Selective right parietal lobe activation during mental rotation
A parametric PET study

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Summary
Regional cerebral blood flow (rCBF) was measured with PET in seven healthy subjects while they carried out a mental rotation task in which they decided whether alphanumeric characters presented in different orientations were in their canonical form or mirror-reversed. Consistent with previous findings, subjects took proportionally longer to respond as characters were rotated further from the upright, indicating that they were mentally rotating the characters to the upright position before making a decision. We used a parametric design in which we varied the mental rotation demands in an incremental fashion while keeping all other aspects of the task constant. In four different scanning conditions, 10, 40, 70 or 100% of the stimuli presented during the scan required mental rotation while the rest were upright. The statistical parametric mapping technique was used to identify areas where changes in rCBF were correlated with the rotational demands of the task. Significant activation was found in only one area located in the right posterior parietal lobe, centred on the intraparietal sulcus (Brodmann area 7). The experimental literature on monkeys and humans suggests that this area is involved in a variety of spatial transformations. Our results contribute evidence that such transformations are recruited during mental rotation and add to a body of evidence which suggests that the right posterior parietal lobe is important for carrying out visuospatial transformations.

Keywords: mental rotation; spatial transformation; PET; right parietal lobe; intraparietal sulcus

Abbreviations: rCBF = regional cerebral blood flow; SPM = statistical parametric mapping

Introduction
Mental rotation refers to the ability to imagine the rotation of an object in space (Shepard, 1984; Corballis, 1997). In a pioneering study, Shepard and Metzler asked subjects to discriminate between novel 3D figures and their mirror images when these stimuli were presented in different orientations (Shepard and Metzler, 1971). They found that response time was proportional to the angular difference between the stimuli. This suggested that subjects attempt to align the two stimuli before making the discrimination and, in the process, they imagine the stimulus passing through intermediate orientations. In a related paradigm, Cooper and Shepard asked subjects to decide whether rotated alphanumeric characters were in their canonical form or mirror-reversed, and again found that reaction time varied linearly as a function of the angular rotation from the upright (Cooper and Shepard, 1973).

While the psychophysical properties of mental rotation are now well established (for a review, see Shepard and Cooper, 1982), its neural basis remains poorly understood. Some studies of patients with brain lesions have reported impairments in mental rotation after damage to the posterior right hemisphere (Ratcliff, 1979; Farah and Hammond, 1988; Ditunno and Mann, 1990), while others found such impairment after posterior left hemisphere lesions (Mehta and Newcombe, 1991). Although the lesions were often large, they almost always involved the parietal lobe, and at least one study has demonstrated mental rotation deficits following lesions confined to the right parietal lobe (Ditunno
and Mann, 1990). Thus, consistent with other findings of parietal involvement in spatial cognition (De Renzi, 1982; Stein, 1991), the lesion data suggest that the parietal lobes play an important role in mental rotation.

Activation of the parietal lobe during mental rotation has been demonstrated consistently in functional MRI and PET studies, although the relative contributions of the left and right parietal lobes remain controversial. Cohen and colleagues (Cohen et al., 1996) reported a functional MRI study in which subjects performed a mental rotation task adapted from Shepard and Metzler (Shepard and Metzler, 1971). Subjects judged whether two 3D figures, presented side by side, were the same or were mirror images; the figures were in different orientations in the experimental condition, but in identical orientation in the control condition. Comparing these conditions identified significant bilateral activations in the superior parietal lobes, the V5 complex (human motion area) (Zeki et al., 1991; Watson et al., 1993), the dorsolateral prefrontal cortex and the premotor areas. The authors attributed the parietal and V5 activations to the mental rotation process per se, while the frontal activations were thought to represent the control of oculomotor functions required for scanning the two stimuli and the processing demands of working memory. Bilateral parietal activation was also reported in a similar PET study (Kosslyn et al., 1997) and in other functional MRI studies using the same paradigm (Tagaris et al., 1996, 1997).

A recent PET study which used rotated alphanumeric characters (the paradigm introduced by Cooper and Shepard, 1973) revealed significant parietal activation only in the left hemisphere, when the mental rotation task was compared with a control condition requiring the mirror discrimination of upright characters (Alivisatos and Petrides, 1997). The left parietal activation was accompanied by increased activity in the right frontal cortex and the right caudate nucleus. This paradigm has the advantage that it employs single characters, thus minimizing eye movements and attentional shifts between stimuli, both of which are known to result in increased activity in the superior aspect of the parietal lobes (Corbetta et al., 1993; Anderson et al., 1994). Therefore, parietal activations observed during this task can be attributed more confidently to mental rotation.

To date, all functional imaging studies of mental rotation have used a cognitive subtraction approach. The validity of this strategy rests on the assumption that components of a cognitive task are separable and can be added to a baseline task without affecting the implementation of other task components. This assumption of ‘pure insertion’ carries with it the additional implication that ensuing differences in brain activity can be attributed to the specific task component under study (Friston, 1998). While this assumption may be appropriate for simple perceptual tasks (e.g. colour and motion processing), it has been shown to be violated in a number of higher cognitive tasks, mental rotation among them. In a series of experiments, Ilan and Miller demonstrated that subjects use a different strategy when deciding whether an upright character is normal or reversed (a judgement that does not involve rotation) depending on whether the character is presented among rotated or upright stimuli (Ilan and Miller, 1994). This demonstration that mental rotation cannot be ‘purely inserted’ into the mirror discrimination task complicates further the interpretation of previous imaging experiments which have relied on cognitive subtraction.

Here we present an attempt to specify the brain areas involved in mental rotation using a different experimental approach, namely a parametric design. The essential difference between parametric and subtraction designs is that, in the former, the components of a cognitive task are treated as dimensions that can be engaged in a graded fashion depending on task demands rather than as categorical entities. Since parametric designs do not rely on the assumption of pure insertion they may be a more robust technique for investigating the neural bases of higher cognitive processes such as mental rotation.

In this study, we used the same paradigm as Alivisatos and Petrides (Alivisatos and Petrides, 1997), but we manipulated the proportion of rotated alphanumeric characters in a set of trials (10, 40, 70 and 100%), thereby requiring subjects to perform more or less mental rotation in each scanning condition. We deliberately did not include a baseline condition with only upright characters, in order to ensure that subjects used the same strategy for the mirror discrimination judgement throughout the experiment. We hypothesized that those brain areas critical for mental rotation would show regional cerebral blood flow (rCBF) changes that correlate significantly with the mental rotation demands of the task. On the basis of previous findings we expected these areas to be located in the parietal lobes, and possibly in the dorsolateral prefrontal cortex and caudate nucleus.

**Method**

**Subjects**

Seven normal volunteers (four males and three females) with a mean age of 47 years (range, 29–66 years) participated in the experiment. All subjects were right-handed according to their scores on the Edinburgh Handedness Inventory (Williams, 1986) and had no history of neurological illness. Written informed consent was obtained prior to participation in the experiment, in accordance with the Declaration of Helsinki. The study was approved by the ethics committees of The Austin Repatriation Medical Centre and The University of Sydney.

**Stimuli and equipment**

The experiment was designed and conducted on a Macintosh computer using the PsyScope software (Cohen et al., 1993). The stimuli were presented in the centre of a 48 cm computer monitor positioned 50 cm from the subject’s face in the PET camera. Responses were recorded via a compatible button
box (Carnegie Mellon University, Pittsburgh, Pa., USA) which recorded reaction time with 1 ms accuracy.

The stimuli were eight asymmetrical alphanumeric characters (F, G, P, R, 2, 4, 5, 7) presented either in their canonical orientation or mirror-reversed. Black characters (Helvetica font, size 100 points), subtending a visual angle of ~4°, were presented in central vision on a white background. The stimuli were rotated clockwise in 40° steps, in the frontal plane, ranging from 0 to 320°.

**Procedure**

The experiment comprised eight scans of a 16 scan PET study. For four of the subjects, the mental rotation experiment was run during scans 1–8, whereas for the other subjects it was run during scans 9–16. The experiment was divided into two blocks of four scans, with 32 stimuli presented per scan. Each block consisted of four conditions in which the proportion of rotated stimuli was manipulated as follows: 10% condition, three of the 32 stimuli were rotated, the rest being upright; 40% condition, 13 stimuli were rotated; 70% condition, 19 stimuli were rotated; 100% condition, all stimuli were rotated. The order of scans within each block was randomized across subjects and counterbalanced within subjects across the two blocks.

Each of the eight characters appeared four times during each scan, twice in its normal orientation and twice reversed. All rotation angles were represented as evenly as possible in each condition. A mean orientation was calculated for each condition by averaging the orientation of the rotated stimuli in that condition. Because previous studies have shown that subjects rotate along the shortest path and that reaction times are symmetrical around 180° (Shepard and Cooper, 1982), this orientation was defined as the absolute angular displacement from the vertical, irrespective of the direction of rotation. The mean orientation of the rotated stimuli was 120, 103, 104 and 100°, for the 10, 40, 70 and 100% conditions respectively. There were no significant differences in stimulus orientation among the conditions. Thus, all aspects of the stimulus material (character, normal versus reversed, mean orientation) were equated across conditions, the only difference being the number of rotated trials in each condition and, therefore, the cognitive load on the mental rotation process.

Scanning was conducted with the lights dimmed and noise kept to a minimum. After being placed in the scanner, each subject received both oral and written instructions and was given 32 practice trials randomly selected from the total pool. For each scan the stimulus began with a blank screen for 2 s, followed by the 32 stimuli presented at the rate of one every 2 s. If the subject responded within the 2 s time limit, the screen went blank until the end of the 2 s interval; otherwise the next stimulus replaced the current one immediately. The subject decided as quickly as possible whether each stimulus was a normal or mirror-reversed character and responded by pressing one of two buttons with the thumb (for mirror-reversed characters) or index finger (for normal characters) of the right hand.

**PET scanning**

Relative rCBF was measured by recording the distribution of cerebral radioactivity following intravenous injection of H215O into one of the small veins of the subject’s left forearm. PET scans were acquired using a Siemens/CTI 951/3IR scanner operated in 3D mode. The scans were reconstructed using a standard image reconstruction algorithm (Kinahan and Rogers, 1989) and a Hanning filter with a cutoff frequency of 0.45 cycles/pixel. Each scan consisted of two acquisition frames with a duration of 30 s (background frame) and 60 s (foreground frame). Data from the background frame were forward decay-corrected and used to correct the foreground frame for residual radioactivity from the preceding scan. The 40 s H215O infusion (mean activity per infusion, 260 MBq), using a highly reproducible automated water generator (Tochon-Danguy et al., 1995), produced a monotonically increasing brain count rate for ~60 s. The scanner acquisition was timed to synchronize the foreground frame with the increasing brain count rate. The 65 s paradigm began 5 s prior to the commencement of the second acquisition frame. A high-resolution MRI scan (Siemens Magnnotom 4000 1.5 T, magnetization prepared rapid acquisition gradient echo protocol; TR (repetition time) = 12.5 ms, TE (echo time) = 5 ms, flip angle = 10°) was also acquired for each subject.

**PET data analysis**

The reconstructed data volume measured 128 × 128 × 31 voxels, with a voxel size of 2.43 × 2.43 × 3.375 mm. An automated image registration algorithm (AIR 3.0, Woods et al., 1998a, b) was used to align the second and subsequent PET images to the first PET image for each subject, using a rigid body transformation with 6 d.f. (degrees of freedom). An average PET image for each subject was formed by summing all of the individual PET images. Each subject’s MRI was edited to remove the scalp and other brain coverings using ANALYZE AVW 2.0 (Biomedical Imaging Resource, Mayo Foundation, Rochester, Minn., USA) (Hanson et al., 1997). Each subject’s average PET image was then aligned to their segmented MRI using an alignment algorithm with 6 d.f. (AIR 3.0), since the voxel dimensions of the PET and MRI had been measured independently beforehand.

Each subject’s segmented MRI was aligned to a standard MRI using a non-linear algorithm with 168 d.f. (AIR 3.0). The standard MRI was chosen from a group of normal MRIs because of its close similarity to the gross dimensions and features of the brain used in the Talairach and Tournoux atlas (Talairach and Tournoux, 1988). The three alignment transformation matrices generated by AIR 3.0 were then combined and applied as a unique transformation to each of the 56 PET images. This meant that each individual image for each subject was resliced only once.
in order to be transformed into Talairach space, sampled at a 2.0 \times 2.0 \times 4.0 \text{ mm}^3 \text{ voxel size}. The transformed images were smoothed using a 3D, 12 mm full-width-at-half-maximum Gaussian blurring function (AIR 3.0), then masked to remove reconstruction artefacts lying outside the cortical surface, as defined by each subject’s MRI. An average image of the seven individual MRIs after non-linear transformation to Talairach space was also generated for the purpose of displaying the data.

Statistical parametric mapping (SPM96; Friston et al., 1995) was used to identify voxels that showed a statistically significant correlation between rCBF change and the proportion of rotated stimuli in each scan. A multi-study covariate design with one subject (and eight scans) per study was used, as this allows for intersubject scaling of global CBF. The percentage of rotated trials in a scan was entered as the covariate of interest, following the standard SPM study-specific ANCOVA (analysis of covariance) normalization of global CBF. Significant correlations were chosen after a Bonferroni-like correction for the number of independent resolution elements in the brain volume. This calculation was determined using the SPM smoothness estimator (Friston et al., 1994). For areas of the brain for which we had no prior hypotheses, significant activations were defined as those having a Z score >4.3 (P_{uncorr} < 0.05), whereas for areas of the brain about which we had prior hypotheses (e.g., parietal lobe, dorsolateral frontal lobe, caudate nucleus), significant activations were determined using a lower threshold (Z = 1.64, P_{uncorr} < 0.05).

Results

Behavioural data

An analysis of reaction time across orientations was conducted in order to verify that subjects engaged in mental rotation for the duration of the experiment. Data for orientations with the same absolute angular displacement from the vertical (e.g., 40° and 320°; 80 and 280°; 120 and 240°; 160 and 200°) were combined, giving five orientations used for analysis (0, 40, 80, 120 and 160°).

The computer only recorded responses given within the 2 s time limit. The seven subjects missed a total of 93 trials (5.2%). A further 12 trials (0.67%) in which reaction time was <500 ms and which followed a missed trial were treated as a delayed response to the previous stimulus and excluded from the analysis. As expected, subjects showed an increase in reaction time as a function of rotation angle (Fig. 1). The mean reaction times for the group were subjected to one-way ANOVA (analysis of variance) with angle of rotation as repeated measures. This revealed a significant linear trend [F(1.6) = 86.13, \( P < 0.0001 \)] with no quadratic component [F(1.6) < 1]. The mean difference in reaction time between the 0 and 160° orientations was 292 ms, implying a mental rotation rate of 547°/s. This rate is within the range of 164–800°/s (mean, 400°/s) reported by Cooper and Shepard (Cooper and Shepard, 1973) and others for the mental rotation of alphanumeric characters. Thus, we can be confident that our subjects were actively engaging in mental rotation throughout the PET experiment.

PET scanning data

There was only one area where changes in rCBF were significantly correlated with mental rotation task demands. This area was located in the right posterior parietal lobe (Talairach coordinates 30, −68, 44; Z = 3.73, P_{uncorr} < 0.0001). As shown in Fig. 2, the activation was centred on the intraparietal sulcus. There was a 3% increase in relative rCBF at this location between the 10% condition (59.5 ml/100 g/min) and the 100% condition (61.3 ml/100 g/min). Lowering the significance threshold to Z = 1.64 (P_{uncorr} < 0.05) failed to reveal additional activations in other areas about which we had prior hypotheses (i.e. left parietal lobe, frontal lobe, caudate nucleus). A small area of activation was apparent in the left parahippocampal gyrus (Talairach coordinates −18, −40, 0; Z = 2.93), but this did not reach the significance threshold set for areas about which we had no prior hypotheses.

Discussion

In this experiment we attempted to specify the brain areas critical for mental rotation, using a parametric design in which we varied the mental rotation demands in an incremental fashion, while keeping all other aspects of the task constant. We isolated one area in the right posterior parietal lobe, centred on the intraparietal sulcus, where rCBF changes were significantly correlated with the mental rotation demands of the task.

We have good evidence that our result reflects neural
Right parietal lobe and mental rotation

Fig. 2 Areas of statistically significant rCBF changes for the group of seven subjects, superimposed on the average MRI of the group. The right of the image corresponds with the subjects’ right. (A) Transverse images through the brain are shown, with distances from the intercommissural (AC–PC) plane as indicated. The only region of statistically significant change ($Z = 3.73, P_{uncorr} < 0.0001$) is situated in the right posterior parietal lobe. (B) Orthogonal images of the activated area (Talairach coordinates, 30, −68, 44). The colour Z scale on the right applies to panels A and B. (C) Surface-rendered view of the activated area in the right posterior hemisphere showing the activation to be centred on the intraparietal sulcus. The statistical threshold of the PET image was lowered to $Z = 1.64$ and the PET and MRI were fused and then surface-rendered at a depth of 12 pixels to enable visualization of the activation just below the cortical surface.
activity related to mental rotation because the reaction time data collected bear the characteristic signature of a mental rotation function. Response time increased linearly as a function of orientation, and the subjects’ rotation rates were similar to those previously reported for the mental rotation of familiar 2D stimuli (Cooper and Shepard, 1973, 1975; Jolicoeur, 1985; Corballis and Cullen, 1986). Furthermore, the experimental design ensured that the only difference between scanning conditions was the proportion of stimuli that had to be rotated to the upright. The conditions did not differ with respect to the identity and number of stimuli, or the response required. In addition, given that the nature of the task and the instructions were the same in each condition, it is unlikely that subjects would have altered their strategy across conditions. A further advantage of our parametric design was that, even if other mental processes changed between conditions, it is unlikely that they would have varied systematically in the manner predicted for the rotation parameter. Therefore, we can confidently attribute the right parietal activation to the mental rotation component of the task.

**Comparison with other mental rotation studies**

Our findings are consistent with those of a recent study that recorded event-related potentials in normal volunteers during a similar mental rotation task (Pegna et al., 1997). These authors reported a significant correlation between the degree of mental rotation required and the duration of an event-related potential component identified at the right parieto-occipital recording site. Thus, their event-related potential findings complement our PET results in identifying a systematic relationship between mental rotation demands and neural activity in the right posterior parietal cortex.

The present findings are also consistent with those of studies of patients with brain lesions that have shown mental rotation abilities to be impaired after damage to the posterior right hemisphere (Ratcliff, 1979; Farah and Hammond, 1988; Ditunno and Mann, 1990). In some of these studies the size of the lesion was too large to allow precise localization, but one study (Ditunno and Mann, 1990) identified mental rotation deficits in patients with lesions confined to the right parietal lobe. A right-hemisphere advantage for mental rotation was also found in experiments with a split-brain patient (Corballis and Sergent, 1988, 1989a, b), in some divided visual field studies with normal subjects (Cohen, 1975; Corballis and McLaren, 1984; Ditunno and Mann, 1990) and in early cerebral blood flow studies (Papanicolau et al., 1987; Deutsch et al., 1988), although of course these techniques do not allow accurate localization within the right hemisphere.

In contrast to the findings outlined above, Mehta and Newcombe found that mental rotation abilities were impaired after left rather than right hemisphere lesions (Mehta and Newcombe, 1991), and some divided visual field studies have likewise found a left hemisphere advantage (Corballis and McLaren, 1984; Fischer and Pellegrino, 1988). However, whereas the studies that reported impairments after right-hemisphere lesions all used single 2D shapes as stimuli, Mehta and Newcombe employed pairs of drawings of 3D shapes similar to those used by Shepard and Metzler (Shepard and Metzler, 1971). It has been proposed that the contribution of the left hemisphere to spatial processing may depend on the complexity and familiarity of the stimulus and the nature of the task (Kosslyn, 1994; Corballis, 1997). For instance, comparing complex stimuli may be accomplished in a piecemeal fashion by focusing on particular salient features rather than the global shape of the stimulus, and this type of processing is more likely to involve the left hemisphere (Corballis, 1997). Moreover, there is some evidence that the left hemisphere becomes more adept at mental rotation with practice (Corballis and Sergent, 1988; Fischer and Pellegrino, 1988). This may account for some of the conflicting findings, as the subjects in different experiments were not equally proficient at the mental rotation tasks.

Differences in stimuli and experimental paradigms may also account for the discrepancy between our findings and those of other functional imaging experiments. Studies that employed pairs of 3D rotated stimuli found bilateral parietal activation during mental rotation (Cohen et al., 1996; Tagaris et al., 1996, 1997; Kosslyn et al., 1998), whereas we used single 2D alphanumeric stimuli and found only right parietal activation. Overall, the majority of the published evidence favours a preferential role for the posterior right hemisphere in mental rotation (at least for familiar 2D stimuli), with increasing contributions from the posterior left hemisphere as the task becomes either more complex or more practiced.

The difference in patterns of activation among functional imaging studies may also be due to other factors not directly related to the mental rotation process. For example, Just and Carpenter demonstrated that, for tasks employing pairs of complex stimuli, the number of saccades increases as the angular disparity between stimuli increases (Just and Carpenter, 1985). This implies that, in experiments using such paradigms, the pattern of eye movements in the rotation condition may differ from that in the control condition. There is good evidence from electrophysiological studies of the monkey cortex, as well as studies of patients with brain lesions and functional imaging experiments with normal subjects, that the superior posterior parietal cortex is involved in directing eye movements towards visual targets (Balint, 1909, translated by Harvey, 1995; Holmes and Horrax, 1919; Andersen, 1989; Anderson et al., 1994). Thus, it is possible that the bilateral parietal activations identified in studies that used pairs of complex stimuli reflect activity related to eye movements in addition to right-sided activity specific to the mental rotation process.

Our results did not confirm Alivisatos and Petrides’ finding of left parietal activation during mental rotation of alphanumeric characters (Alivisatos and Petrides, 1997). The difference between our finding and theirs cannot be explained by differences in the stimuli used, patterns of eye movements...
or the nature of the task, as these were all similar in the two experiments. The most obvious difference between the two studies is in the experimental design: Alivisatos and Petrides used a subtraction paradigm, based on the assumption of pure insertion, whereas we used a parametric design. As mentioned in the Introduction, the assumption of pure insertion of the mental rotation process in a mirror discrimination task may be inappropriate (Ilan and Miller, 1994). This raises the possibility that Alivisatos and Petrides failed to isolate the mental rotation component through their subtraction design, and this in itself may explain the different patterns of activation in the two studies.

Another significant difference between their study and our own was that Alivisatos and Petrides only used three orientations in their mental rotation condition (120, 180 and 240°) and gave their subjects practice trials at these orientations (Alivisatos and Petrides, 1997). These particular orientations were selected because they are typically found to be the most difficult (i.e. they induce the longest reaction times) and, therefore, could reasonably be expected to produce the strongest activation. However, there is good evidence that, given sufficient practice, subjects can store representations of stimuli in different orientations, thus reducing the need to rotate the stimuli back to a canonical orientation (Tarr and Pinker, 1989). This has been shown to be the case particularly for the more difficult orientations and when a block of trials contains highly predictable orientations (Gauthier and Tarr, 1997). Alivisatos and Petrides did not report reaction time data, and the possibility that their subjects were not consistently using a mental rotation strategy cannot, therefore, be ruled out. This may explain why they did not find significant activation in the right parietal lobe, assuming that this area is involved in mental rotation, as our experiment suggests. If this is the case, the left parietal activation found by Alivisatos and Petrides may reflect the encoding of new orientation-specific representations of the characters used in the experiment, rather than mental rotation per se. Although speculative, this is not an unreasonable explanation: the region of the left parietal lobe activated in Alivisatos and Petrides’ experiment included the supramarginal gyrus, which is thought to be responsible for storing letter representations and for phoneme-to-grapheme conversion (Roeltgen, 1983; Penniello et al., 1995). In our experiment, the eight stimuli were presented in eight rotated orientations, making it more difficult for our subjects to encode the 64 different orientation-specific representations during the course of the experiment. Therefore, we argue that our subjects would have been forced to maintain a mental rotation strategy, a contention supported by our reaction time results.

A possible role for the right intraparietal sulcus in mental rotation

Although we found that the right intraparietal sulcus is important for mental rotation, we do not wish to claim that this area necessarily represents a dedicated mental rotation module in the brain. Rather, we will briefly review evidence that the intraparietal sulcus and the superior parietal lobule are involved in implementing a variety of visuospatial transformations and suggest that mental rotation is one of the operations that recruits such transformations.

First, electrophysiological studies of the monkey parietal cortex have shown that the lateral intraparietal sulcus, contains neurons that anticipate the retinal consequences of an intended saccade and fire tonically in response to the memory trace of a visual stimulus (Gnadt and Andersen, 1988; Duhamel et al., 1992). These properties result in a dynamic remapping of retinal information to provide a continuously accurate coding of the location of objects relative to the observer. Secondly, cells in a neighbouring part of the intraparietal sulcus, the anterior intraparietal area, respond selectively to the size and/or orientation of an object, as well as responding to hand and finger movements appropriate for those properties (Sakata et al., 1992). Finally, a third area of the intraparietal sulcus, the ventral intraparietal area, contains neurons that respond strongly to moving stimuli and that code both the direction and the speed of motion (Colby et al., 1993). Recent experiments have also revealed the existence of rotation-sensitive neurons in the posterior parietal cortex of the monkey (Sakata et al., 1994). Evidence from patients with brain lesions and from functional imaging experiments indicates that the intraparietal sulcus and the superior parietal lobule subserve similar functions in humans (Perenin and Vighetto, 1988; Milner and Goodale, 1995; Petit et al., 1997). Therefore, as suggested previously (Stein, 1992; Milner and Goodale, 1995), these regions seem to mediate the visuospatial transformations necessary for our accurate moment-to-moment interaction with the environment.

Our finding of a correlation between mental rotation and neural activity in the right intraparietal sulcus can be interpreted as evidence that mental rotation recruits visuospatial transformations that are implemented in this brain region. Consistent with this, a recent PET study reported increased activation specifically in the right intraparietal sulcus during the early phase of learning to compensate for a rotational displacement when reaching towards a target (Inoue et al., 1997). An inability to invoke such transformation processes may also explain why patients with right parietal lesions often fail to recognize objects seen from unusual perspectives (Warrington and Taylor, 1973). Further research investigating the relationship between rotation of alphanumeric characters versus other kinds of stimuli and directly comparing experimental paradigms may help to clarify the relative contributions of the left and right hemispheres to these transformation processes.

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