Motion in the mind's eye: Comparing mental and visual rotation

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Mental rotation is among the most widely studied visuospatial skills in humans. The processes involved in mental rotation have been described as analogous to seeing an object physically rotate. We used functional magnetic resonance imaging of the whole brain and localized motion-sensitive hV5/MT+ to compare brain activation for stimuli when they were mentally or visually rotated. The results provided clear evidence for activation in hV5/MT+ during both mental and visual rotation of figures, with increased activation for larger rotations. Combined with the overall similarities between mental and visual rotation in this study, these results suggest that mental rotation recruits many of the same neural substrates as observing motion.

In the literature on human visuospatial skills, mental rotation is among the most widely studied tasks. Among other aspects, researchers have explored mental rotation's basic mechanisms (e.g., Bauer & Jolicœur, 1996; D. Cohen & Kubovy, 1993; Cooper & Shepard, 1973a; Corballis, Zbrodoff, & Roldan, 1976; Koriart & Norman, 1984; Robertson, Palmer, & Gomez, 1987; R. N. Shepard & Metzler, 1971; S. Shepard & Metzler, 1988), neural correlates (e.g., M. S. Cohen et al., 1996; Georgopoulos & Pellizzer, 1995; Jagaroo, 2004; Loverock & Modigliani, 1995), role in individual differences (e.g., Just & Carpenter, 1985; Vandenberg & Kuse, 1978), and changes over training and development (e.g., Heil, Rösler, Link, & Bajric, 1998; Kail, Pellegrino, & Carter, 1980; Platt & Cohen, 1981; Snow & Strope, 1990). Although our understanding of the processes involved in mental rotation have come a long way, there are still lingering questions about how mental rotation problems are processed.

Mental rotation has been used to refer to any task that requires participants to consider stimuli at different viewing angles. For example, participants might be asked to determine whether paired images, presented either successively or simultaneously, depict rotated versions of the same figure or two different figures (e.g., R. N. Shepard & Metzler, 1971). Similarly, participants might be asked to make judgments about individual stimuli presented in non-canonical orientations (e.g., letters; Cooper, 1976; Cooper & Shepard, 1973b). The classic result is a monotonic relationship between response latency to make a judgment and the angular disparity either between two figures or

between the canonical and presented orientations (e.g., Kosslyn, 1980; R. N. Shepard & Podgorny, 1978). One of the first explanations for this response latency relationship was the analogue rotation hypothesis (Cooper & Shepard, 1973b). Put simply, this view suggests that mental rotation is just what the name conveys, imagining a figure rotating through space. According to this account, the slope of the response latency curve is indicative of mental rotation speed, with steeper slopes indicating slower rotation.

Much of the debate over the analogue rotation hypothesis has focused on the *analogue* portion of the hypothesis; that is, the claim that the representations of the figures in the brain are somehow analogues of the stimuli in the physical world (e.g., Anderson, 1978; Palmer, 1975; Pylyshyn, 1979). However, regardless of the relationship between the stimulus representation and the physical world, the analogue rotation hypothesis suggests a relationship between the representation/processing of the stimulus in mental rotation and the representation/processing of a stimulus that is perceived while visually rotating. That is, mental rotation is believed to involve representations and processes that are similar to the representations and processes in the perception of visual rotation. By extension, mental rotation and the perception of visual rotation should engage many of the same neural mechanisms. Substantial support already exists for such similarity of processing with mental imagery and visual perception (e.g., Kosslyn, 1981; Kosslyn et al., 1993; Kosslyn, Behrmann, & Jeannerod, 1995; Kosslyn, Ganis, & Thompson, 2001; Sparing et al., 2002), so it is natural to inquire whether this relationship extends to the dynamic case of mental rotation and visual motion perception.

Neuroimaging studies have identified a number of regions of activation correlated with mental rotation, some of which indirectly speak to its relationship to visual motion perception. The most consistent finding has been parietal cortex activation associated with mental rotation, particularly activation focused in the inferior parietal cortex (e.g.,

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Figure 1. Static image of the sample stimuli for the figure matching tasks.

Alivisatos & Petrides, 1997; Barnes et al., 2000; Bonda, Petrides, Frey, & Evans, 1995; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; M. S. Cohen et al., 1996; Gauthier et al., 2002; Harris et al., 2000; Jagaroo, 2004; Richter et al., 2000; Tagaris et al., 1998; Vanrie, Béatse, Wagemans, Sunaert, & Van Hecke, 2002; Vingerhoets, de Lange, Vandemaële, Deblaere, & Achten, 2002; Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999). This region has been associated with processing of higher order motion (Claeys, Lindsey, De Schutter, & Orban, 2003) and lies in close proximity to areas of the human brain sensitive to motion (hV5/MT+; Huk, Dougherty, & Heeger, 2002; Nakamura et al., 2003; Orban et al., 2003; Tootell et al., 1995), suggesting that perhaps mental rotation involves motion imagery that is processed much like visual motion.

The present study was designed to investigate the functional equivalence of mental and visual rotation by focusing on the neural substrates of motion perception. If visual and mental rotations both involve representing rotation, then motion-sensitive brain regions should be commonly activated. In particular, the study was designed to investigate activation in hV5/MT+ during mental and visual rotation tasks. This area has been observed during the presentation of static images (as in mental rotation) when those stimuli convey *implied* motion. That is, when participants observed a still image captured in the midst of a motion, hV5/MT+ showed increased activation in comparison with when they observed still images of non-moving stimuli (Kourtzi & Kanwisher, 2000), suggesting that the representations formed for the still images had representational momentum (Kourtzi, 2004; Senior et al., 2000). For mental rotation, we hypothesize that the presence of two figures at different angular disparities will invoke imagery processes that are similar to those observed in implied motion stimuli, allowing participants to solve the problem by envisioning the motion. As a result, we expect to see activation of hV5/MT+ for both mental and visual rotations.

Upon close examination of the results from previous studies of mental rotation, one finds that they have been mixed, with regard to whether activation associated with mental rotation extends into hV5/MT+. However, important factors may limit the ability to observe or the consistency of observing activation in this region. First,

hV5/MT+ may be nonoverlapping across individuals (Watson et al., 1993), particularly if highly focused activation is expected. This lack of overlap would reduce the power to observe any activation in a typical group-level neuroimaging analysis. Second, direct comparisons with visual motion have been limited. To address these problems, we first established motion-sensitive regions of the brain for each individual separately and then investigated the activation of these regions during both visual rotation and mental rotation. Using the same stimuli under visual and mental rotation conditions allowed a more direct comparison of the underlying processes.

METHOD

Participants

Fourteen healthy, right-handed adults (7 male, 7 female; mean age 22.7 years) participated in return for monetary compensation. The participants were randomly assigned to the task orders defined below.

Rotation Tasks

All stimuli were presented using PsyScope software (J. D. Cohen, MacWhinney, Flatt, & Provost, 1993). The tasks used block figures and required a same/mirror-image judgment (Figure 1). Five different base figures and their mirror reversals were created using Virtus WalkThrough Pro (Virtus Corporation, Cary, NC). For each figure, we captured still images of the figure in 12 different orientations rotated in depth about the vertical axis in 30° increments. For the mental rotation trials, pairs of images (either same or mirror-image figures) were selected to represent three different degrees of angular disparity: 0°, 60°, and 120°. For the visual rotation trials, the same pairs used in mental rotation were used to initiate trials; the rightward figure was a continuous stream of images at intervening angular disparities, to create apparent rotation from the initial angular disparity to 0° disparity. The speed of rotation for 60° and 120° was set to approximately 70° per sec, to mimic the average response latency slopes from extensive pilot data.

For both tasks, each 5,500-msec trial was preceded by a 500-msec fixation cross. The fixation cross remained on the screen throughout the experiment and the participants were instructed to maintain fixation throughout. For each trial, the participants were instructed to make a same/mirror-image discrimination with a buttonpress. In the mental rotation condition, the participants were asked to respond when they were confident in their answer. In the visual rotation condition, the participants were asked to view the stimuli until the rightward figure stopped rotating, and then make a response. This procedure equated the time for visual rotation with the mean time required for mental rotation of the stimulus, a critical feature for determining the sensitivity to degree of motion. On a given trial, the stimuli were visible until a response was made. If the participants made a response within 5,500 msec, the stimuli disappeared and only the fixation cross remained for the duration of the trial. Each task consisted of 50 same trials per angular disparity and 50 mirror-image trials (randomly selected from the three angular disparities). For a given task, the order of the 200 trials was randomized and divided into five 4-min runs of 40 trials each. Each participant completed a total of 10 functional runs (5 mental rotation and 5 visual rotation). Half of the participants performed all 5 mental rotation runs first and half performed all 5 visual rotation runs first. Prior to the first run of each task, the participants were given 6 practice trials to familiarize them with the task and response deadline.¹

MT Localizer

To establish motion-sensitive regions of the brain for each individual, a localizer task was used. The motion-detection task used

3-sec clips of 500 dots moving in random or coherent patterns. Coherent motion has been shown to elicit greater hV5/MT+ activation than does random motion (Nakamura et al., 2003). Using coherent motion therefore allowed us to identify motion-sensitive regions in each participant. For the coherent condition, 100% of the dots moved either to the right or to the left. For the random condition, 5% of the dots moved to either the right or the left among randomly moving dots.

The participants indicated by buttonpress whether the dots were moving to the right or to the left. For the random condition, they were asked to guess. Trials were presented in six blocks each of coherent and random motion. Half of the trials were leftward motion and half were rightward motion, presented randomly within each block. Block order was random in the 3.6-min scan run.

fMRI Data Acquisition

Whole-brain imaging data were acquired on a Philips Gyroscan INTERA 3.0T MRI scanner. Functional images were acquired in twenty 5-mm (+1-mm gap) axial slices using SENSE imaging (Pruessmann, Weiger, Scheidegger, & Boesiger, 1999; 30-msec echo time [TE]; 1,000-msec repetition time [TR]; 70° flip angle; 240-mm field of view; 64 × 64 acquisition matrix). In addition, a high-resolution MPAGE was acquired (150 1-mm slices; minimum TE and TR; 8° flip angle; 256-mm FOV; 256 × 256 acquisition matrix).

fMRI Analyses

Using SPM99 (Wellcome Department of Cognitive Neurology, London, U.K.), all functional data were corrected for slice timing and motion, normalized to a T1 template image, and smoothed with a smoothing kernel of 6 mm. Anatomical and functional images were coregistered to each other to allow common normalization and overlaying of functional activation.

For the motion-detection task, individual block-design models were constructed. In each participant, we looked for greater activation for coherent versus random motion in the bilateral temporoparietal–occipital cortex based on the anatomical locations defined in previous studies (Dukelow et al., 2001; Huk et al., 2002; Sunaert, Van Hecke, Marchal, & Orban, 1999; Tootell et al., 1995; Watson et al., 1993; Zeki et al., 1991).

For the mental and visual rotation tasks, two statistical models (Friston et al., 1995) were constructed using an event-related design for each participant in order to test the effect of rotation with and without the contribution of response latency. In the standard model, the canonical hemodynamic response function (hrf) was modeled without regard for response latency differences, such that differences between rotation and no-rotation could be due all or in part to differences in response latency. In the adjusted model (RT-convolved model) the response latency data were convolved with the hrf in order to isolate novel processes (Christoff et al., 2001). By using the response latency, we were effectively modeling the duration of the trial. As a result, only regions that showed a difference above and beyond differences expected from response latency alone would be evident in this analysis. In both models, regressors were included for each of the three angular disparities in the two tasks, and beta weights were scaled to reflect the percent of signal change relative to the periods of fixation alone. The beta weights for the different conditions were extracted for ROI analyses of motion-sensitive regions. In addition, the contrast images derived from estimating each participant's model were subjected to random effects analyses for rotation versus no-rotation in each task and in a paired *t* test for the difference between mental and visual rotation (Holmes & Friston, 1998). Areas of statistical significance were identified using an uncorrected height threshold of $\alpha = .001$. Clusters with fewer than 10 voxels were then eliminated, yielding a corrected spatial extent threshold of $\alpha = .05$.

RESULTS

Behavioral Results

Accuracy was quite high for all participants in both tasks (hits – false alarms $\geq .90$ in all conditions), so these data were not analyzed further. Mean response latencies were calculated for each participant at each angular disparity for all correct same trials in the mental and visual rotation tasks. These data were subjected to a mixed ANOVA with task order as a between-subjects factor and task and angular disparity as within-subjects factors using a familywise $\alpha = .05$. Figure 2 shows the two key results. First, there was a main effect of angular disparity [$F(2,24) = 425.43$], showing the typical linear relationship [$F(1,24) = 494.04$]. Second, neither task nor its interaction with angular disparity was significant, suggesting that response latency data were remarkably similar in the two tasks. No other effects or interactions reached statistical significance.

fMRI Data

In the motion-detection task, all 14 participants showed significant activation for coherent motion in comparison with random motion in a bilateral region of the occipital–temporal–parietal junction (Table 1). These clusters served as regions of interest (ROIs) to examine the activation in motion-sensitive hV5/MT+. For each individual, the beta weights were extracted for 0°, 60°, and 120° trials for the visual and mental rotation tasks using the two different models (corrected and uncorrected for latency). These data were then subjected to separate ANOVAs, with task order as a between-subjects factor and hemisphere (left or right), task (mental or visual), and angular disparity (0°, 60°, and 120°) as within-subjects factors. We used three criteria for assessing motion-related processing: (1) hV5/MT+ had to be more active for visual rotation than for a no-rotation baseline, (2) hV5/MT+ had to be more ac-

Figure 2. Behavioral task data showing average response latency as a function of angular disparity and task. Error bars reflect ± 1 SEM. MR, mental rotation; VR, visual rotation.

Table 1
Talairach Coordinates for Peak Activation in hV5/MT+ for Each Participant,
Indicating Size and *t* Value Associated With Each Cluster

Subject	Left hV5/MT+					Right hV5/MT+				
	<i>x</i>	<i>y</i>	<i>z</i>	Voxels	<i>t</i>	<i>x</i>	<i>y</i>	<i>z</i>	Voxels	<i>t</i>
1	-38	-64	-4	16	6.04	48	-58	3	26	5.97
2	-42	-68	2	27	7.85	40	-63	2	22	6.48
3	-42	-66	2	32	4.92	42	-62	6	37	3.96
4	-39	-64	6	18	6.98	42	-60	4	23	6.25
5	-48	-63	0	39	5.87	44	-66	6	26	4.83
6	-46	-66	4	26	7.71	42	-62	0	15	4.23
7	-43	-64	3	21	5.26	44	-68	-2	11	7.15
8	-38	-60	-2	33	6.43	40	-62	0	25	5.37
9	-50	-60	4	17	7.81	38	-68	6	24	5.34
10	-45	-58	3	28	8.16	38	-66	0	19	6.29
11	-52	-62	8	15	5.59	48	-65	3	26	5.18
12	-46	-60	0	30	4.23	42	-58	2	29	5.03
13	-36	-68	2	10	6.79	46	-64	-1	11	3.21
14	-40	-60	-1	24	5.64	50	-62	6	12	3.08

tive for mental rotation when compared with a no-rotation baseline, and (3) activation had to increase with increased angular disparity for both visual and mental rotation when analyzed with a model that did not control for response latency.

Figure 3 shows the key results in the hV5/MT+ ROIs. None of the effects or interactions involving task order were significant. The main effect of angular disparity was significant and accounted for large proportions of variance [$F(2,24) = 112.94$ and 72.12 for the standard and the RT-convolved models, respectively]. Pairwise comparisons within each task revealed that 0° was different from 60° and 120° in both the corrected and uncorrected models for all ROIs. In addition, 60° and 120° differed in all ROIs, but only with the standard model, suggesting that response latency was responsible for the difference between the two rotation conditions. In addition to these key findings, we found an interaction between hemisphere and angular disparity [$F(2,24) = 47.28$ and 45.82 , for the standard and the RT-convolved models, respectively], which was largely carried by the simple main effect of angular disparity in the visual rotation condition [$F(2,24) = 46.68$ and 15.47]. This was the result of bigger effects in the left hemisphere during the visual rotation condition, which is consistent with the rotation being presented to the right visual hemifield.

The mental and visual rotation runs were further analyzed in a second-level random effects analysis. Mental rotation and visual rotation were first compared with their respective no-rotation (0°) baselines. The results of these two comparisons were remarkably similar (Figures 4A and 4B). Using the standard model, both tasks showed significant bilateral activation in superior and inferior parietal cortices, a large occipital region, dorsolateral prefrontal cortex (DLPFC, BA 9/46), and a right temporal region in the proximity of the hV5/MT+ regions identified for each participant. The overlap of the regions for mental and visual rotation was further supported by conjoining the individual analyses (Figure 4C). These analyses were

repeated with the RT-convolved model, and all regions remained significant except for the bilateral middle occipital cortex. In a direct comparison of mental and visual rotation, activation was significantly greater for mental rotation than for visual rotation (minus their respective baselines) in the DLPFC region in both the standard and the RT-convolved models.

In order to more closely examine the similarities and differences between mental and visual rotation, the ROIs from the mental and visual rotation contrasts were further interrogated.² For each ROI, individual subject beta weights from the standard model and the RT-convolved model were extracted for each task at each angular disparity and then subjected to a repeated measures ANOVA, with task order as a between-subjects factor and task, angular disparity, and hemisphere as within-subjects factors using a familywise $\alpha = .05$ corrected for violations of sphericity.

In the large middle occipital region (Figure 5A), the only significant effect was angular disparity, and only in the standard model [$F(2,24) = 72.35$]. The significant linear trend [$F(1,24) = 82.67$] accounted for the majority of the effect variance (99%). Together with the absence of any trends when using the RT-convolved hrf model, this trend suggests that this region was largely associated with task duration.

In the superior parietal region (Figure 5B), the standard model revealed a significant main effect of hemisphere [$F(1,12) = 46.49$], with the left hemisphere showing greater activation than the right; however, this was largely attributable to the significant interaction of hemisphere with task [$F(1,12) = 84.97$], showing that the left/right disparity was greater for visual rotation than for mental rotation. The main effect of angular disparity was also significant [$F(2,24) = 345.60$], and could be attributed almost entirely (99%) to the significant linear trend [$F(1,24) = 609.67$]. Using the RT-convolved hrf model, the main effect of hemisphere remained [$F(1,12) = 13.81$], as did its interaction with task [$F(1,12) = 51.74$], again suggesting that the left hemisphere was more active, largely for the

visual rotation task. In addition, there was a main effect of task [$F(1,12) = 238.11$], with more activation for mental rotation than for visual rotation. The main effect of angular disparity was again significant [$F(2,24) = 332.76$], but was no longer carried by the linear trend. Instead, the variance could be entirely accounted for ($>99\%$) by the contrast of 60° and 120° versus 0° [$F(1,24) = 665.26$], indicating that this region was more active for rotation than for no-rotation but that it did not differ as a function of amount of rotation (60° and 120°).³ This trend did not vary as a function of either hemisphere or task.

In the inferior parietal region (Figure 5C), using the standard model revealed main effects of tasks [$F(1,12) = 94.49$], hemisphere [$F(1,12) = 48.75$], and angular disparity [$F(2,24) = 743.25$]. Mental rotation showed greater activation than visual rotation, and there was greater left than right hemisphere activation. The latter effect was again attributable to an asymmetry in the visual rotation task, as evidenced by the interaction of task and hemisphere [$F(1,12) = 94.05$]. The majority of the effect

of angular disparity (98%) could again be attributed to the robust linear trend [$F(1,24) = 1,178.65$]. In this region, the angular disparity showed a significant interaction with task [$F(2,24) = 23.86$], which revealed that the linear trend was significantly larger for mental rotation than for visual rotation [$F(1,24) = 45.45$]. Using the RT-convolved hrf model, all of these effects and interactions remained significant: task [$F(1,12) = 319.44$], angular disparity [$F(2,24) = 561.13$], and task $\times$ angular disparity [$F(2,24) = 330.70$]. As in the superior parietal cortex, the most substantial difference between the standard and RT-convolved hrf models was in the effect of angular disparity. With the RT-convolved hrf, the variance in the effect of angular disparity could be entirely accounted for ($>99\%$) by the contrast of 60° and 120° versus 0° [$F(1,24) = 1,121.78$], indicating that this region is more active for rotation conditions than no-rotation conditions. Moreover, in the task $\times$ angular disparity interaction, this effect is greater for mental rotation than for visual rotation. Indeed, when tested for simple main effects, angu-

Figure 3. Average hV5/MT+ activation as a function of angular disparity, task, and hemisphere estimated from standard (top panel) and RT-convolved (bottom panel) models. Error bars reflect ± 1 SEM.

Figure 4. Group activation for (A) mental rotation (60° and 120°) versus no-rotation (0°) and (B) visual rotation (60° and 120°) versus no-rotation (0°) on the right. These results are based on the model allowing for response time differences. All regions were activated with $p < .05$ corrected. (C) Three axial slices in psychological convention (left = left) showing the conjunction of the two separate analyses.

lar disparity had a marginal effect, at best, in the visual rotation condition [$F(2,24) = 2.00, p = .17$], suggesting that this region participated largely in the mental rotation condition.

Finally, in the DLPFC (Figure 5D), the results were nearly identical using the standard and RT-convolved hrf models (all F s are reported for the standard and RT-convolved models, respectively). The main effect of task was significant [$F(1,12) = 65.79$ and 108.22], with greater activation for mental rotation than for visual rotation. The main effect of angular disparity was significant [$F(2,24) = 207.49$ and 268.90]. Pairwise comparisons revealed that the pattern was the same for both models, showing significant differences for 60° and 120° versus 0° but no difference between 60° and 120°. This effect did not interact with task or hemisphere, suggesting that although mental rotation showed greater activation than visual rotation, both mental and visual rotation showed greater activation than no-rotation.

Together, the results of the ROI analyses support the similarities in activation for mental and visual rotation as well as revealing some differences between them.

DISCUSSION

Previous studies have suggested that mental imagery engages many of the same neural substrates as visual per-

ception (e.g., Kosslyn, 1981; Kosslyn et al., 1993; Kosslyn et al., 1995; Kosslyn et al., 2001; Sparing et al., 2002). The results of the present study extend this similarity to the dynamic imagery involved in mental rotation. Before addressing the key results from the motion-sensitive region, we consider the overall similarity in the brain networks engaged by mental and visual rotation. First, in the whole-brain analysis, we replicated the patterns of activation observed in previous studies, providing additional support for the reliability of our methods. More importantly, this analysis revealed strong similarities in activation patterns for mental and visual rotation. Using a subsequent ROI analysis on the proposed shared regions, we found that a large region of visual cortex was more active for rotation than for no-rotation in both mental and visual rotation, but only when we did not account for the differences in response latencies (i.e., trial duration) across different trial types.

In the superior parietal cortex, the effect of rotation versus no-rotation was evident for both tasks and in both the standard and RT-convolved models. In the standard model, this could be characterized as increased activation with increased angular disparity. However, when we accounted for trial duration, the effect was still apparent for both tasks, but there was only an increase from no-rotation to rotation, and not among the rotation conditions. Moreover, the RT-convolved model showed greater novel recruitment of this area for mental than for visual rotation.

Figure 5. Average activation as a function of angular disparity, task, and hemisphere for the four regions of interest from the whole-brain analysis: (A) occipital cortex, (B) superior parietal cortex, (C) inferior parietal cortex, and (D) DLPFC. Error bars reflect ± 1 SEM.

Activation in the inferior parietal cortex was similar to that in the superior parietal, with a linear increase in activation for mental and visual rotation using the standard model. In addition, the effect was stronger for mental rotation than for visual rotation when we accounted for response latency. However, this difference was far more pronounced, with the effect *only* appearing for mental rotation. This result suggests that the role of inferior parietal cortex for visual rotation is more restricted, tracking closely with response latency, whereas it is preferentially activated for mental rotation, above and beyond the simple trial duration. One possible explanation for this difference is that this region, in addition to playing a role in perception of higher order motion (Claeys et al., 2003), plays a critical role in interpreting the transformational differences and/or computing the necessary transformations to bring figures into alignment. In addition, positing a critical computational role for the inferior parietal cortex would provide some account of why this region is the most consistent area identified with mental rotation in previous studies (e.g., Alivisatos & Petrides, 1997; Barnes et al., 2000; Bonda et al., 1995; Carpenter et al., 1999; M. S. Cohen et al., 1996; Gauthier et al., 2002; Harris et al., 2000; Jagaroo, 2004; Richter et al., 2000; Tagaris et al., 1998; Vanrie et al., 2002; Vingerhoets et al., 2002; Zacks et al., 1999). However, further investigation is warranted before these claims can be substantiated. For example, transcranial magnetic stimulation (TMS) may be able to target more specific roles. Previous TMS studies have strongly suggested a critical role of parietal cortex in mental rotation tasks (e.g., Bestmann, Thilo, Sauner, Siebner, & Rothwell, 2002; Harris & Miniussi, 2003), but these studies have not implicated the inferior parietal cortex specifically.

In addition to the parietal and occipital ROIs, we found an interesting pattern of results in the DLPFC. This frontal region, typically associated with working memory processes (see, e.g., Courtney, Ungerleider, Keil, & Haxby, 1997; Goldman-Rakic, 1984), showed significant activation for rotation in comparison with no-rotation in both tasks. The pattern did not reflect a linear increase with angular disparity and did not change when we accounted for response latency differences. Notably, mental rotation was associated with greater activation than was visual rotation, supporting the subjective experience that mental rotation is the more difficult task. It is worth noting that this difficulty was not reflected in differences in response latency or accuracy, but this is most likely due to the way the tasks were specified. For the mental rotation task, we asked the participants to respond when they knew the correct answer, whereas in the visual rotation task, we specifically asked the participants to watch the stimulus until it stopped and then make a response. As a result, the similarity in the behavioral data may not reflect underlying differences in the difficulty.⁴

Together, these results highlight the similarities in the network of regions recruited by mental and visual rotation, but also support clear differences in both parietal and prefrontal

activations. With these in mind, the more specific question of motion processing can be addressed by considering the results from our motion-sensitive hV5/MT+ ROI analysis.

We predicted that, using the standard model, we should certainly see significant activation in hV5/MT+ in the visual rotation condition that increased with increased angular disparity. Interestingly, we found these results both in the visual rotation and in the mental rotation conditions, indicating that this region is sensitive to mental rotation and that its activation increased as the degree of rotation increased. By using the RT-convolved model, we had the advantage of being able to discriminate whether that activation was strictly correlated with response latency. We should only see hV5/MT+ activation if this area was more active for mental or visual rotation above and beyond what would be predicted from response latency alone. Indeed, we found that the activation differences between the larger (120°) and smaller (60°) rotation conditions seen in the uncorrected model were attributable to response latency differences, whereas the differences between these rotation conditions and the no-rotation baseline were not. This result is consistent with the interpretation that motion drives hV5/MT+ and that more motion translates into more activation. In addition, the fact that we see this activation pattern in hV5/MT+ during mental rotation as well as visual rotation implies that the participants were engaging in processes similar to motion perception during mental rotation.

One concern with the present finding was whether the instructions might have induced the participants to adopt a particular strategy. For example, seeing visual rotation might induce a participant to use an explicit rotational strategy in mental rotation that he or she might not otherwise use. To assess the effect of experience with visual rotation, we ran half of our participants on mental rotation first. These participants had neither experience with nor knowledge of the visual rotation condition. Behavioral and brain activation results from these participants were indistinguishable from those of participants who experienced visual rotation prior to mental. Moreover, our instructions during the mental rotation task were consistent with other studies and stressed "figure matching" as opposed to "mental rotation" in defining the participant's task.

Finally, we consider the implications of our interpretation that the participants were engaging motion perception regions during mental rotation. Whether the participants were mentally manipulating whole figures or parts of figures, whether they were rotating along the expected trajectory or through some other spatial transformation, the key point of our results is that the brain was engaging areas that were also involved in observing motion. These results provide a springboard for more detailed analysis of what this motion might mean. For example, the observed activation of hV5/MT+ could be involved in the response to or the creation of the mental motion. In addition, there may be subtle individual differences in the way this motion is utilized during the task. Answers to such questions require rethinking the mental rotation process as a poten-

tial perceptual phenomenon and may rest on converging evidence from other motion phenomena such as representational momentum (Kourtzi, 2004; Senior et al., 2000).

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NOTES

1. With this procedure, the participants did not have any knowledge of the second task while performing the first task. By not alternating the two tasks, we could analyze the data for task order effects.
2. The right temporal ROI was not interrogated because it was redundant with the hV5/MT+ analysis and showed patterns identical to those in Figure 3.
3. This was also supported in pairwise comparisons. These analyses were not included because they were completely redundant.
4. To test the difficulty hypothesis, 6 participants (3 female) were run in a behavioral version of the task. All 6 participants showed the linear trends for mental and visual rotation, but the visual rotation curves were consistently flatter by a few degrees per sec. The difference was not excessive, but it was consistent. There was no proportionate cost in accuracy, suggesting that the visual rotation task was less difficult.

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