Research Article

Two Forms of Spatial Imagery
Neuroimaging Evidence

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ABSTRACT—*Spatial imagery may be useful in such tasks as interpreting graphs and solving geometry problems, and even in performing surgery. This study provides evidence that spatial imagery is not a single faculty; rather, visualizing spatial location and mentally transforming location rely on distinct neural networks. Using 3-T functional magnetic resonance imaging, we tested 16 participants (8 male, 8 female) in each of two spatial imagery tasks—one that required visualizing location and one that required mentally rotating stimuli. The same stimuli were used in the two tasks. The location-based task engendered more activation near the occipito-parietal sulcus, medial posterior cingulate, and precuneus, whereas the transformation task engendered more activation in superior portions of the parietal lobe and in the postcentral gyrus. These differences in activation provide evidence that there are at least two different types of spatial imagery.*

Mental imagery for spatial relationships is useful across a range of domains, and may be useful in such everyday activities as finding one's way in an unfamiliar neighborhood, packing suitcases into a car, interpreting graphs, solving problems using geometry, and remembering locations of objects around a room. In addition, spatial imagery ability may have consequences for career choice. For example, Wanzel, Hamstra, Anastakis, Matsumoto, and Cusimano (2002) reported that surgical residents with greater competence in mental rotation were better able to learn and perform a complex surgical procedure. In the same vein, Guillot, Champely, Batier, Thiriet, and Collet (2007) reported that anatomy students who had better mental rotation ability performed better on an anatomy test. Moreover, Dror, Kosslyn, and Waag (1993) showed that airplane pilots can perform mental rotation and other spatial judgments better than age-, sex-, and education-matched participants.

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A major finding in cognitive neuroscience is that mental functions generally are not unitary and undifferentiated. Rather, they are carried out by a host of distinct representations and processes. This is true not only at coarse levels of analysis—for example, when one considers faculties such as language, memory, and perception—but also at fine levels of analysis. For example, at least two distinct types of spatial-relation representations can be used to specify location, one that specifies categories (e.g., "left of") and one that specifies metric information (precise distance; e.g., Kosslyn, 2006). In this article, we consider the possibility that spatial imagery can be decomposed into at least two distinct types of processes. On the one hand, such imagery may serve to specify location; on the other hand, it may be involved in representing changes in orientation or mentally simulating such changes.

Many researchers have studied changes in orientation of objects in visual mental images, usually under the rubric of "mental rotation." Neuroimaging has proven to be a useful tool in such investigations, allowing researchers to compare and contrast mental rotation with other abilities. In a review and meta-analysis of mental rotation, Zacks (2008) found consistent activation in parietal cortex, with some extension into superior portions of occipital cortex. Zacks proposed that these regions are likely candidates for implementing the transformation-specific processes involved in mental rotation. Moreover, Zacks and Michelon (2005) proposed that spatial transformations rely initially (and essentially) on memory for spatial locations that are encoded relative to one of three reference frames (object-centric, egocentric, or allocentric), and that spatial transformations per se are executed by a small subset of the common brain regions underlying the spatial imagery system in general.

Previous neuroimaging studies have found that remembering spatial locations of objects also activates portions of parietal cortex. For instance, Moscovitch, Kapur, Köhler, and Houle (1995) reported that Brodmann's area (BA) 40, in inferior parietal cortex, was activated when object location was retrieved (relative to when object identity was retrieved). Such findings are consistent with results from studies of patients with brain

damage. For example, van Asselen et al. (2006) found that stroke patients with damage to parietal cortex (and dorsolateral prefrontal cortex) were impaired relative to control participants in remembering the locations of objects. However, no previous study has directly compared brain areas associated with visualizing location and brain areas associated with visualizing transformations of orientation.

If spatial transformations rely fundamentally on mapping different objects in space relative to a reference frame, then all of the brain areas activated during spatial transformations should also be activated during imagery for spatial location. However, if these processes are distinct, then a direct comparison of the two types of tasks should reveal that each activates at least some distinct brain areas.

METHOD

Participants

Sixteen participants (8 male, 8 female), who were undergraduates, graduate students, or professionals, took part in the study (mean age = 23 years, range = 18–30). Seven additional participants were tested, but were excluded because they failed to complete at least one of the tasks to criterion, or because problems with the functional magnetic resonance imaging (fMRI) scanner or computer equipment prohibited them from completing the session. All participants were tested according to applicable guidelines and regulations governing the use of human participants in research, and the experimental protocol was approved by the Harvard University Faculty of Arts and Sciences Committee on the Use of Human Subjects and the Partners Human Research Committee (which governs research at Massachusetts General Hospital).

Materials

Stimuli included 35 alphanumeric characters created from a variety of standard fonts and modified to fit the circles in which they would eventually appear. The characters were made to appear standard and prototypical in order to maximize clarity and facilitate learning. They consisted of 5 numerals (*1, 2, 3, 7, 9*), 12 lowercase letters (*a, b, d, f, h, i, j, m, n, q, r, t*), and 18 uppercase letters (*A, C, D, E, F, G, H, I, J, L, R, S, T, U, V, W, X, Y*).

For the familiarization phase, each trial consisted of a single character within a circle with a tick mark on top (see Fig. 1 for examples of the types of characters participants learned). For the experimental trials, two sets of stimuli were used. Each set had five characters and appeared within a rectangle; the locations of the characters within the rectangle varied. As in the materials for the familiarization phase, each character was presented within a circle with a tick mark at the top. For each experimental trial we also prepared a circle of the same size as the circles that surrounded the characters during study. The circle was divided into three equal-size sections: one outlined with a bold line, one outlined with a dashed line, and the third outlined with a neutral line (see Fig. 1). A script character (in Apple Chancery font, with minor modifications for some letters to improve clarity) appeared under the circle, to cue participants as to which block character they should visualize in order to perform the task. Each task included 40 trials, presented in two 20-trial blocks.

Procedure

All tasks were computerized and were presented with PsyScope software (J.D. Cohen, MacWhinney, Flatt, & Provost, 1993). During the experimental phase, inside the MRI scanner, the participants received the two blocks of 20 trials for each task. Participants were tested on four tasks, two of which are the focus of this report and are described in detail.

Familiarization Phase (Outside the Scanner)
During familiarization, participants studied the characters that would subsequently be used in the experimental tasks. In turn, each character appeared at the center of the screen, within a circle with a tick mark at the top. Each character appeared for 4 s and then disappeared, followed by a blank circle with a tick mark. Participants were instructed to visualize the character they had just studied as accurately as possible, and then to press a button, which made the character reappear. They were instructed to compare their mental image with the shape of the actual character and to correct any inaccuracies. Once they had done so, they pressed a button, and the next character appeared.

Once participants had completed the familiarization phase, they were asked whether they had any questions. They were told that they would have the opportunity to study some of the characters again and would be asked to practice the tasks that they would be performing later inside the scanner.

When participants were ready, they completed a second familiarization phase, in which they studied only the characters that would be used in the task they were about to perform. This time, participants were instructed to study the characters for as much time as they needed.

Practice Phase (Outside the Scanner)
After familiarization, participants were given instructions for the first task; the order in which the tasks were practiced was counterbalanced across participants. For each task, participants were instructed that a rectangular box containing some of the characters from the familiarization phase would appear on the screen, and that they should remember the box and the characters to perform the task that followed. For the spatial-location memory task, they were told that they should pay attention to and remember the locations of the characters within the box. For the spatial-transformation task, they were told that they should pay attention to and remember the shapes of the characters (i.e., "what the characters look like").
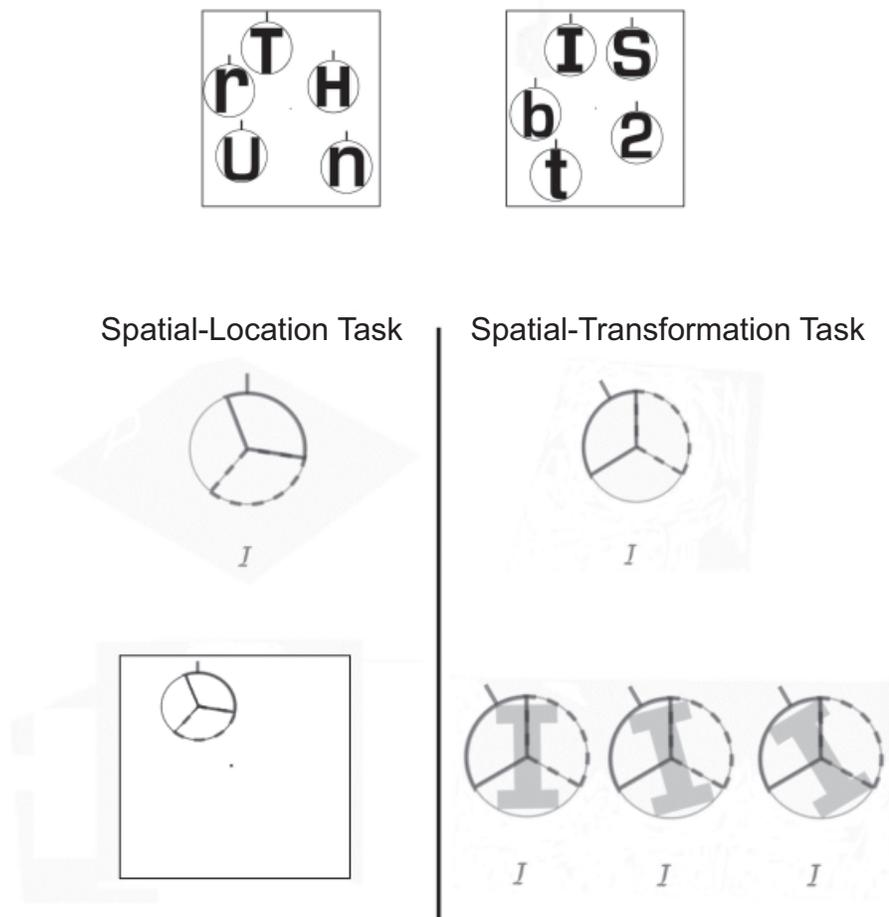
Fig. 1. Example of a trial in the spatial-location task and spatial-transformation task. In both tasks, participants first studied the block characters in two boxes that were presented sequentially for 30 s each. On each trial in the spatial-location task, participants saw a trisected circle with a vertical tick mark at the top and a script character below (middle left). The script character cued them to re-member the location of the corresponding block character that they had studied and to visualize the trisected circle in the location where that character had appeared (bottom left). After having mentally placed the trisected circle in the appropriate location within the box, participants decided whether the bold or dashed section of the circle was closer to the center point of the box. In the example shown, the correct response would have been ''dashed.'' On each trial in the spatial-transformation task, participants saw a trisected circle with a tick mark displaced from the vertical and a script character below (middle right). The script character cued the block character to be visualized. Participants visualized the character in the circle and mentally rotated it to align with the tick mark, in order to decide which section of the circle (bold or dashed) would contain more of the character when it was rotated (bottom right). In the example shown here, the correct response would have been ''bold.''

Regardless of the specific task, a rectangular box then appeared at the center of the screen. The box contained five alphanumeric characters, each placed within a circle with a tick mark indicating the top of the circle. The characters were placed in different locations within the box (see the top of Fig. 1 for examples). Participants studied the box with the characters for 30 s. (Note that a single study box was used on practice trials, whereas two boxes were shown sequentially in the experimental trials conducted inside the scanner.) After the box disappeared, participants were told that the practice trials were about to begin. The practice phase for each task consisted of five trials. During this phase, the computer beeped if the participant answered incorrectly.

Spatial-Location Task. On each trial of the spatial-location task, participants were shown a trisected circle stimulus (see the left side of Fig. 1 for a sample experimental trial for this task). A smaller, script version of one of the characters previously shown in the study box was displayed below the trisected circle. This script character cued participants to mentally place the circle in the location where the corresponding block character had appeared in the study box. The task was to decide whether the bold or dashed segment of the circle would be closer to the center of the display if the circle appeared in that location. Thus, participants did not need to visualize the characters in order to perform the task; the only information required to perform the

task was the location where the circle associated with the character had originally appeared.

Spatial-Transformation Task. As was the case for the spatial-location task, on each trial of the spatial-transformation task (see the right side of Fig. 1, which illustrates mental rotation in a sample experimental trial), a trisected circle appeared, and below the circle was a script character. The character cued participants to visualize the corresponding block character they had studied within the study box. A tick mark was positioned on the contour of the circle (not at the top, but rather at another location on the circle's circumference; see the right side of Fig. 1). Participants were instructed to mentally rotate the visualized character until its top was aligned directly under the tick mark (as schematized at the bottom of the right side of Fig. 1). After performing this rotation, participants judged whether more of the character would be in the bold or dashed section of the circle; the segments were arranged so that this judgment was easy (i.e., the rate-limiting step was mental rotation itself).

Experimental Trials (Inside the Scanner)

The experimental trials had the same format as the practice trials, except that (a) none of the characters used in practice trials were used in experimental trials (but all of the characters used in the experimental trials had been learned in the familiarization phase); (b) the computer did not beep if participants made an error; (c) the stimulus duration varied across trials; (d) each task was administered twice, and each block of each task comprised 20 trials; and (e) participants were given two new study boxes (presented in sequence for 30 s each) at the beginning of each scan (i.e., for every 20 trials). Each task was performed once before either task was repeated. The interstimulus interval (ISI) varied from 6 to 14 s, in 1-s increments. ISIs were programmed according to a pseudorandom schedule and were varied to allow deconvolution of the hemodynamic response, and also to require participants to remain vigilant.

fMRI Methods

Images were obtained with a 3-T Siemens Allegra scanner and a standard head coil. Participants recorded responses with a fiber-optic button box. T1-weighted anatomical images were acquired using a magnetization-prepared rapid gradient echo (MP-RAGE) sequence (repetition time = 25 ms, echo time = 3.25 ms, flip angle = 40°, field of view = 256 × 256 mm, acquisition matrix = 256 × 256, 128 slices, slice thickness = 1.33 mm, no gap, resolution of 1 × 1 × 1.33 mm).

Functional images were acquired using echoplanar imaging (repetition time = 2,000 ms, echo time = 30 ms, flip angle = 90°, field of view = 256 × 256 mm, acquisition matrix = 64 × 64, 35 slices, slice thickness = 4 mm isotropic, no gap, 110 time points for each run).

Images were transformed to be made compatible with the Statistical Parametric Mapping program (SPM2; Wellcome Trust Centre for Neuroimaging, London, United Kingdom). Preprocessing included slice-time correction, motion correction, and spatial normalization to Montreal Neurological Institute coordinates. To maximize the spatial resolution of the results, we did not spatially smooth the data. To model the hemodynamic response related to the processing of interest, we modeled events using the canonical hemodynamic basis function within SPM. Events were entered as vectors starting at the onset of each stimulus and ending at each participant's response. Only trials with correct responses were analyzed (i.e., trials with incorrect responses and trials in which participants did not provide a response were not included in the analyses). We used one-tailed *t* tests within a random-effects analysis to identify brain regions that were consistently active across our group of participants.

We contrasted each of the two tasks with the other and also compared each task with the baseline period, defined as the interval between the point when a participant responded on a given trial and the presentation of the next stimulus. Because each stimulus remained on the screen after the participant responded until a new stimulus was presented, the baseline condition had the same visual stimulation as each of the task conditions, but without the task-specific processing associated with spatial-location memory or spatial transformation.

Corrections for Multiple Comparisons

To correct for multiple comparisons, we conducted a Monte Carlo simulation using custom software written in MATLAB (The Mathworks, Natick, MA; Slotnick, 2008a). Because clusters of activation are increasingly improbable as they become larger, it is possible to determine the probability of a given spatial extent of activity (or larger) and then enforce an extent threshold to yield the desired Type I error rate. Three-dimensional spatial autocorrelation (full-width at half-maximum) of the random-effects contrast images was estimated to be 7.5 mm using custom software written in MATLAB to model smoothness in the data (Slotnick, 2008b). After running 1,000 simulations, we determined that for an individual voxel threshold of $p < .001$, a cluster-extent threshold of 15 contiguous voxels was necessary to correct for multiple comparisons to achieve a significance level of $p < .05$. Thus, only clusters of activation meeting or exceeding that size were considered significantly activated. (For further details regarding cluster-extent threshold correction for multiple comparisons, see Slotnick, 2008a, and Slotnick & Schacter, 2006).

RESULTS

Behavioral Results

We analyzed response time (RT) and error data using analysis of variance (ANOVA) with a 2 (task: spatial location vs. transformation) × 2 (block: first vs. second) × 2 (gender: female vs. male) design. The only effect to emerge from the RT analysis was a main effect of task. As Table 1 shows, participants required

TABLE 1

Mean Response Time and Error Rate for Each Task and Block

	Response time (ms)		Error rate (%)	
Task	First block	Second block	First block	Second block
Spatial location	3,984 (173)	3,962 (115)	22.2 (3.5)	25.9 (3.0)
Spatial transformation	4,419 (171)	4,432 (177)	26.6 (2.2)	27.8 (2.5)

Note. Standard errors of the mean are presented in parentheses.

more time to respond in the transformation task than in the location task, $t(15) = 2.91$, $p_{rep} = .96$. No significant effects were found in the analysis of errors (see Table 1).

fMRI Results

We contrasted each of the tasks against the other to compare directly the activation associated specifically with spatial-location memory and spatial transformation.

Spatial Location Versus Spatial Transformation

Contrasting spatial location with spatial transformation (Table 2 and Fig. 2) revealed peak activation in the vicinity of the occipito-parietal sulcus, near the precuneus and posterior cingulate cortex. This region was also activated more during the spatial-location task than during the baseline, which indicates that the differences in this area between the two tasks were clearly a result of increases in activation during the spatial-location task, rather than deactivations during the transformation task. Activations in this region were bilateral. We also found greater activation in the medial lingual gyrus (BA 18) in the location task than in the transformation task, although this difference was in

fact a result of deactivation in the transformation task compared with the baseline, rather than an increase in the location task. Other portions of the lingual gyrus and the cuneus were also activated in the location task compared with the transformation task, although the differences between the two main conditions and the baseline were subthreshold, so these activations are more difficult to interpret. (For all of these regions, comparison with the baseline yielded nonsignificant positive z scores for the location task and nonsignificant negative z scores for the transformation task, which suggests a trend that may have proven significant with greater power.)

Spatial Transformation Versus Spatial Location

When we contrasted activation in the spatial-transformation task with activation in the spatial-location task (see Table 3 and Fig. 2), we found peak activation bilaterally in the superior parietal lobule (BA 7) and in the postcentral gyrus (BA 2/5/7). In addition, we found activation in the right inferior parietal cortex (BA 40). However, some portions of the left superior parietal cortex and right inferior parietal cortex were not more significantly activated in the transformation task than during the

TABLE 2

Areas of Activation Identified by Contrasting the Spatial-Location Task With the Spatial-Transformation Task

	MNI coordinates			z score		
Region	x	y	z	L − T	L − B	T − B
Occipito-parietal sulcus, precuneus, posterior cingulate (BA 18/30/31, Cluster 1)	15	−69	12	4.14*	3.94*	0.59
Occipito-parietal sulcus, precuneus, posterior cingulate (BA 31, Cluster 2)	−21	−66	18	3.91*	3.23*	1.30
Lingual gyrus (BA 18/19, Cluster 1)	9	−81	30	4.19*	−0.23	−4.23*
Lingual gyrus (BA 18, Cluster 3)	−9	−72	−12	3.85*	1.34	−3.02
Cuneus (BA 18/19, Cluster 1)	21	−72	12	4.15*	2.32	−2.95
Cuneus (BA 23/31, Cluster 3)	−9	−75	6	3.55*	2.43	−1.78
Lingual gyrus (BA 18, Cluster 3)	−6	−66	0	3.82*	2.93	−1.46

Note. Locations of the foci (peak voxels) of activation are given in Montreal Neurological Institute (MNI) coordinates. Each locus of activation is identified by the Brodmann's area (BA) where it is located, as well as the cluster (of the three identified by the Statistical Parametric Mapping program) to which it belongs. Cluster sizes were as follows: Cluster 1 = 229 voxels; Cluster 2 = 16 voxels; Cluster 3 = 111 voxels. For each activation, z scores are provided for the main contrast between the two tasks (spatial location vs. spatial transformation, or L − T) and for the contrast between each task and the baseline (spatial location vs. baseline, or L − B; spatial transformation vs. baseline, or T − B). Significant z scores (individual-voxel threshold, $p < .001$; corrected for multiple comparisons at $p < .05$) are denoted with an asterisk.

Fig. 2. Differential activity associated with the spatial-location task (ovals) and the spatial-transformation task (rectangles) when the two tasks were contrasted with each other (top left: anterior view; top right: posterior view; middle left: right lateral view; middle right: left lateral view; bottom left: inferior view; bottom right: superior view). Note that some apparent activations do not reflect increases relative to the baseline and may be due to deactivations in the opposite task (see the text and Tables 2 and 3 for details).

baseline, and one region of the right inferior parietal cortex was also activated more during the spatial-location task than during the baseline. These findings provide evidence that spatial transformation may rely partly on areas responsible for mapping spatial location (note that the activation maps for the two tasks when contrasted with baseline were largely similar, as shown in Fig. 3). Unlike in the reverse comparison, we did not find activation in the precuneus, in the posterior cingulate, or at the occipito-parietal junction. Instead, we documented activation in parietal regions near the junction of the superior and inferior lobules and extending into the postcentral gyrus. Classically, these areas have been associated with mental rotation (e.g., see

M.S. Cohen et al., 1996; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Kosslyn, Thompson, Wraga, & Alpert, 2001) and are generally more superior and lateral than those associated with the spatial-location task.

Medial Activations
Although we found no significant activation within 5 mm of midline, activations tended to be closer to the medial surface in the location task than in the transformation task. Figure 4 provides a medial view through a peak region of activation in the location task (identified by the contrast with the transformation task). This region, near the occipito-parietal junction, was activated

TABLE 3

Areas of Activation Identified by Contrasting the Spatial-Transformation Task With the Spatial-Location Task

Region	MNI coordinates			z score		
	x	y	z	T − L	T − B	L − B
Inferior parietal lobule, postcentral gyrus (BA 40/2, Cluster1)	48	−39	63	4.31*	4.24*	2.23
Superior parietal cortex (BA 7, Cluster 2)	18	−48	57	4.03*	3.37*	0.11
Superior parietal cortex (BA 7, Cluster 2)	12	−54	69	3.82*	3.90*	2.35
Postcentral gyrus (BA 5, Cluster 3)	−30	−45	66	3.76*	4.37*	2.00
Postcentral gyrus (BA 5, Cluster 2)	27	−48	66	3.63*	3.25*	1.65
Postcentral gyrus, superior parietal cortex (BA 5/7, Cluster 3)	−24	−48	60	3.52*	3.28*	2.50
Inferior parietal cortex (BA 40, Cluster 1)	45	−39	45	3.87*	4.43*	4.09*
Inferior parietal cortex (BA 40, Cluster 1)	57	−36	54	3.51*	1.34	−1.72
Superior parietal cortex (BA 40/7, Cluster 3)	−24	−48	72	3.51*	2.10	0.90

Note. Locations of the foci (peak voxels) of activation are given in Montreal Neurological Institute (MNI) coordinates. Each locus of activation is identified by the Brodmann's area (BA) where it is located, as well as the cluster (of the three identified by the Statistical Parametric Mapping program) to which it belongs. Cluster sizes were as follows: Cluster 1 = 23 voxels; Cluster 2 = 25 voxels; Cluster 3 = 20 voxels. For each activation, z scores are provided for the main contrast between the two tasks (spatial transformation vs. spatial location, or T − L) and for the contrast between each task and the baseline (spatial transformation vs. baseline, or T − B; spatial location vs. baseline, or L − B). Significant z scores (individual-voxel threshold, $p < .001$; corrected for multiple comparisons at $p < .05$) are denoted with an asterisk.

bilaterally, and to a greater degree in the location task than in either the transformation task or the baseline. Therefore, our data suggest that it plays a specific role in memory for object location.

DISCUSSION

Our results document a clear dissociation between spatial imagery that relies on transformational processes and spatial imagery that relies on memory for location. This result is important because it demonstrates that spatial imagery, like mental imagery more generally, is not a unitary function. This finding allows us to refine the conclusions of Kozhevnikov, Kosslyn, and Shephard (2005), who demonstrated that visualizers should be divided into two types: those who prefer object imagery (i.e., imagery for shapes) and those who prefer spatial imagery. Kozhevnikov et al. showed that spatial imagers tend to be con-
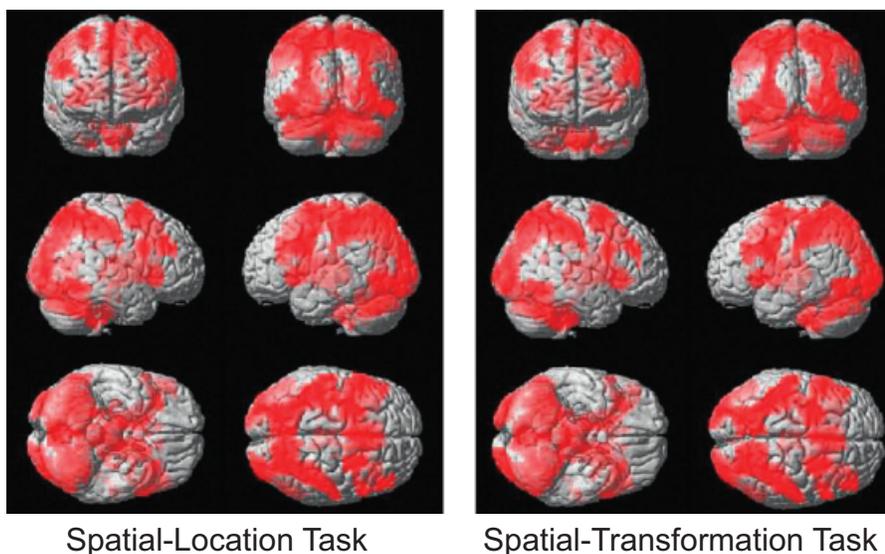

Spatial-Location Task   Spatial-Transformation Task

Fig. 3. Activation associated with the spatial-location and spatial-transformation tasks when compared with the baseline (top left: anterior view; top right: posterior view; middle left: right lateral view; middle right: left lateral view; bottom left: inferior view; bottom right: superior view).
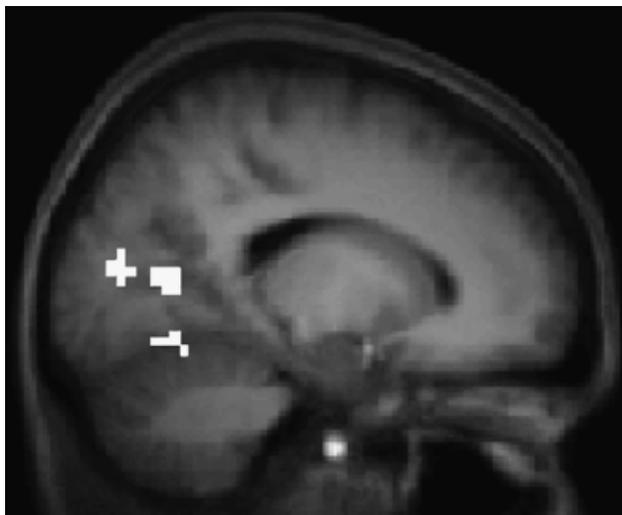
Fig. 4. Medial sagittal view of activation near the right occipito-parietal junction (first focus of activation listed in Table 2) associated with the spatial-location task when contrasted with the spatial-transformation task (activation in this region was also elevated in the spatial-location task relative to the baseline). Activation in more inferior lingual gyrus can be seen, although the activity in this region was not significantly elevated relative to the baseline.

centrated in certain professions and tend to interpret graphic representations differently than object imagers do. However, Kozhevnikov et al. sorted object imagers and spatial imagers according to reported preference, rather than ability, and focused on mental manipulations and transformations. Perhaps more important, they treated spatial imagery as a single capacity. Clearly, spatial imagery ability should be divided into more fine-grained capacities.

Kosslyn's (1994) theory posits that information about the locations and orientations of objects is organized into a single map, which is implemented primarily in the right parietal lobe. Our results are consistent with this claim, in that we found more activation for the location task, relative to the transformation task, in cortex near the right occipito-parietal junction. Moreover, the observed activation in the precuneus/posterior cingulate area in this same comparison may reflect this region's role in directing information to processes that operate on this map. In contrast, Kosslyn's theory posits that spatial transformations occur when a process operating on this map in turn changes the mapping function from inferotemporal areas (where visual memories are activated) to more posterior cortex; changing the mapping function alters the location or orientation of the object in the image. Our findings suggest that portions of the parietal lobe near the junction of the superior and inferior lobules may play a crucial role in spatial-transformation processes. Previous results (M.S. Cohen et al., 1996; Kosslyn et al., 1998) have also documented activation of motor and premotor regions during mental rotation (at least when certain strategies are used). These findings are consistent with the activation observed in the current study.

In interpreting our results, it is important to note that not all of the regions activated more in one task than the other necessarily implement the functions used to perform that task. In particular, portions of the lingual gyrus in BA 18 and BA 19 were clearly more activated in the location task than in the transformation task—but this was because of deactivation during the transformation task relative to the baseline (the activation in this region did not change in the location task relative to the baseline; see Table 2). Thus, we must caution that such differences in activation cannot be ascribed to the region's playing a role in the type of spatial imagery that underlies memory for location. Rather, it is possible that the transformation task (which our behavioral data indicate is more cognitively demanding than the location task) might require greater attention, and thus could require inhibiting regions where activation might interfere with task-specific processing. A static picture of fMRI results is inadequate to represent the dynamic, shifting nature of brain activations and deactivations. Not only may regions that might interfere with accomplishing a task be actively inhibited, but also resources such as blood flow and blood volume might be redistributed away from less useful regions toward essential ones. Given that spatial and shape-based imagery rely on different general processes (e.g., Kozhevnikov et al., 2005), and given the difficulty of the transformation task, resources may have shifted from object-based ventral-stream visual areas (e.g., BA 18) toward dorsal regions critical for spatial transformations.

The precuneus/posterior cingulate region, which was more activated in the location task than in the transformation task, has also been associated with the *default-mode network* (see Mason et al., 2007). However, it is unlikely that the activation in this region reflected "default" brain activation during the less-demanding spatial-location task: This region was more strongly activated bilaterally in the location task than in the baseline, which suggests that the activation was a result of the region's playing an active role in task-specific processing for location memory. Activations (compared with the transformation task) in other regions of the cuneus and lingual gyrus that were statistically unchanged from baseline may have reflected non-task-related processing (or stimulus-independent thought; Mason et al., 2007); however, the lack of statistical difference from baseline may also reflect a lack of statistical power.

Although we cannot with confidence interpret all the activation differences identified in the direct comparison of the two task conditions, the data reveal that there is a clear dissociation between two types of spatial imagery, and that a small, distinct set of brain areas is specific to each. These results support the claim that some processes map spatial locations and other processes transform spatial-relations representations (cf. Zacks & Michelon, 2005).

If spatial imagery ability (rather than simply "imagery ability") is useful in such tasks as learning geometry and anatomy, navigating an environment, and learning surgical techniques, then it is also important to know the particular spatial imagery

ability (or abilities) that comes into play in each circumstance. Such knowledge is essential in investigating the parameters that define the training and transfer of skill in a particular domain, and, ultimately, in designing training programs to fit a specific set of skills (cf. Wright, Thompson, Ganis, Newcombe, & Kosslyn, 2008). Progress has been made in identifying subcomponents of mental imagery (see Kosslyn, Thompson, & Ganis, 2006), including those functions that underlie processing shape and those that underlie processing spatial relations (see, e.g., Farah, Hammond, Levine, & Calvanio, 1988; Kosslyn, Ganis, & Thompson, 2001; Kozhevnikov, Hegarty, & Mayer, 2002). The present study was designed to further current understanding of spatial mental imagery by decomposing this construct into two component parts. Our results support the view that at least two different, broad types of spatial imagery exist.

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