parity judgments is the requirement that participants form a mental image of the character prior to mental rotation.

Posterior Parietal Cortex

Our results are consistent with those of previous studies in showing activation in the IPS elicited by the parity task. This activation was bilateral, in conformity with some previous studies (e.g., Podzebenko et al., 2002), but contrary to those showing unilateral activation in the right (e.g., Harris et al., 2000) or the left (e.g., Alivisatos & Petrides, 1997) IPS. Further, the linear increase in activation with angular orientation was evident only in the posterior portion of the dIPS, suggesting that only this portion of the IPS is involved in the process of mental rotation itself. This explanation is consistent with previous studies showing that the IPS consists of a number of functionally distinct regions, both in humans and in monkeys (Orban et al., 2006).

Activation unique to the parity task was observed within the vIPS, an area posterior to the portion of the IPS involved in mental rotation (see below). This area may correspond to one of the four motion-sensitive sections of the IPS (Orban et al., 2006). Orban et al. (2006) suggest that the vIPS is a human homologue of the LIP area in the macaque cortex. The lateral intraparietal area (LIP) has been shown to be involved in visuospatial attention, motor planning, and decision making (Freedman & Assad, 2006). Hemispheric asymmetries were also observed within this region for the parity task, with larger activation on the right than on the left.

Inferior Frontal Gyrus

The inferior frontal gyrus was the only prefrontal region that showed increases in response to the parity task that did not vary as a function of stimulus orientation. Activation in areas that do not show orientation dependence might reflect areas that respond to the increases in attentional and working-memory demands for the parity task, rather than areas involved in the process of mental rotation per se. Task-related hemispheric differences were also observed in this area, with increases in activation on the left for both category and parity tasks, and only parity-task-related increases on the right.

Mental Rotation

Linear increases in RTs and the BOLD signal as a function of angular orientation were found only in response to the parity task. Increases in RTs as a function of stimulus orientation are commonly associated with mental rotation (e.g., Cooper & Shepard, 1973). We hypothesized that comparable effects should be seen in the

BOLD signal originating in the areas that are involved in mental rotation per se. The observation that linear effects were only associated with the parity task provides additional support for the idea that linear increases in the BOLD signal are, indeed, neural correlates of mental rotation. Only a subset of areas involved in the parity judgment task showed linear increases in BOLD activation with larger angular orientations. The mental rotation–related effects were restricted to a subregion of the IPS—the dIPSm, and to specific prefrontal areas—the lateral and the medial pre-SMA. These findings support the notion that mental rotation is subserved by both parietal and higher-order premotor regions.

The frontal modulation with increased mental-rotation demands with the alphanumeric parity task is of particular significance because some models of mental rotation, namely that of Carpenter et al. (1999), have attributed activation within those regions to eye movements or shifts of attention between simultaneously presented stimuli, as is typically the case in paradigms using torus shapes. In contrast, the role of parietal cortex activation is the transformation of the spatial coordinates of the image required for mental rotation. Given that the current paradigm involved single stimulus displays, the higher-order premotor activation cannot be due to eye movements or shifts of attention between stimuli.

Somewhat paradoxically, Harris et al. (2000) suggested that eye movements are specifically related to the parietal activation. They suggested that eye movements translate into a spatial coordinate system, and that this information is continuously updating object location, direction, and speed of motion, as well as changes in stimulus orientation. Because eye movements are coded by a fronto-parietal network, the explanation proposed by Harris et al. could also account for the frontal activation reported in this study, and thus, further support the conclusion that mental rotation is critically dependent on a fronto-parietal network, rather than just on the parietal cortex.

Another possibility is that the fronto-parietal involvement reflects activation of the network that underlies visually guided action. The parallel between mental rotation, which is often considered viewed as a higher cognitive function, and visual perception for action is not often made, although the interpretation of mental rotation as an action-oriented process was proposed by Jordan et al. (2001). Nevertheless, it is important to note that although experimental study of mental rotation began with a parity-discrimination task (Shepard & Metzler, 1971), visuomotor rotation paradigms also elicit orientation-dependent performance suggestive of that mental rotation (Georgopoulos & Massey, 1987).

The distinction between visual processing leading to perception and visual processing leading to interaction with the environment has been made by Goodale and Milner (1992) and mapped to the ventral and dorsal visual pathways, respectively. More recently, the idea of three visual systems has been developed (Rizzolatti & Gallese, 2006; Creem & Proffitt, 2001). Rizzolatti and Gallese (2006) likewise have proposed three rather than two functional pathways: One, culminating in the superior parietal lobule, would be specifically related to visual processing leading to action. Another, leading to inferior temporal cortices, would be specifically related to visual recognition. And the third, terminating in the inferior parietal lobe, would associate visual object processing with object-related interaction both in terms of spatial perception, motor action preparation, and understanding.

Rizzolatti and Gallese (2006) argued that spatial information is ''coded'' in terms of motor experience. If this is the case, visuospatial processing that does not lead to action would still, by definition, depend on cognitive and neural mechanisms comparable to mechanisms leading to action. Thus, viewing mental rotation as a higher cognitive process divorced from object-related action may be erroneous. Although the functional role of mental rotation is not necessarily clear, it is highly likely that a complex process such as this would evolve so we could imagine what spatial arrangements would look like before we go through the effort of actually moving or rearranging objects; and thus, brain regions that are involved in motor preparation and planning may also be recruited. Similarly, the pattern of behavioral performance, increase in reaction times with larger rotations, indicates that the mental rotation is performed in an analogue manner, comparable to the act of rotating a physical object (Shepard & Metzler, 1971). The development of mental-rotation abilities would critically depend on prior experience of seeing objects going through a trajectory, either by an individual moving around an object, or by manipulating objects themselves. Mental rotation may therefore recruit circuits that are related to physical rotation of objects.

Another possibility is that these effects do not reflect mental rotation itself, but rather increased duration of attention and working memory associated with increased RTs. This seems plausible given that the duration of BOLD signal is highly correlated with RTs in both the frontal and the parietal regions (Lamm et al., 2001; Richter et al., 1997, 2000). The localization of these effects corresponds closely to the dorsal fronto-parietal network, which mediates both visuospatial attention as well as visuospatial working memory (e.g., Corbetta, Kincade, & Shulman, 2002), and involves both the IPS and higher-order premotor areas identified in this study.

If this is the case, then it may be useful to consider how mental rotation is instantiated in the brain. Jagaroo (2004) provided a comprehensive discussion of the two possible interpretations of parietal activation in mental-rotation tasks. One is that the parietal activation reflects rotational image transformation, possibly akin to a neuronal population vector that shifts with rotation of the image (see Georgopoulos, Lurito, Petrides, Schwartz, &

Massey, 1989). The other interpretation is that the parietal activation reflects a multitude of parietal functions, none of which is unique to mental rotation. The current study does not resolve these two views, but the results strongly suggest that higher-order premotor areas and the PPC follow the same activation patterns as a function of mental-rotation demands. Therefore, it seems very difficult to attribute activation within the parietal lobe to mental rotation per se and within the higher-order premotor areas to processes other than mental rotation.

A possibility remains that the prefrontal activation may be a result of prominent anatomical connections between the PPC and the premotor areas, given that, in some cases, anatomically connected cortical regions will show coactivation even if only one of those areas is actively involved in the task (Rorden & Karnath, 2004). Mental rotation is disrupted by damage to either the left (Mehta & Newcombe, 1991) or right (Ditunno & Mann, 1990) PPC, by stimulation of the parietal lobe with TMS (Harris & Miniussi, 2003), or by deep cortical stimulation (Zacks et al., 2003). In contrast, mental rotation is apparently unaffected by lobotomy of either the left or the right prefrontal cortex (Alivisatos, 1992).

However, it is debatable whether the results reported by Alivisatos (1992) are conclusive given that some of the patients, particularly in the left frontal lobotomy group, showed considerably slower mental-rotation rates than either temporal lobotomy or normal controls. Alivisatos reported no systematic difference between the extent of frontal resection between subjects who showed a reduction in mental-rotation rates and those who did not. Interestingly, Silberstein, Danieli, and Nunez (2003) found EEG synchronization between *left* frontal and *right* parietal regions when subjects mentally rotated the 3-D ''torus'' shapes used by Shepard and Metzler (1971) in their original mental-rotation experiment. It seems likely that time-varying processes such as mental rotation involve large populations of neurons, involving both parietal and frontal regions (Georgopoulos, Taira, & Lukashin, 1993). Therefore, it may of interest investigate the contribution of higher-order premotor regions using a neurodisruptive technique such as TMS.

Conclusion

Linear modulation of the BOLD response was observed only during the parity task and was characterized by increases in activation with an increase in angular rotation from upright. These effects were restricted to a subset of areas that showed increases in activation in response to the parity task and included the posterior portion of the dIPS, the lateral and medial pre-SMA, and the anterior insular region. No hemispheric asymmetries were observed for the effects of orientation, indicating that neither hemisphere can be seen as dominant for mental rotation.

Hemispheric asymmetries *were* observed for the parity task, but not in the areas that showed linear increases in BOLD signal amplitude associated with mental rotation. Firstly, larger right- than left-hemispheric activation was observed in the vIPS, the IFG, as well as the lateral and medial pre-SMA (anterior to the areas that showed linear increases in response to the parity task). Secondly, the parity task elicited more activation than the category task in all these regions on the right, but not on the left. This pattern of results suggests that the hemispheric asymmetries may be related to visuospatial processing other than mental rotation per se.

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