Graded Functional Activation in the Visuospatial System with the Amount of Task Demand

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Abstract

♦ Two studies examined how the amount and type of computational demand are related to fMRI-measured activation in three bilateral cortical regions involved in the Shepard-Metzler (1971) mental-rotation paradigm. The amount of demand for the computation of visuospatial coordinates was manipulated by presenting mental rotation problems with increasing angular disparity (0, 40, 80, or 120°). Activation in both the left and right intraparietal sulcal regions increased linearly with angular disparity in two separate studies. Activation also occurred in the fusiform gyrus and inferior temporal regions, regions that are primarily associated with the processes of object and object-part identification. By contrast, the demand for object recognition and

rotation processes was relatively low, and the demand for executing saccades was high in a control condition that required making a systematic visual scan of two grids. The grid-scanning condition resulted in relatively less activation in the parietal and inferior temporal regions but considerable activation in frontal areas that are associated with planning and executing saccades, including the precentral gyrus and sulcus into the posterior middle frontal region. These data suggest that the amount of activation in the various cortical regions that support visuospatial processing is related to the amount, as well as to the type, of computational demand. ♦

INTRODUCTION

Functional neuroimaging studies typically measure cortical activation to assess the involvement of a particular region in a given task. The qualitative properties of the task are assumed to be critical to the pattern of activation. The current study goes beyond the qualitative aspects to examine the quantitative properties of the task demand. More specifically, we relate the graded amount of rotation task demand, as expressed in a computational model of mental rotation, to the amount of cortical activity in specific areas, as measured with functional magnetic resonance imaging (fMRI). The major objective is to determine how the amount of neural activation in a network of brain regions is modulated by the amount of mental rotation that is required in a given condition. This network consists at least of the left- and right-hemisphere intraparietal regions (part of the dorsal stream or the so-called where system), as well as the left and right ventral (what) stream of processing, and the motor system that is involved in guiding eye movements. The results indicate how this network of areas works together to perform a spatial thinking task, dynamically varying the contribution of a given area or subsystem with the particular demands of a given set of stimulus items.

Before outlining the predictions in more detail, we briefly describe the paradigm and the computational model and their mapping to the neural level of functioning. In a typical mental rotation paradigm, a participant judges whether two pictures depict either the same object (but possibly at different orientations) or two mirror-image isomers of the object (Arnoult, 1954; Shepard & Metzler, 1971), as illustrated in Figure 1. Participants report that they imagine one figure rotating into the orientation of the other figure, and the average decision time increases monotonically with the angular disparity between two pictures of the same object (Shepard & Cooper, 1982; Shepard & Metzler, 1971). Shepard proposed that during mental rotation, the represented orientation of the object passes through at least some intermediate states corresponding to intermediate orientations, abstractly isomorphic to aspects of a physical rotation of an object. The present research focuses on the functional properties of the rotation process and their implementation in the cortical neural systems. The computational model of the task performance provides a hypothesized decomposition of the component cognitive processes that are required to perform the task, beyond the rotation process itself.
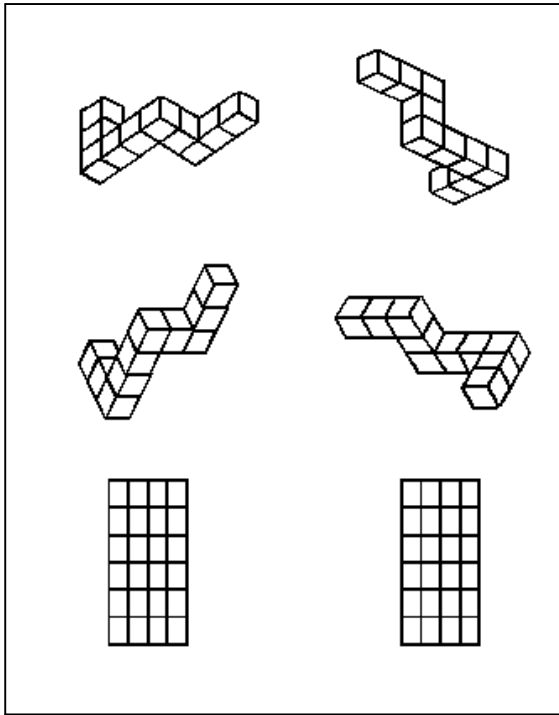
Figure 1. Example problems involving 80° of angular disparity, two mirror image figures, and the grids used in the grid-scanning condition.

its representation and that of its tentative counterpart in the target figure are sufficiently similar in orientation for their figural identity to be compared. As the amount of required mental rotation increases, there is an increase in the activation resources needed to support the computation of additional orientations and the maintenance of intermediate representations. For example, mentally rotating a figure through 120° requires more activation resources than mentally rotating it through 40° because the figure is represented at a greater number of intermediate orientations. If such functional resources have correlates at the neural level, mental rotation tasks that are more demanding of resources may also engender more activation in the neural systems that implement the computations.

The functional resources in the computational model may have multiple correlates in the cortical systems, including the neuronal, circulatory, and glial components that ensure appropriate neurotransmitter and metabolic functioning of the cortical systems that perform the various computations. The expenditure of neural resources may even depend on the structural connectivity that ensures the coordinated communication of the parallel and serial networks that subserve the visuospatial computations. The fMRI-activation measure is interpreted as assessing one facet that relates to the activation level of the large-scale neural networks that implement such computations.

The mapping from the computational model to the activation of large-scale neural systems entails three visuospatial systems of primary interest. The major focus is on the so-called where system, a processing stream that is thought to project from the occipital cortex to the parietal region and that participates in the computation of extrapersonal and personal spatial localization (Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Haxby, 1994). This system is expected to play a primary role in mental rotation because performance requires the computation of the spatial coordinates of the object being mentally rotated and its comparison to the represented coordinates of the target object. A second relevant system, the so-called what system, is associated with a stream that projects from the occipital region to the inferior temporal gyrus and participates in the computation of object identity. These two systems may interact with each other and with a third set of systems, namely, the motor systems that compute the head and eye movements in response to internal switches of attention. Such eye movements can occur in response to the visuospatial computations of mental rotation (Just & Carpenter, 1976). In simple tasks requiring visually guided saccades, these motor systems activate regions in the precentral sulcus (Luna et al., 1998); in the present research, the relevant area includes the precentral gyrus, the posterior middle frontal gyrus, and other areas around and including the interhemispheric fissure.

Furthermore, the model provides a theoretical measure of the duration of the processing as a function of angular disparity, as wen as individual differences in response times and errors (Carpenter & Just, 1997; Just & Carpenter, 1985). The model is expressed in 3CAPS, an activation-based hybrid architecture that has proven useful for simulating high-level cognition. A recent development in the simulation architecture is the incorporation of a resource dimension to implement the theoretical claim that mental computations and information maintenance are accompanied by the consumption of activation resources (Just & Carpenter, 1992).

In the computational model, resources are construed as a limited amount of activation that fuels both processing and the temporary maintenance of intermediate products. Representational elements have associated activation levels that can be incremented or decremented. A representational element is considered to be activated when its activation level is above some threshold, at which time the presence of that element can participate in initiating other processes. The elements include representations of objects, object parts, and spatial operations, each of which can be thought of as constituting complex processing networks. Processes such as mental rotation are implemented as increases or decreases in the activation levels associated with the representation of an encoded segment of a figure at successive orientations (differing by fairly large steps) until

The hypothesis that the parietal region is particularly implicated in computing spatial coordinates during mental rotation is supported by both neuroimaging and event-related potential (ERP) studies. In a study involving the Shepard-Metzler rotation task, fMRI-measured activation was found in the left and right parietal regions [Brodmann's areas (BA) 7a and 7b and sometimes BA 40] when a rotation condition was compared to a 0° rotation condition (Cohen et al., 1996). Parietal involvement has also been found in several ERP studies of a simpler rotation task in which participants judged whether a letter was normal or mirror-imaged (Desrocher, Smith, & Taylor, 1995; Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989). AU three studies found that as the angular disparity increased, there was increasing negativity in the ERP waveforms in the latency range of 350 to 800 msec, particularly in the parietal and occipital leads, which was interpreted as reflecting rotation. Systematic effects are also found in central leads (Desrocher et al., 1995; Roshler, Heil, Bajric, Pauls, & Henninghausen, 1995) and occipital leads (Peronnet & Farah, 1989), but the effects are more pronounced over the parietal leads. Finally, a PET study found activation in the left posterior-superior parietal cortex when comparing the activation during the mental rotation of letters to a condition requiring a simple discrimination of normal and mirror- image upright letters (Alivisatos & Petrides, 1997). These studies all implicate the parietal region in some aspect of rotation. The current study examines how the FMRI- measured activation varies as a function of increasing task demand, as operationalized by increasing amounts of mental rotation.

Although the theoretical analysis of mental rotation tasks understandably focuses on the rotation or mental transformation of orientation, the eye fixation studies and the computational model make it clear that object-identification processes also participate in that task (Carpenter & Just, 1976; Just & Carpenter, 1985). At least in the case of figures of this degree of structural complexity, the figure segments are identified and locally matched to determine which initial segments are to be rotated into alignment. After this initial encoding, subjects appear to focus on one particular structural segment of each figure, alternating their point of regard between the two potentially corresponding segments in the two depictions of the figures. This segmentation and attempt to find potentially corresponding segments of the two figures could centrally involve the ventral object recognition system. Also, after the mental rotation of the segments, the representations must be maintained at successive spatial orientations, and at each step, they are compared to determine the orientation similarity between the segments. Finally, once each major segment has been rotated, the subject must decide whether the major segments are identical in their structural arrangement. Thus, the paradigm involves extensive recognition and comparison of objects and object parts.

This analysis leads to the prediction that there should be activation in the object recognition system, the system that is most closely associated with the processing stream that projects from the occipital lobe to the fusiform gyrus and the inferior temporal region.

Besides the processing of figural structure and orientation, the task clearly involves eye movements and the associated cortical activity. This study includes a control condition in which participants systematically scanned back and forth between two 2-dimensional grids, looking between corresponding cells in the grids. The grids have the same number of lines and the same mean angular separation as the figural stimuli. This control grid condition provides a comparison to the eye movements in the rotation conditions. The grid-scanning task is "difficult" by a time-based measure because it requires figure encoding, visual scanning and matching, and the execution of numerous eye fixations. However, because the grids are constant across trials and the scanning pattern is fixed, there should be relatively little computational demand on the systems that compute the figure's spatial coordinates or the object's identity. If fMRI-measured activation is a function of computational demand, rather than simply due to a time-based measure of difficulty, there should be less activation in the where region associated with computing the spatial orientation of the encoded grids. By contrast, the cortical motor regions involved in the planning and execution of eye fixations may show more similar amounts of fMRI-measured activation in the rotation and grid-scanning conditions. Indeed, PET studies have shown that the execution of either visually guided saccades or prelearned horizontal saccades (compared to fixation of an imagined central point) activates similar subcortical and cortical regions, including cortical motor areas and also parts of the superior parietat cortex (Petit, Orssaud, Tzourio, Crivello, Berthoz, & Mazoyer, 1996; Sweeney et al., 1996). Thus, the grid-scanning task's emphasis on saccade planning and execution should attenuate the activation differences between it and the rotation conditions in cortical regions that primarily support motor planning and execution.

In sum, the present study assesses fMRI-measured activation in three major cortical regions of interest (ROIs) in each hemisphere: the posterior parietal, the inferior temporal, and the motor regions (including the precentral sulcus and surrounding gyri). These regions are assumed to include large-scale interacting neural networks that together support the computation of visuospatial coordinates, viewer invariant figural identity, and motor planning and execution. Although cortical areas may preferentially support one function, there probably is not a one-to-one association of cortical region to function (Mesulam, 1990). Thus, the predictions concern the relative degree of activation and the modulation of activation by the increased demand for visuospatial computations, as operationalized by the amount of mental rotation required to solve the problem.

The experimental conditions involved a graded manipulation of the amount of angular disparity and hence the amount of mental rotation required, either 0, 40, 80, or 120°, as well as the grid-scanning condition. The steady-state activation in each of several major neural areas for the five conditions was compared to a condition in which the participant simply fixated a central point, which was the baseline condition. Conditions occurred in four separate 25 to 30-sec epochs, appropriately counterbalanced. The two major dependent measures were (1) the number of voxels that were significantly activated compared to the fixation baseline condition using a *t* test (t > 4.5) as a threshold and (2) a measure of the amplitude of the activation, namely, the percentage of increase in the magnetic resonance (MR) signal intensity over the fixation condition baseline level in any voxel (in a ROI) that was significantly activated in any of the five conditions.

An initial study, using a 1.5 Tesla (T) GE scanner and 7 to 9 coronal slices, focused almost exclusively on activation in the parietal region. The second study used the same paradigm with a 3.0T scanner and 14 slices in an axial orientation, which enabled us to quantify the activation in more cortical regions, including most of the inferior temporal region and the frontal regions. Scanning was done at the MR Research Center of the University of Pittsburgh Medical Center.

RESULTS AND DISCUSSION

Response Time and Errors

The response times and error rates increase monotonically with angular disparity from 0 to 120° as shown in Figure 2. The increase is consistent with the hypothesis that larger angular disparities involve the activation of the rotated representation at some intermediate orientations. The slope for the 3.0T study was 914 msec/40° increment (standard error = 98 msec); the slope for the 1.5T study was 1097 msec/40° increment (standard error = 150 msec). Overall, the behavioral results for the two studies are similar to each other and other behavioral data for this task (Just & Carpenter, 1976; Shepard & Metzler, 1971). Also, the average response time for the grid-control condition was relatively long, even greater than the mean for the 120° angular disparity condition, which indicates that the grid condition was successful in eliciting a large number of saccades. The average difference between the response time for the grid condition and the mean of the four rotation conditions was 2040 msec (standard error = 749 msec) for the 3.0T study and 1978 msec (with standard error = 600 msec) for the 1.5T study. In spite of this long mean response time, we will show that the grid condition elicited relatively little fMRI-measured activation in the parietal regions, consistent with the claim that the grid condition makes relatively less demand on the computation of visuospatial coordinates than does the rotation task.

Although the average response time differs among conditions, the epoch durations of the five conditions

Figure 2. The response time and errors increase as a function of the angular disparity of the rotation conditions, consistent with the hypothesized mental rotation process, for both the 3.0T (left panel) and 1.5T (right panel) studies. Also note that the grid condition elicits a mean response time that exceeds that of the 120° rotation condition. The error bars for the rotation conditions are the standard error of the slope of the increase. For the grid condition it is the standard error of the difference between the grid and mean for the rotation conditions.
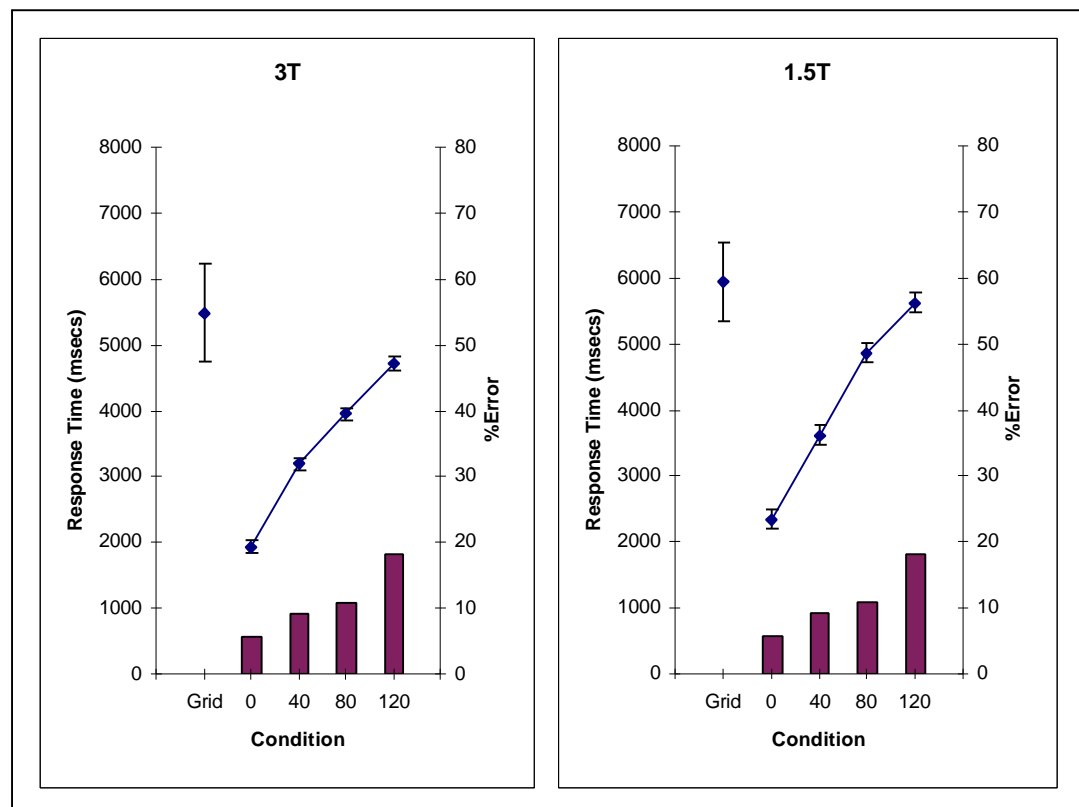
were equated experimentally by presenting more items per epoch for the conditions with shorter processing times per item. In addition, in the data analysis, any residual disparities were removed by truncating the epoch durations to that of the minimum epoch duration across conditions so that differential sampling intervals would not influence the comparisons. These aspects of the study work against the hypothesis to lessen the activation increase as a function of disparity.

The major analyses concerned fMRI-measured activation in three cortical regions in each hemisphere: the parietal region, the fusiform gyrus and inferior temporal regions, and the frontal regions, including the precentral gyrus and sulcus and the posterior middle frontal gyrus and also a few other regions, such as the dorsolateral prefrontal cortex and a region including the interhemispheric fissure. To illustrate how these regions were sampled, Figure 3 shows the placement of 14 axial slices on the midline sagittal image of a typical participant in the 3.0T study. For four individuals, the most superior slice was higher, in order to more completely sample the precentral sulcus and associated motor regions.

Figure 4 illustrates the type of data that were obtained for the grid condition and four rotation conditions (0, 40, 80, and 120°) in three slices for the individual shown in Figure 3. The white areas indicate the voxels that were activated above baseline (the fixation control condition), and these activated voxels are superimposed on the corresponding structural image. The images are displayed using radiological convention-as though one were looking toward the patient from the foot of the bed, with the right side of the image depicting the left hemisphere of the participant. The first row in Figure 4 (slice 2 from the top in Figure 3) is through the centrum semiovale.

The activation is in the area of the precentral sulcus (the frontal eye fields) and along the cortex of the interhemispheric fissure (supplementary eye field), and it tends to be high and similar in the grid and four rotation conditions. The second row, through the cingulate gyrus, shows activation in the intraparietal sulcus and gyri. The number of activated voxels is relatively low in the grid condition and much higher in the rotation conditions, where it tends to increase with angular disparity. As Figure 4 suggests for a single slice, the multi-slice analysis showed that the number of significantly activated voxels in and around the region of the intraparietal sulcus increased with angular disparity. For most of the participants, activation is found continuously through the intraparietal sulcus into the transverse occipital sulcus. The third row, through the inferior temporal-occipital lobes, shows activation to be high in the rotation conditions and lower in the grid condition. This general description of the results is supported by the analyses of multislice ROIs across the participants.

Activation in Parietal Regions

A primary motivation for the study was to test whether larger angular disparities, which consume more activation resources in the computational model, are associated with increased fMRI-measured activation. In the model, mental rotation through larger angular disparities requires the consumption of more activation resources to compute and maintain the coordinates of the figure being mentally rotated, which leads to a prediction of an increase in fMRI-measured activation in the parietal regions.

Figure 3. This shows the positions of the 14 axial slices for a typical individual in the 3.0T study.
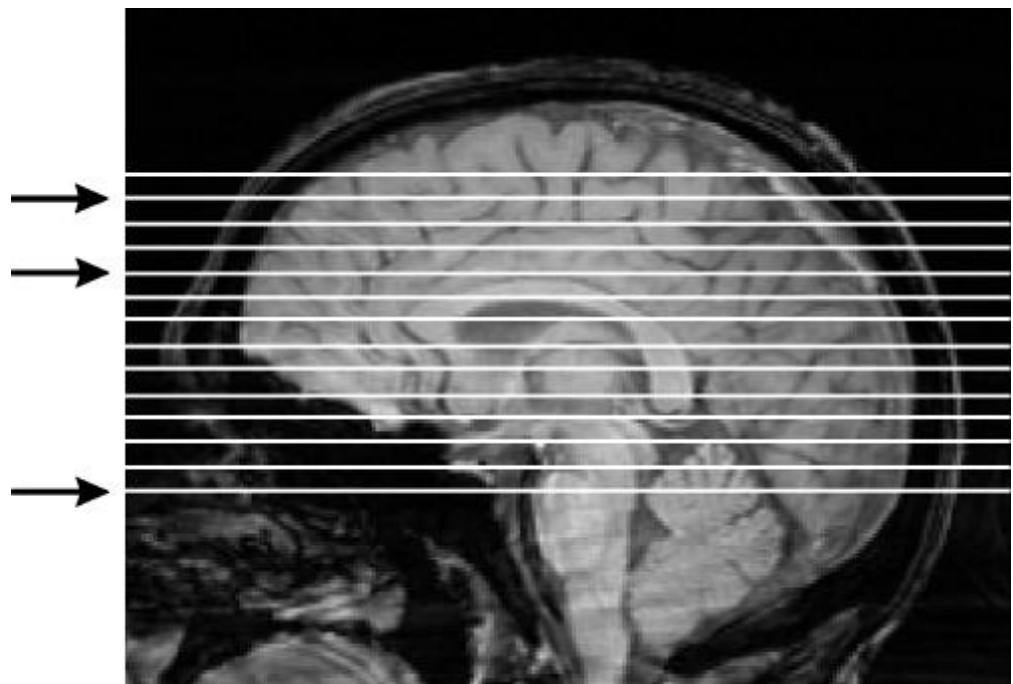
Figure 4. *The pattern of activated voxels for the five experimental conditions (the columns) superimposed on structural images for three slices (the rows) for the individual in Figure 3. The top row, a superior slice, shows some of the activation along the precentral sulcus, which tends to occur in all five conditions. The middle row shows activation in and around the intraparietal sulcus that increases with angular disparity and is very low for the grid condition. The bottom row shows activation in the fusiform gyrus and the inferior temporal region, which tends to be relatively high in the rotation conditions and much less for the grid condition.*
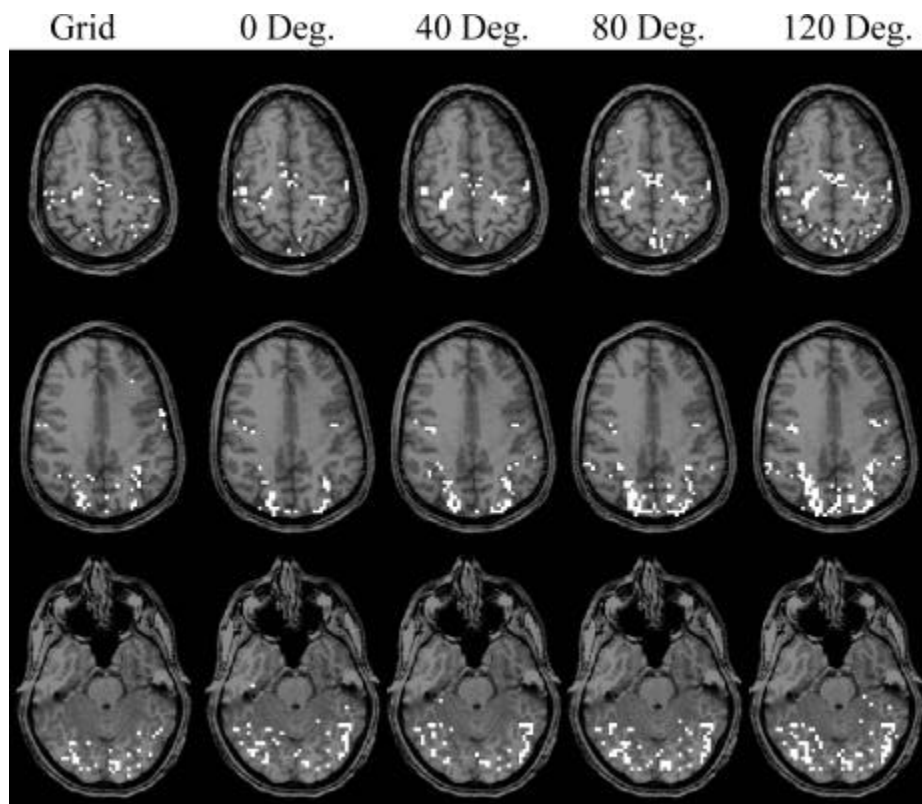

Figure 5 shows that the average number of significantly activated voxels (compared to the fixation baseline condition) increases with angular disparity for the left and right parietal regions for the 3.0T study. A linear contrast of the means for the four main rotation conditions is significant for both the left parietal region ($F(l, 7) = 24.85, p < 0.01$) and the right parietal region ($F(1, 7) = 15.35, p < 0.01$). The overall main effect of the four rotation conditions also is significant, $F(3,21) = 13.32, p < 0.01$, and $F(3, 21) = 6.2l, p < 0.01$, for the left and right parietal regions, respectively, but neither the quadratic nor cubic trends are significant for either data set. The slope of the increase is 13.2 (±2.4) and 9.6 (±2.4) voxels per 40° increment for the left and right parietal regions, respectively. The equivalent expressions in terms of the increase in the volume of activated brain tissue are increases of 14.8 mm^3 per degree and 10.8 mm^3 per degree, respectively. These data demonstrate two important properties. First, the linear trend shows the quantitative impact of the amount of a particular type of task demand on activation as assessed with FMRI, which constitutes major support for the approach. Second, the bilaterality of the effects indicates the involvement of both hemispheres in this visuospatial task. The bilaterality is most asymmetric at O', where the right hemisphere is noticeably more responsive than the left, suggesting that bilaterality may increase with the task's demand.

A second measure of activation is the amplitude of fMRI-measured activation, specifically, the percentage of increase in MR signal intensity over the fixation baseline for voxels in an ROI that were activated above threshold in any of the five experimental conditions. As Figure 5 indicates, the mean percentage increased with angular disparity, with a slope of 0.221%/40° increment (±0.028) and 0.173%/40° increment (±0.037) for the left and right hemispheres, respectively. There is significant variation among the four rotation conditions, $F(3, 21) = 14.75$, $p < 0.01$ and $F(3,21) = 6.86$, $p < 0.01$, and this variation had significant linear trends, $F(l, 7) = 52.51$, $p < 0.01$, and $F(l, 7) = 18.88$, $p < 0.01$, for the left and right hemispheres, respectively. Thus, both the number of activated voxels and their average amplitude of activation show effects of increasing computational demand.

Figure 6 shows a similar increase in the mean number of voxels and in the amplitude of MR intensity for the parietal ROI in the 1.5T study.[1] The number of voxels significantly activated above the rest condition increases linearly with angular disparity. The rate of increase was 6.4 (±1.6) and 5.6 (±1.2) voxels/40° increment for the left and right parietal regions, respectively. A linear contrast among the rotation means was significant for both the left parietal ($F(l, 8 = 12.86$, $p < 0.01$) and the right parietal regions ($F(l, 8) = 16.27$, $p < 0.01$), and the overall variation among the four rotation conditions is significant for the left parietal

Figure 5. The average number of activated voxels for the left and right parietal regions increase as a function of the increase in angular disparity (left panel) and so does the mean percentage of increase in MR signal intensity over the fixation condition (right panel) for the 3.0T study. By contrast, the grid condition results in relatively few voxels that are significantly activated and a significantly lower increase in mean activation level. The results for the right hemisphere are shown by filled symbols and for the left, by open symbols.[2]
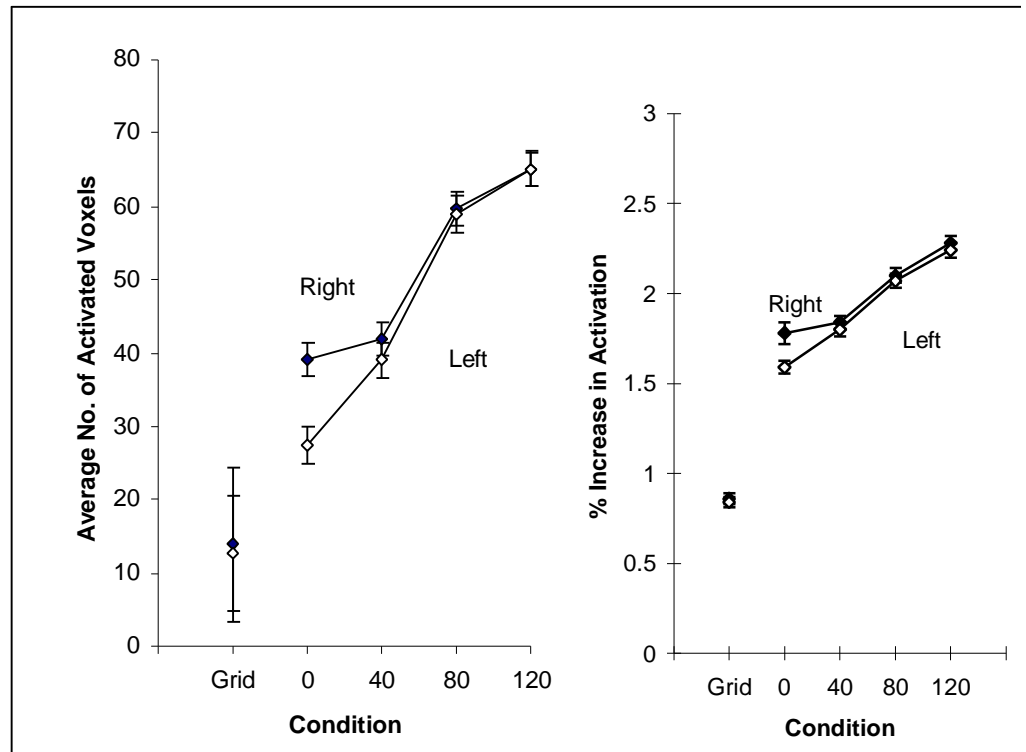
$(F(3,24) = 9.20, p < 0.01)$ and right parietal regions $(F(3,24) = 7.26, p < .01)$, and neither the quadratic nor the cubic trends were significant for either region.

The amplitude of the activation over the baseline condition also increased significantly with angular disparity, as it did in the 3.0T study, with a slope of 0.285%/40° increment (±0.048%) and 0.187%/40° increment (±0.029%) for the left and right hemispheres, respectively. For the left parietal region, there was an overall difference among the four rotation conditions,

$F(3, 24) = 19.64, p < 0.01$, and this increase had a significant linear trend, $F(1, 8) = 35.45, p < 0.01$. For the right parietal region, there was also an overall difference, $F(3, 24) = 12.83, p < 0.01$, and this increase also had significant linear and quadratic trends, $F(1, 7) = 43.98$ and 4.51. In sum, both studies showed a monotonic increase in the number of voxels and the amplitude of fMRI-measured activation in the parietal regions as a function of the amount of mental rotation. The increase supports the hypothesis that the amount of cortical activation is modulated by the

Figure 6. The average number of activated voxels for the left and right parietal regions increase as a function of the increase in angular disparity (left panel) and so does the mean percentage of increase in MR signal over the fixation condition (right panel) for the 1.5T study. By contrast, the grid condition results in relatively few voxels that are significantly activated and a significantly lower increase in mean activation level. The results for the right hemisphere are shown by filled symbols and for the left, by open symbols.
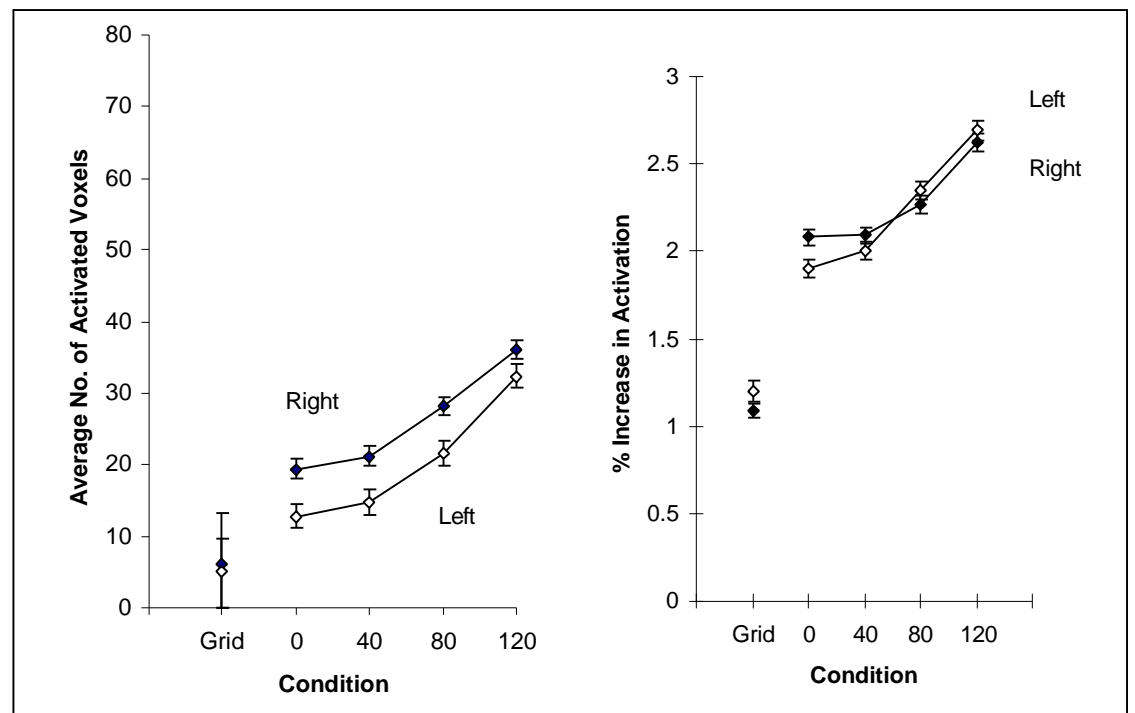
relevant task demand, as operationalized here by the amount of mental rotation.

A second purpose of this study was to contrast the effect of the grid-scanning condition to that of the rotation conditions. As predicted, the grid condition activated relatively few voxels (12.6 for the left and 13.9 for the right in the 3.0T study, and 5.0 for the left and 6.1 for the right in the 1.5T study) and produced small increments in signal intensity (averaging 0.86% for the 3.0T and 1.15% above baseline for the 1.5T study). These indices of activation were lower than those obtained for the mean of the rotation conditions, in spite of the higher response times for the grid condition. Figures 5 and 6 show the associated standard errors of the mean for the difference between the grid and mean of the four rotation conditions bracketing each of the relevant measures for the grid condition. The lower level of activation for the grid condition is consistent with lesser computational demand associated with scanning grids in fixed positions compared to the demand required to compute and compare the coordinates of two unusual objects on each trial in the rotation conditions. More generally, the low level of fMRI-measured parietal activation for the grid condition illustrates how a process may take time but not necessarily make certain types of computational demands and, correspondingly, not consume activation in the model.

Most of the voxels that are activated in the various conditions may be seen as drawn from overlapping pools of voxels rather than from spatially distinct voxels that are particular to a condition. On average, 85% of the voxels that were significantly activated in one condition were also activated in at least one of the other five conditions in the 3.0T study. The complementary set, the proportion of voxels that were significantly activated in only one condition, increased with angular disparity. Eight percent of the voxels activated in the 0° condition were not activated in any other condition. For the 40°, 80°, 120°, and grid conditions, the corresponding percentages were 12, 15, 20, and 20%, respectively. Of course, the overlap is also a function of the resolution of the neuroimaging technique, and it is conceivable that with a higher level of resolution, there would be less measurable overlap associated with the different rotation conditions. In addition to the increases in the number of activated voxels, the larger angular disparities also involve significantly higher increases in the amplitudes of activation, which is also consistent with the postulated greater demand on visuospatial computations.

These neuroimaging results are consistent with previous ERP studies of mental rotation described in the introduction that have shown evidence of increased activity in the parietal region as a function of the degree of angular disparity in mental rotation. Finally, although we have focused on mental rotation, there is reason to believe that the parietal region is involved in spatial transformations beyond rotation. For example, one ERP study found substantially similar parietal ERPs for both mental rotation and mental size scaling (when the two stimuli differ in size) (Rosler et al., 1995).

The similarity suggests that the parietal lobe is involved in other types of spatial transformations, and it is consistent with the more general characterization that this region is implicated in the computation of spatial orientation and position.

Activation in Inferior Temporal Regions

In performing the mental rotation task, the computational model attempts to match up potentially corresponding segments of the two figures, leading to the prediction that there should also be activation in the what system, a system that is associated with the inferior temporal regions. We examined the degree to which this system was activated in the mental rotation conditions compared to the grid-scanning condition. Although the grid condition involves extensive figural matching, the demand to compute novel figural information is relatively low because the two-dimensional grids are much less complex than Shepard-Metzler figures, and the grids and their positions are invariant across trials. As predicted, the rotation conditions led to significantly more activation in the inferior temporal ROIs, an average of 62.6 voxels activated, compared to 9.3 voxels for the grid condition, combined across the two hemispheres. A difference in the same direction (albeit smaller) was found in the 1.5T study as well (15.1 versus 9.2 voxels for the rotation versus grid conditions, respectively), al- though that study involved only the more posterior inferior temporal region by virtue of the limited number of coronal slices. By definition, the inferior temporal ROI included multiple anatomical areas, including the fusiform gyrus and the inferior temporal lobe, and it was difficult to determine the degree to which activation appeared continuously or in distinct subregions.

In both studies, although a relatively large number of voxels was significantly activated above rest, the number did not vary systematically among the four rotation conditions, as shown in Figure 7. The amplitude of activation increase did not vary systematically with rotation angle in the left inferior temporal ROI in either study, but there was marginally significant variation in the right ROI that had a slight linear trend for the 3.0T study ($F(1, 7) = 3.31$), with an increase of 0.074%/40° increment and a quadratic trend for the 1.5T study ($F(1, 8) = 1.89$ and 11.38 for the linear and quadratic trends, respectively). The fact that the right inferior temporal region shows a similar but not identical pattern to the left is consistent with the patient studies reviewed by Farah (1990), who showed asymmetries in the type of recognition proc- esses most strongly associated with lesions of the occipital-temporal region of the two hemispheres. The increase in the amplitude of activation for the higher angular disparities for the right ROI is consistent with the existence of feedback and feedforward relations between the where and what systems. One tentative hypothesis is that mental rotation is accomplished by the coordination of activation in both the what and where systems.

Figure 7. The average number of activated voxels for the left and right inferior temporal ROIs are elevated for the rotation conditions, as is the mean percentage of increase in MR intensity over the fixation condition (right panel). By contrast, the grid condition results in relatively few voxels that are significantly activated and a significantly lower increase in mean activation level. The results for the right hemisphere are shown by filled symbols and for the left, by open symbols. The data in both panels are for the 3.0T study.
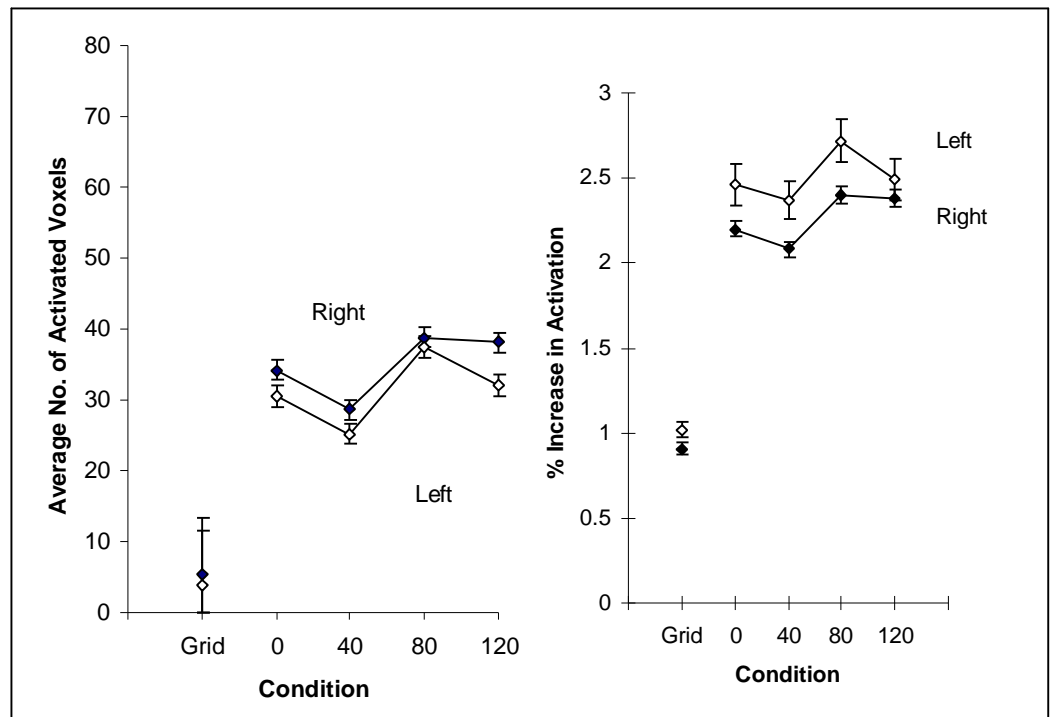
The inferior temporal region may subserve not only viewer-invariant object identification but also to a lesser extent, the computation of orientation. Of course, the presence or even the pattern of fMRI-measured activation as a function of condition does not uniquely identify the particular types of computations occurring in any area. The presence of the inferior temporal activation clearly indicates the involvement of the system, but the results do not specify its computations.

Activation in Frontal Regions

The grid condition was designed to increase the amount of motor activity (specifically, the number of saccades) compared to the rotation conditions while imposing relatively little computational demand for determining the location of the figural display or the associated eye fixations. To compare the activation associated with

Figure 8. The average number of activated voxels (left panel) and the mean percentage of increase in MR intensity (right panel) for the left and right frontal ROIs are elevated for the rotation conditions and for the grid-scanning condition. The grid condition was designed to particularly involve a relatively large number of saccades. In spite of this, there is still a slightly higher level of activation for the rotation conditions for both measures, the number of activated voxels, and the amplitude of activation increase. The results for the right hemisphere are shown by filled symbols and for the left, by open symbols. The data in both panels are for the 3.0T study.
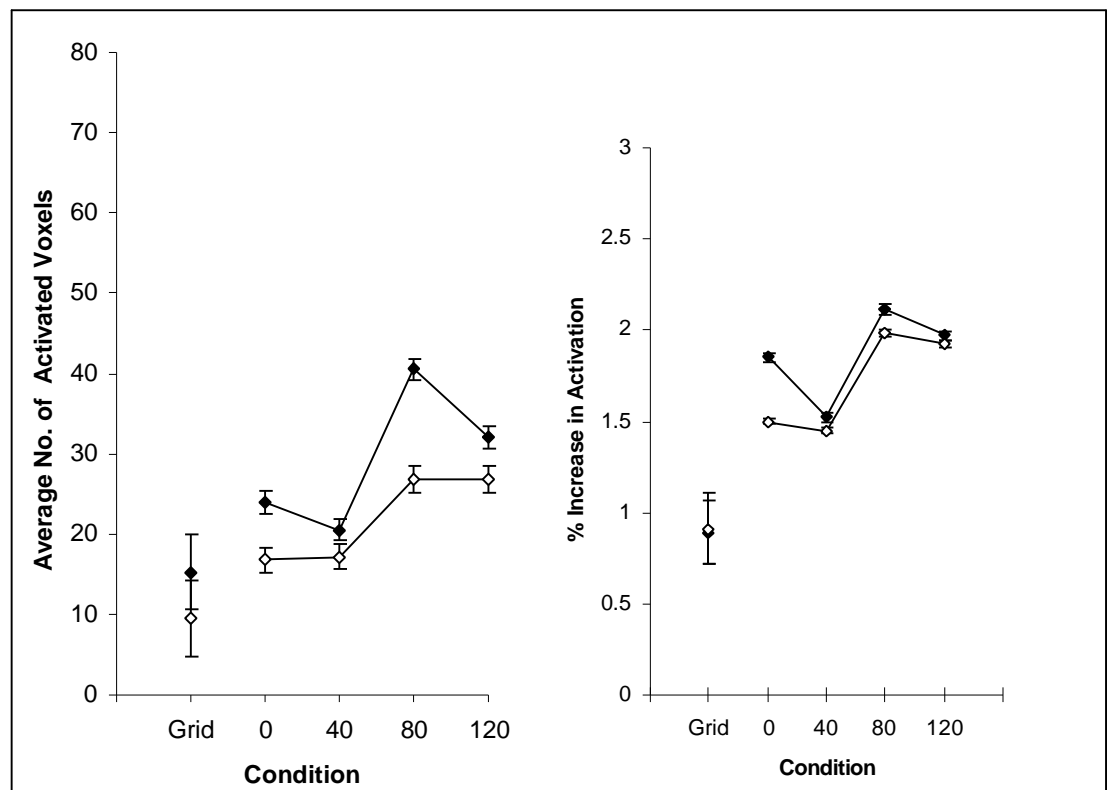
oculomotor activity, we quantified the fMRI-measured intensity of a 'frontal-motor" ROI that included the precentral gyrus and sulcus and the posterior middle frontal gyrus, which formed one region of continuous activation, and for ROIs that included the interhemispheric fissure and the dorsolateral prefrontal cortices for four individuals in the 3.0T study.

Figure 8 shows the average number of significantly activated voxels and the amplitude of the MR signal increase for the grid condition and the four rotation conditions for the frontal-motor ROI. The rotation conditions are associated with much higher levels of activation than the grid condition, even though the grid condition was designed to involve a large number of saccades, even more than the average rotation condition. The greater activation for the rotation conditions occurs when all five conditions are truncated to an equal duration and when the results are biased in favor of the grid condition by comparing the activation for the longer, untruncated grid condition to that for the rotation conditions that have been truncated. This difference suggests that the so-called motor regions are not simply involved in motor planning and execution. The amount of activation in the frontal region may also reflect the greater computational demand in computing the object's spatial presentation in the rotation conditions.

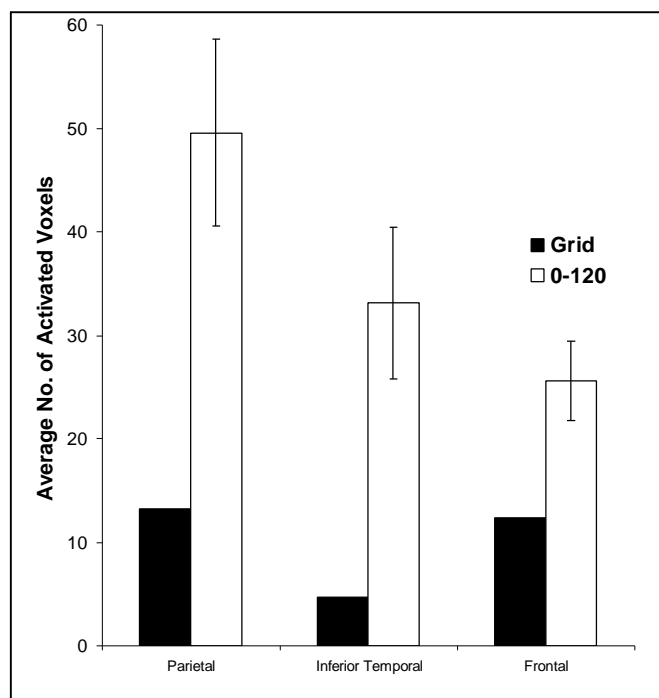Although the frontal regions show the effect of rotation

demand, the difference between the grid condition and the rotation condition is certainly less for the frontal ROIs than it is for the parietal or temporal ROIs. Figure 9 shows the average number of activated voxels for the grid condition compared to the average of the four rotation conditions for each of the three frontal ROIs and for the parietal and inferior temporal ROIs. To conservatively test the significance of this interaction, we added across the precentral sulcus, gyrus, and posterior middle frontal area ROIs because activation is contiguous through these regions. The number of activated voxels in the grid condition compared to the mean of the rotation conditions was significantly more similar for these frontal areas (the precentral gyrus, sulcus, and posterior middle frontal area ROIs) than for the parietal ROI, $t(3) = 3.02$, $p < 0.05$. This interaction suggests that the cognitive computations related to mental rotation have relatively more impact on the parietal and inferior temporal regions than on the frontal regions; the sheer amount of motor movement has more effect on the activation in the frontal regions than in the parietal or inferior temporal regions.

Another frontal region that showed small amounts of activation is the dorsolateral prefrontal cortex, a region that is often associated with executive processing in complex tasks. All four individuals had activation in this region, with a mean number of activated voxels equal to approximately 1 voxel for the rotation conditions and 0.5 voxel for the grid condition. Another compatible interpretation is that some of the frontal regions are implicated in the maintenance of spatial information over short time periods (Goldman-Rakic, 1988; Jonides et at., 1993). Some activation in this region, in combination with activation in the parietal and inferior temporal region, may represent the activation of networks that help maintain and process visuospatial information and, hence, some of the constitute components of a visuospatial working-memory system.

General Discussion

The initial goal of this research was to test for the effect of graded task demand in the computation of spatial coordinates on fMRI-measured activation in the visuospatial system. In addition to obtainning results consistent with this view, the findings also provided an illuminating view of an entire network of cortical areas coactivating in the mental rotation task. We address these two main issues next.

Figure 9. The mean number of activated voxels (averaged across the left and right hemispheres) for each of the major ROIs in the 3.0T study showing the asymmetry between the grid condition compared to the average of the rotation conditions. The asymmetry is much greater for the parietal and inferior temporal ROIs than for the frontal areas, specifically the precentral gyrus, the posterior middle frontal area, and the supplementary motor area.

Graded Activation and Capacity Utilization

The theoretical approach uses the concept of capacity utilization, a concept adopted from economics but which applies to any dynamic system and which relates the amount of demand on a system's resources relative to the supply of resources. In the computational model of mental

rotation, resources are operationalized as the activation that is used in computing and maintaining the object's represented spatial orientations. The consumption of resources may abstractly be taken as an index of the efficiency of a neural system relative to the demand that is being imposed. The implication of this approach is that to understand neural function, the cognitive task analysis must be expanded from a description of the qualitative nature of processes to include a quantitative consideration of the amount of demand across various experimental conditions. The brain activation results are consistent with the conclusion that mental rotation processes make more demand on resources as the rotation angle increases.

The finding that the cortical region most responsive to the manipulation of angular disparity is the parietal area is consistent with the recent fMRI results of Tagaris et al., (1997), which in turn converge with the earlier cited results associating the computation of spatial coordinates with the parietal system. In the Tagaris et al., study, clustering techniques were used to analyze the pattern of activation change in several frontal and parietal neural areas, along with behavioral measures, including error rate and rotation rate. In general, the activation changes in most of the parietal areas clustered more with the behavioral measures, particularly the error rates, than did the activation changes in most of the frontal areas (their oblique slices did not include the inferior frontal regions). Their results and the current ones sup- port the view that the parietal activation relates to the demand imposed by increasing the amount of angular disparity.

The results also usefully distinguished between what makes a process long versus what makes a process demanding. The grid control condition, which took as long as the most demanding rotation condition, was associated with the least amount of parietal activation, consistent with the small demand on the kinds of visu- ospatial computations thought to be executed primarily in the parietal region. The current study suggests that task demand is a major determinant of the underlying neural functioning. More specifically, in the 3CAPS theory, the demand of a successfully performed task relates to the amount of activation required in the model to perform the activation-based processes and to maintain intermediate representations. This measure is both conceptually and empirically distinguishable from a simple response time measure (Carpenter, Just, & Shell, 1990; Just & Carpenter, 1992).

The two measures of activation in this study, the number of activated voxels and the amplitude of activation, are not identical but neither are they necessarily independent. The information that each measure conveys is partially relative to the neuroimaging technique's resolution. If a voxel's size exceeds that of the relevant neural system, partial voluming could cause a higher level of response to appear as an additional area of activity. Alternatively, a system could signal its responsivity to greater demand through either dimension by recruiting nearby units and by increasing its own activity level.

In sensory systems, both increases in neuronal firing frequency and in the number of activated neurons are ways of respond- ing to increases in stimulus intensity. of course, we are not suggesting any simple mapping of single neuron activity to fMRI-measured activation because FMRI is a physiological index of the functioning of large-scale net- works, which includes patterns of neuronal activation and deactivation. The partial separability of the two measures at least indicates the importance of continuing to assess both in future neuroimaging studies.

Collaboration among Neural Systems

The results indicated a coactivation in a number of neural systems in association with the need for rotation, in areas like the left and right parietal and inferior temporal regions. Some frontal regions were also activated, but the difference between the grid and rotation conditions was less in the frontal regions, suggesting a wide-spread but nonuniform distribution of the effect of the rotation demand. Even if a region like the parietal area is specialized for rotation, there must be feedback among regions, such that the extra rotation processing has an impact on multiple regions. For example, it is easy to imagine why both a what and a where system might be influenced by the angular disparity in a mental rotation task. If the what system constructs a representation of an object or object segment at a given orientation, even if the mental rotation were performed by the where system, it may be necessary for the what system to re-represent that segment at a new orientation and to compare the new representation with the unrotated representation. The more rotation there is to be done (presumably by the where system), the more work there might be for the what system. It is also likely that the inferior temporal what system also directly supports the computation of spatial coordinates. Correspondingly, neural elements in the parietal region may support the computation of figural identity or gaze location. In this view, the specialization of neural systems is partial, such that each system performs not only its own preferred computation but may also participate in the computations performed by its collaborating systems. Such a view is consistent with the findings of neurons in the parietal region that fire in association with saccades and neurons in the frontal eye fields that contain well-defined receptive fields (Mesulam, 1990; Goldberg & Segraves, 1987; Lynch, Mountcastle, Talbor, and Yin, 1977). The idea that particular cognitive functions are not necessarily isolated to particular brain areas has been made in various contexts by several researchers, including Goldman-Rakic (1988), Posner, Petersen, Fox, and Raichle (1988) and Mesulam (1990). The current contribution is to operationalize a method that reveals such collaboration during the performance of a complex visualization task.

The bilaterality of the parietal activation, indicating that both hemispheres contribute to the task performance, is a striking and consistent result of both studies. It suggests that mental rotation processes are not confined to the right hemisphere, the hemisphere that decades of clinical studies have associated with spatial processing. The discrepancy between the high degree of symmetry in brain activation and the great lack of symmetry in the effect of brain lesions can have several possible resolutions. One possibility is that mental rotation contrasts with certain other visuospatial processes in its lateralization. Indeed, mental rotation tasks have not been associated with consistent laterality effects in several clinical studies using clinical populations with circumscribed lesions (Mehta, Newcombe, & Ratcliff, 1989; Newcombe & Ratcliff, 1989). In contrast to the study of rotation, some neuroimaging studies of the control of visual spatial attention have been interpreted to suggest an asymmetry in the two hemispheres (Nobre et al., 1997). Also, the degree of lateralization could vary partly as a function of the amount of visuospatial demand. The apparent bilaterality of the current results could reflect the recruitment of the left hemisphere by the right as demand increases, a recruitment that could be blocked if the right hemisphere were injured. Alternatively or in addition, the two hemispheres could have slightly different roles in the decomposition and transformation processes that underlie this complex rotation task. For example, visuospatial processes that require relatively fast configural judgments and less coordination over time may be more right-lateralized. This interpretation follows from the finding that the right-left asymmetry is substantial at 0° and almost nonexistent at the other rotation conditions for both dependent measures (number of voxels activated and percentage of change in signal intensity). This interpretation might also account for the differential laterality effects found in simple delayed-match-to-sample tasks involving spatial positions versus verbal material Jonides et al., 1993). Although a definitive conclusion about the contributions of the two hemispheres is premature, it is clear that in the current task with normal individuals, both hemispheres are highly and similarly responsive.

The present research suggests the reconstrual of the theory of the visuospatial working memory system in a way that focuses on the ability of the systems to actively compute and not just passively maintain visuospatial information. In this view, it may be more fruitful to consider the visuospatial systems as a dynamic and flexible configuration of several large-scale neural systems that have various specialties, including the computation of orientation with respect to various frames of reference, object and object part identification, and information maintenance. The computations may emerge through interactions among the various subsystems, and the functional subsystems need not map exclusively onto single cortical areas.

In the monkey, even the maintenance of a representation of an object in a particular orientation and location (without much additional computation) may occur through the interaction of several neural areas, including the parietal region and principal sulcus area (Goldman-Rakic, 1992). According to the current proposal, the relative amount of activation in each area would depend on both the nature and amount of computational demands that the task entails. Tasks that involve relatively more computations related to orientation or position may produce more activation in the parietal region, the inferior occipitotemporal pathway, and some frontal motor areas. By contrast, routine visual scanning tasks, which involve maintaining information about an object in a particular position and/or orientation, may result in relatively less activation in the parietal region and somewhat more in the frontal regions. Thus, the visuospatial performance may be the emergent product of dynamic interactions among various subsystems that together are capable of complex perceptual and imaginal computations, in addition to passive information maintenance.

We have observed similar principles of neural organization in fMRI studies of sentence comprehension, which showed that increasing syntactic complexity resulted in increased activation in a network of cortical areas (Just, Carpenter, Keller, Eddy, & Thulborn, 1996). These areas included the posterior superior temporal gyrus (Wernicke's area) and its right homologue and the inferior frontal gyrus (Broca's area) and its right homologue. Thus, both the sentence comprehension and the mental rotation task produced evidence of coordinated activation in a network of areas, modulated by the size of the demand. Such data suggests that it is not wise to attempt to construct a "cognitive atlas" that maps cognitive functions to particular brain areas solely on the basis of a qualitative description of the type of operation.

Other neuroimaging studies have also shown in- creased activation in some neural regions with cognitive demand. For example, in the continuous performance task, the participant has to keep track of from one to three alphanumeric items in a running list. The amount of fMRI-measured activation increases with the number of items being tracked and rehearsed, in prefrontal and inferior frontal areas (Braver, Cohen, Jonides, Smith, & Noll, 1997; Cohen et al., 1997; also Jonides et al., 1997). A similar result was found with a positron emission tomography (PET) study of a traditional word-span task (Grasby et al., 1994). Thus, a growing body of neuroimaging studies indicate that computational demand is associated with increases in cortical neural activation in certain regions relevant to the task (Just, Carpenter, & Miyake, 1997). The more general conclusion to be drawn may be that there are general principles that govern the relation of active thinking to the cortical systems that subserve those mental processes. Just as physical energy systems require resources, so do

neural energy systems. It is the consumption of different types of resources that may be indexed by various metabolically based neuroimaging measures, including fMRI. Specifically, greater task demand translates into greater resource demand.

METHOD

Participants

In the 1.5T study, the participants were nine right-handed volunteer college students (three females). In the 3.0T study, the participants were eight right-handed volunteer college students (three females). Each participant gave signed, informed consent (approved by the University of Pittsburgh and the Carnegie Mellon Institutional Review Boards). Participants were familiarized with the scanner, the fMRI procedure, and the mental rotation task before the study commenced.

fMRI Design

The fMRI-measured activation is interpreted as an index of neural activity because transient increases in neuronal activation are accompanied by an increase in blood supply and an increase in the oxygen concentration in the small capillaries serving relatively local regions. MR senses such changes in blood oxygenation using a method called BOLD contrast (blood oxygenation level dependent), which does not require an exogenous contrast agent (Kwong et al., 1992; Ogawa, Lee, Kay, & Tank, 1990).

During the scan repetition time (typically, 1500 msec for the 1.5T study), images of the MR signal intensity are taken in seven or nine 5-mm-thick coronal slices coverng the posterior parietal lobes. A new image is acquired every 214 msec, and each slice is imaged every 1500 msec. For the 1.5T study, gradient echo, resonant echo planar pulse sequence was used with TR (repetition time) = 1500 msec, TE (echo time) = 50 msec, flip angle = 90°, and a 128 x 64 matrix of voxels of size 3.125 x 3.125 x 5 mm with 1-mm gap. For the 3.0T study, the acquisition parameters for the gradient echo, resonant echo planar images were TR = 3000 msec, TE = 25 msec, flip angle = 90°, and the same voxel sizes with 14 axial slices. The studies were performed with commercial birdcage, quadrature-drive radio-frequency coils.

Experimental Paradigm

The experiment has four mental rotation conditions, involving 0, 40,80, and 120° of angular disparity, and two control conditions: (1) a fixation rest condition, in which the subject simply looked at a fixation point for 24 sec (this condition was treated as a baseline) and (2) a grid comparison task. The grid condition provided a measure of cortical activation under conditions in which individuals

executed many of large and small saccades, in addition to encoding and comparing two figures. For the grid condition, the stimuli consist of two 4 by 6 rectangular grids with approximately the same total length of line segments as a pair of figures. The participant fixated each part of the top row of the left grid, went across to fixate the corresponding part of the right grid, looked back to the second row of the left grid, and so forth until each grid had been entirely scanned, and then responded "Same." Hence, the response times in this condition are measures of visual scanning time.

Multiple trials with the same angular disparity between the two figures were blocked into epochs that took approximately 24 sec in order to allow the hemodynamic response to be sampled at its steady-state level. The rotation condition epochs are intermixed with grid condition epochs, such that each occurs four times in a session in an appropriately counterbalanced order, and rest epochs occur between each set of experimental epochs and at the beginning and end of the sequence of epochs. Successive epochs are separated by 6-sec rest periods during which individuals fixated an asterisk in the middle of the screen. Data from this 6-sec rest interval and from the first 6 sec of the following epoch are discarded to accommodate the rise and fall of the hemodynamic response (Bandettini, Wong, Hinks, Tokofsky, & Hyde, 1992), leaving a total duration to be analyzed of approximately 80 sec per experimental condition per participant.

A response time and accuracy measure are obtained for each trial within each epoch. Sixteen percent of the trials are Different trials, to ensure that participants were performing the task, and the rest are Same trials. Each trial (except for the rest condition) is self-paced by the participant and terminates with the subject's button- press response. To approximately equate epoch durations across condition, slightly more trials per epoch are included for smaller angular disparity epochs than larger ones because the response times are typically slightly faster. For most individuals, there were 10 trials per epoch for the 0° condition, 8 trials per epoch for the 40° condition, and 6 trials per epoch for the 80° and 120° conditions. However, the number of trials per epoch were reduced for the few individuals who had very long response times in the practice set in order to keep the duration of each epoch approximately 24 sec. During the data analysis, the epoch durations were truncated to equal length across all conditions including the grid control condition on an individual participant basis so that no differential effect of trial times could affect the means or variances of the activation across conditions.

Data Analysis

ROIs are defined using the parcellation method originally described by Rademacher, Galaburda, Kennedy, Filipek, and Caviness (1992) and further refined by Caviness,

Meyer, Makris, and Kennedy (1996). This approach uses limiting sulci and anatomically landmarked coronal planes to segment cortical regions. A mean of the functional images is registered to a high-resolution, T1-weighted, structural volume scan. For the 1.5T study, these were conventional spin echo images with TR = 400 msec, TE = 11 msec, 256 x 256 acquisition matrix, 5-mm slice thickness, and a 1-mm gap and taken in the same coronal planes as the functional images. For the 3.0T study, they were 3D SPGR, TR = 25, TE = 4, flip angle = 40°, field of view (FOV) = 24 cm x 18 cm, 124 slices, resulting in voxel dimensions of 0.9375 x 0.9375 x 1.5 mm thick taken axially. Limiting sulci and cerebral land- marks were identified by viewing the structural images simultaneously in the three orthogonal planes. The functional images were then segmented in the axial or coronal plane by manually tracing the regions of interest on each slice.

Because the main hypotheses concerned the parietal and temporal regions, the major analyses focused on ROIs in these regions. In the Caviness et al., (1996) nomenclature, the parietal ROI corresponded to the superior parietal lobule (SPL, BAs 5 and 7), the posterior supramarginal gyrus (SGp, BAs 40), and the angular gyrus (AG, BAs 39). The interior temporal ROI included the fusiform gyrus regions (TOF and TF, BAs 36, 37, and 20) and the inferior temporal gyrus areas (TO3 and TFp or BAs 37 and 20). The superior temporal ROI corresponds to the superior temporal gyrus (T1a and T1p or BA 22) and the middle temporal gyrus regions (T2a, T2p, and T02 or BAs 21,22, and 37). These six ROls were analyzed for all participants in both studies, but most of the statistical analyses focused on the parietal ROIs for both studies and the temporal ROIs for the 3.0T study; the coronal slices in the 1.5T study gave a very incomplete sample of the temporal ROIs.

To quantify the relative amount of activation in areas associated with eye movement control and execution, three separate ROIs in the frontal lobes were defined for a subset of four volunteers in the 3.0T study. These ROIs corresponded to the Caviness et al. (1996) parcellation units for the supplementary motor area UPL or medial BA 6), the precentral gyrus (PRG or BAs 6 and 4), and the posterior portion of the middle frontal gyrus (F2 or BAs 6 and 8). The division of the anterior and posterior portions of the middle frontal gyrus was defined by a coronal plane perpendicular to the anterior commissure-posterior commissure (AC-PC) line at the anterior edge of the genu of the corpus callosum at midline. We note that the precentral gyrus ROI and the posterior middle frontal ROI could be considered a single functional region because activation was fairly continuous through these two regions. In addition, to assess the activation of the dorsolateral prefrontal cortex, a separate ROI was defined representing the middorsolateral prefrontal cortex (corresponding to the anterior portion of parcellation unit F2 or BAs 9 and 46).

The image preprocessing corrected for head motion and signal drift using procedures and software developed by William Eddy and his colleagues in the Carnegie Mellon statistics department (Eddy, Fitzgerald, Genovese, Mockus, & Noll, 1996). The in-plane head motion of the 17 participants in the two studies never exceeded 0.2 voxels in the slices of interest; several other data sets with greater in-plane or out-of-plane head motion were discarded.

The data analysis focuses on quantifying the volume of fMRI-measured activation using two measures. The first was the average number of voxels that have an activation level that is significantly above the rest control baseline. For each voxel in the a priori defined ROIs, the distribution of intensities in an experimental condition is compared to that for the rest condition using a t test with a threshold of $t > 4.5$, a conservative threshold. [3] A second but related measure quantified the increase in the amplitude of activation over the rest condition for any voxel that had a statistically significantly elevated activation level in any of the five conditions. These voxels were selected for having activation that was significantly above threshold but with no bias concerning any specific pattern, such as an increase as a function of angular disparity. This measure was analyzed with an ANOVA for each anatomical ROI, with voxels nested within the eight or nine individuals for each study and crossed with four main experimental conditions. We report an even more conservative analysis in which the average activation was measured for each individual and analyzed with a repeated measure ANOVA.

For several reasons, the activation effects are believed to primarily reflect changes in the microvasculature that are induced by changes in cortical neuronal activity rather than in large veins. First, to reduce the possible influence of larger vessels, we excluded from analysis any voxels showing a large percentage change in signal intensity (greater than 6.2%) that were likely to reflect the activity of blood vessels. In the 3.0T study, this constituted 1.4% of the 15,752 total voxels of the parietal ROIs for the eight volunteers and 3.2% of the 6705 voxels of the inferior temporal ROIs. In the 1.5T study, it was 2.5% of the 16,522 total voxels of the parietal ROIs for the nine volunteers and 3.2% of the 6949 voxels of the inferior temporal ROIs. Second, a lack of influence of large veins was consistent with the observed pattern of intercorrelations between the activation patterns over time of three kinds of voxels (voxels containing known veins, voxels containing cerebral spinal fluid, and the voxels of primary interest in the ROIs). The patterns for voxels containing the superior sagittal sinus and the straight sinus correlate significantly with each other and with that for voxels containing cortical veins. However, the patterns did not correlate with the activation pattern for voxels included in the ROIs in either the parietal region or the inferior temporal region. Conversely, the patterns of voxels in the ROIs correlated with each other but not with the pattern for voxels containing the sinuses or cerebral spinal fluid.

Third, the regions of activation map to gray matter rather than to spaces occupied by cerebrospinal fluid in which large vessels are found. Moreover, the nonlinear distribution of activation confined to a discrete volume within the imaging space does not represent the known venous drainage pattern of the parietal and temporal lobes. Finally, although it appears that these measures were successful in quantifying fMRI-measured activation associated with the microvasculature, we note that the issue of localization is not central in the current context because the primary question concerns the effect of task demand rather than the absolute localization of function.

Notes

1. Compared to the 3.0T results, the 1.5T study showed the same quantitative trends but a lower number of voxels overall and higher amplitudes of MR signal intensity in those voxels that were activated significantly in any condition. Both differences are consistent with the higher signal-to-noise ratio (by a factor of 2; Thulborn et al., 1996) and with the higher sensitivity for magnetic susceptibility effects of the 3.0T compared to the 1.5T systems. In fact, the increased susceptibility of the 3.0T (approaching a quadratic power; Thulborn, Waterton, Matthews, & Radda, 1982) increases the sensitivity to the microvasculature that biases toward the smaller vessels. Both the higher signal-to-noise ratio and increased sensitivity would enable one to detect smaller increases in activation. This would increase the number of voxels that would be found to be significantly activated (hence, the greater number) even though their in- crease in activation level n-tight be relatively lower (hence, the lower average increase in activation amplitude).

2. The error bar for each rotation condition represents the standard error of the *slope* of the linear increase as a function of 40° increment in disparity. For the grid condition, it gives the standard error of the difference between the mean of the rotation conditions and the grid condition (calculated initially within each participant). These estimates reflect the statistics used to estimate the slope and to test the difference between the grid and rotation conditions, respectively. Conventionally, error bars depict that the between-subject variance for an observation, which is irrelevant to the major hypotheses here because this study has a within-subject design with graded variation of the main variable (see Loftus & Masson, 1994, for a related point concerning variances to be reported for within-S designs).

3. An analysis of the effect of different t-value thresholds on the count of the number of significantly activated voxels indicates that the monotonicity across conditions holds for different t-thresholds varying from 3.5 to 6 and is not dependent on the particular threshold that was used (t = 4.5).

The analysis also suggests that it is important that individuals be able to perform the task throughout the range of task difficulty. Two of three participants who had very high error rates for the 80 and 120° conditions showed more activated voxels in the 80° condition than in the 120° condition, suggesting that they may have resorted to guessing or to a less effective strategy, thereby expending less effort in the 120° condition than in the 80° one.

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