

Imagining rotation by endogenous *versus* exogenous forces: Distinct neural mechanisms

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Previous neuroimaging studies of mental image transformations have sometimes implicated motor processes and sometimes not. In this study, prior to neuroimaging the subjects either viewed an electric motor rotating an angular object, or they rotated the object manually. Following this, they performed the identical mental rotation task in which they compared members of pairs of such figures, but were asked to imagine the figures rotating as they had just seen the model rotate. When

results from the two rotation conditions were directly compared, motor cortex (including area M1) was found to be activated only when subjects imagined the rotations as a consequence of manual activity. Thus, there are at least two, qualitatively distinct, ways to imagine objects rotating in images, and these different strategies can be adopted voluntarily. *NeuroReport* 12:2519–2525 © 2001 Lippincott Williams & Wilkins.

Key words: Mental imagery; Mental rotation; PET; Primary motor area

INTRODUCTION

One of the most striking discoveries in cognitive psychology was first reported by Shepard and Metzler [1], who found that when people compare two similar objects at different orientations, they mentally rotate the objects until they are at the same orientation. Moreover, this rotation process is incremental: the farther an object must be rotated, the more time is required [2–4]. This finding suggested that when people visualize objects moving, the objects move much as they do during actual physical transformations. This is a mystery because in imagery there are no actual physical constraints that dictate the trajectories of such transformations. In this report we show that at least two distinct mechanisms can give rise to this effect.

One possible account for the increase in time to mentally rotate objects greater amounts is that people imagine that they physically turn the objects, and thus the mental rotation result reflects physical constraints on our movements (which must pass through trajectories, as opposed to making instantaneous translations). Although some previous studies have suggested a role for motor processing in mental rotation [5–9], other studies have produced ambiguous evidence for such processing [10,11]. One earlier study [12] revealed that when people mentally rotate pictures of the multiarmed block-like objects designed by Shepard and Metzler [1], posterior parietal areas are engaged. In contrast, when they mentally rotate pictures of hands, parts of motor cortex are activated in addition to

posterior parietal areas. These results suggested that there are two distinct ways to rotate objects in images: either by imagining the consequences of an external force's manipulating an object, or by imagining the consequences of oneself physically manipulating it. In the second case (when the force is endogenous), but not the first (when the force is exogenous), motor processes would play a role in the rotation process [13].

The present study was designed with two aims. First, we wanted to demonstrate that there are in fact two distinct methods for mentally rotating inanimate objects *per se* (not simply body parts *vs* other objects), only one of which draws on motor processes. Second, we wanted to show that people can voluntarily adopt one or the other method. Crucially, to address these aims we use the identical task, and vary only the instructions; thus, any observed differences cannot be attributed to intrinsic properties of the task itself. We used the original Shepard and Metzler task [1], in which subjects see pairs of multiarmed block-like figures and decide whether the two shapes in each pair are identical or one is a mirror-reversed version of the other. In the baseline condition, the shapes were always at the same orientation; in the test condition, the shape on the right was rotated relative to that on the left. Subjects responded as quickly and accurately as possible, and after each response another pair was presented. PET was used to monitor regional cerebral blood flow (rCBF) while the subjects performed the tasks.

The key manipulation was that prior to testing we showed the subjects a specific way to visualize the objects rotating. In the external action (EA) condition, they observed a scale model of one of the objects being rotated by an electric motor, and were told that they would soon be asked to imagine this event. In the internal action (IA) condition, they observed a scale model that could be rotated by physically turning it, and were asked to do this and observe the results; again, they were told that they soon would be asked to imagine this event. Thus, the task was identical, only the instructions about how to imagine carrying out the rotation were varied.

MATERIALS AND METHODS

Subjects: Ten males volunteered to participate as paid subjects. The data from two of these subjects were discarded because they either had an error rate > than 50% or had excessively slow response times that prevented us from comparing response times for every angle of rotation. Thus, data from eight subjects were retained. (All analyses in this report rely on the data obtained from these eight subjects). The subjects were between 18 and 39 years of age (mean 24), and all were right-handed and had normal or corrected-to-normal vision. This research was approved by the Harvard University and Massachusetts General Hospital/Partners Institutional Review Boards. All subjects provided written informed consent prior to their participation in this study and all were tested in accordance with local laws and regulations.

Stimuli: The same Shepard and Metzler [1] stimuli used by Kosslyn *et al.* [12] were used here. These stimuli were individually placed in a circle, and then rotated in 20° increments. Rotations were performed separately for each of the three major axes (X, Y, and Z), which produced 28 different images: a stimulus at 0° of orientation, and at each orientation from 20° to 180° in each of the three planes. A mirror-reversed version of each stimulus was then created, producing a total of 56 stimuli. These stimuli were paired. In one set of pairs, for the rotation condition, a vertical version of each stimulus was positioned to the left of a rotated version of the same stimulus; each rotated version was paired with the vertical version. In the other set of pairs, for the baseline condition, the figure at the left was displayed at the same angle as that on the right, with half the pairs including mirror-reversed versions and half including identical versions. The entire stimulus, including both objects and their encompassing circles, subtended ~15 cm along the widest axis, corresponding to approximately 16.4° of visual angle as viewed by the subject from a distance of about 52 cm.

Task procedure: Subjects were told that on each trial two shapes would appear, and they were to determine whether the shapes were the same or mirror images. Prior to each testing condition the subjects participated in a familiarization phase. In each familiarization phase they were shown a single Shepard-Metzler object (constructed from cubes of wood, 2 cm per side, in a configuration that did not appear during testing) mounted by Velcro on the rotating knob of an Illusionator (Lafayette Instrument Company, Lafayette, IN). In the familiarization phase of the EA condition, the

investigator rotated the object by switching on the Illusionator motor. It rotated at a rate of 78 r.p.m. for 45 s along each of the x, y, and z axes, and in clockwise and counter-clockwise directions. The process was then repeated, for a total rotation time of 9 min. Subjects were asked to observe the object being rotated by the motor, in preparation for later visualizing this sort of motion. The subjects were instructed to notice how the object was rotated by the external force of the motor, independent of any other force. When subjects made the same/different discriminations during the testing phase, they were instructed to use the strategy of mentally rotating the object as if it were being rotated by a motor, as they saw in the training phase demonstration.

In the familiarization and training phase of the IA condition, subjects viewed the same object affixed to the Illusionator, but were asked to turn it manually with their dominant hand. Because all subjects were right-handed, they all used their right hands to turn the stimuli. They were instructed to grasp the object around its center with their dominant hand and rotate it along the specified axis at a comfortable speed until asked to stop. The conditions and duration of rotation were identical to those in the EA condition, except that subjects controlled the rate of rotation. Given that we later found (see below) that the subjects mentally rotated images at the same rate in both conditions, any differences in rate during the familiarization phase did not appear to influence performance in the task. During familiarization they were told to notice how the figure rotated through the force of their own hand. During the testing phase, they were asked to use a strategy in which they imagined grasping the figure and turning it with their own hand.

Prior to the trials in a given block, the subjects read the instructions and then paraphrased them for the investigator; any misconceptions were corrected. They then received nine practice trials, three per axis, using stimuli that did not appear in the test sequence; after this, they were asked to describe what they did during these trials. At this point, we corrected any misconceptions about the nature of the task, or the specific strategy they were to use. The test trials began with a fixation point, which remained on the screen for 500 ms; following this, a pair of figures appeared and the subjects were to evaluate whether the identical shape appeared twice or whether a shape and its mirror image were on the screen. Subjects indicated their response by pressing a foot pedal under their left or right foot (foot of response was counterbalanced over subjects). The subjects were asked to keep their hands by their sides at all times during testing, and possible movements were restricted by the stand that supported the computer's monitor. The trials were presented in a random order except that the same response could not occur three times in a row, the same figure could not appear twice within three trials, and the same orientation and axis of rotation were miniblocked (i.e. they could not appear twice until all variations had appeared once, nor three times until all had appeared twice, etc.). In addition, different sets of stimuli were shown in the IA and EA conditions and different orders were presented for each replicate, to avoid subjects' implicit encoding of the ordering of correct responses. The sets of stimuli and orders were counterbalanced over conditions.

All subjects began with the baseline trials first; we were concerned that they might attempt to rotate stimuli in this condition if they had just received the rotation condition. In the baseline condition, subjects were presented with paired Shepard-Metzler stimuli at the same angle, and were asked to decide, as quickly and accurately as possible, whether the two stimuli were the same or mirror-reversed. No mental rotation was required and no instructions concerning strategy were given to the subjects at that time. After the baseline condition, two other activation conditions were administered before the present test conditions were administered (these involved mental rotation, but did not involve using a specific strategy; these results will be reported in a separate paper). Approximately 20 min separated these last conditions from the beginning of the present test conditions. Each condition was replicated in two scans, however because of time limitations and constraints related to the other conditions that were tested in this session, two subjects participated only once in the baseline condition. The order of the test conditions was counterbalanced over subjects. Subjects participated in the entire 9 min familiarization and training phase prior to each scan in the test conditions, whether it was an original scan or a replicate. Figure 1 illustrates the design of the study.

PET acquisition: The PET acquisition procedure has been described in detail elsewhere [12,14]. To summarize, the subjects first were placed in the scanner and then aligned

relative to the cantho-meatal line; following this, they each were fitted with a thermoplastic head holder, a set of nasal cannulae, and a vacuum mask. Next, an orbiting rod source was used to obtain transmission measurements prior to scanning. Scanning was accomplished by having the subjects inhale $C^{15}O_2$ mixed with room air, beginning 15 s after the subjects began the task and continuing for 60 s. Each condition began about 10 min after the previous one. The PET machine was a GE Scanditronix PC4096 15-slice whole body tomograph that produced contiguous slices 6.5 mm apart (center to center; axial field = 97.5 mm), and the axial resolution was 6.0 mm full width at half maximum (FWHM) [15].

PET statistical analysis: Data were analyzed with the SPM technique, using SPM95 software [16]. The PET data were normalized to a global mean of 50 ml/min/100 g, and then the data in all voxels were fit by the method of least squares to a linear model. Planned contrasts between conditions were evaluated using *t*-statistics; data from all conditions were used to compute the appropriate error term. The threshold for statistical significance was set at $Z > 4.26$ ($p < 0.0001$ uncorrected, two-tailed) except for regions that were hypothesized to be activated in a given contrast, for which the threshold was set to $Z > 3.09$ ($p < 0.01$ uncorrected for multiple comparisons, one-tailed). This threshold was a compromise between those suggested by Gaussian fields theory, which assumes no hypotheses regarding the anatomic localization of activations, and

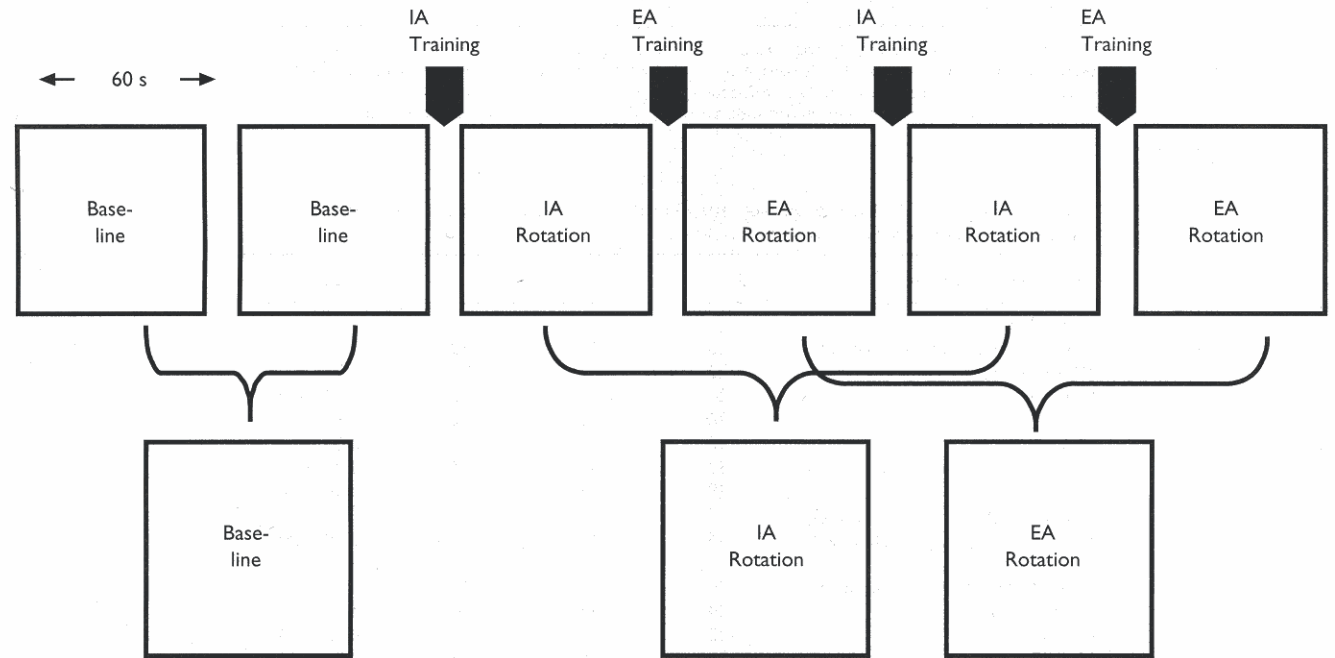


Fig. 1. The experimental design. Subjects participated in three separate conditions, all of which featured Shepard-Metzler figures: (1) a baseline where two figures at the same orientation were presented, and subjects judged whether they were identical or mirror-reversed (no mental rotation was required); (2) a mental rotation condition in which subjects imagined their dominant hand physically grasping and mentally rotating one of the figures into congruence with the other (internal action (IA) rotation); (3) a mental rotation condition in which subjects imagined one figure being rotated by a motor (external action (EA) rotation). For greater statistical power, results from the two replicates of the same condition were averaged. The baseline task was always performed first, whereas the order of the internal action and external action rotation conditions was counterbalanced over subjects. A 9 min familiarization and training session on imagery of IA or EA rotation preceded each of the rotation scans.

theories that ignore the spatial correlations that characterize PET and other neuroimaging data [17]. In this study, a strong hypothesis existed only for the primary motor cortex (M1) premotor and supplementary motor areas (roughly corresponding to Brodmann's areas 4 and 6).

We recognize that some investigators may have specific hypotheses related to regions other than the ones for which we expected differences in activation; thus in Table 1 and Table 2 we present a list of all regions attaining Z-scores > 3.09, although we stress that we do not consider the non-hypothesized regions to be significant unless they reach a Z-score of ≥ 4.26. Regions with Z-scores of 3.09–4.26 for which we did not have a pre-existing hypothesis are labeled as non-significant (NS) in the tables and are not discussed in the text.

RESULTS

The behavioral data are presented in Fig. 2. Figure 2a shows the typical increase in response time with amount of

rotation ($F(4,28)=8.08, p<0.0001$) and this effect was comparable in the EA and IA conditions ($F<1$ for the interaction). Similar patterns were found with error rates (Fig. 2b); errors increased with increasing angular disparity ($F(4,28)=4.66, p<0.005$) and the effect was comparable in the two conditions ($F<1$ for the interaction). It is important to note that there were no overall differences between the rotation conditions in either response times or error rates ($p>0.2$ in both cases); thus, any differences between a direct comparison of the blood flow results from the two rotation conditions cannot reflect simply the total amount of processing. These findings not only provide evidence that subjects performed the task appropriately, but also suggest that both methods can in fact be used to perform mental rotation.

In addition, the subjects responded more quickly in the baseline condition than in either rotation condition ($p<0.0001$ for both comparisons of response times). These faster times resulted in the subjects' seeing and evaluating

Table 1. Areas in which there was activation in the IA condition compared with the EA condition and vice versa.

IA versus EA	x	y	z	Z score
Activation in the IA condition:				
M1 (area 4)	-22	-16	56	3.44
Parahippocampal gyrus (area 36)	28	-28	-16	3.44 (NS)
Junction of inferior/superior parietal lobule (areas 7/40)	-32	-38	52	3.38 (NS)
Activation in the EA condition:				
Inferior frontal gyrus (area 47)	-28	22	-16	3.31 (NS)

The Talairach and Tournoux [21] coordinates are provided, along with the Z-score. Areas are presented in descending order of Z-score. For regions with a localized hypothesis, a Z-score of ≥ 3.09 was considered significant. For non-hypothesized regions, a Z-score of ≥ 4.26 was required. Non-significant regions attaining a Z-score of ≥ 3.09 are presented for information purposes only and are marked as being non-significant (NS).

Table 2. Areas in which there was activation in the IA condition compared with the baseline and in the EA condition compared with the baseline.

EA and IA versus baseline	X	Y	Z	Z score
IA baseline:				
Superior parietal lobule (area 7)	26	-60	48	5.19
PMA (area 6)	-22	-2	52	4.21
Area 19	24	-78	32	3.94 (NS)
Area 19	-36	-80	12	3.81 (NS)
Area 18	-36	-88	-4	3.69 (NS)
Inferior frontal gyrus (areas 45/47)	-32	32	4	3.63 (NS)
DLPFC (area 46)	-28	36	16	3.56 (NS)
Junction of IF/DLPFC (areas 44/9)	-44	20	24	3.44 (NS)
Inferior temporal gyrus (area 37)	-44	-58	-8	3.19 (NS)
EA baseline:				
Superior parietal lobule (area 7)	26	-56	48	5.56
DLPFC (area 9)	-44	22	24	4.31
Area 19	-32	-76	32	4.13 (NS)
Area 19	28	-76	32	3.94 (NS)
PMA (area 6)	-20	4	52	3.69
Area 18	-34	-90	-4	3.63 (NS)
Inferior temporal gyrus (area 37)	-48	-56	-8	3.38 (NS)

The Talairach and Tournoux [21] coordinates are provided, along with the Z-score. Areas are presented in descending order of Z-score. For regions with a localized hypothesis, a Z-score of ≥ 3.09 was considered significant. For non-hypothesized regions, a Z-score of ≥ 4.26 was required. Non-significant regions attaining a Z-score of ≥ 3.09 are presented for information purposes only and are marked as being non-significant (NS).

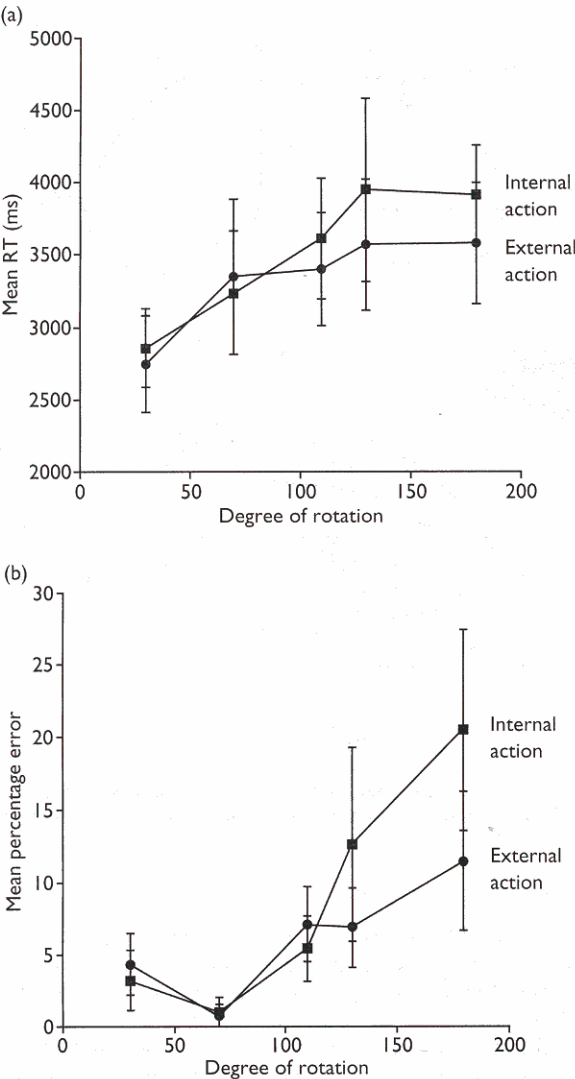


Fig. 2. Mean response times (a) and error rates (b) for same/different decisions in the rotation conditions. Stimuli were preceded either by a demonstration of EA rotation (i.e., rotation driven by an electric motor) or IA rotation (i.e., rotation driven by manual turning of a crank). Each data point represents the average of two angles of rotation.

more stimuli in the baseline condition than in the rotation conditions. Indeed, on average subjects received and evaluated an average of 23.5 stimuli per block in the IA condition, 24.7 stimuli per block in the EA condition, and 50.7 stimuli per block in the baseline condition. An analysis of variance showed that there was a difference in the total number of trials completed between the three conditions ($F(2,7) = 84.1, p < 0.0001$). Planned contrasts revealed that the number of trials completed was not significantly different in the two rotation conditions ($p < 0.62$), but was different between the baseline and the rotation conditions ($p < 0.0001$). Thus, comparisons to the baseline condition must be made with caution, given the possibility that differences may reflect in part differences in the number of different trials processed.

Because the two rotation conditions differ only in one

respect, in the instructions, and we have strong hypotheses about the consequences of this difference, we began by directly comparing the neuroimaging results from these conditions. As evident in Fig. 3 and Table 1, when we examined which areas are more activated in the IA condition than in the EA condition, we found clear activation in primary motor cortex (area M1); in contrast, no region was significantly more activated in the EA condition than in the IA condition.

We next compared each rotation condition with the baseline, as shown in Table 2 and Fig. 4. Of greatest importance, in both conditions there was activation in the pre-motor area (PMA, area 6), which plays a critical role in movement production [18]. As is evident in Table 2, other areas were also activated, as will be discussed shortly.

In addition to the SPM analyses, we performed a second-tier region of interest (ROI) analysis to examine any possible differences between the conditions in M1 or PMA that may have been missed by the more general SPM-based analysis. We traced a circle of 5 mm in radius around each of the three loci in motor regions (in areas M1 and PMA) reported to be activated in any of the comparisons. All of the findings from SPM were confirmed, and no new significant results emerged from this analysis.

Finally, we also performed the reverse contrasts, observing activation in the baseline condition compared to the rotation condition. Although several areas were more strongly activated, none of them involved motor cortex.

DISCUSSION

When we directly compared the two types of rotation, the results were clearcut: When subjects imagined objects

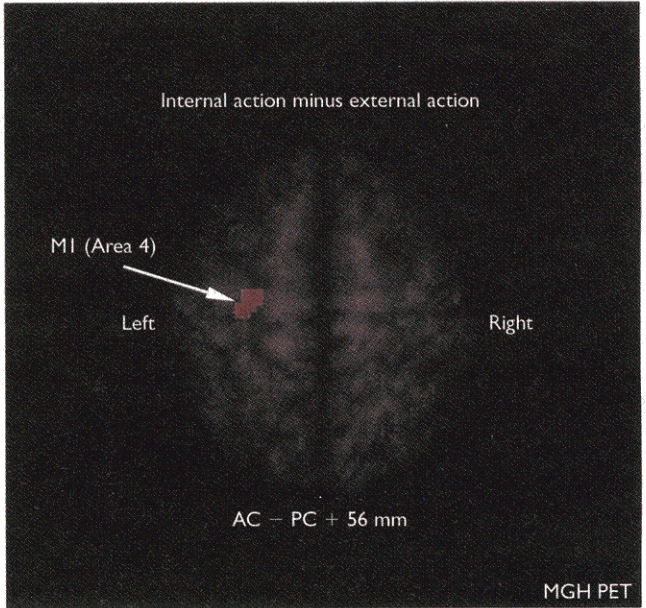


Fig. 3. A transverse PET image, 56 mm above the AC-PC line, showing activation in the primary motor area when activation in the EA condition is subtracted from activation in the IA condition. This result shows that motor areas of the brain can play a role in the mental rotation of an abstract figure, and that different types of advance training on the task may induce different strategies for accomplishing the task.

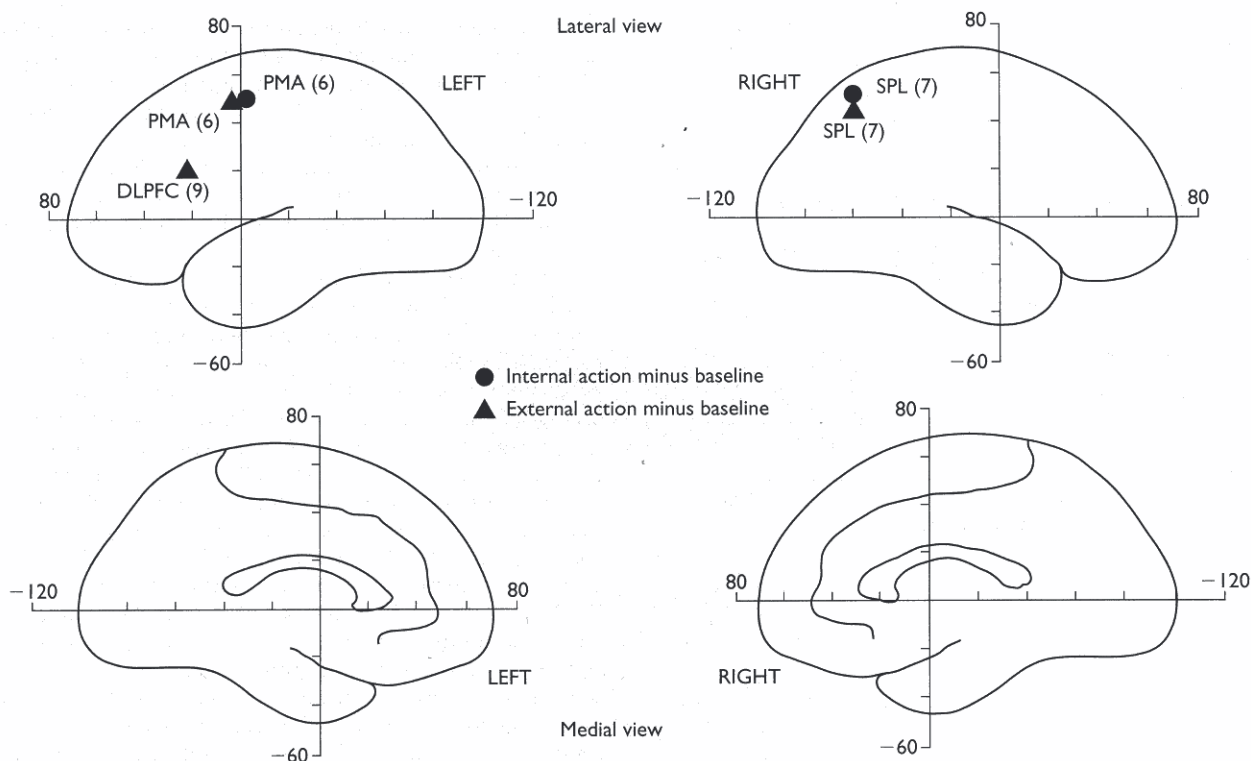


Fig. 4. Areas of activation when the IA (circles) and EA (triangles) conditions were compared individually to the baseline. Lateral views are presented at the top, medial views at the bottom. The left hemisphere is represented on the left side of the panel, and the right hemisphere is represented on the right side. Each tick mark represents a distance of 20 mm.

rotating as a consequence of their own motor activity, primary motor cortex and other motor areas were activated; when they imagined objects rotating as a consequence of an external force, primary motor cortex was not activated. These findings provide support for two conclusions: First, there are at least two distinct mechanisms that can be used to mentally rotate objects, one that involves motor processing and one that does not; and second, people can voluntarily adopt one or the other strategy. When we compared the rotation results to the baseline, we found evidence that premotor cortex was activated in both cases. This result could indicate that some motor processes are used whenever we imagine objects rotating [9], but such processing remains at a relatively abstract level if we do not imagine that we ourselves are manipulating the object.

Could the activation in motor cortex have occurred because the subjects actually moved? We asked the subjects to keep their hands by their sides at all times during testing, and they responded by pressing pedals under their left or right foot. The part of area M1 that controls the feet is at the very top of the motor strip, far from the area that controls the hands. Thus, we were pleased to discover activation in the region of M1 that is close to the hand area [19], particularly on the left side, which controls the right hand (the one used to turn the figure during pre-training). However, we did not record EMGs, and thus cannot definitively rule out the possibility that the subjects made subtle movements while they were rotating, although

observation during testing indicated that no gross hand or arm movements were made. If such twitches occurred, they may themselves have been incidental concomitants of internal processing or could have played a functional role in facilitating mental rotation. In fact, transcranial magnetic stimulation delivered over M1 immediately prior to mental rotation of hands does disrupt processing [20]. Thus, M1 played a functional role in this sort of motor rotation, and probably played a functional role in the present study as well.

Although our conclusions are supported by the analysis in which we directly compared the two rotation conditions, when these conditions are compared to the same baseline, we do not find evidence of activation of primary motor cortex. This finding suggests either that M1 was partially activated in the baseline condition, or that the activation in the IA condition was subthreshold in this comparison. However, a close look at the results from the IA condition did not reveal subthreshold activation in area M1. Consider two additional accounts for this puzzling aspect of the results. First, we have no theory for how subjects compare the shapes in the baseline condition, and it is possible that they imagine mentally moving one figure over, until it covers the other. If so, motor processes may be involved in this process. Second, there were more trials in the baseline condition than in the rotation conditions, and thus even if subjects imagined moving the figures only on a percentage of trials, there may have been enough such processing to activate M1, which in turn obscured the

activation in M1 due to image rotation when that condition was compared to this baseline.

In the comparisons with the baseline condition, in addition to the premotor cortex, we also found activation in area 7 in both rotation conditions; this area is involved in spatial processing and has consistently been activated in studies of mental rotation [5,12].

When we compared the EA condition with baseline, we found a similar pattern of activation to what we found when the IA condition was compared with baseline. Indeed, we again found strong activation in areas involved in spatial processing (area 7 and the portion of DLPFC that may be involved in working memory). We also discovered activation of area 6, the premotor area. As noted earlier, it is possible that relatively high-level motor commands play a role in both types of mental rotation [7,9].

CONCLUSION

The fact that many areas were activated in both conditions underscores the point that all cognitive processing is accomplished by a host of areas working in concert, not a single area or center. Nevertheless, certain areas appear to play key roles in different ways of accomplishing a task. In this example, we found that there are two ways to imagine an object rotating, and that people can voluntarily adopt one or the other method. This is the thin edge of a wedge; we suspect that there are many ways to accomplish any given task, each relying on some distinctive brain areas. For example, if subjects had been asked to imagine physically rotating by spinning the forms with their index finger, we would have expected different activation what was found here; similarly, if they imagined moving the

forms with their big toes, this probably would produce yet another pattern of brain activation, and so on. The brain may be the body's most flexible organ.

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