# Changes in cortical activity during mental rotation
# A mapping study using functional MRI

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## Summary

*Mental imagery is an important cognitive method for problem solving, and the mental rotation of complex objects, as originally described by Shepard and Metzler (1971), is among the best studied of mental imagery tasks. Functional MRI was used to observe focal changes in blood flow in the brains of 10 healthy volunteers performing a mental rotation task. On each trial, subjects viewed a pair of perspective drawings of three-dimensional shapes, mentally rotated one into congruence with the other, and then determined whether the two forms were identical or mirror-images. The control task, which we have called the 'comparison' condition, was identical except that both members of each pair appeared at the same orientation, and hence the same encoding, comparison and decision processes were used but mental rotation was not required. These tasks were interleaved with a baseline 'fixation' condition, in which the subjects viewed a crosshair. Technically adequate studies were obtained in eight of the 10 subjects. Areas of increased signal were identified according to sulcal landmarks and are described in terms of the Brodmann's area (BA) definitions that correspond according to the atlas of Talaraich and Tournoux. When the rotation task was contrasted with the comparison condition, all subjects showed consistent foci of activation in BAs 7a and 7b (sometimes spreading to BA 40); 88% had increased signal in middle frontal gyrus (BA 8) and 75% showed extra-striate activation, including particularly BAs 39 and 19, in a position consistent with area V5/human MT as localized by functional and histological assays. In more than half of the subjects, hand somatosensory cortex (3-1-2) was engaged, and in 50% of subjects there was elevated signal in BA 18. In frontal cortex, activation was above threshold in half the subjects in BAs 9 and/or 46 (dorsolateral prefrontal cortex). Some (four out of eight) subjects also showed signal increases in BAs 44 and/or 46. Premotor cortex (BA 6) was active in half of the subjects during the rotation task. There was little evidence for lateralization of the cortical activity or of engagement of motor cortex. These data are consistent with the hypothesis that mental rotation engages cortical areas involved in tracking moving objects and encoding spatial relations, as well as the more general understanding that mental imagery engages the same, or similar, neural imagery as direct perception.*

Keywords: functional MRI; mental imagery; mental rotation; brain mapping

Abbreviations: BA = Brodmann's area; fMRI = functional MRI

## Introduction
### The mental rotation task

Shepard and Metzler (1971) showed subjects pairs of perspective line drawings of chiral shapes, and asked whether the shapes were identical or one was a mirror-image of the other. The figures in each pair were presented at different degrees of angular disparity, and the subjects' response times increased almost linearly as the angle between the figures increased. Most remarkably, the slope of the curve relating response time to rotation angle was the same when the object was rotated rigidly in the picture plane and when it was rotated in depth. These behavioural data suggested that the decision process was made by the subjects' visualizing a

constant velocity rotation of the rigid three-dimensional object; this interpretation is consistent with the subjective reports of volunteers performing this task. Moreover, Cooper (1976) subsequently estimated the rates of rotation for individual subjects, and then asked them to begin mentally rotating a stimulus when given a cue. At a specific interval after the cue, a probe figure was presented, and the subjects were to decide whether it was identical to the figure being mentally rotated; the probe figure was oriented so that it should have lined up with the imaged figure or should have been 'ahead' or 'behind' it by a specific amount. The subjects evaluated the probe figure most quickly when it was aligned with the image—regardless of its actual orientation, as though the 'image was caught on the fly' by the probe figure. Moreover, the subjects required more time for greater angular disparities between the imaged and probed figures, exactly as expected if they had to engage in additional mental rotation to align the two.

Although the behavioural results have been replicated many times [for reviews, *see* Kosslyn (1980, 1994) and Shepard and Cooper (1982)], little is known yet of the neural mechanisms that underlie mental rotation. Most of the research on the neural basis of such processing has focused on its possible cerebral lateralization. Many researchers have performed divided-visual-field studies with normal subjects, which have produced ambiguous results. Although some researchers have reported faster response times when stimuli are presented in the left visual field, and hence are processed initially in the right cerebral hemisphere [for example, *see* Cohen (1975) and Ditunno and Mann (1990)], others have found faster response times when stimuli are presented in the right visual field, and hence are processed initially in the left hemisphere [for example, *see* Fischer and Pellegrino (1988)]. Furthermore, others have not found any evidence of hemispheric differences (Simion *et al.*, 1980; Jones and Anuza, 1982; Corballis and McLaren, 1984; Corballis *et al.*, 1985*a, b*; Van Strien and Bouma, 1990; Uecker and Obrzut, 1993).

Mental rotation has also been studied in the isolated cerebral hemispheres of split-brain patients. For example, Corballis and Sergent (1988) asked a patient to mentally rotate letters to their standard upright positions and decide whether they faced normally or were mirror-reversed. The patient could perform this task faster and more accurately when the stimulus was presented to the right hemisphere than when it was shown to the left hemisphere. However, with sufficient practice, he was able to perform the task when stimuli were presented to his left hemisphere, but this hemisphere remained slower and made more errors than the right. Corballis and Sergent (1992) tested this patient again, and demonstrated that this left-hemisphere deficit was not a consequence of problems in identifying the stimuli or in making the normal/mirror-reversed judgment (for convergent results, with another split-brain patient, *see* LeDoux *et al.*, 1977).

In addition, Herrmann and van Dyke (1978) showed that

left-handed subjects had shorter response times than right-handers in the same task, which they suggested may indicate that rotation relies on processes implemented in the right hemisphere. However, it is not entirely clear that all left-handers have reversed laterality, nor is it clear that the subjects in the two groups were entirely equated on a number of other possibly relevant variables. This asymmetry was noted also by Yamamoto and Hatta (1980) in the rotation of tactually presented figures.

Evidence for lateralized processing was also reported by Deutsch *et al.* (1988), who asked subjects to perform the Shepard–Metzler mental rotation task while their brains were scanned using the Xe-133 technique; they found increased blood flow in the right hemisphere, extending from the frontal to the posterior parietal lobes. Although the spatial resolution of this technique allows one to draw inferences about laterality, it is not sufficiently precise to allow one to characterize the pattern of neural activity. No evidence of lateralization was reported by Peronnet and Farah (1989), who measured event-related-potentials while subjects performed mental rotation; however, they did find late electrical negativity in posterior scalp regions that varied systematically with the rotation task.

Kosslyn *et al.* (1985) reported studies on two patients with left-hemisphere brain damage who had selective difficulty performing mental rotation, relative to some other imagery tasks. Apparently, not all of the processing that underlies mental rotation may be implemented in the right hemisphere. In addition, Alivisatos (1992) found that patients who had damage to the frontal or temporal lobes were not able to use advance information about the orientations of objects to prepare for them. However, these patients were still able to perform rotation tasks, and thus they may have had difficulty using rotation strategically, not in performing rotation *per se*.

The results from all of these studies are most consistent with the view that mental rotation, like all other complex cognitive activities, is performed by a host of processes working together; these processes being carried out in different parts of the brain. Depending on the precise nature of the task, various aspects of the system may be more or less important, and hence may play a large role in determining the behaviour (for development of this idea, *see* chapter 10 in Kosslyn, 1994). If so, then we should see a system of neural activity when mental rotation is performed, not simply activity in one or another locus. Further, by observing which regions are most active during the rotation task, we can gain insight into the components of the task, as performed by the brain.

However, we must note that it is by no means clear that visual mental rotation relies on visual mechanisms. For example, Marmor and Zaback (1976) showed that even congenitally blind subjects require more time to mentally rotate tactually presented objects by greater amounts. This result is consistent with the presence either of a modality-independent neural substrate, or of separate but similar modality-dependent cortical loci. In addition, linear increases

in response time with increased rotation were reported by Georgopoulos and Massey (1987) in a motor task, in which the subjects were asked to move a 'manipulandum' in a stimulus direction or at an angle from it. These researchers recorded the activity of neurons in area M1 in monkeys who were anticipating moving their arms a specific amount, and found that activity systematically shifted across populations of neurons that encoded the orientation of the arm, shifting from a representation of the initial orientation, through various intermediate orientations, to the target orientation. These results do not show, however, that mental rotation was actually being performed in M1; it could have been performed in another area, which, in turn, drove activity in M1. Moreover, such results may only occur when the arm must be controlled.

Other data have been marshalled as evidence for the argument that visual mental rotation does not rely on visual mechanisms. For example, Rock *et al.* (1989) reported that if subjects are asked to visualize what a novel three-dimensional object looks like from a different vantage point, they are unable to do so unless they use strategies to circumvent the visualization process. They conclude that the relationship between response times and rotation angle in the results reported by Shepard and Metzler (1971) and Shepard and Cooper (1982) is simply a consequence of the difficulty of performing the comparison itself [this view, however, fails to explain results like those of Cooper (1976) summarized earlier]. A critical review of the evidence that visual imagery does not require activation of primary visual cortex was published recently by Roland and Gulyás (1994), who conclude from the published evidence that visual mental imagery does not require the involvement of early visual areas and that it is not necessarily subject to the same cortical organization (e.g. retinotopy) as direct perception (Kosslyn *et al.*, 1995).

Clearly, then, there are numerous open issues surrounding the neural mechanisms that underlie mental rotation. In this report we consider three. (i) Are there reliable hemispheric asymmetries in normal brains? (ii) Are motor areas involved in all types of rotation? (iii) Is primary visual cortex active during rotation? To investigate these questions, we studied the neural basis of mental rotation with functional MRI, a new technique that reveals localized changes in blood flow associated with neural activity during sensorimotor processing (Kwong *et al.*, 1992; Ogawa *et al.*, 1992*a*, *b*; Cohen and Bookheimer, 1994) and mental activity (Le Bihan *et al.*, 1992).

# Material and methods
## Subjects
Ten normal volunteers participated in this experiment under approval and oversight by the Massachusetts General Hospital sub-committee on human studies, accession number 90–7063. Our human welfare assurance from the office of
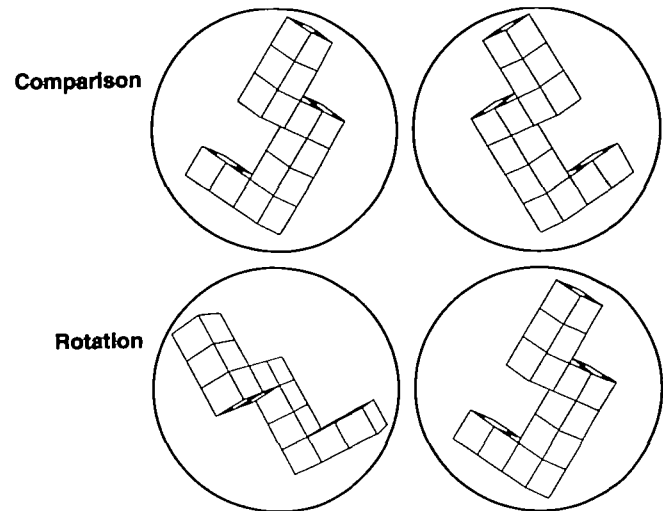


**Fig. 1** Example of stimuli used in the mental rotation task. In the comparison condition (*top*), the subjects were asked to determine whether two pictures were identical or different. Only identical or mirror-image figures were shown. In the rotation condition (*bottom*), the subjects were asked to make the same judgment, but the figures were presented at different orientations. In the example above, both the control and rotation figures are different.

protection from research risks at the National Institute of Health indicates compliance with national and international regulations concerning human subjects according to the declaration of Helsinki. All subjects gave their informed consent to participate. Our MPA number is M1331–01. There were seven (all right-handed) males and three (two right-handed and one left-handed) females ranging in age from 20 to 35 years. Prior to scanning, the subjects were trained in the rotation task with a block of practice trials, consisting of one trial of every possible degree, before entering the scanner (described below). All subjects reported that they were able to perform the task within the instrument without difficulty.

## Rotation task
The figures for the original Shepard and Metzler (1971) mental rotation task were kindly supplied by Professor Shepard, and were scanned digitally to create Apple Macintosh PICT files. They were thus as described in the 1971 report, consisting of three-dimensional perspective drawings of 10 cubes arranged in chiral patterns and viewed from a variety of rotation angles (*see* Fig. 1). Two versions of the task were created. In the control (which we call the 'comparison') condition, subjects were shown a pair of figures, half of which were identical and half of which were mirror-reversed shapes. A control, reversed, pair is illustrated at the top of Fig. 1. Each of the 10 possible angled-shapes (0–180° in 20° increments) appeared in each type of pair. The stimulus ordering consisted of a set of blocks, so that each of the stimuli appeared once before any stimulus appeared twice, and each appeared twice before any appeared three times, and so forth. Within each of these blocks, the

stimuli were in a random order except that the same stimulus could not appear twice within three successive trials. Moreover, half of the pairs within each block included identical figures and half included mirror-reversed figures. No more than three consecutive trials could have the same response.

The second version of the task ('rotation') was identical to the first except that the members of each pair were presented at different orientations. The left member was always presented so that the major axis was vertical, as illustrated at the bottom of Fig. 1. The right member was presented at nine possible angles (20–180° in 20° increments) from vertical. In addition, three sets of these rotation trials were constructed, which included rotations around different major axes; one set included rotations around the $x$-axis, another around the $y$-axis, and another around the $z$-axis. These stimuli were presented in separate sets. Within each set, the stimulus trials were ordered so that each orientation appeared once before it would appear again, once with identical stimuli and once with mirror-imaged stimuli, within each balanced subgroup of 18 trials. The same orientation could not appear twice within three consecutive trials. Otherwise, the ordering was the same as in the control condition.

A third 'resting' or 'fixation' condition was interleaved between the 'control' and 'rotation' tasks as described below. As indicated in the results, this was likely processed as an active task by the subjects, and we will thus refer to it as the fixation condition. During the fixation intervals, the subjects were asked to maintain their gaze on a small centrally located crosshair.

### Rotation task procedure

The subjects were asked to look at each pair, and to decide whether the figures were identical or were mirror-images and to indicate their choice by pressing one of two buttons. In the control condition, subjects were simply asked to respond as quickly and accurately as possible. In the rotation condition, they were told to visualize the right-hand stimulus rotating until it was aligned with the left-hand stimulus, and then were to decide whether the two shapes were identical or were mirror reversed. Again, they were to respond as quickly and accurately as possible by pressing the appropriate button. The subjects responded with a small keypad that was placed under their dominant hand. The stimuli were projected from a Sharp video projector onto the rear of a translucent screen, which was visible from the inside of the magnet. From the subject's central point of view, the images subtended approximately 13×7.5 cm (16×8.5° of visual angle). On each trial, a centred fixation point appeared for 500 ms and was replaced by pair of cube figures. The stimuli remained visible until the subject responded and were immediately replaced by the next fixation point; thus, 500 ms after a response, a new stimulus pair was presented. Stimulus presentation was controlled by a modified version of the
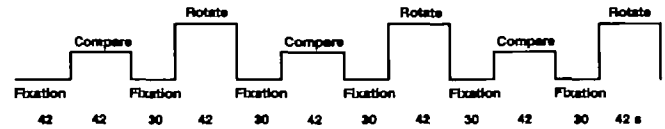


**Fig. 2** Schematic of protocol used in the mental rotation studies. Numbers indicate the block duration in seconds. Stimuli were presented in blocks of 42 s duration, separated by rest periods of 30 s, during which the subject viewed a fixation point. Stimulation periods alternated between the comparison and rotation figures described above. During each trial lasting ~8 min, there were three separate comparison and rotation periods and six rest periods. Each subject completed three or four trials in a single imaging session.

MacLab program (Costin, 1988), which also recorded responses and response times. The buttons were interfaced to the control computer through a low impedance DC path that controlled a series of electromagnetic reed switches located outside the magnet room (which was radio frequency and magnetically shielded); this system avoided the introduction of artifacts into the images.

The trials were presented in blocks consisting of an initial fixation period, followed by alternating blocks of control, fixation and rotation periods. Control and rotation task blocks were 42 s long, as was the initial fixation block; all other fixation blocks were 30 s long. During the rotation task, each 42 s block included rotations around the same axis ($x$, $y$ or $z$). The order of stimulus presentation was balanced in the same manner for both control and rotation conditions. Figure 2 shows schematically the relationship of the scan times and protocol. The entire behavioural and scanning protocol, as described in Fig. 2, was repeated from two to four times per subject.

### Scanning

Subjects were scanned in the head coil of a General Electric 1.5 Tesla Signa (Waukesha, Wisc., USA) modified for echo planar imaging by Advanced NMR Systems (Wilmington, Mass., USA). We began by obtaining a high resolution series of $T_1$-weighted (spin echo TR/TE/NEX/matrix 600/11/1/256×192) anatomical images for each subject in contiguous sagittal sections to serve as a basis set for the determination of anatomical landmarks and coordinates. Using an automated procedure (Reese et al., 1993), the magnetic field was shimmed on each individual subject. Following this, a series of seven 10 mm slices with angiographic contrast (SPGR TR/TE/Flip/NEX/matrix 50/17/55/2/256×256) was collected in the scan planes of interest, parallel to the calcarine fissure; note that this resulted in considerable variation in slice angle with respect to other landmarks, such as the AC–PC line. High resolution echo planar imaging scans were then collected in the same planes using a $T_2$-weighted (TR/TE 3000/80) partial K-space acquisition (Weisskoff and Rzedzian, 1989; Cohen and Weisskoff, 1991), which produced a 256×128 matrix with 1.5×1.5 mm in-plane resolution.

Functional images were acquired using a susceptibility-

weighted asymmetric spin echo acquisition, a modification of the susceptibility method of Kwong *et al.* (1992) and Ogawa *et al.* (1992*b*). To introduce susceptibility weighting, the Hahn echo and gradient echo were offset by 25 ms (Baker *et al.*, 1992; Hoppel *et al.*, 1993). Images with a 128×64 matrix were acquired in each plane every 3200 ms in interleaved slice order. In each functional series, 146 images were acquired in each location, resulting in a time per functional study of 7 min and 48 s. Figure 2 shows schematically the relationship of the scan times and protocol.

## Functional MRI data analysis

A variety of statistical procedures were explored in comparing the comparison and rotation conditions. We evaluated the use of the Kolmogorov–Smirnov statistic (Stuart and Ord, 1991) for its ability to detect differences in response distributions and variance as well as Student's *t* test for differences in the mean. Although the tests varied in the relative *P* values assigned each pixel, the pattern of activation was essentially identical, suggesting that the activity differences were characterized well by differences in the mean signal intensity. The significance assigned each pixel was generally greater using the *t* test, which is consistent with its relatively high power in detecting differences between mean values. The probability of significant activation was estimated from the *t* statistic using standard algorithms (Press *et al.*, 1992). The resulting *t* values were not corrected for any possible temporal autocorrelation, as the nominal independence of successive time points remains poorly characterized. In any event, such autocorrelation is likely to be quite small in this study, given that individual time points were separated by an interval of 3.2 s. We present our data as raw *t* statistics, as these do not over-specify our confidence in the transformation to probability levels.

Motion artifact is a common problem in fMRI (Cohen and Bookheimer, 1994; Hajnal *et al.*, 1994) because small head motions can result in relatively large signal changes. Such artifacts typically appear as areas of unusually high or low signal intensity at interfaces between structures having large signal differences (e.g. at the edge of the skull). Because a head coil was used for all imaging experiments, in-plane rotations and displacements typically resulted in areas of high intensity at one surface, with a complementary low signal intensity area on the opposite surface; through-plane motion could result in more circularly symmetric artifacts, as illustrated in Fig. 3. Frequently, it was possible to detect frank motion by viewing the entire temporal series from a subject as a ciné loop. Where motion was detected, or suspected using the above subjective criteria, the data set was re-registered using a modified version of the Woods algorithm (Woods *et al.*, 1993). The signal intensity of images within the radio frequency coils used for MRI is never completely homogeneous, and gross susceptibility effects from tissue inhomogeneity cause additional non-uniformities if displacements are even moderately large. Thus, the simple

re-registration algorithms cannot completely correct for the effects of motion. Data that continued to show signs of motion artifact after re-registration were excluded from further analysis.

For visual analysis, we first generated maps of statistical significance of a difference in mean between two conditions (rest versus stimulation or rotation versus comparison), assigning a colour of red for $t = 3.62$ (two-tailed) ranging to yellow for $t \geq 7.36$ (two-tailed) in six of the eight subjects. These maps were then superimposed onto coplanar anatomical echo planar imaging data for subsequent localization of cortical regions. This format is used in the accompanying figures. Anatomical locations of the activation foci were described by identifying the major sulci and gyri (Ono *et al.*, 1990) and were labelled according to the Brodmann (1909) nomenclature indicated in the atlas of Talairach and Tournoux (1988). The individual data suggested substantial variability of the response foci across subjects in several areas. This is consistent with the reported data on anatomical variability of the higher visual centre, V5 (sometimes called human MT) (Watson *et al.*, 1993), which is seen to vary in position by nearly 3 cm relative to stereotaxically transformed coordinates but which bears a consistent relationship to sulcal landmarks. For this reason, no attempt was made to combine the activation data (Fox *et al.*, 1988), which would likely have resulted in artifactually diminished magnitudes of activation for several regions in several brains. Instead the major areas of activation are characterized by anatomical description. The data were later grouped across subjects by indicating the number of subjects showing increased activity $(t > 3.62)$ in each of these anatomically defined regions. When interpreting these data, it is important to recognize that some of these areas are quite large, thus some differences in individual patterns of activation will not be detected.

## Results

Technically acceptable (i.e. free from obvious motion artifact) imaging studies were acquired in eight of 10 subjects. Unless specifically mentioned, the results reported below refer only to these subjects.

## Behaviour

We recorded responses and response times on-line, allowing us to determine whether the 'behavioural signatures' of mental rotation are present; i.e. mental rotation is a covert and private event, and we needed some way to verify that subjects were engaged in the kind of processing we wanted to study. The well-documented effects of orientation on response times provide one such indication, and we would have good reason to be confident that our fMRI data reflected the neural basis of mental rotation if we obtained these effects from our subjects while they were being scanned. Thus, we submitted the response times to an ANOVA. We analysed only those times from rotation trials when subjects
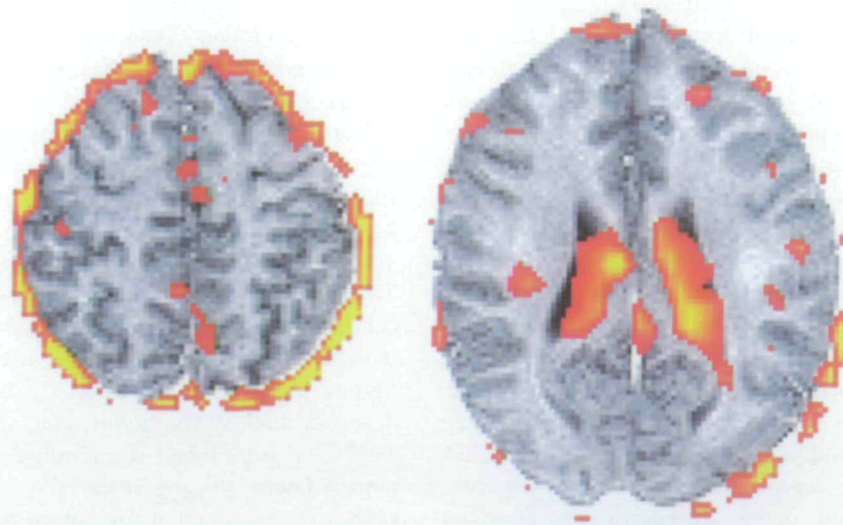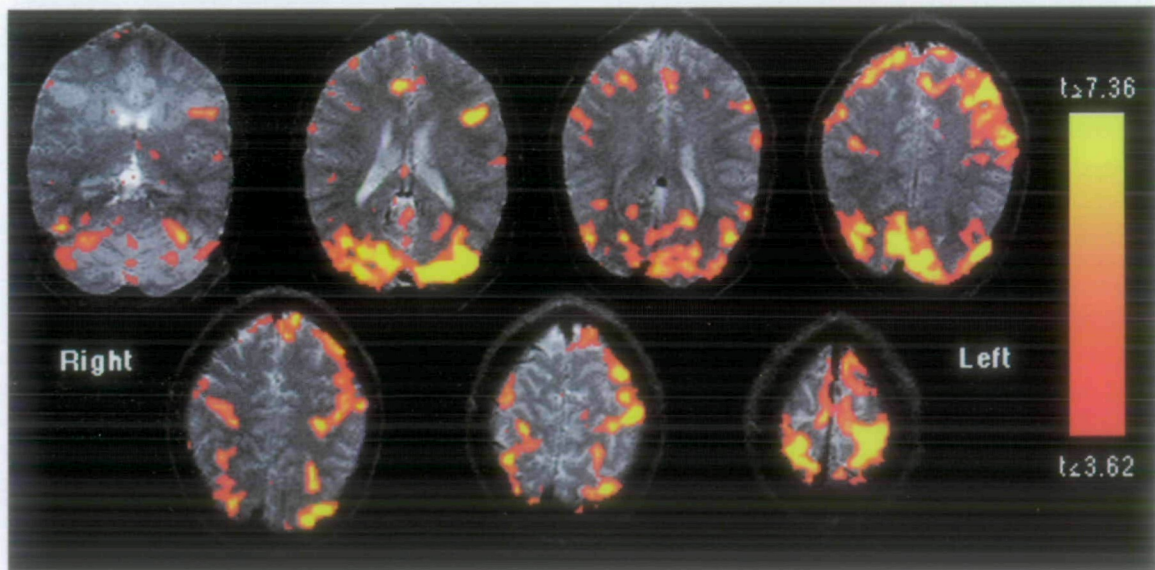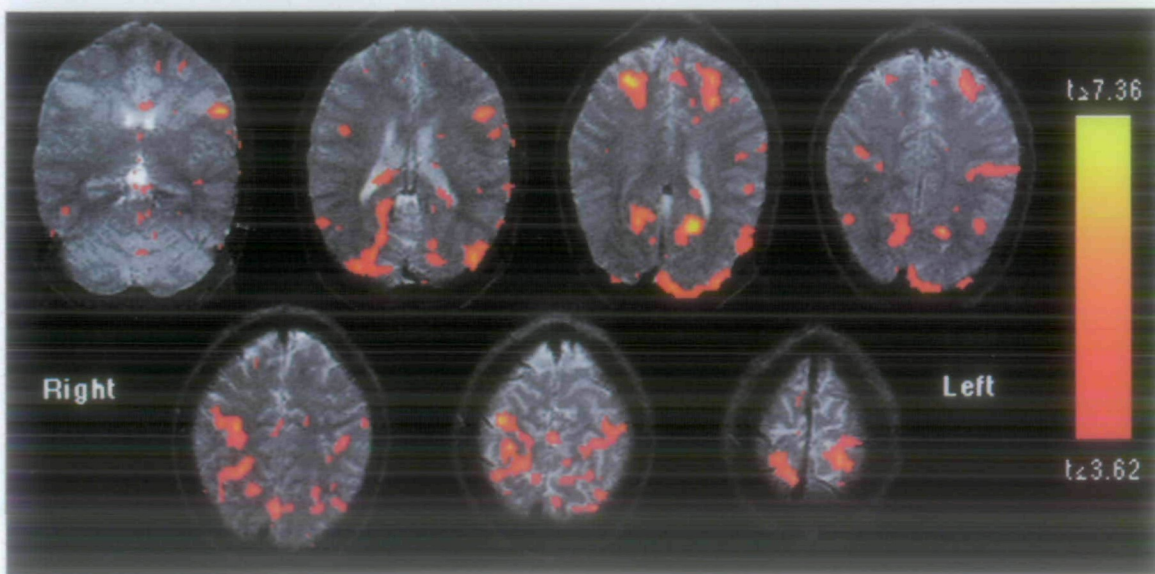
**Fig. 3**

**Fig. 4**

**Fig. 5**

made a correct response, and eliminated outliers prior to analysis (an outlier was defined as a time >3 SDs from the mean of the times in that condition for that subject). In all subjects, the response time increased appropriately with angular disparity. An ANOVA documented that (i) subjects required more time in the rotation condition than in the control condition [$F(1,7) = 22.872$, $P < 0.002$] (control: M = 849 ms; rotation: M = 2412 ms), (ii) times varied for the different angles [$F(1,8) = 6.302$, $P < 0.0001$] and (iii) the angle affected response times in the rotation condition but not in the control condition, as indicated by an interaction of condition and angle [$F(1,8) = 7.005$, $P < 0.0001$].

The accuracy data were analysed in the same way. We found that the subjects made more errors when evaluating pairs that incorporated different amounts of angular disparities. The ANOVA documented that (i) subjects made more errors in the rotation condition than in the control condition [$F(1,7) = 8.261$, $P < 0.02$] (control: M = 5%; rotation: M = 9%), (ii) errors varied for the different angles [$F(1,8) = 20.627$, $P < 0.0001$] and (iii) angle affected error rates in the rotation condition but not in the control condition, as indicated by an interaction of condition and angle [$F(1,8) = 8.430$, $P < 0.0001$].

### Stimulation versus rest

To verify our ability to detect cortical activation, we compared the signal intensity during the combined control and rotation blocks to signal intensity in the fixation periods. In all scans, including those discarded from further analysis because of motion contamination, this comparison showed strong focal activation in the midline occipital cortex. Specifically, we observed strong activations in the midline occipital cortex in the three planes superior to, through, and inferior to the calcarine fissure and extending approximately to the parieto-occipital sulcus, engaging Brodmann's areas 17, 18 and 19. Signal intensity changes were also evident in all experimental (free from motion artifact) subjects along the central sulcus 2–3 cm from the superior pole (BAs 4 and 3–1–2). As illustrated in Fig. 4, some activity could be seen in the majority (six out of eight) of subjects in the superior frontal gyrus in BA 6 in this comparison.

### Rotation versus control

The key comparison here was between the rotation and the control tasks, both of which required the subjects to encode

the shapes, to compare them, and to make a decision. Thus, additional activity in the rotation trials will not reflect these other processes, but rather can be identified with the rotation process *per se*. An example study showing the regions active in a single subject is given in Fig. 5.

In all eight of our subjects who could be analysed (and bilaterally in seven), we observed strong activation diffusely throughout the posterior parietal lobe, in BA 7a and 7b. In seven out of eight subjects, activation was seen in the middle frontal gyrus, corresponding to BA 8; this activity was bilateral in six out of eight. In addition, a smaller focus of signal change appeared consistently ($n = 7/8$) in the region of the parieto-occipital (39/19) border. In about half of the cases, the signal was increased in the neighbourhood of BAs 46 and 44 in dorsolateral prefrontal cortex ($n = 4/8$), and in the superior postcentral regions (3–1–2). The difference in the BA 8 activation was less in comparing the rotation and control tasks than in comparing stimulation and fixation (as reported above). Comparison of the control and fixation conditions confirmed that these regions showed higher signal during the fixation condition. Our data do not show strong or consistent evidence of lateralization, to left or right, of activity in this comparison. In fact, most individual regions were activated bilaterally. The overall results of this comparison are summarized in Fig. 6.

## Discussion

This work was motivated by three general issues, and it is useful to consider the results in this context. First, we asked whether mental rotation relies on processes that are implemented primarily in one cerebral hemisphere. Although we did find some asymmetries in individual brains, there was remarkably little consistency over subjects in these asymmetries. Deutsch *et al.* (1988), who used the Xe-133 regional cerebral blood flow method, reported more activation in the right cerebral hemisphere during mental rotation. However, their data were averaged over subjects, and it was not clear how many showed this asymmetry (nor how strongly most subjects showed it). Additional relevant results were reported in an abstract of a study, similar to ours, in which the investigators used fMRI (Tagaris *et al.*, 1994). They reported that in the four experimental subjects BA 7, primarily in the left parietal cortex, was activated during rotation, relative to a passive control condition. Their reported control

**Fig. 3** Functional MRI data are extremely sensitive to motion artifacts. The figure above, excluded from the final data set, shows the effect of through-plane motion on the functional images. Criteria used to exclude these data included (i) areas of significant signal change outside of the brain, (ii) areas of large signal change at regions of large intensity gradients (such as the edge of the brain, longitudinal fissure, and the top of the lateral ventricles), and (iii) a characteristic ring of signal change around the brain. The calculated functional 'activation' maps are shown overlaid onto echo-planar images.

**Fig. 4** The activation pattern seen in a single subject, comparing resting image intensities to those seen during the combined control and rotation conditions.

**Fig. 5** Functional MRI data from the same subject as Fig. 4, indicating areas of increased signal intensity during the mental rotation task as compared with comparison conditions. Areas of activation are seen in right inferior frontal gyrus, bilaterally in the inferior parietal lobule and superior frontal gyrus, as well as diffuse centres of activation throughout the precuneus, primarily BA 7.
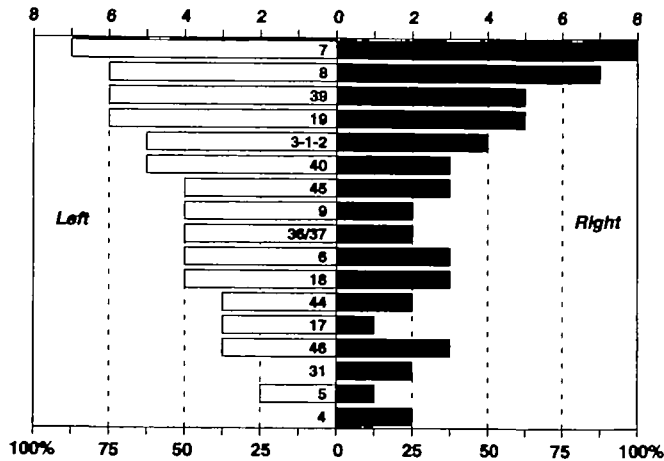
**Fig. 6** Number of subjects showing activation, on the left and right, in each anatomical area in which a significant intensity difference was found in at least two subjects. Figures on the upper axis indicate the number (out of a possible eight) of subjects showing activity. The figures at the bottom indicate the percent of same. The numbers in each bar indicate the Brodmann's area designation.

task differed, however, consisting of observation of identical flat rectangles and pushing a button. Further, the scan planes used in that study were parallel to the AC–PC line and were thus angled somewhat differently than those used here; hence, it was unlikely that the superior parietal activations would have been seen.

Our data suggest that any hemispheric dominance in mental rotation is quite variable, even across a study of right-handed subjects; in this sense, our data are consistent with the published studies of the lateralization of mental rotation processes, whose conclusions are highly variable (Ratcliff, 1979; Yamamoto and Hatta, 1980; Corballis and Sergent, 1988, 1989; Deutsch *et al.*, 1988; Fischer and Pellegrino, 1988; Ditunno and Mann, 1990; Mehta and Newcombe, 1991; Burton *et al.*, 1992; Wendt and Risberg, 1994). Wilson, in particular, reported that measured asymmetries in cerebral blood flow were correlated with task performance (Wilson *et al.*, 1994), which suggests that cognitive/neural strategies may differ across individuals. Our results confirm and extend Tagaris' other observations. These data suggest a possible role for the ventral intraparietal area (Colby *et al.*, 1993*a, b*) in mental rotation, consistent with its anatomically identified input (in the macaque) from area MT. We believe that the activity seen in BA 7a and 7b is likely to be associated with the encoding of spatial relations and allocation of visual attention.

We next asked whether motor areas are involved in mental rotation. We did find activation in the postcentral gyrus in five out of eight subjects, but failed to see consistent activity in precentral regions, except in BA 6 (supplementary motor area). This result is unlikely to be related to motor planning for the behavioural response, given that the similar planning and execution were involved in the control condition. Rather, it is possible that the supplementary motor area is activated

in difficult tasks that require substantial attention; may have a role in supplementary motor area of the anterior attentional system described by Posner and others (Passingham *et al.*, 1989; Posner and Petersen, 1990; Deiber *et al.*, 1991; Bench *et al.*, 1993).

Finally, we asked whether areas involved in visual perception are recruited during visual mental rotation. In our studies we saw little activity in the immediate vicinity of the calcarine fissure that would suggest involvement of primary visual cortex in mental rotation. However, the visual stimulation in the control task was well matched to the stimulation in the rotation task (the identical figures were presented in identical stimulus conditions), and thus we should not be surprised by this result. Kosslyn *et al.* (1993) suggested that visual mental images may be generated by activating long-term visual memories (in the inferior temporal lobes), which in turn activate early visual area via descending efferent pathways. They report activation in the medial occipital lobe during visual mental imagery, as measured by PET (but *see* Kosslyn and Ochsner, 1994). The lack of activity detected in this region in the rotation minus control comparison suggests that such descending input does not play a role in the kind of mental rotation task we studied, which does not require one to form images on the basis of remembered information (the to-be-compared stimuli both are physically present during the task).

We did, however, find evidence that some 'higher' visual areas were activated during mental rotation. For example, cortical area V5 (human MT), known to respond to motion of stimuli (Watson *et al.*, 1993; Tootell *et al.*, 1994, 1995*a*), was apparently active in the rotation task. (N.B. Most of the literature on the region cortical area V5 comes from animal data, in which 'MT' refers to the middle temporal region. The functionally similar region in humans, however, is not in the same topographical location. It may thus be more proper to refer to this by a functional terminology, labelling it as 'V5'. We do not wish to contaminate this literature further, and thus opt to use both terms: V5/MT for the remainder of this communication.) This is interesting because no actual motion was present (unfortunately, we did not anticipate this result and did not perform functional localization studies with moving stimuli to confirm this more directly). Tootell has noted that the perception of motion, even illusory motion, is correlated strongly with increased activity in this area as seen using fMRI (Tootell *et al.*, 1995*b*). Several reports have shown that, behaviourally, subjects are considerably better at imagining the rotation of an object than they are at imagining themselves moving to see the object from a different vantage, though the final object views might well be identical (Koriat and Norman, 1984; Farah and Hammond, 1988; Rock *et al.*, 1989). Although, to our knowledge, this has not been tested, we suspect that imagining smooth transformation of the whole visual field as the subject moves would be a less effective activator of this region. Further, electrically recorded activity in the parietal visual areas, lateral intraparietal (Gnadt and

Andersen, 1988; Colby *et al.*, 1993*a*) and ventral intraparietal areas (Colby *et al.*, 1993*b*), that in the monkey include BA 7, suggest a role for the superior parietal lobule in the multiple spatial representations of visual objects (Colby *et al.*, 1995). We surmise that the neural machinery for mental rotation is like that of direct perception in utilizing cortical regions typically involved in the detection and analysis of form and motion.

In addition, the strong activation difference observed in the frontal eye fields is consistent with a role for these regions in scanning of the visual field (Anderson *et al.*, 1994). Indeed, it is known that there is considerable saccadic scanning during performance of this task. Just and Carpenter (1985) analysed patterns of eye movements during this task, and argued that subjects, in fact, encode and rotate parts individually, which involves fixating on corresponding parts of each figure. Clearly, these eye movements were not an artifact of simply encoding the shapes, comparing them, or reaching the decision; these processes were also required in the control condition.

Our finding of higher signal intensity during the fixation condition than during the control task was unexpected. A plausible interpretation is that active fixation requires more conscious control of eye position than does the simple same/different recognition task. This interpretation emphasizes a troubling aspect of currently available analysis tools for fMRI, PET and single photon emission computed tomagraphy: namely, the presence of large activations implies high local neural activity and perhaps, at least in some cases, inefficient data processing. Indeed, several investigators have shown diminished activation magnitude (Raichle *et al.*, 1994) and systematic variations of cortical extent (Pascual-Leone *et al.*, 1994) with task mastery.

Finally, we found activation of BA 46, which has been identified as playing a role in 'working memory' for spatial location by Goldman-Rakic (1987), in monkeys; Jonides *et al.* (1993) in humans, and in BA 9. We did not find the right lateralization, however, that might have been predicted based on the reports of Jonides *et al.* (1993). This activation is consistent with the analysis of Just and Carpenter (1985), who characterized patterns of eye movements during this task. They argued that subjects, in fact, encode parts individually in the process of rotation, which requires remembering where individual parts of each figure are located. Such a task clearly would involve the kind of spatial working memory that has been identified with BA 46; this inference is also consistent with the claim that BAs 7a and 7b are involved in the encoding of spatial relations and the allocation of visual attention. This region of dorsolateral prefrontal cortex has been implicated in a wide variety of self-initiated ('willed') behaviours, e.g. Frith *et al.* (1991). Brodmann's areas 9 and 46 are connected reciprocally to BA 8 and the dorsomedial eye fields, and receive heavy input from parietal BA 7a; in lesion studies of monkeys, these areas are essential for delayed response tasks that require monkeys to guide their choice by spatial location and information held in working memory (for review, *see* Passingham, 1993). In our data set, these regions were seen in less than half of the subjects, making any mechanistic interpretation of their involvement premature.

## A plausible neural mechanism for mental rotation

Based on the data at hand, we believe that the neural structures most involved in mental rotation as performed in this protocol are the frontal eye fields (probably primarily in control of oculomotor function in scanning these complex visual images), the extrastriate visual regions of the superior parietal lobule and V5/MT. The superior parietal lobe, especially BAs 7 and 8 is typically activated in visuospatial processing tasks. We posit that the bulk of the computation for the mental rotation, as studied here, is performed in this cortical area. Interestingly, current theory suggests a role for these regions in determining the position of an object with respect to the observer (Colby *et al.*, 1995), a point of view consistent with the theory that the figures are rotated as solid objects with three-dimensional extent. The activity in putative area V5/MT is perhaps even more intriguing. The engagement of this motion sensitive area by a non-moving stimulus has been reported previously as subjects looked at a figure yielding illusory motion (Zeki *et al.*, 1993). When performing the rotation task, however, our subjects do not perceive motion. Instead, they may well perform a computation that is based on the object motion, and therefore engage this region as a processing centre.

As a whole, our data support an important role for fMRI in the study of higher order mental functions. These results demonstrate that the technique makes it possible to detect the neural activity underlying mental states (e.g. performing mental rotation). Moreover, this can be performed for individual subjects, which circumvents problems in normalizing scans and then averaging over them. This advantage is meaningful if genetics and experience produce significant individual differences in brain structure and function, as appears to be the case.

Further, these data strongly support a sort of conservation principle of mental events: that the machinery of primary sensation, imagery and perhaps perception might well be the same. This view of the brain, and of mental imagery, differs profoundly from the typical subjective view of a separate, conscious, observer of sensory events, suggesting instead that the neural substrates of sensation and conscious perception (accepting that imagery in this case is a conscious event) are one and the same.

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