

# Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography

STEPHEN M. KOSSLYN,<sup>a,b</sup> GREGORY J. DIGIROLAMO,<sup>a</sup> WILLIAM L. THOMPSON,<sup>a</sup>  
AND NATHANIEL M. ALPERT<sup>c</sup>

<sup>a</sup>Department of Psychology, Harvard University, Cambridge, MA, USA

<sup>b</sup>Department of Neurology, Massachusetts General Hospital, Boston, USA

<sup>c</sup>Department of Radiology, Massachusetts General Hospital, Boston, USA

## Abstract

Twelve right-handed men participated in two mental rotation tasks as their regional cerebral blood flow (rCBF) was monitored using positron emission tomography. In one task, participants mentally rotated and compared figures composed of angular branching forms; in the other task, participants mentally rotated and compared drawings of human hands. In both cases, rCBF was compared with a baseline condition that used identical stimuli and required the same comparison, but in which rotation was not required. Mental rotation of branching objects engendered activation in the parietal lobe and Area 19. In contrast, mental rotation of hands engendered activation in the precentral gyrus (M1), superior and inferior parietal lobes, primary visual cortex, insula, and frontal Areas 6 and 9. The results suggest that at least two different mechanisms can be used in mental rotation, one mechanism that recruits processes that prepare motor movements and another mechanism that does not.

**Descriptors:** Mental rotation, Mental imagery, Positron emission tomography, Cognitive neuroscience

Objects in visual mental images can be manipulated much like actual objects, which can help one to reason about the consequences of the corresponding physical manipulation (see Shepard & Cooper, 1982). Indeed, Shepard and Metzler (1971) found that when people compared two similar objects at different orientations, an increment of time is required for each degree of angular disparity between the objects. These and similar findings (for reviews, see Kosslyn, 1980, 1994; Shepard & Cooper, 1982) indicate that people perform such tasks by “mentally rotating” an object as if it were moving through the intermediate positions along a trajectory, as would occur if the object were physically rotated. But there is a mystery here: objects are constrained by the laws of physics to move along trajectories, whereas internal representations are not. The laws of physics do not prevent a mental image from undergoing instantaneous translation from one position to the next. The present study was designed to test one possible account for the fact that people visualize objects rotating through trajectories.

One type of account we considered was inspired in part by two

very different sets of findings. First, Parsons (1987, 1994) found that people can rotate images of body parts more easily if the parts move in natural ways; for example, it is easier to visualize a hand rotating if the rotation corresponds to a comfortable movement than if it does not (see also Cooper & Shepard, 1975; Sekiyama, 1983). Second, Georgopoulos, Lurito, Petrides, Schwartz and Massey (1989) found that neurons in the motor strip discharge before a monkey begins to shift a lever in a specific arc and that there is an orderly sequence of activity over time: Neurons that are tuned for orientations near the starting point of the lever fire first, neurons that are tuned for slightly displaced orientations fire next, and so on.

Both sets of results suggest that motor processes play a role in mental rotation. Kosslyn (1994) offered a theory of how such a mechanism might operate: He suggested that visual mental images arise via the same mechanisms that “prime” the representations of expected objects during perception, but during imagery an individual anticipates seeing an object so strongly that its visual representation is activated from memory and a spatial pattern is reconstructed in topographically mapped visual cortex (cf. Neisser, 1976). According to this theory, an imaged object rotates through a trajectory because the person is anticipating what he or she would see if the object were physically manipulated, and objects are physically constrained to move along trajectories.

A recent positron emission tomography (PET) result appears to be consistent with this view. Alivisatos and Petrides (1997) asked participants to decide whether alphanumeric characters faced normally or were mirror-reversed in two conditions: in one, the letters were upright; in the other, the letters were tilted various amounts

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Gregory J. DiGirolamo's present address: Department of Psychology, University of Oregon, Eugene, OR 97403, USA.

Address reprint requests to: S. M. Kosslyn, Department of Psychology, Harvard University, 830 William James Hall, 33 Kirkland Street, Cambridge, MA 02138, USA. E-mail: smk@wjh.harvard.edu.

from the upright position. Cooper and Shepard (1973) showed that participants require increasing amounts of time to make this judgment for characters that are rotated increasing amounts from the upright position. When Alivisatos and Petrides compared these two conditions, they found more activation during rotation in parietal areas (Areas 7 and 40, both in the left hemisphere), in two regions of the right frontal lobe (Areas 45 and 8), and in the right head of the caudate nucleus. It is possible that the two parietal regions were both involved in motor processing. Andersen (1989) concluded that neurons in the posterior parietal lobe of nonhuman primates “generally have both sensory and movement-related responses. Cells responding to reaching behavior also have somatosensory inputs, and cells responding to smooth pursuit, saccades, or fixations also respond to visual stimuli” (pp. 397–398). In addition, it is particularly intriguing that the striatum was activated—this structure clearly plays a key role in motor control in receiving inputs from the neocortex and sending outputs through the basal ganglia to frontal areas involved in motor planning and execution (see, Graybiel, Aosaki, Flaherty & Kimura, 1994).

Similarly, Deutsch, Bourbon, Papanicolaou, and Eisenberg (1988) asked participants to view pairs of the angular, multiarmed stimuli used by Shepard and Metzler (1971) and to decide whether the shapes in each pair were the same or mirror-reversed. One shape was rotated relative to the other, and thus mental rotation was required in this task. Deutsch et al. assessed brain activity during this task with the Xe-133 technique and found increased blood flow in the right hemisphere. The activated region extended from the frontal to the posterior parietal lobes and included many motor areas. Peronnet and Farah (1989) used event-related potentials to measure brain activity in a letter mental rotation task (similar to the study by Alivisatos & Petrides, 1997). They found a late electrical negativity over the posterior scalp that varied systematically with the amount of necessary rotation; it is possible that at least some of this activity reflects motor processes in the posterior parietal lobes.

Finally, Parsons et al. (1995) used PET to study a task that appears to involve mental rotation of hands. On each trial, a picture of a hand appeared in one of several orientations for 150 ms in either the left or right visual field (with separate conditions for each visual field). Predominately left hands were presented in the right visual field in one condition, and predominately right hands were presented in the left visual field in the other condition. Participants decided whether each stimulus was a left or right hand. Parsons et al. hypothesized that participants would use an implicit movement to identify the hands, mentally rotating a representation of their own hand into congruence with the stimulus. Activation engendered by the hand-identification task was compared with that associated with a fixation condition.

In both visual field conditions, frontal, parietal, basal ganglia, and cerebellar areas were active, as was Area 17. Supplementary motor cortex was strongly activated in the left hemisphere in both conditions. Although prefrontal and insular premotor areas were solely active in the hemisphere contralateral to the stimulus handedness, the anterior cingulate and the superior premotor area were activated bilaterally in both conditions (although both were more strongly activated in the left hemisphere). Notably, primary motor and somatosensory cortices were not activated in any condition. Parsons et al. interpreted the left hemisphere activations present in both conditions as evidence of generic motor programming in the dominant hemisphere, whereas the contralateral activations were taken to reflect programming of specific movements. The authors concluded that this sort of mental rotation relies on intermediate or

high-order cortical systems that involve motor processes but does not require primary cortices.

The findings of Parsons et al. (1995) suggest that motor imagery is involved in implicit transformations of the viewer rather than of the object. These results make sense given that the stimuli were hands but do not rule out the possibility that object-based motor imagery underlies all forms of mental rotation (cf. Decety, 1996). In this case, one would visualize what one would see if one manipulated an object in a specific way. Indeed, Cohen et al. (1996) used functional magnetic resonance imaging (fMRI) to study the original Shepard–Metzler task and found activation of motor areas. Specifically, in this study, the participants viewed identical pairs of stimuli in the test and baseline conditions, and in both conditions decided whether they were the same or mirror-imaged shapes. The only difference in conditions was that the stimuli were presented in different orientations in the test condition and in the same orientations in the baseline condition. Thus, by comparing the two conditions, it was possible to examine activation due to mental rotation *per se*. Of particular interest here, the results revealed activity in premotor Area 6 (in half the participants), and more than half of the participants displayed clear evidence of activation in hand somatosensory cortex (Areas 3, 2, and 1). In addition, all participants had activation in Areas 7a and 7b (which sometimes spread to Area 40), and 88% of the participants had evidence of activation in the middle frontal gyrus (Area 8). The supplementary motor area was also active bilaterally for some participants, which could reflect planned (but unexecuted) motor movements (cf. Deiber et al., 1991), or this bilateral activation could reflect greater attentional processing needed during the rotation condition (see Posner & DiGirolamo, 1998). The method of analyzing these data may not have been as powerful as group-based methods, however, and thus it is possible that activation in other motor areas was not detected.

In the present study, we directly compared, in the same participants, mental rotation of hands and mental rotation of the three-dimensional multiarmed figures used by Shepard and Metzler (1971). If image rotation occurs when one anticipates what one would see if one manipulated an object, then motor areas should be active during all mental rotation. Indeed, if priming underlies mental rotation, then we not only expect activation in higher-level motor control areas, such as the supplementary motor area, premotor area, and posterior parietal lobe, but we also expect activation in low-level motor areas, such as M1 (the area from which Georgopoulos et al., 1989, recorded in the monkey). Furthermore, if objects in general are rotated by imagining that one is twisting them, then we should find similar results in the two tasks.

However, the notion that objects in images rotate through trajectories because of the constraints imposed by the motor system does not imply that the observer's own motor system must be manipulating the object. It is possible that objects can be rotated by imagining that someone else is manipulating them. Moreover, one could imagine that objects are shifted by inanimate forces, in which case motor processes would not be involved at all. Thus, we have three classes of theories, only one of which implies that motor areas in the brain should be activated when one performs mental rotation. We need not assume that only one process is used to mentally rotate objects. Indeed, it is possible that the method used is tailored to the specific task or to the specific stimuli. If so, then we may find evidence of motor processing when hands are rotated but not when Shepard–Metzler objects are rotated. Thus, in the present study, we investigated whether there is more than one way in which objects in images can be rotated.

## Method

### Participants

Twelve members of the Harvard University and Massachusetts General Hospital community volunteered to be paid participants. All participants were healthy right-handed men with a mean age of 20 years and 1 month (with a range of 18 years and 5 months to 24 years and 9 months). The participants were not aware of the purposes or predictions of the experiment until after test completion. The experiment and its protocol were approved by both the Harvard University and the Massachusetts General Hospital Institutional Review boards. All of the participants gave informed consent.

### Materials

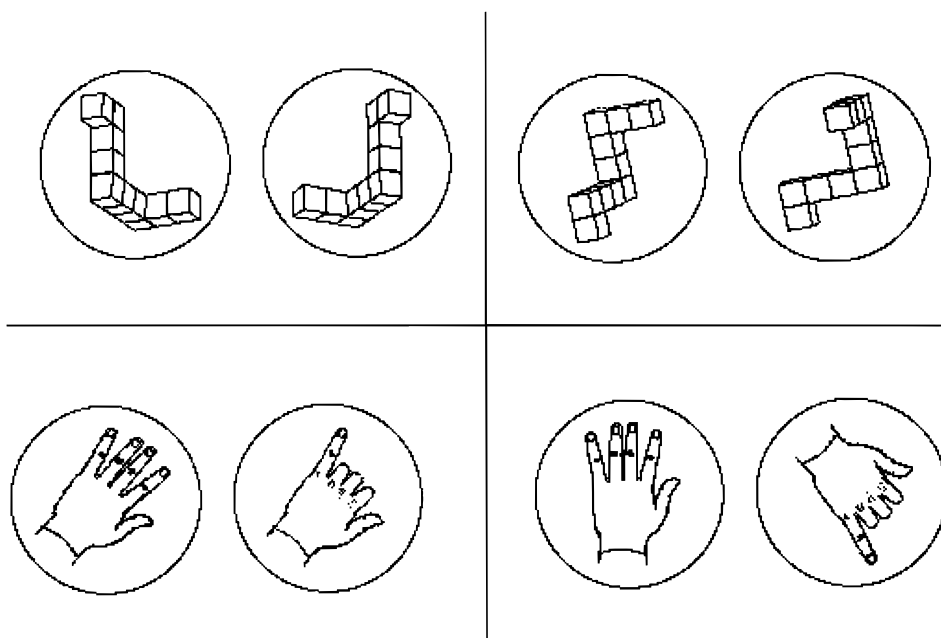
Three sets of three-dimensional three-armed angular figures were constructed from Shepard and Metzler's (1971) drawings, as illustrated in Figure 1. The arms were constructed by juxtaposing cubes, and thus we shall refer to these as the *cubes figures*. The figures were digitized using a Microtek ScanMaker 600ZS, which scanned the images in black and white at 75 dots per inch to create bit-mapped files. Each stimulus object was placed in a circle and then rotated in 20° increments separately along all three major axes (X, Y, and Z). This procedure created 56 different images: a normal and mirror-reversed cubes figure at 0° of orientation and a normal and mirror-reversed cubes figure at each orientation from 20° to 180° in each of the three planes. For the rotation condition, a vertical version of each stimulus was paired with a copy that was rotated to each of the nonvertical orientations; similarly, a vertical version of each stimulus was paired with a mirror-imaged version of itself rotated at each possible angle. For the baseline task, duplicates of each figure at each angle were created and paired; similarly, each figure at each angle was paired with its mirror image at the same angle.

The bit-mapped images were resized to make the entire figure (both stimuli and their encompassing circles) approximately 15 cm along the widest axis, which corresponded to about 16.4° of visual

angle from the participants' viewing distance of approximately 52 cm.

A similar series of figures was also created for two-dimensional line drawings of hands (cf. Cooper & Shepard, 1975). The stimuli were drawn by hand and scanned into bit-mapped files. Again, a series of images of the hands was created by orienting the stimuli in 20° increments from 0° to 180° through the X-axis plane. Eight sets of hand stimuli were created: a palm-facing-participant version and back-of-hand-facing-participant version for four different finger configurations. The finger configurations of the hands consisted of (a) all five fingers raised; (b) the thumb, index finger, and middle finger raised with the ring finger and little finger folded; (c) the thumb, index finger, and little finger of the hand raised and the two middle fingers folded; and (d) just the little finger raised with the other three fingers and thumb folded. Images of each of these finger configurations were produced in a palm-facing version and a back-of-hand facing version and at all nine orientations of rotation. This process created 160 images: a left- and right-handed version of each of the possible eight configurations (palm and back for each of the four finger configurations) at 0° and eight sets of nine images rotated from 20° to 180° in 20° increments through the X-axis plane with a left-handed and right-handed example of each figure.

As illustrated in Figure 1, pairs of hands were presented, with each enclosed in the same-sized circles and subtending the same visual angle as the cubes stimuli. In the rotation condition, the stimulus on the left side was always a left hand, whereas the hand on the right side could be either a right or left hand. (We wanted to avoid a type of Stroop interference that might have occurred if the hands appeared in the opposite locations, and hence anchored the left with the left hand.) In addition, the hand on the left was always upright, whereas the one on the right appeared at each nonvertical angle; half of the pairs had left hands and half had a left and a right hand. In the baseline condition, each figure at each angle was paired with another left hand or a right hand at the same angle; at each angle, half were



**Figure 1.** Illustrations of "same" and "different" stimuli used in the cubes conditions (top) and in the hands conditions (bottom). The left panels illustrate stimuli in the baseline conditions, and the right panels illustrate stimuli in the rotation conditions.

paired with the identical figure and half were paired with the opposite hand.

For both types of stimuli, the pairs were arranged randomly into blocks of 9 in the rotation condition and into blocks of 10 in the baseline; in each block, equal numbers of identical and mirror-imaged cube stimuli or equal numbers of left and right hands were presented, with the plane of rotation of the cubes completely randomized. The trials within and between these blocks were arranged randomly except that there were no more than three of the same type in succession (i.e., identical and mirror for the cubes and left and right for the hands), and the same angular disparity could not appear twice before every other angular disparity had appeared once and could not appear three times until every other had occurred twice, and so on. Each hand configuration and each plane of rotation appeared once before being repeated, and each appeared twice before any appeared three times, and so forth. This procedure was used to ensure that samples from every angle of disparity, plane of rotation, and hand configuration would be completed during the PET acquisition procedure. Finally, a practice condition was constructed for both types of stimuli in both conditions. The practice trials were constructed in the same manner as the test trials, with one example of each angular disparity; there were 10 practice trials for each baseline condition and 9 practice trials for each rotation condition.

### Procedure

**PET procedure.** Each participant was tested individually in a custom-built suite designed for the PET procedure. After informed consent was given, each participant was placed on the scanner bed and a custom thermoplastic mask (TRUE SCAN, Annapolis, MD) was fitted. After the participant's head was aligned relative to the canthomeatal line and stabilized by securing the mask to the scanner bed, we attached a nasal cannule to the inflow line from a radiolabeled gas source and put a vacuum mask over the participant's face. Several transmission measurements with an orbiting-rod source were acquired before the testing scans.

We began the experiment by measuring residual background from previous studies with the camera acquisition program; 15 s later, stimulus presentation began, and the participant performed the task. Fifteen seconds after the participant began the task, [ $^{15}\text{O}$ ]CO $_2$ -radiolabeled gas, delivered at a concentration of 2,800 MBq/L at a rate of 2 L/min was administered and continued for the next 60 s. The participant was asked to stop performing the task as soon as the gas stopped flowing. The gas was diluted by mixture with room air such that the measured peak count rate from the brain was 100,000–200,000 events/s.

The PET scanner was a GE Scanditronix PC4096 15-slice whole-body tomograph used in the stationary mode (see Rota-Kops, Herzog, Schmid, Holte, & Feinendegen, 1990); 6.5-mm continuous slices (center-to-center) were produced with an axial resolution of 6 mm full width at half maximum (FWHM) and an axial field of 97.5 mm. The lighting was dim and indirect and there was no distracting noise.

**Task procedure.** The stimuli were displayed using a modified version of the MacLab program (Costin, 1988) on a Macintosh Classic II computer; responses and response times were recorded by the MacLab program via foot pedals. Half the participants began with the cubes conditions, and half began with the hands conditions. The baseline task was always administered before the corresponding rotation task; we were concerned that participants might try unnecessarily to rotate the baseline stimuli if they had

just performed the rotation task. After completing the baseline and rotation task with one set of stimuli, the participants received those conditions for the other set of stimuli.

Each condition began when instructions appeared on the computer screen. The participant was asked to read and then paraphrase the instructions. Only after the participant had correctly paraphrased the instructions were the practice trials presented. Each trial began when a fixation point appeared for 500 ms; the fixation point was then replaced by one of the stimulus pairs, and the participant indicated whether the figure on the right was the same as that on the left (i.e., an identical or mirror-reversed cube, or the same hand). Participants responded by pressing one foot pedal if the stimuli were the same and another foot pedal if they were different. The foot response assignment was counterbalanced across participants. Participants were asked to respond as quickly and as accurately as possible. Immediately after a response, a fixation point appeared and the sequence started over.

After the participants completed the practice trials for the first baseline condition, any additional questions were answered. Following this question-and-answer session, the participants performed the baseline trials while being scanned. After the scan for the baseline trials, participants read the instructions for the corresponding rotation trials. The rotation instructions asked the participants to rotate the image on the right into congruence with the figure on the left and to determine whether the two objects were identical or mirror images (for cubes) or were the same or different hands. All participants reported using this rotational strategy when queried after the test trials. After the participant reported understanding the instructions, the rotation trials were administered.

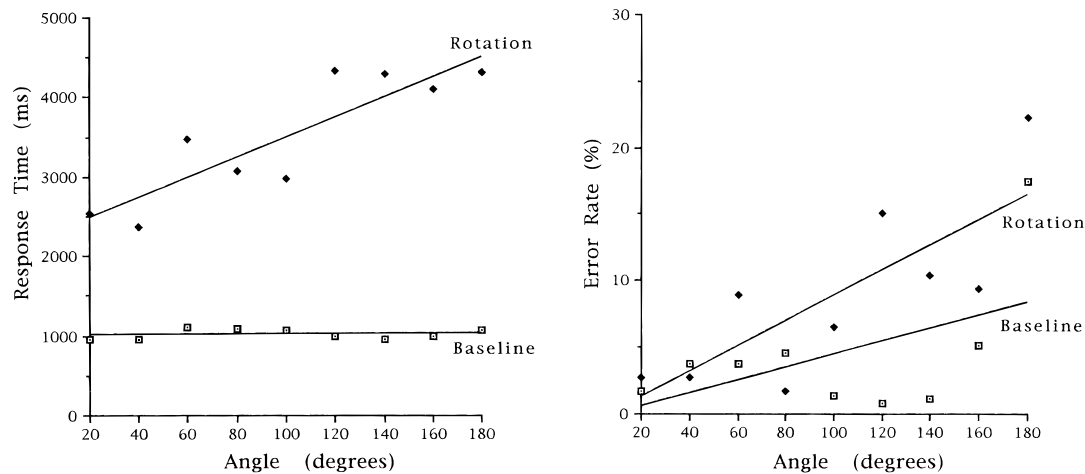
In all conditions, participants began the test trials 15 s before the PET scan was initiated and continued for a total of 75 s until the scan ended. No scans were conducted during the instructions or practice trials, and each scan began at least 10 min after the completion of the previous scan. This entire procedure was repeated for both conditions for both stimulus types.

## Results

### Behavioral Results

We analyzed response times and error rates to ensure that the participants did in fact perform the task. If they did, they should have required more time when more mental rotation was required (see Shepard & Cooper, 1982). Response times and error rates were considered in separate analyses of variance (ANOVA) for each condition. Response times were trimmed before analysis by discarding all times that were more than 2.5 times the mean of the times in that cell (defined by angle and condition) for that participant; this procedure eliminated 1.0% of the data for all participants in the hand rotation condition (the largest amount of discarded data for a single participant was 2.5%, 1 of 40 trials) and 0% of the data for the cubes rotation. In addition, in both baseline conditions, only trials with stimuli oriented from 20° to 180° (the range of angles used in the rotation analysis) were analyzed. This analysis provided the clearest behavioral analogy between the two tasks and the neuroimaging results. This paring excluded 10% of the baseline trials for both the hands and cubes. Only times from correct responses were analyzed. All effects and interactions not noted were not significant,  $p > .15$  in all cases.

**Cubes figures.** As evident in Figure 2, times varied for the different angular disparities,  $F(8,80) = 5.16$ ,  $p < .0001$ ; moreover, the effects of angular disparity differed for the baseline and



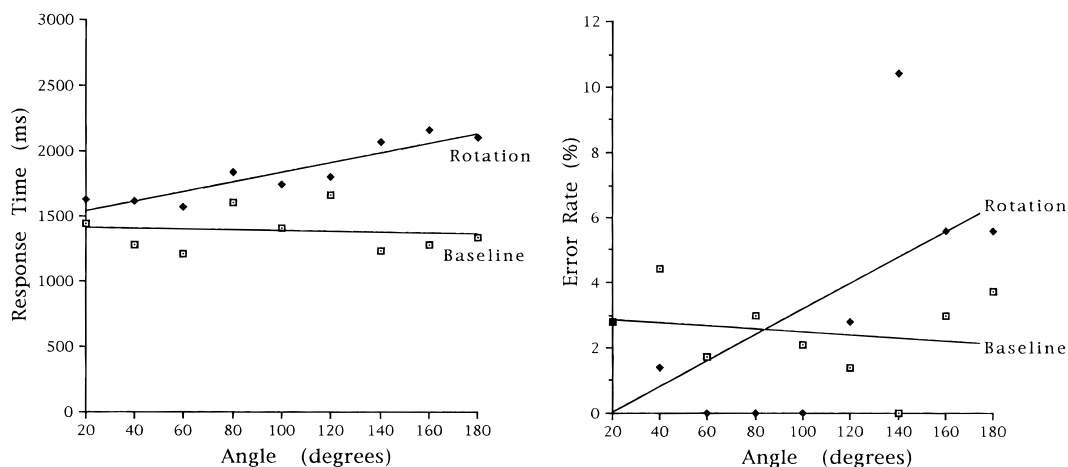
**Figure 2.** Response time (left) and error rates (right) in the cubes conditions. Times increased linearly with angular disparity in the rotation condition but not in the baseline condition.

rotation conditions,  $F(8,80) = 4.90$ ,  $p < .0001$ , for the interaction of condition and angle. A planned linear contrast revealed that the participants required more time when more rotation was necessary,  $F(1,80) = 31.72$ ,  $p < .0001$ , whereas another contrast revealed that participants did not require different amounts of time for the different angles in the baseline condition,  $F < 1$ . Not surprisingly, the participants required more time overall to decide whether the cubes figures matched in the rotation condition (3,496 ms) than in the baseline condition (1,018 ms),  $F(1,10) = 61.52$ ,  $p < .0001$ . The times did not vary for the different counterbalancing conditions,  $F < 1$ , nor was there an interaction of angle with counterbalancing order,  $F < 1$ .

The participants made different numbers of errors for stimuli at different angles,  $F(8,80) = 20.53$ ,  $p < .0001$ . A planned linear contrast was highly significant,  $F(1,80) = 20.53$ ,  $p < .0001$ . Participants made the fewest errors for stimuli at 20° (2.2%), and the greatest number of errors for stimuli at 180° (19.8%). There was no interaction of angle and condition in the error rates, with  $F(8,80) = 1.20$ ,  $p > .3$ , nor was there even a hint of an angle by

order interaction,  $F < 1$ ; however, a planned linear contrast revealed a highly significant effect of angle in the rotation condition,  $F(1,80) = 19.41$ ,  $p < .0001$ , and a significant effect in the baseline condition,  $F(1,80) = 5.08$ ,  $p < .02$ . The effect in the baseline condition reflected a large number of errors at 180° (17.4%), whereas the effect in the rotation condition reflected a trend over all angles. As in the response time data, the order of stimulus presentation had no effect on error rates, with participants making on average 5.6% errors for cubes figures following hands and 7.6% errors for cubes figures preceding hands,  $F(1,10) = 1.04$ ,  $p > .33$ . However, as expected, participants tended to make more errors in the rotation condition (8.8%) than the baseline condition (4.4%),  $F(1,10) = 4.65$ ,  $p < .06$ .

**Hands.** As illustrated in Figure 3, response times varied for the different angular disparities,  $F(8,80) = 2.23$ ,  $p < .03$ , and the effects of angular disparity differed for the baseline and rotation condition,  $F(8,80) = 2.54$ ,  $p < .02$  for the interaction of condition and angle. As evident in Figure 3, a planned linear contrast re-



**Figure 3.** Response time (left) and error rates (right) in the hands conditions. Times increased linearly with angular disparity in the rotation condition but not in the baseline condition.



vealed that the participants required more time when more rotation was necessary,  $F(1,80) = 9.70$ ,  $p < .003$ , whereas another contrast revealed that participants did not require different amounts of time for the different angles in the baseline condition,  $F < 1$ . When participants had to rotate the stimuli to make their decision, they required more time than in the baseline condition,  $F(1,10) = 27.92$ ,  $p < .0004$ . Participants responded faster in the hands condition after the cubes condition than when the hands condition preceded the cubes condition, with means of 1,310 and 1,907 ms, respectively,  $F(1,10) = 5.17$ ,  $p < .05$ . There was no interaction of order and angle,  $F(8,80) = 1.49$ ,  $p > .17$ .

In addition, differences in angle did not affect the participants' error rates,  $F < 1$ . We did find a tendency for errors to vary differently for the angles in the two conditions,  $F(8,80) = 1.86$ ,  $p < .08$  for the interaction of angle and condition; a planned linear contrast revealed that errors increased with angle in the rotation condition,  $F(1,80) = 7.82$ ,  $p < .007$ , but not in the baseline condition,  $F < 1$ . We did not find an interaction of Angle  $\times$  Order,  $F < 1$ , nor were there differences in the numbers of errors participants made based on the order of stimuli presentation,  $F < 1$ ; participants made on average 3.4% errors when the hands condition preceded the cubes condition and 2.2% errors when cubes were presented before hands. There was no difference,  $F < 1$ , between errors when participants rotated the objects and errors when the task did not require rotation, with mean error rates of 3.2% and 2.5%, respectively.

In short, we found good behavioral evidence that the participants did in fact rotate the stimuli during the rotation conditions, and did not rotate them during the baseline conditions. These results give us reason to infer that the PET scanning results reflect the processing underlying rotation in the experimental conditions, but not in the baseline conditions. Because the rotation and baseline condition (for each type of stimuli) required the identical task and used the identical stimuli, by comparing the two we can discover which processes underlie mental rotation of the two types of stimuli.

### PET Statistical Analyses

The PET analysis had a number of steps. After the blood flow images were reconstructed, a correction was computed to account for head movement (rigid body translation and rotation) using a least squares fitting technique (Alpert, Berdichevsky, Levin, Morris, & Fischman, 1996). The voxel-by-voxel mean over all of the conditions was then computed and used to determine the transformation to the standard coordinate system of Talairach and Tournoux (1988). This transformation was performed by deforming the 10-mm parasagittal brain-surface contour to match the contour of a reference brain (Alpert, Berdichevsky, Weise, Tang, & Rauch, 1993). Following spatial normalization, scans were filtered with a two-dimensional Gaussian filter, FWHM set to 20 mm. Statistical analysis followed the theory of statistical parametric mapping (SPM; Friston, Frith, Liddle, & Frackowiak, 1991; Friston et al., 1995; Worsley, Evans, Marrett, & Neelin, 1992). Data were analyzed with SPM95 (from the Wellcome Dept. of Cognitive Neurology, London, UK). The PET data at each voxel were normalized by the global mean and fit to a linear statistical model with scan condition considered as the main effect and participants as a block effect. Hypothesis testing was performed using the method of planned contrasts at each voxel. Data from all four conditions were used in the computation of the error term for all reported contrasts. When a priori hypotheses were available to provide anatomic localization a  $z$  threshold of 3.0 was considered to be statistically significant.

This threshold was chosen as a compromise between the higher thresholds provided by the theory of Gaussian fields, which assume no a priori knowledge regarding the anatomic localization of activations, and simple statistical theories, which do not consider the spatial correlations inherent in PET and other neuroimaging techniques.

### PET Results

We compared each rotation condition to the corresponding baseline condition and then compared the two types of rotation directly. The coordinates of the single most-activated pixel in each area were then identified in the Talairach and Tournoux (1988) atlas and are reported below.

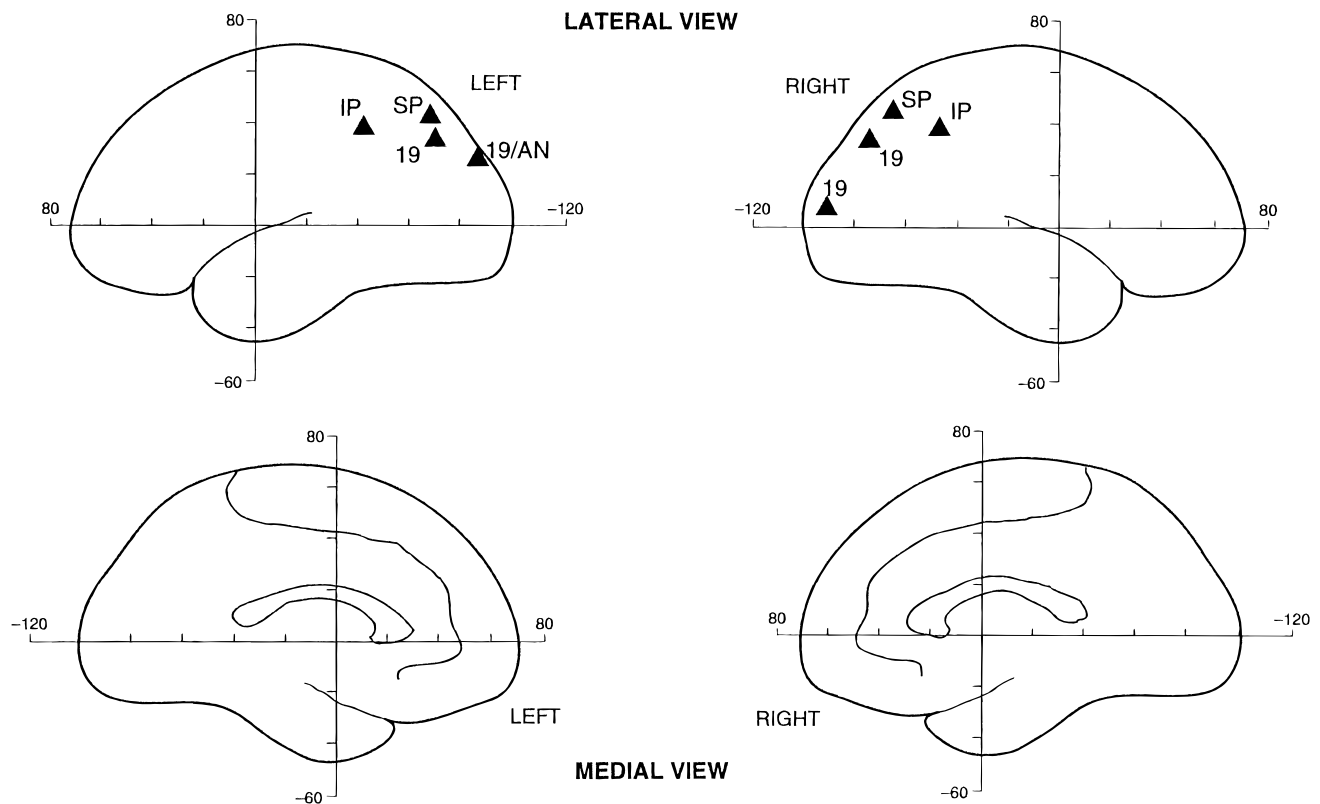
*Cubes figures.* We compared blood flow in the cubes rotation condition with that in the cubes baseline condition. These results are presented in Figure 4 and Table 1. As is evident, none of the frontal motor areas was activated by this kind of rotation. However, we did find activation in the inferior and superior parietal lobes bilaterally; such activation may reflect in part the contribution of motor processes (e.g., Milner & Goodale, 1995) and spatial attention (e.g., Posner & Petersen, 1990). We also found activation in the rotation condition in four portions of Area 19 (two in each hemisphere).

*Hands.* We next compared blood flow in the hands rotation condition with that in the hands baseline condition. These results are presented in Figure 5 and Table 2. As is evident, we found activation in the left precentral gyrus, which corresponds to primary motor cortex. We also found activation in the left premotor area (Area 6), the left superior parietal lobe, two portions of the left inferior parietal lobe, left insula and left superior frontal cortex (Area 9). No activity at all was observed in the right hemisphere, which is in striking contrast to the results reported by Deutsch et al. (1988) with the Shepard-Metzler figures. Finally, Area 17 was activated along the midline. This last result could indicate that participants encoded more visual information in the rotation condition, or could reflect the top-down priming mechanism that may underlie rotation (cf. Kosslyn, Thompson, Kim & Alpert, 1995).

*Comparing tasks.* We next subtracted blood flow in the cubes baseline condition from that in the cubes rotation condition, and compared this difference map with that obtained when we subtracted blood flow in the hands baseline condition from that in the hands rotation condition. No areas were activated more in the cubes figures rotation task than in the hands rotation task.<sup>1</sup> We next compared the two difference maps in the opposite way, observing which areas were more activated during hands rotation than during cubes figures rotation. These results are presented in Figure 6 and Table 3.

As is evident, we found greater activation during hands rotation in four regions of the left hemisphere: area M1 (the motor strip), Heschl's gyrus (primary auditory cortex), the insula, and dorsolateral prefrontal cortex. Again, no activation was over threshold in the right hemisphere.

<sup>1</sup> Although there are significant differences between cubes rotation and baseline conditions in the right hemisphere and no significant differences between the hands rotation and baseline conditions in the right hemisphere, the difference of those differences was not significant. A discussion of such nontransitivity can be found in Menard et al. (1996; see also Toga & Mazziotta, 1996).



**Figure 4.** Areas in which there was significantly greater blood flow in the cubes rotation condition than in the cubes baseline condition. Points indicate the location of the most significant pixel in an area. The axes indicate location in 20-mm increments relative to the anterior commissure. IP = inferior parietal, SP = superior parietal, AN = angular gyrus, 19 = Area 19.

## General Discussion

According to one hypothesis, visualized objects appear to move along trajectories because one anticipates what one would see if the objects were being physically manipulated. Alternatively, one could visualize the consequences of someone else's, or an external force's, moving the object. Moreover, we considered the possibility that different ways of rotating objects would be used for different types of stimuli.

**Table 1.** Comparison of Regional Cerebral Blood Flow When Participants Mentally Rotated the Cubes: Stimuli With Regional Cerebral Blood Flow in the Cubes Baseline

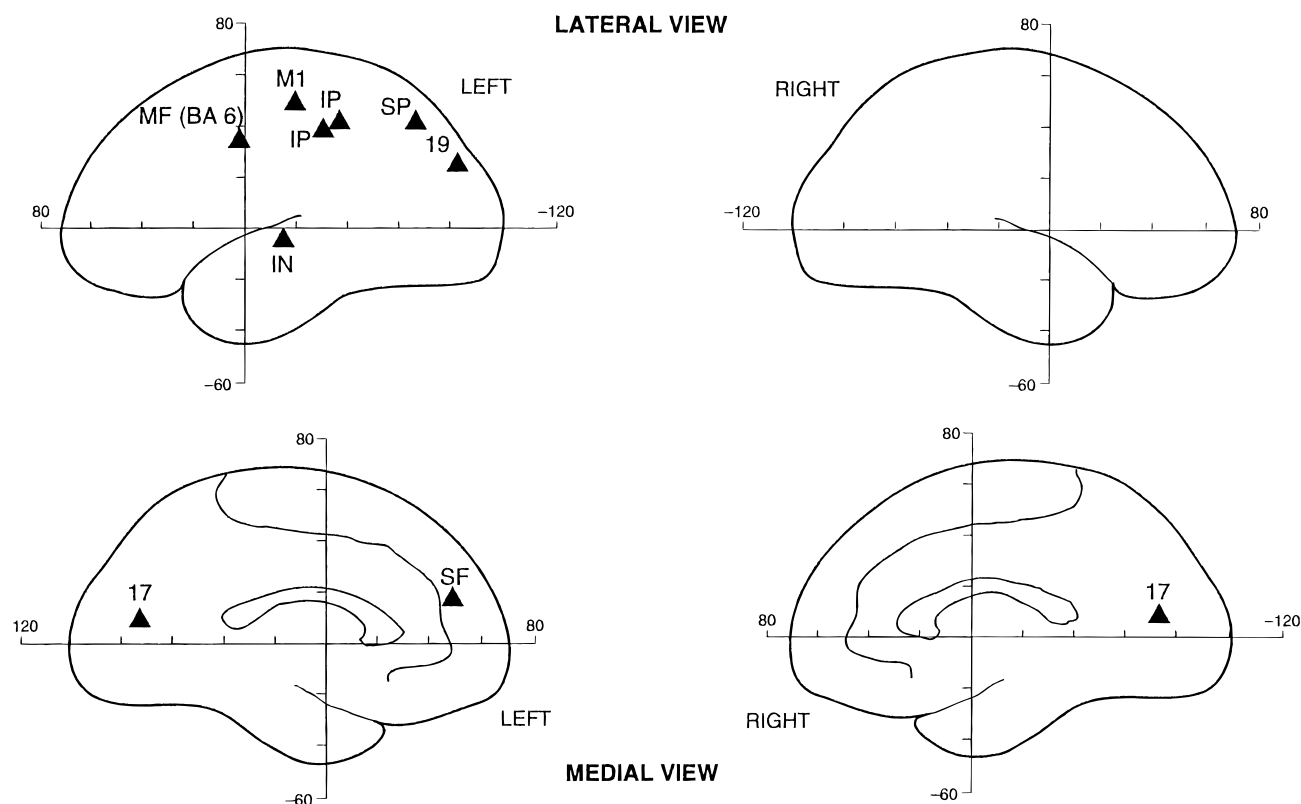
Area	X	Y	Z	Z score
Left hemisphere regions				
Area 19/ Angular gyrus	-27	-85	28	3.35
Area 19	-29	-71	36	3.33
Superior parietal	-15	-68	44	3.74
Inferior parietal	-33	-42	40	3.10
Right hemisphere regions				
Area 19	39	-90	8	3.14
Area 19	27	-79	36	3.12
Superior parietal	12	-65	48	3.89
Inferior parietal	35	-46	40	3.22

Note: Only areas with  $Z > 3.0$  are listed.

We found substantial activation in motor areas for the hands task, including primary motor cortex (M1), premotor cortex, and the posterior parietal lobe. In contrast, when we considered the areas that were activated in the cubes conditions, we found activation in parietal regions, but none in frontal motor regions. The results of the cubes conditions are similar to those of Cohen et al. (1996), who also found parietal activation in all participants. Thus, we have evidence that, in general, low-level motor processes were only recruited when one mentally rotates hands.<sup>2</sup>

The strongest activations during rotation of hands were in the precentral gyrus (M1) and Area 6. These areas, along with superior parietal Area 7 (which was also activated during mental rotation of hands), may prepare one to move one's hands. Taira, Mine, Georgopoulos, Murata, and Sakata (1990) showed that many posterior parietal neurons in the monkey fire when the monkey reaches out to grasp an object. Moreover, the motor information supplied to these posterior cells may arise from premotor Area 6. Area 6 is intimately connected with the posterior parietal lobe (Area 7b in the monkey), and both areas project directly to motor cortex. Rizolatti et al. (1988) demonstrated that Area 6 is associated with grasping behavior; moreover, Sakata and Taira (1994) suggested

<sup>2</sup> Participants were watched to see whether they solved the hands task by actually rotating their own hands, which they did not appear to do. Moreover, it was impossible for them to see their hands (because of the mask holding their head in place and the position of the monitor), and if they tried we would have found huge movement artifacts when we registered the PET images.



**Figure 5.** Areas in which there was significantly greater blood flow in the hands rotation condition than in the hands baseline condition. Points indicate the location of the most significant pixel in an area. The axes indicate location in 20-mm increments relative to the anterior commissure. MF = middle frontal, M1 = primary motor cortex, IP = inferior parietal, SP = superior parietal; 19 = Area 19, IN = insula, SF = superior frontal, 17 = Area 17.

that connections between Area 6 and the posterior parietal cortex provide information that allows a match between sensory input and motor output to take place in the parietal lobe. Mountcastle, Lynch, Georgopoulos, Sakata, and Acuna (1975) described “reach” cells in Area 7b that also project to Area 6.

In contrast, when the cubes figures were rotated, we found activation in areas that may calculate the orientation of an object in

a way that can be used to guide action but does not actually set up a motor program to reach toward and grasp the object. The results suggest that motor processes may be involved to some degree in even this type of rotation, but we did not find simple quantitative differences between our cubes and hands conditions; rather, qualitatively different areas were activated—some of which involve the motor system in the hands task but not in the cubes figures task. Thus, the data suggest that there are at least two ways in which objects in images can be rotated, one that relies heavily on motor processes and one that does not.

We have good evidence that both sets of results really do reflect the processes underlying mental rotation per se. First, the tasks were

**Table 2.** Comparison of Regional Cerebral Blood Flow When Participants Mentally Rotated the Hands Stimuli With Regional Cerebral Blood Flow in the Hands Baseline Condition

Area	X	Y	Z	Z score
Left hemisphere regions				
Area 19	-22	-83	28	3.33
Superior parietal	-20	-68	44	3.18
Inferior parietal	-38	-37	44	3.54
Inferior parietal	-50	-32	40	3.46
Precentral gyrus (M1)	-29	-21	52	3.60
Middle frontal (area 6)	-34	2	36	3.72
Insula	-26	15	-4	3.01
Superior frontal (area 9)	-20	49	20	3.56
Midline regions				
Area 17	4	-74	8	3.10

Note: Only areas with  $Z > 3.0$  are listed.

**Table 3.** Comparison of Regional Cerebral Blood Flow When Participants Mentally Rotated the Hands (Minus the Hands Baseline) With When Participants Mentally Rotated the Cubes (Minus the Cubes Baseline)

Area	X	Y	Z	Z score
Left hemisphere regions				
M1 (paracentral lobule)	-7	-35	60	4.16
Heschl's gyrus	-45	-16	8	3.14
Insula	-35	-8	-4	3.51
Middle frontal	-20	51	20	3.80

Note: Only areas with  $Z > 3.0$  are listed.



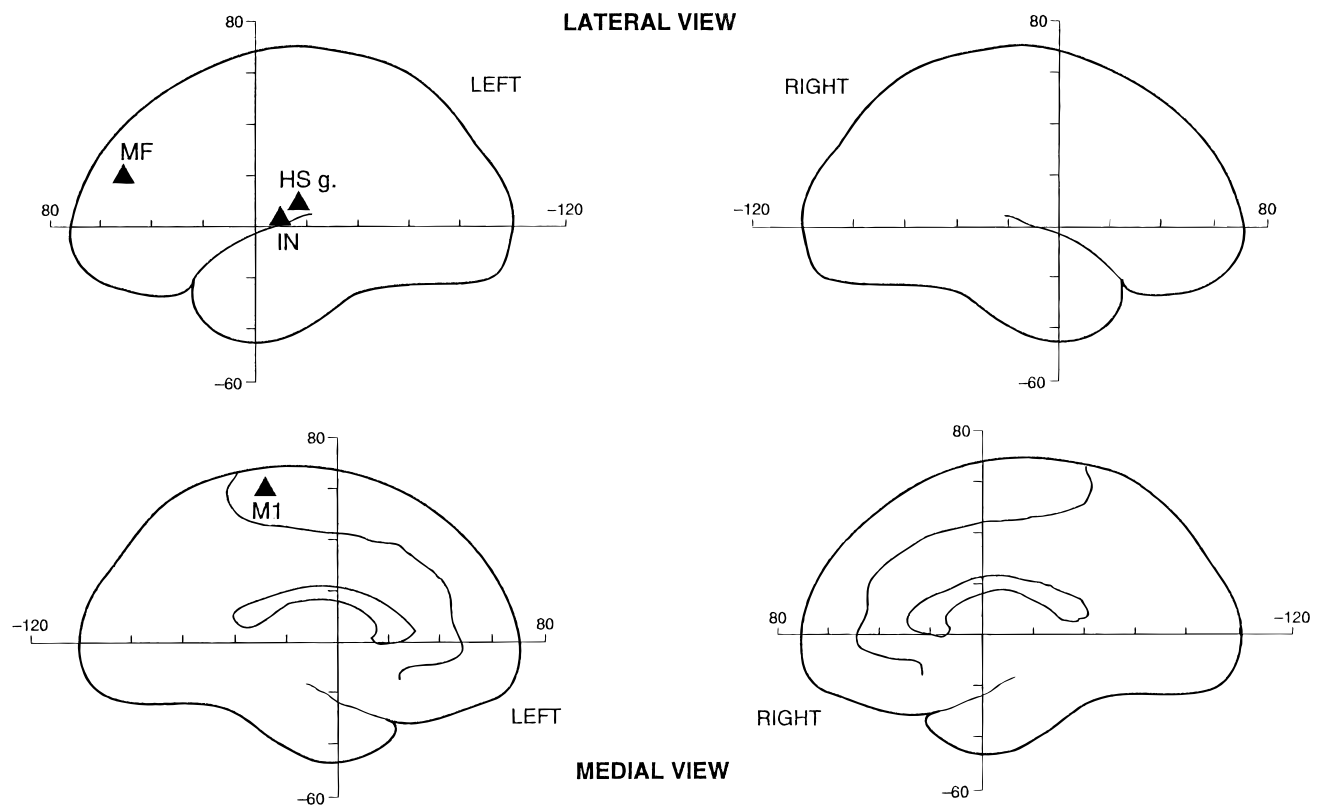
chosen because they were already in the literature and much is known about them. In particular, Shepard, Cooper, and their collaborators have offered a large amount of data indicating that mental rotation is in fact used in these tasks (e.g., see Shepard & Cooper, 1982). Second, the "hallmark" of mental rotation, namely the increased time with increased angular disparity, allows us to justify our inference that rotation was in fact used. No other task produces the same behavioral signature; the only similar phenomenon we know of is the increase in time to name misoriented pictures, but these times typically "dip" at 180° and the slopes are much shallower than those observed in mental rotation experiments (e.g., see Jolicoeur, 1990). Third, the baseline tasks and stimuli were identical to those in the rotation condition, except for the necessity to use rotation, so any additional processing accompanied rotation.

At first glance, the relatively large response times we recorded might suggest that the cubes task involves more general cognitive processes, which are not involved in rotation *per se*. However, such long response times are not atypical in this task. Rotation, like many other types of cognitive processing, can be more or less difficult depending on the precise stimuli and the difficulty of the comparisons required. In addition, the intercepts of the functions illustrated in Figures 2 and 3 would be much more similar if we had included the 0° rotation in these analyses (we did not because they were presented in a separate condition). However, even if the intercepts were different in the two rotation tasks, this difference could reflect a longer "start up" time to begin rotating in the cubes condition compared with that for the hands. Given that the baseline

trials were at the same angles as the rotated stimuli in the rotation condition, it is difficult to see how an increased intercept would reflect longer comparison times to make the decision in the cubes condition or longer times to encode the stimulus pair. The design of the studies ensures that the additional processing we assessed accompanied rotation *per se*; only this variable distinguished the rotation and baseline conditions. We cannot, however, specify exactly what role was played by all processes involved in mental rotation.

Our results underscore that mental rotation is not a simple process, as is evident in attempts to develop precise models of mental rotation (for reviews, see Kosslyn, 1980, 1994). Like most cognitive processes, mental rotation appears to be carried out by a system of operations working together. Understanding the contributions of different operations to the overall process will require a series of additional studies. The present goal was more modest, simply to explore whether there are (at least) two different ways to mentally rotate objects, which draw on different brain systems. The results suggest that there are at least two different ways to perform mental rotation, one that involves processes that execute movements and one that may not. It would be of interest to discover whether one or the other strategy can be chosen voluntarily, or whether motor-based processing only occurs when one visualizes moving body parts.

The present results also bear on another issue concerning mental rotation. The relatively large literature that addresses the possible cerebral localization of mental rotation contains mixed results.



**Figure 6.** Areas in which there was significantly greater blood flow in the hands rotation condition than in the cubes rotation condition. Each condition's respective baseline is subtracted out. Points indicate the location of the most significant pixel in an area. The axes indicate location in 20-mm increments relative to the anterior commissure. MF = middle frontal, HS g. = Heschl's gyrus, IN = insula, M1 = primary motor cortex.

In divided-visual-field studies with normal participants, evidence has been gathered that rotation is more effective in the right hemisphere (e.g., see Cohen, 1975; Dittunno & Mann, 1990) or in the left hemisphere (e.g., see Fischer & Pellegrino, 1988), and evidence exists that suggests the task is performed using both hemispheres (e.g., Corballis, Macadie, & Beale, 1985; Corballis, Macadie, Crotty, & Beale, 1985; Corballis & McLaren, 1984; Jones & Anuza, 1982; Simion, Bagnara, Bisiacchi, Roncato, & Umlitá, 1980; Uecker & Obrzut, 1993; Van Strien & Bouma, 1990). Research with split-brain patients has suggested that the right hemisphere may be better at mental rotation than the left, but over time both hemispheres could perform the task (e.g., Corballis & Sergent, 1988, 1989). However, studies of individuals with focal brain lesions are not entirely consistent with these results. For example, Kosslyn, Berndt, and Doyle (1985) found that two left-hemisphere-damaged aphasic patients had difficulty performing mental rotation. In contrast, Ratcliff (1979) found that patients with right hemisphere damage were selectively impaired at this ability.

The present results illustrate that areas in both cerebral hemispheres are used in the cubes versions of the task. In contrast, in

the hands task, only the left hemisphere was activated. Given that the figures were in free view and participants were not forced to fixate in the center, it is unlikely that this left hemisphere effect arose because the participants only encoded the figure on the right. However, it is possible that participants visualized manipulating their right hands to evaluate the figure on the right, and this processing may have occurred primarily in the left hemisphere (cf. Parsons et al., 1995).

Clearly, the type of rotation has a major role in which brain systems are recruited. This fact may help to explain some of the inconsistencies in the literature. Indeed, it is even possible that participants can use a mixture of the two types of processing, which would produce particularly complex results; as Decety (1996) suggested, implicit motor imagery may be important in a variety of cognitive tasks including mental rotation. The present results underscore the fact that the brain is a complex mechanism, which can—and clearly does—perform tasks in different ways. To understand neural information processing, we must take care to consider the importance of the specific type of stimulus being processed.

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