

Neuroimaging Studies of Mental Rotation: A Meta-analysis and Review

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Abstract

■ Mental rotation is a hypothesized imagery process that has inspired controversy regarding the substrate of human spatial reasoning. Two central questions about mental rotation remain: Does mental rotation depend on analog spatial representations, and does mental rotation depend on motor simulation? A review and meta-analysis of neuroimaging studies help answer these questions. Mental rotation is accompanied by increased activity in the intraparietal sulcus and adjacent regions. These areas contain spatially mapped representations, and activity in

these areas is modulated by parametric manipulations of mental rotation tasks, supporting the view that mental rotation depends on analog representations. Mental rotation also is accompanied by activity in the medial superior precentral cortex, particularly under conditions that favor motor simulation, supporting the view that mental rotation depends on motor simulation in some situations. The relationship between mental rotation and motor simulation can be understood in terms of how these two processes update spatial reference frames. ■

INTRODUCTION

Mental rotation is a hypothetical psychological operation in which a mental image is rotated around some axis in three-dimensional space. Mental rotation was first revealed in behavioral experiments (Cooper & Shepard, 1973; Shepard & Metzler, 1971) in virtue of a striking finding: The time to make a judgment about a rotated object often increases in a near-linear fashion with the amount of rotation required to bring the object into alignment with a comparison object or with a previously learned template. Participants in mental rotation experiments generally report strong introspective impressions that they perform the experimental tasks by forming a mental image of the stimulus and imagine it rotating until aligned. That is, they intuit that they are performing an operation on *analog spatial representations*, in which “the intermediate stages of the internal process have a demonstrable one-to-one relation to intermediate stages of the corresponding external process” (Shepard & Cooper, 1982, p. 13).

Mental rotation has been controversial since the first reports. The experimental results have been taken as evidence for the existence of analog spatial representations in the mind/brain (Shepard & Cooper, 1982); however, alternative interpretations have attempted to explain the behavioral patterns in mental imagery experiments without recourse to analog representations (Pylyshyn, 1981). Neuropsychological and neuroimaging data have provided further evidence in the larger im-

agery debate, supporting the analog representation view (Kosslyn, 1994; but see Pylyshyn, 2003). Neuroimaging studies of mental rotation provide a valuable means to test the hypothesis that mental rotation, in particular, operates in virtue of analog spatial representations. Imaging evidence for such representations should satisfy two criteria. First, activation should be observed in areas known to be spatially mapped. Second, the observed activation should be modulated by the amount of mental rotation performed in a given trial or block of trials; this can be indexed by variables such as the angular distance of the rotation or participants’ response time. If spatially mapped regions of the brain consistently show increases in activation with increasing amounts of mental rotation, this would provide good evidence that mental rotation depends on analog spatial representations.

More recently, a debate has emerged about the role of motor processes in mental rotation. Early neuroimaging studies found activity during mental rotation tasks in areas in the posterior frontal cortex that are associated with motor planning and execution (Cohen & Bookheimer, 1994). These findings and others have led researchers to ask whether motor simulation plays an important role in mental rotation tasks. Neuroimaging studies can also contribute to answering this question. To do so, it is important to dissociate activity in motor regions of the brain due to motor demands of a task (e.g., pressing a response button) from activity related to spatial reasoning.

There are now several dozen neuroimaging studies of mental rotation (see Appendix A), so one might hope that the available data would help settle these outstanding controversies: Does mental rotation depend on analog

spatial representations, and does mental rotation depend on motor simulation? Unfortunately, however, the body of extant data is difficult to navigate: Foci of brain activity associated with mental rotation have been reported in every lobe of the cerebrum and in the cerebellum. The range of experimental and control tasks has varied widely, which may contribute to this variability. In such situations, the statistical technique of *meta-analysis* is particularly valuable (Turkeltaub, Eden, Jones, & Zeffiro, 2002). In the rest of this article, I describe a meta-analytic study of neuroimaging studies of mental rotation, delving into more detail on neuroimaging and other data relevant to the motor imagery question, and discuss the implications of these data for the two controversies.

SELECTION OF ARTICLES AND META-ANALYSIS PROCEDURE

Articles were identified by searching the PsycInfo (www.apa.org/psycinfo) and MedLine (www.nlm.nih.gov/pubs/factsheets/medline.html) databases in July 2006 for articles whose titles, abstracts, or keywords included the term “mental rotation” and any of the following terms: “PET,” “positron emission tomography,” “fMRI,” “MRI,” or “neuroimaging.” This returned 68 documents. Documents were excluded if they were not peer-reviewed journal articles publishing new data (e.g., dissertations, review articles, $n = 8$), did not report a positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) study (e.g., behavioral experiments, $n = 13$), did not study mental rotation of visual stimuli (e.g., spatial navigation or mental rotation of haptic stimuli, $n = 6$), or if they did not present the data in a form from which a stereotactic coordinate could be extracted (e.g., only sulci/gyri or Brodmann’s areas reported, or a small number of transverse slice images, $n = 9$). The remaining 32 articles are listed in Appendix A. In all experiments, participants either decided whether two objects matched or decided whether an object matched a prototype (e.g., whether an alphanumeric character was facing forward). The majority of experiments ($n = 19$) used Shepard and Metzler (1971) objects or similar stimuli. Other stimulus sets included alphanumeric characters ($n = 7$), drawings or photographs of objects ($n = 4$), drawings or photos of hands ($n = 4$), abstract 2-D line figures ($n = 3$), abstract 3-D cubes ($n = 3$), and drawings of bodies ($n = 1$).

For each article, the task comparisons reported were categorized as *transformation-specific* or *omnibus*. Transformation-specific contrasts isolated within-task effects of mental rotation, for example, by comparing a condition involving stimuli with large rotations to stimuli with small rotations during the same task. Task comparisons were identified as omnibus if they compared a mental rotation task to a loose control, for example, looking at a fixation crosshair. Each reported focus of

activation was converted to the stereotactic coordinate system of Talairach and Tournoux (1988) and entered into a database. When a paper reported multiple analyses that reused the same degrees of freedom, the most tightly controlled task comparison was used. For results reported in figures or described verbally, the stereotactic coordinates of each focus of activation were recorded using CARET (Van Essen et al., 2001; <http://brainmap.wustl.edu/caret>) and the PALS atlas (Van Essen, 2005; <http://brainmap.wustl.edu:8081/sums/directory.do?id=679528>). (This required subjective judgments as to the centroid of each focus based on the reported data.) A total of 320 activation foci were identified, 213 transformation-specific foci and 107 omnibus foci. These are listed in Appendix B.

Volume-wise probability maps were generated using the method and software described by Turkeltaub et al. (2002). Each focus of activation was located in a common stereotactic space (Talairach & Tournoux, 1988 space) and convolved with a Gaussian kernel ($SD = 6.0$ mm) to model the spatial uncertainty associated with the focus’s location. The resulting Gaussian distributions were summed, projected onto a 2-mm isotropic lattice, and thresholded to control the voxelwise false-positive rate at $p \leq .001$, based on the Monte Carlo simulations reported by Turkeltaub et al. Three maps were generated: one based on the transformation-specific foci, one based on the omnibus foci, and one based on all of the foci. After thresholding, contiguous clusters of above-threshold voxels were identified. Above-threshold voxels within the cortex were visualized using the PALS atlas and using CARET. The complete dataset, including the individual foci and probability maps, is available at http://sumsdb.wustl.edu/sums/directory.do?id=6617254&dir_name=JCogNeuro_07.

EFFECTS OF MENTAL ROTATION TASKS ON LOCAL BRAIN ACTIVITY

The results of the meta-analysis are shown in Table 1 and Figure 1. Brain regions that were consistently activated included the superior parietal, frontal, and inferiorotemporal cortex. Activity was observed bilaterally in most areas; however, in the parietal cortex, activity was somewhat more consistently observed in the right hemisphere, whereas in the frontal cortex, activity was more consistently observed in the left hemisphere.

Posterior Parietal/Occipital Cortex

A large number of studies reported foci of activation in the superior parietal cortex and adjacent areas, leading to a large significant region of activation centered in the intraparietal sulcus and extending into the transverse occipital sulcus, including Brodmann’s areas 7, 19, 39, and 40. The consistent activation of the superior parie-

Table 1. Brain Regions That Were Consistently Activated in a Meta-analysis of Neuroimaging Studies of Mental Rotation

Talairach Coordinates			Volume (cm ³)	Brodmann's Area	Description
x	y	z			
All Task Comparisons					
23.6	−64.8	42.7	29.35	7/19	Intraparietal sulcus
−27.3	−63.6	41.3	21.45	7/19	Intraparietal sulcus, temporal–occipital sulcus
−38.3	5.2	34.7	8.94	6	Precentral sulcus, superior frontal sulcus
−36.0	−83.4	4.2	3.28	19	Lateral occipital sulcus
42.6	15.3	21.0	2.42	44/46	Inferior frontal sulcus, inferior precentral sulcus
29.8	−7.5	46.9	2.26	4/6	Precentral sulcus, superior frontal sulcus
−0.1	15.2	42.3	0.83	8/9/32	Superior frontal gyrus
15.3	17.6	35.8	0.78	24/32	Anterior cingulate sulcus
−0.7	−5.5	53.7	0.12	6	Cingulate sulcus
−8.1	−89.9	−0.9	0.06	17	Calcarine fissure
Omnibus Task Comparisons					
24.9	−66.7	47.1	5.26	7/19	Superior parietal lobule
−31.3	−79.0	31.9	2.66	19	Intraparietal sulcus, temporal–occipital sulcus
−40.4	−2.1	42.1	1.83	6	Precentral sulcus
39.1	24.7	35.9	1.75	9/46	Inferior frontal sulcus
39.8	17.0	14.7	1.39	13	Insula
35.8	−0.1	41.9	1.32	6	Precentral sulcus
−19.5	−64.5	51.7	1.28	7	Intraparietal sulcus
−38.3	20.6	26.5	1.06	44/46	Inferior frontal sulcus, inferior precentral sulcus
−0.6	−2.7	53.2	0.60	6	Medial precentral gyrus
−1.5	14.3	46.9	0.42	8	Superior frontal gyrus
−44.0	−33.8	56.7	0.27	2	Postcentral sulcus
50.9	−20.5	5.0	0.15	44/45	Frontal operculum
Transformation-specific Task Comparisons					
23.2	−64.7	41.6	26.74	7/19	Intraparietal sulcus, temporal–occipital sulcus
−29.3	−64.6	34.8	21.77	19	Intraparietal sulcus, temporal–occipital sulcus, lateral occipital sulcus
−30.4	−3.7	43.7	2.06	6	Precentral sulcus
−43.9	19.2	22.0	1.70	44/45/46	Superior frontal sulcus
27.7	−9.7	49.1	1.58	6/8	Precentral sulcus
15.0	17.8	35.4	1.18	24/32	Anterior cingulate sulcus
45.8	11.3	23.2	0.43	44/45/46	Inferior frontal sulcus, inferior precentral sulcus
−47.5	−59.5	−10.0	0.18	37	Posterior inferior temporal sulcus

Coordinates are for the center of mass of a contiguous above-threshold probability cluster.

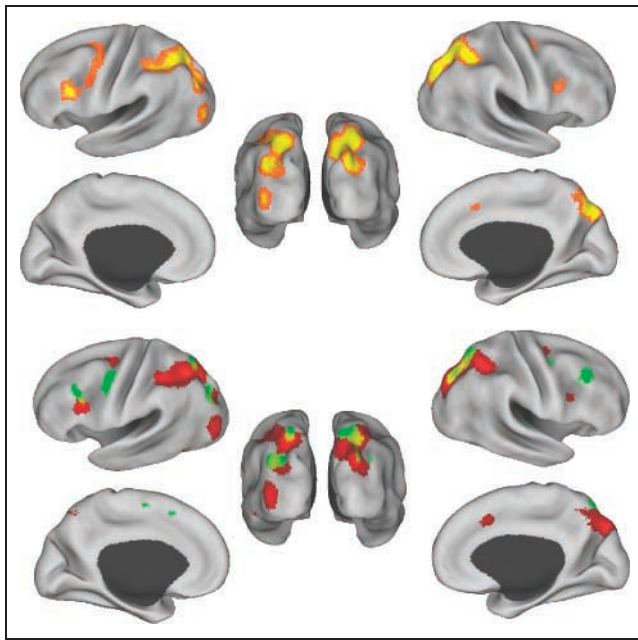


Figure 1. Meta-analysis of neuroimaging studies of mental rotation. The top panel shows the regions that responded above chance ($p \leq .001$, corrected for multiple comparisons) in mental rotation task comparisons across all studies. Brighter colors indicate stronger responses. The bottom panel compares two more specific types of task contrast ($p < .001$, corrected for multiple comparisons): *Red*: transformation-specific contrasts compared different degrees of mental rotation demand within a single task. *Green*: omnibus contrasts compared mental rotation tasks to loose control tasks, for example, fixating on a crosshair. *Yellow*: regions that were significantly associated with both transformation-specific and omnibus task comparison. In both panels, the meta-analysis results are projected on medial, oblique lateral, and posterior views of the cortical surface.

tal cortex during mental rotation tasks converges with neuropsychological data (Ratcliff, 1979) in indicating an important role for this region in visuospatial image transformations. As can be seen in the bottom of Figure 1, activity in this region was consistently observed in transformation-specific comparisons.

The superior parietal cortex is known to implement maps of space that code the locations of targets of intended actions. This can be seen most clearly in electrophysiological studies of eye movements and reaching in the monkey (Andersen & Buneo, 2002; Colby & Goldberg, 1999). Individual cells in monkey superior parietal cortex frequently represent locations in eye-centered coordinates, but these eye-centered responses are modulated by the monkey's head or body position (Snyder, Grieve, Brotchie, & Andersen, 1998), making it possible to read off location in body- or world-centered reference frames. Converging with the monkey data, patients with neglect syndrome, in which one part of space is ignored, often have lesions in the parietal cortex (Robertson, 2004; but see Karnath, Ferber, & Himmelbach, 2001), and this neglect can manifest itself in eye-, body-, or world-centered reference frames.

Thus, the results of the meta-analysis satisfy two key criteria for supporting the hypothesis that mental rotation depends on analog spatial representations. First, activity was observed in a brain area known to implement spatial maps, namely, the superior parietal cortex. Second, activity in this region was consistently related to the amount of mental rotation performed in a trial or block of trials; activations were observed in transformation-specific comparisons, not only in omnibus comparisons. This result reduces the likelihood that activity in the posterior parietal cortex during mental rotation tasks reflects incidental task features such as encoding a visual stimulus or making a manual response.

Motor Regions in the Precentral Cortex

The top pane of Figure 1 indicates that a number of studies reported activity during mental rotation tasks in the precentral sulcus, bilaterally. Regions in the precentral cortex are associated with motor planning and execution, and have been identified with mental rotation since the first neuroimaging studies of mental rotation (Cohen & Bookheimer, 1994). It has been suggested that precentral activity may reflect the use of motor simulation (computations that map to the specifics of joint angles and/or torques; Michelon, Vettel, & Zacks, 2006) to solve mental rotation problems. In other words, participants may simulate moving objects with their hands. However, an alternative is that activation in motor areas may be caused by incidental features of the tasks used—in particular, the need to make a manual response in nearly every study. Thus, does “motor” activity during mental rotation tasks reflect the use of motor simulation to solve the problems, or does it simply reflect the demands of planning and executing a motor response?

Inspection of Figure 1 and Table 1 provides part of an answer to this question. Foci of activation during transformation-specific contrasts were confined largely to the medial superior portion of the precentral sulcus. This region is described in the motor control literature as the *supplementary motor area* (SMA; Picard & Strick, 2001). The SMA is known to be responsive during motor imagery tasks and projects to both the *primary motor cortex* (M1) and the spinal cord, placing it in a good position to play a role in motor control and simulation. Foci of activation during the omnibus contrasts were largely confined to the lateral inferior portion of the precentral sulcus. These activations likely overlapped both M1 and *lateral premotor cortex* (PM).¹ Like SMA, M1 and PM both contain projections to the spinal cord, but these are denser in M1 (Dum & Strick, 2002). PM appears to code for actions at a more abstract level, representing the distal targets of actions as well as the proximal effectors (Schubotz & von Cramon, 2003). One possibility is that the activation of these areas during omnibus contrasts reflects the planning and execution of the task's motor response. In transformation-

specific contrasts, these components are better controlled because the tasks' motor response is constant throughout the within-task conditions being compared. Thus, the medial superior activations, likely corresponding to activity in the SMA, may well be due to mental rotation.

A series of PET experiments by Kosslyn, DiGirolamo, Thompson, and Alpert (1998) have probed the conditions under which mental rotation tasks activate motor areas. Their results converge in suggesting that, under some conditions, people are more likely to engage in motor simulation to solve mental rotation problems, and that when people engage this strategy, medial/superior motor areas are activated. The first experiment compared a mental rotation task involving hands with a task using abstract figures (Kosslyn et al., 1998). Mental rotation of hands produced greater activity in the left precentral gyrus. Another study used all abstract figures but manipulated participants' training before scanning (Kosslyn, Thompson, Wraga, & Alpert, 2001). In one condition, participants were trained to imagine an object rotated by an external force; in the other condition they imagined turning an object with their right hand. Activity in a region of the precentral cortex was reliably greater when participants imagined turning the object. (The authors identify this region as M1, but its stereotactic coordinates place it in the precentral sulcus, within the medial superior cluster shown in Figure 1. This may correspond to SMA rather than M1.) A third study (Wraga, Thompson, Alpert, & Kosslyn, 2003) used a transfer paradigm, in which participants first performed mental rotation of either hands or abstract objects, and then all participants performed mental rotation of abstract objects during scanning. Those participants who had previously rotated hands showed greater activity in the precentral cortex bilaterally than those who had not. A recent event-related fMRI study compared a task requiring right-left judgments about pictures of hands to right-left judgments about alphanumeric characters (de Lange, Hagoort, & Toni, 2005). This experiment identified two sets of regions in the precentral sulcus whose activity was positively correlated with the degree of rotation required on each trial. One set increased in activity with increasing rotation during mental rotation of both hands and characters, whereas the other set increased with increasing rotation only during hand rotation. Interestingly, the regions with hand-selective rotation responses also appeared to respond to the motor demands of the task, which further strengthen the interpretation that they performed motor simulations. One block-design fMRI study that compared mental rotation of hands and tools (Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002) failed to find significant differences between the two in motor areas, although there was a trend toward greater activity in the right precentral cortex during hand rotation. In sum, these data indicate that activity in parts of the precentral sulcus during mental rotation tasks is greatest when the task situation affords the use of a

motor simulation strategy. This supports the hypothesis that activity in these regions during mental rotation reflects motor simulation.

Prefrontal Cortex

The lateral inferior prefrontal cortex has not typically been highlighted in discussions of mental rotation data; however, eight different studies (studies 5, 9, 13–15, 23, and 30–31 in Appendix A) identified foci of activation in this area in transformation-specific contrasts and the responses were tightly clustered, leading to significant regions of activation in the meta-analysis. In two of these studies (Kosslyn et al., 1998, 2001), activation in the left inferior frontal cortex was specific to mental rotation tasks that were designed to encourage motor simulation (see above). As can be seen in Figure 1, the overlapping locations were in BA 44 and 45. This region has long been associated with speech production; more recently, it has been implicated in motor control and imitation (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Therefore, one possibility is that this activation, like that in SMA, reflects the use of motor simulation in some mental rotation tasks.

IMPLICATIONS

The present meta-analysis allows for two strong conclusions regarding the neural substrate of mental rotation. First, the posterior parietal cortex (as well as regions extending down into the superior posterior occipital cortex) is consistently activated during mental rotation across a range of tasks, imaging modalities, and statistical analysis strategies. This region is therefore a good candidate for implementing the transformation-specific computations required to carry out mental rotation tasks. This finding converges with data from neuropsychological studies (Farah, 1989) and from a transcranial magnetic stimulation study (Harris & Miniussi, 2003). The fact that these areas are known to contain multiple spatial maps provides support for the view that mental rotation is based on analog spatial representations. However, such inferences from *where* brain activity is observed in a task to *what* that brain region is doing are relatively weak, particularly as in this case when the areas in question respond during tasks unrelated to the task of interest (Poldrack, 2006). The inference can be strengthened in this case, however, because activation in this area was found in transformation-specific as well as omnibus comparisons. Moreover, several studies have conducted parametric analyses of brain activity as a function of response time, accuracy, proportion of rotated stimuli, or rotation angle, and have observed graded effects in these areas (Gauthier et al., 2002; Podzebenko, Egan, & Watson, 2002; Zacks, Ollinger,

Sheridan, & Tversky, 2002; Harris et al., 2000; Tagaris, Kim, Strupp, & Andersen, 1996). (This does not, however, necessitate that mental rotation operate holistically on whole objects rather than on object parts; see, e.g., Just & Carpenter, 1985.) Together with the meta-analytic result, these provide relatively good support for the hypothesis that mental rotation is a continuous transformation performed on **analog spatial representations**.

Second, motor areas in the posterior frontal cortex are clearly activated during many mental rotation paradigms. However, these activations appear to reflect at least two different processes. Activity in lateral inferior precentral regions, overlapping M1 and PM, likely reflects incidental features of some mental rotation tasks such as the need to execute a motor response. Activity in medial superior regions, most likely in the SMA, probably reflects computational processes that are specific to the mental image transformations. In particular, activity in these regions may reflect the use of motor simulation strategies when the task affords it. Studies using transcranial magnetic stimulation have provided converging evidence consistent with this hypothesis, although they do not have the spatial resolution to distinguish between M1, the SMA, and the premotor cortex. Three studies have reported that temporarily lesioning the left motor cortex impairs mental rotation of hands, but not of alphanumeric characters or feet (Tomasino, Borroni, Isaja, & Ida Rumiati, 2005; Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000).

Modulation of activity in the precentral cortex may reflect the degree that participants adopt a motor simulation strategy to solve a mental rotation task. (The lateral inferior prefrontal cortex and the superior parietal cortex also play important roles in motor planning, and thus, may also be modulated by the use of motor simulation.) That activity also may reflect the use of a motor transformation strategy, which could be implemented by transformations of a neural representation of a reaching movement (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989). The hypothesis that motor simulation sometimes interacts with mental rotation receives further support from behavioral studies that have identified interactions between mental and manual rotation (Wexler, Kosslyn, & Berthoz, 1998; Wohlschläger & Wohlschläger, 1998). In these experiments, participants were asked to mentally rotate a picture in order to make a spatial judgment, while turning a knob or joystick. Manual rotation in the same direction as the mental rotation sped response times, whereas manual rotation in the opposite direction slowed response times. This interaction between motor performance and mental rotation indicates that when motor simulation arises in mental imagery tasks, it is not merely epiphenomenal; instead, motor processes interact with visuospatial processes.

How are we to understand such interactions computationally? One way is to analyze mental imagery tasks in terms of the spatial reference frames on which they

depend (Zacks & Michelon, 2005). Performing most mental rotation tasks requires coordinating two different reference frames: an *object-centered* reference frame and an *environmental* reference frame. Object-centered reference frames locate things relative to the intrinsic axes of objects. For example, a car has a well-defined top (roof), bottom (undercarriage), front (grille), and back (trunk). Environmental reference frames locate things relative to the larger environment. For example, a movie theater has a well-defined front (screen), back (exits), top (ceiling), and bottom (floor). For visually presented stimuli, both of these reference frames must be computed by the brain from information initially coded in an eye-centered reference frame. One possibility is that object-centered and environmental reference frames in the superior parietal cortex are distributed representations constructed in the superior parietal cortex by gain fields, which modulate the eye-centered responses of individual cells based on signals coding the current position of the head and body (Andersen & Buneo, 2002). When mentally rotating an object, a person updates the relationship between the object's object-centered reference frame and an environmental frame. If the task requires one to compare two objects to decide if they are identical, updating is used to align the two objects' object-centered reference frames, so that the locations of object features can be compared in a common environmental reference frame. Interactions among cell populations in the superior parietal cortex may be the mechanism by which these two frames are brought into a particular relation. Such interactions may be governed by associations learned from a lifetime of experience observing rotational motion.

In some situations, it may be possible to bring to bear yet another reference frame when performing mental rotation tasks: *effector-centered* reference frames, which are defined relative to one's hands or feet. When one grasps an object, an effector-based reference frame becomes coupled to the object's object-based reference frame. When one moves the object by hand, this coupled reference frame is updated relative to the larger environmental reference frame. It is well established that people can simulate the updating of effector-based reference frames; this type of updating is at the core of motor imagery (Jeannerod & Frak, 1999). Adult humans have extensive experience with grasping and carrying. For some mental rotation tasks, people may tend to bring this experience to bear, updating not just an object-based reference frame but also a coupled object- and effector-based frame. This may be advantageous because it allows one to bring additional computational resources to bear. Large numbers of cells in the precentral cortex are known to code locations in effector-based coordinates (Colby, 1998). Therefore, during some mental imagery tasks, people may update effector-based reference frames in addition to object-based reference frames, leading to activation in the precentral cortex.² In short, the nervous

system has specialized mechanisms for updating effector-centered reference frames. When those mechanisms can be used to help solve mental rotation problems, this increases activity in motor regions of the brain.

APPENDIX A

Articles in the meta-analysis

1. Alivisatos, B., & Petrides, M. (1997). Functional activation of the human brain during mental rotation. *Neuropsychologia*, 35, 111–118.
2. Barnes, J., et al. (2000). Cortical activity during rotational and linear transformations. *Neuropsychologia*, 38, 1148–1156.
3. Berns, G. S., Chappelow, J. D., & Zink, C. F. (2005). Neurobiological correlates of social conformity and independence during mental rotation. *Biological Psychiatry*, 58, 245–253.
4. Carpenter, P. A., Just, M. A., Keller, T. A., Eddy, W., & Thulborn, K. (1999). Graded functional activation in the visuospatial system with the amount of task demand. *J Cognitive Neuroscience*, 11, 9–24.
5. Cohen, M. S., et al. (1996). Changes in cortical activity during mental rotation. A mapping study using functional MRI. *Brain*, 119, 89–100.
6. Dietrich, T., et al. (2001). Effects of blood estrogen level on cortical activation patterns during cognitive activation as measured by functional MRI. *Neuroimage*, 13, 425–432.
7. Halari, R., et al. (2006). Comparable fMRI activity with differential behavioural performance on mental rotation and overt verbal fluency tasks in healthy men and women. *Experimental Brain Research*, 169, 1–14.
8. Harris, I. M., et al. (2000). Selective right parietal lobe activation during mental rotation: A parametric PET study. *Brain*, 123, 65–73.
9. Johnston, S., Leek, E. C., Atherton, C., Thacker, N., & Jackson, A. (2004). Functional contribution of medial premotor cortex to visuo-spatial transformation in humans. *Neuroscience Letters*, 355, 209–212.
10. Jordan, K., Heinze, H. J., Lutz, K., Kanowski, M., & Jancke, L. (2001). Cortical activations during the mental rotation of different visual objects. *Neuroimage*, 13, 143–152.
11. Just, M. A., Carpenter, P. A., Maguire, M., Diwadkar, V., & McMains, S. (2001). Mental rotation of objects retrieved from memory: A functional MRI study of spatial processing. *Journal of Experimental Psychology: General*, 130, 493–504.
12. Just, M. A., et al. (2001). Interdependence of nonoverlapping cortical systems in dual cognitive tasks. *Neuroimage*, 14, 417–426.
13. Kosslyn, S. M., Digirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. *Psychophysiology*, 35, 151–161.
14. Kosslyn, S. M., Thompson, W. L., Wraga, M., & Alpert, N. M. (2001). Imagining rotation by endogenous versus exogenous forces: Distinct neural mechanisms. *NeuroReport*, 12, 2519–2525.
15. Ng, V. W., et al. (2001). Identifying rate-limiting nodes in large-scale cortical networks for visuospatial processing: An illustration using fMRI. *Journal of Cognitive Neuroscience*, 13, 537–545.
16. Podzebenko, K., Egan, G. F., & Watson, J. D. (2002). Widespread dorsal stream activation during a parametric mental rotation task, revealed with functional magnetic resonance imaging. *Neuroimage*, 15, 547–558.
17. Podzebenko, K., Egan, G. F., & Watson, J. D. G. (2005). Real and imaginary rotary motion processing: Functional parcellation of the human parietal lobe revealed by fMRI. *Journal of Cognitive Neuroscience*, 17, 24–36.
18. Richter, W., et al. (2000). Motor area activity during mental rotation studied by time-resolved single-trial fMRI. *Journal of Cognitive Neuroscience*, 12, 310–320.
19. Richter, W., Ugurbil, K., Georgopoulos, A., & Kim, S.-G. (1997). Time-resolved fMRI of mental rotation. *NeuroReport*, 8, 3697–3702.
20. Silk, T., et al. (2005). Fronto-parietal activation in attention-deficit hyperactivity disorder, combined type: Functional magnetic resonance imaging study. *British Journal of Psychiatry*, 187, 282–283.
21. Tagaris, G. A., Kim, S.-G., Strupp, J. P., Andersen, P., et al. (1997). Mental rotation studied by functional magnetic resonance imaging at high field (4 Tesla): Performance and cortical activation. *Journal of Cognitive Neuroscience*, 9, 419–432.
22. Tagaris, G. A., et al. (1998). Functional magnetic resonance imaging of mental rotation and memory scanning: A multidimensional scaling analysis of brain activation patterns. *Brain Research Reviews*, 26, 106–112.
23. Thomsen, T., et al. (2000). Functional magnetic resonance imaging (fMRI) study of sex differences in a mental rotation task. *Medical Science Monitor*, 6, 1186–1196.
24. Vanrie, J., Bâeatse, E., Wagemans, J., Sunaert, S., & Van Hecke, P. (2002). Mental rotation versus invariant features in object perception from different viewpoints: An fMRI study. *Neuropsychologia*, 40, 917–930.
25. Vingerhoets, G., de Lange, F. P., Vandemaele, P., Deblaere, K., & Achten, E. (2002). Motor imagery in mental rotation: An fMRI study. *Neuroimage*, 17, 1623–1633.
26. Vingerhoets, G., et al. (2001). Regional brain activity during different paradigms of mental rotation in healthy volunteers: A positron emission tomography study. *Neuroimage*, 13, 381–391.
27. Weiss, E., et al. (2003). Sex differences in brain activation pattern during a visuospatial cognitive task: A functional magnetic resonance imaging study in healthy volunteers. *Neuroscience Letters*, 344, 169–172.
28. Windischberger, C., et al. (2003). Fuzzy cluster analysis of high-field functional MRI data. *Artificial Intelligence in Medicine*, 29, 203–223.

29. Windischberger, C., Lamm, C., Bauer, H., & Moser, E. (2003). Human motor cortex activity during mental rotation. *Neuroimage*, 20, 225–232.

30. Wraga, M., Thompson, W. L., Alpert, N. M., & Kosslyn, S. M. (2003). Implicit transfer of motor strategies in mental rotation. *Brain and Cognition*, 52, 135–143.

31. Zacks, J., Rypma, B., Gabrieli, J. D., Tversky, B., & Glover, G. H. (1999). Imagined transformations of

bodies: An fMRI investigation. *Neuropsychologia*, 37, 1029–1040.

32. Zitzmann, M., Weckesser, M., Schober, O., & Nieschlag, E. (2001). Changes in cerebral glucose metabolism and visuospatial capability in hypogonadal males under testosterone substitution therapy. *Experimental and Clinical Endocrinology and Diabetes*, 109, 302–304.

APPENDIX B

Activation foci entered in the meta-analysis. (See Appendix A for ID numbers. All coordinates reported in Talairach '88 space. T = transformation-specific; O = omnibus. This table can be downloaded from http://sumsdb.wustl.edu/sums/directory.do?id=6617254&dir_name=JCogNeuro_07.)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	x	y	z
1	115	Table 3	Mental rotation minus mirror image task	T	N	−39	−54	45
1	115	Table 3	Mental rotation minus mirror image task	T	N	−13	−68	48
1	115	Table 3	Mental rotation minus mirror image task	T	N	38	32	3
1	115	Table 3	Mental rotation minus mirror image task	T	N	20	10	47
1	115	Table 3	Mental rotation minus mirror image task	T	N	8	17	6
2	1152	Table 1	Rotational transformation	O	N	−17	−64	53
2	1152	Table 1	Rotational transformation	O	N	−26	−72	31
2	1152	Table 1	Rotational transformation	O	N	−40	−39	59
2	1152	Table 1	Rotational transformation	O	N	−43	0	42
2	1152	Table 1	Rotational transformation	O	N	17	−61	59
2	1152	Table 1	Rotational transformation	O	N	38	−61	−2
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	−22	−1	70
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	−31	−51	70
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	23	−1	70
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	27	−48	70
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	0	3	55
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	−47	−31	55
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	−22	−69	55
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	28	−59	55
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	−45	1	34
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	46	12	34
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	−25	−72	34
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	30	−73	34
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	−27	−90	8
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	31	−91	8
3	249	Figure 4	Baseline mental rotation (red areas)	O	Y	0	−16	8
4	14	Figure 4	Mental rotation in 40-degree increments	O	Y	0	−9	55
4	14	Figure 4	Mental rotation in 40-degree increments	O	Y	−22	−30	57

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
4	14	Figure 4	Mental rotation in 40-degree increments	O	Y	19	−28	57
4	14	Figure 4	Mental rotation in 40-degree increments	O	Y	−15	−84	55
4	14	Figure 4	Mental rotation in 40-degree increments	O	Y	12	−72	55
4	14	Figure 4	Mental rotation in 40-degree increments	O	Y	−37	−81	−18
4	14	Figure 4	Mental rotation in 40-degree increments	O	Y	30	−80	−18
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−46	11	−10
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	21	−98	26
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−44	−77	26
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−43	18	26
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	26	39	35
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−20	36	35
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	17	−56	35
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−14	−60	35
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−25	−94	35
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	12	−64	39
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	0	−97	39
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−48	−21	39
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−30	41	39
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	39	−11	47
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	42	−44	47
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	34	−41	54
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−41	−17	54
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	24	−56	68
5	94	Figure 5	Mental rotation minus control for single subject	T	Y	−27	−47	58
6	429	Text	Mental rotation	O	Y	−38	−76	36

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
6	429	Text	Mental rotation	O	Y	38	-76	36
7	6	Table 2	Males, rotation minus control	T	N	-34	-76	22
7	6	Table 2	Males, rotation minus control	T	N	-32	-82	2
7	6	Table 2	Males, rotation minus control	T	N	34	-70	22
7	6	Table 2	Males, rotation minus control	T	N	-36	-4	52
7	6	Table 2	Males, rotation minus control	T	N	32	-62	52
7	6	Table 2	Males, rotation minus control	T	N	26	-54	62
7	6	Table 2	Females, rotation minus control	T	N	-28	-78	12
7	6	Table 2	Females, rotation minus control	T	N	-38	-78	10
7	6	Table 2	Females, rotation minus control	T	N	-34	-78	-2
7	6	Table 2	Females, rotation minus control	T	N	-38	-40	56
7	6	Table 2	Females, rotation minus control	T	N	12	-52	62
7	6	Table 2	Females, rotation minus control	T	N	16	-58	58
8	68	Text	Mental rotation	O	N	30	-68	44
9	210	Text	Mental rotation minus control	T	N	5.94	-57.3976	51.669
9	210	Text	Mental rotation minus control	T	N	1.98	16.0472	44.627
9	210	Text	Mental rotation minus control	T	N	-41.58	17.5304	0.805
10	149	Table 3	3-D object rotation versus controls	T	N	-28	-64	48
10	149	Table 3	3-D object rotation versus controls	T	N	36	-52	52
10	149	Table 3	Abstract object rotation versus controls	T	N	-24	-64	48
10	149	Table 3	Abstract object rotation versus controls	T	N	24	-56	56
10	149	Table 3	Abstract object rotation versus controls	T	N	32	-48	44
10	149	Table 3	Abstract object rotation versus controls	T	N	-32	-4	40
10	149	Table 3	Letter rotation versus controls	T	N	-24	-64	48
10	149	Table 3	Letter rotation versus controls	T	N	24	-52	56
11	422	Table 1	Mental rotation	O	N	-52	-19	6
11	422	Table 1	Mental rotation	O	N	51	-21	5
11	422	Table 1	Mental rotation	O	N	-29	-52	44
11	422	Table 1	Mental rotation	O	N	29	-54	42
11	422	Table 1	Mental rotation	O	N	3	-72	8
11	422	Table 1	Mental rotation	O	N	-26	-70	3
11	422	Table 1	Mental rotation	O	N	32	-67	4
11	422	Table 1	Mental rotation	O	N	-34	25	35
11	422	Table 1	Mental rotation	O	N	32	33	35
11	422	Table 1	Mental rotation	O	N	0	13	35
11	422	Table 1	Mental rotation	O	N	-37	18	18
11	422	Table 1	Mental rotation	O	N	40	21	13
11	422	Table 1	Mental rotation	O	N	-40	-1	45

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
11	422	Table 1	Mental rotation	O	N	38	2	41
11	422	Table 1	Mental rotation	O	N	−1	16	48
11	422	Table 1	Mental rotation	O	N	−35	−8	49
11	422	Table 1	Mental rotation	O	N	37	−5	45
11	422	Table 1	Mental rotation	O	N	1	−2	56
11	422	Table 1	Mental rotation	O	N	1	−55	−12
12	497	Table 1	Mental rotation	O	N	−17	−60	47
12	497	Table 1	Mental rotation	O	N	21	−60	48
12	497	Table 1	Mental rotation	O	N	−35	−53	40
12	497	Table 1	Mental rotation	O	N	38	−47	42
12	497	Table 1	Mental rotation	O	N	−39	17	20
12	497	Table 1	Mental rotation	O	N	40	18	19
12	497	Table 1	Mental rotation	O	N	−36	27	34
12	497	Table 1	Mental rotation	O	N	32	24	42
12	497	Table 1	Mental rotation	O	N	−52	−29	3
12	497	Table 1	Mental rotation	O	N	53	−18	8
12	497	Table 1	Mental rotation	O	N	−35	1	47
12	497	Table 1	Mental rotation	O	N	35	3	46
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	−27	−85	28
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	−29	−71	36
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	−15	−68	44
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	−33	−42	40
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	39	−90	8
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	27	−79	36
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	12	−65	48
13	157	Table 1	Rotation of Shepard–Metzler cubes minus baseline condition	T	N	35	−46	40
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−22	−83	28
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−20	−68	44
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−38	−37	44
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−50	−32	40

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−29	−21	52
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−34	2	36
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−26	15	−4
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	−20	49	20
13	158	Table 2	Rotation of hand stimuli minus baseline condition	T	N	4	−74	8
14	2522	Table 2	IA – baseline	T	N	26	−60	48
14	2522	Table 2	IA – baseline	T	N	−22	−2	52
14	2522	Table 2	IA – baseline	T	N	24	−78	32
14	2522	Table 2	IA – baseline	T	N	−36	−80	12
14	2522	Table 2	IA – baseline	T	N	−36	−88	−4
14	2522	Table 2	IA – baseline	T	N	−32	32	4
14	2522	Table 2	IA – baseline	T	N	−28	36	16
14	2522	Table 2	IA – baseline	T	N	−44	20	24
14	2522	Table 2	IA – baseline	T	N	−44	−58	−8
14	2522	Table 2	EA – baseline	T	N	26	−56	48
14	2522	Table 2	EA – baseline	T	N	−44	22	24
14	2522	Table 2	EA – baseline	T	N	−32	−76	32
14	2522	Table 2	EA – baseline	T	N	28	−76	32
14	2522	Table 2	EA – baseline	T	N	−20	4	52
14	2522	Table 2	EA – baseline	T	N	−34	−90	−4
14	2522	Table 2	EA – baseline	T	N	−48	−56	−8
15	540	Table 1	Mental rotation	T	N	14	−64	42
15	540	Table 1	Mental rotation	T	N	−6	−64	48
15	540	Table 1	Mental rotation	T	N	−38	−42	48
15	540	Table 1	Mental rotation	T	N	32	−72	20
15	540	Table 1	Mental rotation	T	N	35	−72	4
15	540	Table 1	Mental rotation	T	N	52	11	26
15	540	Table 1	Mental rotation	T	N	−6	−58	37
15	540	Table 1	Mental rotation	T	N	17	−69	37
15	540	Table 1	Mental rotation	T	N	26	−78	−7
15	540	Table 1	Mental rotation	T	N	8	−70	55
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	−30	−82	36
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	22	−78	54

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	−42	−54	46
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	36	−70	−32
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	34	−56	54
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	−36	−90	4
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	32	−12	56
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	44	12	8
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	−4	−64	64
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	28	−54	44
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	−44	−82	−14
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	42	−86	−10
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	24	−84	42
16	552	Table 1	Mental rotation region correlated with proportion of stimuli rotated	T	N	−36	20	4
17	31	Table 3	Rotating alphanumerics minus stationary alphanumerics	T	N	26	−86	38
17	31	Table 3	Rotating alphanumerics minus stationary alphanumerics	T	N	−54	−82	10
17	31	Table 3	Rotating alphanumerics minus stationary alphanumerics	T	N	52	−76	8
17	31	Table 3	Rotating alphanumerics minus stationary alphanumerics	T	N	−38	−90	0
17	31	Table 3	Stationary alphanumerics minus rotating alphanumerics	T	N	−4	−90	10
17	31	Table 3	Rotating abstracts minus stationary abstracts	T	N	−28	−60	64
17	31	Table 3	Rotating abstracts minus stationary abstracts	T	N	−54	−82	8
17	31	Table 3	Rotating abstracts minus stationary abstracts	T	N	52	−80	6
17	31	Table 3	Rotating abstracts minus stationary abstracts	T	N	−40	−88	2
18	3700	Figure 2	Rotation-control contrast	T	Y	−21	−94	21
18	3700	Figure 2	Rotation-control contrast	T	Y	22	−94	14
18	3700	Figure 2	Rotation-control contrast	T	Y	−15	−94	3

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
18	3700	Figure 2	Rotation-control contrast	T	Y	24	−94	−2
19	312	Figure 3	Mental rotation	T	Y	−25	−20	57
19	312	Figure 3	Mental rotation	T	Y	36	−26	57
19	312	Figure 3	Mental rotation	T	Y	0	−7	57
19	312	Figure 3	Mental rotation	T	Y	−32	−61	57
19	312	Figure 3	Mental rotation	T	Y	33	−58	57
19	312	Figure 3	Mental rotation	T	Y	−6	−66	57
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	27	9	54
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	36	9	18
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	45	18	21
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	−15	−90*	24
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	21	−6	51
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	15	−75	42
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	30	−84	3
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	48	−39	3
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	3	27	39
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	−51	3	24
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	39	12	80
20	283	Text	Mental rotation minus baseline, ADHD subjects	O	N	24	27	−18
21	423	Figure 5	Mental rotation	O	Y	44	27	40
21	423	Figure 5	Mental rotation	O	Y	12	24	58
21	423	Figure 5	Mental rotation	O	Y	−33	−82	31
21	423	Figure 5	Mental rotation	O	Y	−39	−15	62
21	423	Figure 5	Mental rotation	O	Y	−42	−30	62
21	423	Figure 5	Mental rotation	O	Y	−12	24	58
21	423	Figure 5	Mental rotation	O	Y	−13	59	−4
21	423	Figure 5	Mental rotation	O	Y	44	27	40
21	423	Figure 5	Mental rotation	O	Y	0	30	16
21	423	Figure 5	Mental rotation	O	Y	13	59	−4
21	423	Figure 5	Mental rotation	T	Y	35	−52	56

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
21	423	Figure 5	Mental rotation	T	Y	33	−82	31
21	423	Figure 5	Mental rotation	T	Y	−19	−97	2
21	423	Figure 5	Mental rotation	T	Y	19	−97	2
21	423	Figure 5	Mental rotation	T	Y	−35	−52	56
21	423	Figure 5	Mental rotation	T	Y	42	−30	62
21	423	Figure 5	Mental rotation	T	Y	39	−15	62
22	112	Figure 1	Visual mental rotation	O	Y	16	−66	60
22	112	Figure 1	Visual mental rotation	O	Y	25	−55	62
22	112	Figure 1	Visual mental rotation	O	Y	−18	−61	59
22	112	Figure 1	Visual mental rotation	O	Y	44	−21	57
22	112	Figure 1	Visual mental rotation	O	Y	49	−3	43
23	1192	Table 4	MR task minus control task: males only	T	N	22	−69	42
23	1192	Table 4	MR task minus control task: males only	T	N	−27	−50	43
23	1192	Table 5	MR task minus control task: females only	T	N	22	−77	38
23	1192	Table 5	MR task minus control task: females only	T	N	40	24	22
23	1192	Table 5	MR task minus control task: females only	T	N	−20	−58	46
23	1192	Table 5	MR task minus control task: females only	T	N	−38	20	22
24	922	Table 1	Rotation-control contrast	T	N	27	1	54
24	922	Table 1	Rotation-control contrast	T	N	51	39	27
24	922	Table 1	Rotation-control contrast	T	N	25	−57	57
24	922	Table 1	Rotation-control contrast	T	N	37	−67	−24
24	922	Table 1	Rotation-control contrast	T	N	13	−60	4
24	922	Table 1	Rotation-control contrast	T	N	39	−36	39
24	922	Table 1	Rotation-control contrast	T	N	34	−78	16
24	922	Table 1	Rotation-control contrast	T	N	3	30	45
25	387	Table 1	Mental rotation	T	N	−42	−6	48
25	387	Table 1	Mental rotation	T	N	−15	−72	63
25	387	Table 1	Mental rotation	T	N	18	21	39
25	387	Table 1	Mental rotation	T	N	18	21	39
25	387	Table 1	Mental rotation	T	N	−6	−87	0
25	387	Table 1	Mental rotation	T	N	−57	−15	−3
25	387	Table 1	Mental rotation	T	N	−3	39	45
25	387	Table 1	Mental rotation	T	N	−9	−69	−3
25	387	Table 1	Mental rotation	T	N	−12	−27	72
25	387	Table 1	Mental rotation	T	N	−37.8	−9.1	41.5
25	387	Table 1	Mental rotation	T	N	−14	−73.2	51.4
25	387	Table 1	Mental rotation	T	N	15	17	34.9
25	387	Table 1	Mental rotation	T	N	15	17	34.9

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	x	y	z
25	387	Table 1	Mental rotation	T	N	-6.1	-87.7	-4.8
25	387	Table 1	Mental rotation	T	N	-51	-17.9	0.4
25	387	Table 1	Mental rotation	T	N	-3.4	34.5	41.1
25	387	Table 1	Mental rotation	T	N	-8.7	-70.3	-6.5
25	387	Table 1	Mental rotation	T	N	-11.4	-29.5	61.6
26	1628	Table 2	EH – CH	T	N	17	-89	-19
26	1628	Table 2	EH – CH	T	N	-25	-48	31
26	1628	Table 2	EH – CH	T	N	29	-50	50
26	1628	Table 2	EH – CH	T	N	-24	-9	50
26	1628	Table 2	EH – CH	T	N	26	-9	52
26	1628	Table 2	EH – CH	T	N	33	-85	-12
26	1628	Table 2	ET – CT	T	N	-4	-31	-25
26	1628	Table 2	ET – CT	T	N	1	-40	-27
26	1628	Table 2	ET – CT	T	N	-24	-69	-23
26	1628	Table 2	ET – CT	T	N	24	-60	-32
26	1628	Table 2	ET – CT	T	N	-29	-58	53
26	1628	Table 2	ET – CT	T	N	17	-67	48
26	1628	Table 2	ET – CT	T	N	-25	-3	51
26	1628	Table 2	ET – CT	T	N	-22	-79	22
26	1628	Table 2	ET – CT	T	N	24	-81	25
27	171	Text	Mental rotation minus control	T	N	32	24	-4
27	171	Text	Mental rotation minus control	T	N	-52	4	32
27	171	Text	Mental rotation minus control	T	N	28	-8	52
27	171	Text	Mental rotation minus control	T	N	-28	-8	64
27	171	Text	Mental rotation minus control	T	N	0	16	40
27	171	Text	Mental rotation minus control	T	N	36	-44	40
27	171	Text	Mental rotation minus control	T	N	-40	-40	52
28	217	Figure 9	Mental rotation versus rest condition	O	Y	-29	-88	33
28	217	Figure 9	Mental rotation versus rest condition	O	Y	14	-92	33
28	217	Figure 9	Mental rotation versus rest condition	O	Y	-56	-2	12
28	217	Figure 9	Mental rotation versus rest condition	O	Y	-45	31	9
28	217	Figure 9	Mental rotation versus rest condition	O	Y	48	-16	20
28	217	Figure 9	Mental rotation versus rest condition	O	Y	-31	-79	38
28	217	Figure 9	Mental rotation versus rest condition	O	Y	31	-79	38
29	231	Figure 5	Activation during task processing	O	Y	-42	18	32
29	231	Figure 5	Activation during task processing	O	Y	39	23	32
29	231	Figure 5	Activation during task processing	O	Y	45	-59	46
29	231	Figure 5	Activation during task processing	O	Y	33	-69	50

APPENDIX B (continued)

ID	Page	Table or Figure	Condition/Contrast	Class	Coordinates			
					Hand-entered?	<i>x</i>	<i>y</i>	<i>z</i>
29	231	Figure 5	Activation during task processing	O	Y	0	16	50
29	231	Figure 5	Activation during task processing	O	Y	-21	4	55
29	231	Figure 5	Activation during task processing	O	Y	27	15	55
30	141	Table 2	Hand – baseline	T	N	-38	44	-12
30	141	Table 2	Hand – baseline	T	N	-40	0	28
30	141	Table 2	Hand – baseline	T	N	-32	-12	-4
30	141	Table 2	Hand – baseline	T	N	-8	-42	16
30	141	Table 2	Hand – baseline	T	N	-22	40	24
30	141	Table 2	Object – baseline	T	N	22	-64	44
30	141	Table 2	Object – baseline	T	N	46	12	24
30	141	Table 2	Object – baseline	T	N	28	-74	28
30	141	Table 2	Object – baseline	T	N	-20	-62	48
30	141	Table 2	Object – baseline	T	N	-34	24	-12
30	141	Table 2	Object – baseline	T	N	-48	-62	-8
30	141	Table 2	Object HO – baseline	T	N	-10	-76	36
30	141	Table 2	Object HO – baseline	T	N	0	-62	4
30	141	Table 2	Object HO – baseline	T	N	26	-12	52
30	141	Table 2	Object OO – baseline	T	N	24	-62	44
30	141	Table 2	Object OO – baseline	T	N	30	-70	32
30	141	Table 2	Object OO – baseline	T	N	44	10	24
30	141	Table 2	Object OO – baseline	T	N	-36	-40	40
31	1035	Figure 4	Inverted – upright	T	Y	-45	26	20
31	1035	Figure 4	Inverted – upright	T	Y	-44	10	32
31	1035	Figure 4	Inverted – upright	T	Y	48	19	32
31	1035	Figure 4	Inverted – upright	T	Y	3	30	32
31	1035	Figure 4	Inverted – upright	T	Y	-19	12	50
31	1035	Figure 4	Inverted – upright	T	Y	-43	-57	50
31	1035	Figure 4	Inverted – upright	T	Y	12	-83	50
31	1035	Figure 4	Inverted – upright	T	Y	12	-83	50
31	1035	Figure 4	Inverted – upright	T	Y	12	-83	50
31	1035	Figure 4	Inverted – upright	T	Y	12	-83	50
31	1035	Figure 4	Inverted – upright	T	Y	12	-83	50
32	304	Table 1	Mental rotation	O	N	28	-92	-8

MR = mental rotation; IA = internal action; EA = external action; ADHD = attention deficit disorder; EH = experimental hands; CH = control hands; ET = experimental tools; CT = control tools; HO = hand-object; OO = object-object.

*This coordinate appears in the original publication as -15, 90, 24; this erratum was corrected for the analyses.

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Notes

1. Using this meta-analysis technique, it is possible that such patterns can arise due to incidental differences between a small number of studies, if each study contributes several nearby foci to the analysis. This was not the case in the present instance: In the left hemisphere, 12 separate studies were represented; in the right hemisphere, 8 separate studies were represented.
2. The parietal cortex and the frontal cortex contain cells that code information that can be read out in effector-based coordinates (Andersen & Buneo, 2002; Colby, 1998). Therefore, it is possible that some of the variations in activation in parietal regions across mental rotation paradigms reflect the engagement of these representations.

REFERENCES

- Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, 25, 189–220.
- Cohen, M. S., & Bookheimer, S. Y. (1994). Localization of brain function using magnetic resonance imaging. *Trends in Neurosciences*, 17, 268–277.
- Colby, C. L. (1998). Action-oriented spatial reference frames in cortex. *Neuron*, 20, 15–24.
- Colby, C. L., & Goldberg, M. E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience*, 22, 319–349.
- Cooper, L. A., & Shepard, R. N. (1973). The time required to prepare for a rotated stimulus. *Memory & Cognition*, 1, 246–250.
- de Lange, F. P., Hagoort, P., & Toni, I. (2005). Neural topography and content of movement representations. *Journal of Cognitive Neuroscience*, 17, 97–112.
- Dum, R. P., & Strick, P. L. (2002). Motor areas in the frontal lobe of the primate. *Physiology and Behavior*, 77, 677–682.
- Farah, M. J. (1989). The neuropsychology of mental imagery. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (pp. 395–413). Amsterdam: Elsevier.
- Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex*, 10, 175–180.
- Gauthier, I., Hayward, W. G., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (2002). BOLD activity during mental rotation and viewpoint-dependent object recognition. *Neuron*, 34, 161–171.
- Georgopoulos, A. P., Lurito, J. T., Petrides, M., Schwartz, A. B., & Massey, J. T. (1989). Mental rotation of the neuronal population vector. *Science*, 243, 234–236.
- Harris, I. M., Egan, G. F., Sonkkila, C., Tochon-Danguy, H. J., Paxinos, G., & Watson, J. D. G. (2000). Selective right parietal lobe activation during mental rotation: A parametric PET study. *Brain*, 123, 65–73.
- Harris, I. M., & Miniussi, C. (2003). Parietal lobe contribution to mental rotation demonstrated with rTMS. *Journal of Cognitive Neuroscience*, 15, 1–9.
- Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current Opinion in Neurobiology*, 9, 735–739.
- Just, M. A., & Carpenter, P. A. (1985). Cognitive coordinate systems: Accounts of mental rotation and individual differences in spatial ability. *Psychological Review*, 92, 137–172.
- Karnath, H.-O., Ferber, S., & Himmelbach, M. (2001). Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature*, 411, 950–952.
- Kosslyn, S. M. (1994). *Image and brain: The resolution of the imagery debate*. Cambridge: MIT Press.
- Kosslyn, S. M., DiGirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. *Psychophysiology*, 35, 151–161.
- Kosslyn, S. M., Thompson, W. L., Wraga, M., & Alpert, N. M. (2001). Imagining rotation by endogenous versus exogenous forces: Distinct neural mechanisms. *NeuroReport*, 12, 2519–2525.
- Michelon, P., Vettel, J. M., & Zacks, J. M. (2006). Lateral somatotopic organization during imagined and prepared movements. *Journal of Neurophysiology*, 95, 811–822.
- Picard, N., & Strick, P. L. (2001). Imaging the premotor areas. *Current Opinion in Neurobiology*, 11, 663–672.
- Podzebenko, K., Egan, G. F., & Watson, J. D. (2002). Widespread dorsal stream activation during a parametric mental rotation task, revealed with functional magnetic resonance imaging. *Neuroimage*, 15, 547–558.
- Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, 10, 59–63.
- Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, 88, 16–45.
- Pylyshyn, Z. W. (2003). Return of the mental image: Are there really pictures in the brain? *Trends in Cognitive Sciences*, 7, 113–118.
- Ratcliff, G. (1979). Spatial thought, mental rotation and the right cerebral hemisphere. *Neuropsychologia*, 17, 49–54.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, 3, 131–141.
- Robertson, L. C. (2004). *Space, objects, minds and brains*. New York: Psychology Press.
- Schubotz, R. I., & von Cramon, D. Y. (2003). Functional-anatomical concepts of human premotor cortex: Evidence from fMRI and PET studies. *Neuroimage*, 20(Suppl. 1), S120–S131.
- Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge: MIT Press.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.
- Snyder, L. H., Grieve, K. L., Brotchie, P., & Andersen, R. A. (1998). Separate body- and world-referenced representations of visual space in parietal cortex. *Nature*, 394, 887–891.
- Tagaris, G. A., Kim, S.-G., Strupp, J. P., & Andersen, P. (1996). Quantitative relations between parietal activation and performance in mental rotation. *NeuroReport*, 7, 773–776.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: 3-Dimensional proportional system, an approach to cerebral imaging*. Stuttgart: Thieme.
- Tomasino, B., Borroni, P., Isaja, A., & Ida Rumati, R. (2005). The role of the primary motor cortex in mental rotation: A TMS study. *Cognitive Neuropsychology*, 22, 348–363.

- Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *Neuroimage*, *16*, 765–780.
- Van Essen, D. C. (2005). A Population-Average, Landmark- and Surface-based (PALS) atlas of human cerebral cortex. *Neuroimage*, *28*, 635–662.
- Van Essen, D. C., Drury, H. A., Dickson, J., Harwell, J., Hanlon, D., & Anderson, C. H. (2001). An integrated software suite for surface-based analyses of cerebral cortex. *Journal of the American Medical Informatics Association*, *8*, 443–459.
- Vingerhoets, G., de Lange, F. P., Vandemaele, P., Deblaere, K., & Achten, E. (2002). Motor imagery in mental rotation: An fMRI study. *Neuroimage*, *17*, 1623–1633.
- Wexler, M., Kosslyn, S. M., & Berthoz, A. (1998). Motor processes in mental rotation. *Cognition*, *68*, 77–94.
- Wohlschläger, A., & Wohlschläger, A. (1998). Mental and manual rotation. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 397–412.
- Wraga, M., Thompson, W. L., Alpert, N. M., & Kosslyn, S. M. (2003). Implicit transfer of motor strategies in mental rotation. *Brain and Cognition*, *52*, 135–143.
- Zacks, J. M., & Michelon, P. (2005). Transformations of visuospatial images. *Behavioral and Cognitive Neuroscience Reviews*, *4*, 96–118.
- Zacks, J. M., Ollinger, J. M., Sheridan, M. A., & Tversky, B. (2002). A parametric study of mental spatial transformations of bodies. *Neuroimage*, *16*, 857–872.