

Implicit transfer of motor strategies in mental rotation

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Accepted 11 October 2002

Abstract

Recent research indicates that motor areas are activated in some types of mental rotation. Many of these studies have required participants to perform egocentric transformations of body parts or whole bodies; however, motor activation also has been found with nonbody objects when participants explicitly relate the objects to their hands. The current study used positron emission tomography (PET) to examine whether such egocentric motor strategies can be transferred implicitly from one type of mental rotation to another. Two groups of participants were tested. In the Hand–Object group, participants performed imaginal rotations of pictures of hands; following this, they then made similar judgments of pictures of Shepard–Metzler objects. The Object–Object group performed the rotation task for two sets of Shepard–Metzler objects only. When the second condition in each group (which always required rotating Shepard–Metzler objects) was compared, motor areas (Area 6 and M1) were found to be activated only in the Hand–Object group. These findings suggest that motor strategies can be covertly transferred to imaginal transformations of nonbody objects.

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Keywords: Mental imagery; Mental rotation; Motor learning; PET

1. Introduction

Some 30 years ago Roger Shepard and colleagues first reported that participants who are asked to compare two misoriented objects mentally rotate the objects into alignment (e.g., Shepard & Metzler, 1971; Shepard & Cooper, 1982). This finding was important not only because it documented that people can transform objects in images, but also because it showed that the mental rotation process is incremental: Response times increase linearly with greater angular disparity between objects. This result suggests that participants transform objects in the mind similarly to the way objects are physically transformed, despite the fact that the physical constraints of the environment need not apply to imaginal space.

More recently investigators have begun using neuro-imaging techniques to examine the neural underpinnings of mental rotation. One intriguing finding is that participants use motor strategies to perform some types of mental rotation, as indicated by activation in motor areas of the brain such as the premotor area (PMA) and primary motor cortex (M1). Many of these studies require participants to mentally transform body parts (e.g., Bonda, Petrides, Frey, & Evans, 1995; Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Parsons et al., 1995). For example, Parsons et al. (1995) used positron emission tomography (PET) to study brain activation while participants judged whether drawings depicted left or right hands. Parsons (1987) previously had hypothesized that participants solved this task by comparing the rotated representation of their own hand to that of the stimulus. Mapping the coordinates of one body reference frame to another (i.e., hand-to-hand) is an

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egocentric transformation (Howard, 1982). When participants' brains were scanned while they performed the hand rotation task, Parsons et al. (1995) found activation of brain areas involved in motor control, specifically in premotor areas as well as the superior parietal lobule.

In another PET study Kosslyn et al. (1998) compared performance on same/different judgments of hand drawings and Shepard–Metzler (1971) cube figures. Rotation of the latter requires a mapping of object-relative reference frames rather than egocentric reference frames (Howard, 1982). Kosslyn et al. found that motor and premotor areas were activated during the hand rotation task but not the object rotation task. Further evidence for the role of motor areas in egocentric transformations was reported by Ganis et al. (2000), who used transcranial magnetic stimulation (TMS) to impair primary motor cortex transiently, which hindered participants' performance on an imaginal hand and, to a lesser extent, foot rotation task. These findings collectively suggest that mental rotation tasks involving body parts elicit motor strategies.

Motor activation also has been reported when participants mentally transform nonbody objects (e.g., Barnes et al., 2000; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Cohen et al., 1996; Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Richter et al., 2000; Tagaris et al., 1997; Vingerhoets et al., 2001). Using functional magnetic resonance imaging (fMRI), Cohen et al. (1996) studied mental rotation of the original Shepard–Metzler figures and found premotor activation in half of their participants. More recently Kosslyn, Thompson, Wraga, and Alpert (2001) used PET to demonstrate that when participants are led to use motor strategies, motor areas are activated even when they mentally rotate nonbody objects. When participants were instructed to imagine Shepard–Metzler objects being rotated by their dominant hand (i.e., object-to-hand mapping), Kosslyn et al. found activation in contralateral M1 regions. In contrast, they found no such activation when participants imagined the objects being rotated by an external (nonbody) source (i.e., object-to-object mapping). These findings suggest that motor strategies are not defined by their reliance on mental rotation of a body-related stimulus per se, but rather may be defined as strategies that can be used in tasks requiring egocentric transformations.

In the present study we investigated whether motor strategies can be transferred *implicitly* from a task involving egocentric transformations to one that does not. Research on motor sequence learning has shown that primary and secondary motor areas are involved in implicit transfer of motor skills (Grafton, Hazeltine, & Ivry, 1995; Grafton, Hazeltine, & Ivry, 1998). In the current study, we examined whether motor strategies adopted during mental rotation of hands would carry

over to mental rotations of objects, under conditions where participants received no explicit instructions on relating the objects to their hands. We hypothesized that participants can perform mental rotation in two ways, either by imagining themselves rotating the object or by imagining an external force rotating it, and that the strategy they adopt depends in part on what they have been doing immediately prior to the task.

2. Method

2.1. Participants

Sixteen right-handed males (aged 18–39 years) volunteered to take part in the study as paid participants. All participants gave written informed consent prior to the study, and all were tested in accordance with local laws and regulations as stipulated and approved by the Harvard University and Massachusetts General Hospital/Partners Institutional Review Boards.

2.2. Materials

The stimuli were identical to those used by Kosslyn et al. (1998). The object stimuli were depictions of three-dimensional, multi-armed cube figures enclosed in a circle, based on the figures originally used by Shepard and Metzler (1971). The figures were rotated in 20° increments from 20° to 180° in each of the three planes of rotation (*X*, frontal; *Y*, transverse; *Z*, sagittal), for a total of 27 versions. We then created a mirror-reversed version of each stimulus. The addition of normal and mirror-reversed figures at 0° resulted in a total of 56 stimuli. For the rotation condition, a vertical version of each stimulus was positioned to the left of each tilted version of the same stimulus. For the baseline condition, each stimulus of the pair appeared at the same angle of orientation, with half the pairs including mirror-reversed versions and half including identical versions. We divided the full group of stimuli in half, which resulted in two stimulus sets per condition. We administered a different stimulus set for each block, counterbalancing so that each stimulus set appeared equally often in each condition within a task. Thus, participants in the Object–Object group could not repeat the task with the same objects. Each stimulus set had equal numbers of all angles and axes of rotation, but not every angle/axis combination, which would have required the full set of 112 stimuli.

The hand stimuli consisted of two-dimensional line drawings of hands, each of which was enclosed in a circle. We created four finger configurations: (a) all five fingers raised; (b) thumb, index finger, and middle finger raised with ring and little finger folded; (c) thumb, index finger, and little finger raised with middle

and ring finger folded; and (d) only little finger raised. In addition, we created a palm-facing and back of the hand-facing version of each finger configuration. These figures were rotated in 20° increments from 20° to 180° in the *X* plane of rotation. The total set consisted of 160 stimuli, including normal and mirror-reversed (i.e., right and left hand) versions of all 8 sets of stimuli (4 finger configurations \times 2 versions) and 8 stimuli at 0°. For the rotation condition, we paired the hands so that the stimulus on the left side of the screen was always an upright left hand, and the stimulus on the right side of the screen was always a rotated left or right hand. For the baseline condition, each pair of hands appeared at the same angle of orientation, with half of the pairs including identical figures and half including opposite hands.

For both sets of stimuli, the pair of figures (including the surrounding circles) was 14.9 cm at its maximum width. As viewed by the participant from a distance of about 52 cm, this corresponded to approximately 16.3° of horizontal visual angle.

2.3. Procedure and design

Stimuli and instructions were displayed on a Macintosh PowerBook 1400cs computer using MacLab software (Costin, 1988). Participants were divided into two groups. The Hand–Object group received one set of trials with Hand stimuli followed by a set with Object stimuli; the Object–Object group received two sets of trials with Object stimuli only. Each sequence of scans consisted of a block of baseline trials followed by a block of rotation trials. The baseline trials were always administered first to ensure that participants evaluated them without using mental rotation. For the baseline trials, participants viewed two Object or two Hand stimuli presented 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 participants received no instructions concerning strategy. After the baseline condition, participants received the corresponding rotation condition, where they viewed pairs of Object or Hand stimuli at different angles with respect to each other. The participant's task was again to decide as quickly and accurately as possible whether the stimuli were identical or mirror-reversed.

At the outset of each block, participants first read the instructions on the computer screen and paraphrased them to the investigator, who corrected any misconceptions. Participants then performed nine practice trials with feedback, one trial at each angle of rotation from 20° to 180° and equal numbers of trials from all three axes, using stimuli that did not appear in the test trials. Before the test trials were administered for a given condition, the investigator reiterated the instructions

and reminded the participant of the importance of following them. Each test trial began with a fixation point that remained on the screen for 500 ms. A pair of figures then appeared. Participants indicated their “same” or “mirror” response by pressing foot pedals with their left and right feet (foot of response was counterbalanced across participants). Participants were instructed to keep their hands by their sides at all times during testing; the investigators observed them during trials to ensure that they complied with this instruction. The stand supporting the computer laptop, which fit snugly against the participants' shoulders and sides, also served to restrict their movements.

Trials in all blocks were presented in a pseudo-random order with the following restrictions: the same response could not occur three times in succession and the same angular orientation and axis of rotation could not be repeated until all variations had appeared once.

During debriefing, participants provided written feedback of their experience, including whether they had followed the directions for each condition or had used a different strategy. They then discussed their written answers with the investigators.

2.4. Behavioral analysis

The computer recorded responses and response times (RTs) for the rotation and baseline conditions of each task. For each statistical comparison, we performed a 2 (task: hand vs. object) \times 2 (condition: rotation vs. baseline) \times 5 (degree) mixed-design analysis of variance (ANOVA) on RTs and error rates.

2.5. PET acquisition

The PET acquisition procedure has been described in detail elsewhere (Kosslyn et al., 1994, 1998). To summarize, each participant was first placed in the scanner and aligned relative to the cantho-meatal line. The participant then was fitted with a thermoplastic face mask and provided with a set of nasal cannulae and a vacuum mask. Next, an orbiting rod source was used to obtain transmission measurements. For the scanning procedure, the participant inhaled $^{15}\text{O}-\text{CO}_2$, mixed into room air, 15 s after beginning the behavioral 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; the axial field was equal to 97.5 mm), and the axial resolution was 6.0 mm full width at half maximum (FWHM) (Kops, Herzog, Schmid, Holte, & Feinendegen, 1990). The $^{15}\text{O}-\text{CO}_2$ was delivered at a concentration of 2800 MBq/L at a flow rate of 2 L/min and was mixed with room air so that the measured peak count rate from the brain was 100,000–200,000 events/s.

2.6. PET statistical analysis

Data were analyzed with the Statistical Parametric Mapping (SPM) technique, using the SPM95 software (Friston et al., 1995). The PET data from all scans were realigned to the position of the first scan. The data were then normalized to a global mean of 50 ml/min/100 g. Thus, variations between individuals and between scans due to global factors such as inhaled tracer concentration, or arterial $p\text{CO}_2$, were removed. The data for each subject were spatially normalized to the coordinates of the Talairach and Tournoux (1988) atlas using locally developed software. Using the Advanced Visual Systems (AVS, Waltham, MA) platform, a set of landmarks (midline, right and left margins, PC point) was identified and positioned as input in order to reslice the brain images to fit the standardized template. The data in all voxels were then fit to a linear model by the method of least squares. Planned contrasts among conditions were evaluated using t statistics; data from all conditions were used to compute the appropriate error term. The between-group analyses were performed using a “multi-study, different conditions” design within SPM, whereas the within-group analyses were performed using a “multi-subjects, different conditions” design, “with replicates,” if appropriate to the analysis. The threshold for statistical significance was set at $z > 3.72$ ($p < .0001$ uncorrected), for nonhypothesized regions. In cases where we had a localized hypothesis, a Z -score of 3.09, corresponding to $p < .001$, uncorrected for multiple comparisons, was considered to be significant.

3. Results

3.1. Behavioral results

In debriefing, no participants reported imagining rotating their own hand as a method of rotating the stimulus in any of the object rotation conditions, even when directly asked about this possible strategy.

We will refer to the first condition in the Object–Object group as the Object task, and the task that followed it as Object_{OO}. We will refer to the first task in the Hand–Object group as the Hand task, and the task that followed it as Object_{HO}.

We conducted separate analyses to compare rotation and baseline conditions of the first task performed in each group, and of the second task performed in each group (i.e., Hand vs. Object; Object_{HO} vs. Object_{OO}). To provide the clearest comparison between rotation and baseline conditions, we eliminated 0° trials from all baseline data: Analyses were performed on 20–180° trials for both conditions. Fig. 1a shows mean response time (RT) for the Hand–Object comparison. The results are

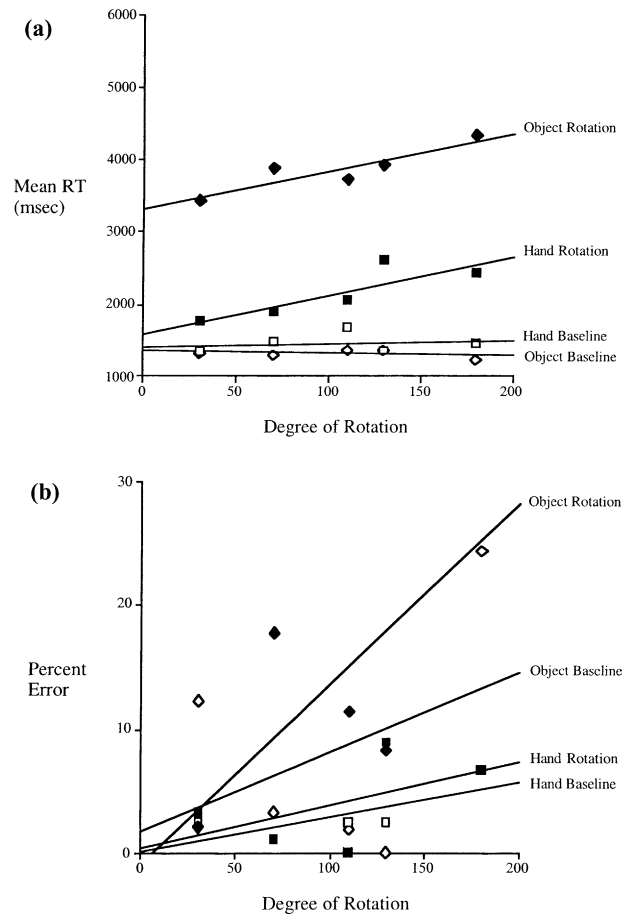


Fig. 1. (a) Mean response times and (b) mean percent error for same/different judgments in the Hand and Object rotation conditions. With the exception of 180° trials, each data point represents the average of two angles of rotation.

very similar to those reported by Kosslyn et al. (1998) for identical tasks. The ANOVA performed on the data yielded main effects of task, $F(1, 14) = 7.21$, $p < .018$, and condition, $F(1, 14) = 96.05$, $p < .001$, and a significant Task \times Condition interaction, $F(1, 14) = 32.16$, $p < .0001$. Performance in the Hand task was generally faster than performance in the Object task. Across both tasks, performance was faster in the baseline conditions than in the rotation conditions. Analysis of the Task \times Condition interaction revealed that faster performance in the Hand task was largely driven by the rotation rather than baseline conditions. We also found a significant effect of degree, $F(4, 56) = 5.32$, $p < .001$, and this effect was again driven by the rotation conditions rather than the baseline conditions, as indicated by a significant Condition \times Degree interaction $F(4, 56) = 4.46$, $p < .003$. As expected if the participants were in fact performing the task, a linear contrast revealed that they required more time when the stimuli had increasingly different orientations, $F(1, 56) = 22.15$, $p = .0001$. A similar contrast for the baseline condition revealed no linearity effect, $p > .5$.

Fig. 1b shows the results for mean error rates. The ANOVA performed on the error data yielded only main effects of task, $F(1, 14) = 6.70$, $p < .05$, and degree, $F(4, 56) = 5.69$, $p < .001$, and a significant Task \times Degree interaction, $F(4, 56) = 3.19$, $p < .02$. Performance in the Hand task was again more accurate than in the Object task. Errors varied for different orientations, but assessment of the Task \times Degree interaction revealed that this result was driven predominantly by the Object task rather than the Hand task. A linear contrast revealed that for the rotation conditions, there was a significant increase in errors with increasing angular disparity, $F(1, 56) = 5.98$, $p < .02$. A similar contrast for the baseline conditions also showed such an increase, $F(1, 56) = 6.38$, $p < .02$. Least square means comparisons with Bonferroni corrections revealed that this effect was carried entirely by higher error rates for 180° trials, $t(1, 56) = 3.09$ – 5.61 , $p < .03$ in all cases.

Fig. 2a shows the mean RT for the comparison of the second task in each group (i.e., Object_{HO} versus Object_{OO}). The ANOVA performed on the data yielded only main effects of condition, $F(1, 14) = 50.35$, $p < .0001$, and degree, $F(4, 56) = 3.63$, $p < .011$, and a significant Condition \times Degree interaction, $F(4, 56) = 2.57$, $p < .05$. In contrast to the previous comparison, we found no effect of task ($p > .05$); thus, participants in Object_{HO} and Object_{OO} tasks performed comparably. Participants again were faster in the baseline conditions than in the rotation conditions. RT also increased for the different orientations, and assessment of the Condition \times Degree interaction revealed that this finding was driven by the rotation rather than baseline conditions. For the rotation conditions, a linear contrast revealed that RT did in fact increase as a function of angular disparity between stimuli, $F(1, 56) = 11.02$, $p < .002$. Although the slope for Object_{OO} rotations appears to be steeper than that of Object_{HO} rotations, this difference was not significant, $p > .05$. Linear contrasts for the baseline conditions revealed no effect, $p > .05$.

Fig. 2b shows the corresponding results for mean error rates. The ANOVA performed on the data yielded only main effects of condition, $F(1, 14) = 10.49$, $p < .006$, and degree, $F(4, 56) = 17.76$, $p < .0001$, and a significant Condition \times Degree interaction, $F(4, 56) = 11.56$, $p < .0001$. Similar to the RT results, participants in the Object_{HO} and Object_{OO} tasks performed comparably (task effect: $p > .05$). However, participants made more errors in the baseline conditions than in the rotation conditions, and this effect was related to the Condition \times Degree interaction. Linear contrasts revealed no effect of angular disparity on error rate in the rotation conditions, $p > .05$, but a similar contrast revealed a significant effect of angle for the baseline conditions $F(1, 56) = 12.77$, $p < .0007$. Bonferroni-corrected least square means comparisons between all pairs of angle groupings in the baseline conditions revealed that participants made more errors for stimuli at 20–40° than for stimuli at 100–120° ($t(1, 56) = 3.46$, $p < .01$) and 140–160° ($t(1, 56) = 3.59$, $p < .007$). The participants made more errors for stimuli at 180° than for stimuli at all other angles, $t(1, 56)$, 4.72–8.31, $p < .001$, in all cases. This pattern of errors held true for participants in both tasks.

The fact that there were no overall differences in either RTs or error rates across Object_{HO} and Object_{OO} tasks is noteworthy: Any brain areas that are more active in one of the tasks than in the other are likely to reflect qualitative differences in processing, not simply differences in the overall amount of processing per se.

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3.2. PET results

We designed this study to investigate whether motor activation from an egocentric hand rotation task would implicitly transfer to an object rotation task. We assessed this possibility by directly comparing the patterns of regional cerebral blood flow (rCBF) in the Object_{HO}

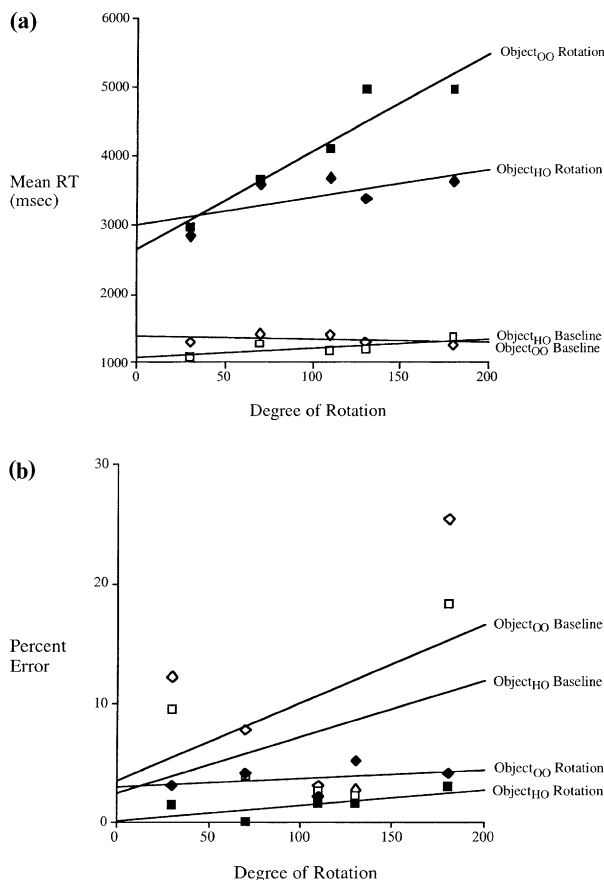


Fig. 2. (a) Mean response times and (b) mean percent error for same/different judgments in the Object_{HO} and Object_{OO} rotation conditions. With the exception of 180° trials, each data point represents the average of two angles of rotation.

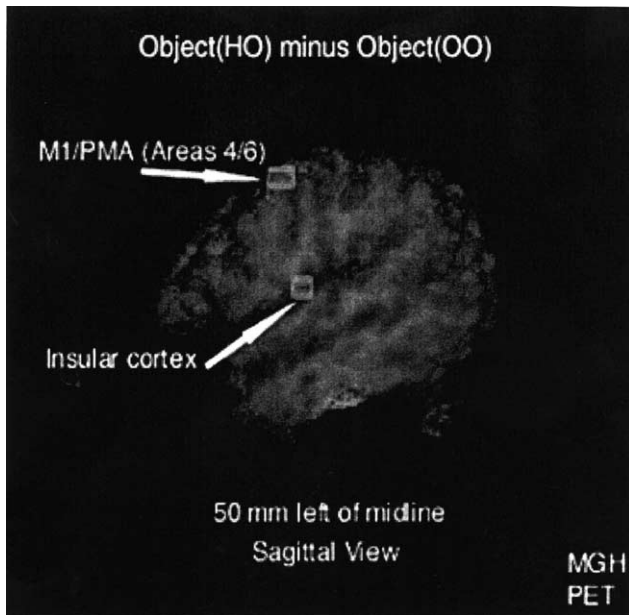


Fig. 3. A sagittal PET image illustrating the primary motor activation discovered when activation in the Object_{OO} condition was subtracted from activation in the Object_{HO} condition. This slice is 50 mm left of the midline and also reveals activation found in the insular cortex. The threshold for this image was set to a Z-score of 3.72. The MRI image, fused with the PET data, is a composite average of a group of brain images (not from participants in this study) normalized to Talairach and Tournoux (1988) coordinates and is presented here in order to show the approximate locations of the regions of activation.

and Object_{OO} rotation conditions. As shown in Fig. 3 and Table 1, we did in fact find greater rCBF in several motor areas in the Object_{HO} condition than in the Object_{OO} condition. We found bilateral activation in the

premotor area (PMA: Area 6), left activation at the junction between PMA and primary motor cortex (Area M1), and left activation in the insula, which may be involved in the representation of egocentric space (Bottini et al., 2001). In addition, we found greater rCBF in several visual processing areas, including right activation of primary visual cortex (V1) and secondary visual areas (Areas 18/19). Other activated areas included the supplementary motor area (SMA: Area 6), the superior frontal gyrus (BA10) and dorsolateral prefrontal cortex (DLPFC: Area 46), all of which are involved in spatial working memory. The results of performing the reverse contrast, of Object_{OO} versus Object_{HO} are also shown in Table 1. This comparison revealed bilateral activation of secondary visual areas (Areas 18/19), and right activation of the superior parietal lobule (Area 7), an area typically found in spatial transformations of objects. This contrast also revealed activation in the right occipito-temporal junction (Areas 37/19).

We next compared the rotation conditions with their respective baselines (see Table 2). In general, the results for the Hand and Object tasks are similar to those reported by Kosslyn et al. (1998) for the identical manipulations. The comparison of the Hand rotation condition to its baseline revealed activation in PMA (Area 6); in contrast, the comparison of the Object rotation condition to its baseline revealed no such activation. Instead, we found bilateral activation of spatial processing areas (Area 7). For the Object_{HO} rotation condition, in which an object rotation occurred after a hand rotation, we found activation in the medial occipito-parietal junction (Areas 19/7) and also activation

Table 1

Areas of activation in the Object_{HO} group compared to the Object_{OO} group (top), and vice versa (bottom). Talairach and Tournoux (1988) coordinates are provided, along with Z-scores. Areas of activation are presented in descending order of Z-scores

	X	Y	Z	Z-score
Object _{HO} –Object _{OO}				
V1 (Area 17)	12	–64	8	5.56
Area 19	24	–80	44	5.44
PMA (Area 6)	26	–14	56	5.13
Insula	–30	–22	16	5.06
Posterior cingulate (Area 31)	8	–44	32	4.50
PMA/M1 (Areas 6/4)	–50	–2	44	4.13
Area 19	–30	–86	28	4.13
Cingulate (Area 32)	–4	42	16	3.94
Area 18	12	–78	24	3.94
Superior frontal gyrus (Area 10)	22	50	4	3.94
DLPFC (Area 46)	–48	30	24	3.88
PMA (Area 6)	–20	–14	52	3.88
Pre-SMA (Area 6)	2	6	52	3.81
Pre-SMA (Area 6)	–2	4	48	3.75
Object _{OO} –Object _{HO}				
Areas 18/19	38	–74	–4	4.19
Area 19	–44	–80	4	4.13
Superior parietal lobule (Area 7)	28	–42	44	4.00
Occipito-temporal junction (Areas 37/19)	48	–58	0	3.88

Table 2

Areas of activation in the hand task compared to its baseline, and in the three object tasks compared to their baselines. Talairach and Tournoux (1988) coordinates are provided, along with Z-scores. Areas are presented in descending order of Z-scores

	X	Y	Z	Z-score
Hand-baseline				
Orbital frontal gyrus (Area 11)	−38	44	−12	4.44
PMA (Area 6)	−40	0	28	4.13
Insula	−32	−12	−4	4.00
Posterior cingulate (Area 30)	−8	−42	16	3.94
DLPFC (Areas 9/10/46)	−22	40	24	3.88
Object-baseline				
Superior parietal lobule (Area 7)	22	−64	44	5.56
DLPFC/IF (Areas 9/44)	46	12	24	4.75
Area 19	28	−74	28	4.63
Superior parietal lobule (Area 7)	−20	−62	48	4.38
Inferior frontal gyrus (Area 47)	−34	24	−12	3.94
Inferior temporal gyrus (Area 37)	−48	−62	−8	3.81
Object _{HO} -baseline				
Cuneus (Area 19)	−10	−76	36	5.44
Occipito-parietal junction (Areas 19/7)	0	−62	4	3.81
PMA (Area 6)	26	−12	52	3.38
Object _{OO} -baseline				
Superior parietal lobule (Area 7)	24	−62	44	4.94
Occipito-parietal junction (Areas 19/7)	30	−70	32	4.81
Inferior frontal gyrus (Area 44)	44	10	24	4.06
IF/DLPFC (Areas 44/9)	−36	−40	40	3.75

in PMA (Area 6). Thus, the object rotation task in this condition appeared more “hand”-like. In contrast, we found no evidence of motor activation in the Object_{OO} rotation condition; however, we did find activation in right spatial processing areas (Area 7 and Areas 19/7).

4. Discussion

In line with our hypothesis, motor activation from an imaginal hand rotation task transferred implicitly to an imaginal object rotation task, despite the fact that participants were given no instructions to relate the objects to their hands. In contrast, we did not find motor activation in an imaginal object rotation task that was preceded by another object rotation task. This finding adds a new twist to those of previous studies, which either reported motor activation during mental rotation of human body parts or during object rotation tasks in which participants explicitly were instructed to relate the objects to their hands. The present results suggest that human beings can adopt motor strategies in mental rotation of nonbody objects without explicit knowledge.

Our hypothesis is most strongly supported by the comparison of the two second conditions, which were identical (both requiring rotation of object stimuli from the same set). This analysis revealed activation in premotor (Area 6) and primary motor (M1) areas when this task followed the Hand rotation condition. These areas may be involved in preparatory hand movements. For

example, Area 6 has direct connections to both M1 and the posterior parietal lobe (He, Dumm, & Strick, 1995). Single-cell recordings in nonhuman primates have revealed cells in Area 6 that fire to grasping movements (Rizzolatti et al., 1998). Moreover, Grafton et al. (1998) have argued that M1 activation found during implicit learning may reflect anticipatory priming from motor planning regions such as Area 6. The activation we found in the region of M1 was close to the hand area (Boling, Olivier, Bittar, & Reutens, 1999) and was specific to the left hemisphere (which controls the right hand — the dominant hand for all our participants, and thus the hand most likely to be involved in an object-hand mapping strategy for mental rotation). We found similar results in a task in which participants explicitly were instructed to imagine rotating the stimulus object with their right hands (Kosslyn et al., 2001). We also found activation in the insula, which is thought to be involved in the representation of egocentric space (Bottini et al., 2001). These findings collectively suggest that the implicit transfer of motor activation from Hand to Object_{HO} tasks in the present study reflects a covert strategy of relating the stimulus object to the participant's hand.

The results of additional analyses buttress these conclusions. We essentially replicated the results of Kosslyn et al. (1998) when we compared individual Object and Hand conditions to their respective baselines. The contrast in the Object task revealed activation primarily in spatial processing areas of the posterior parietal lobule (Area 7) but no activation of motor

areas; the contrast in the Hand task revealed activation of premotor areas. One notable exception to the findings of Kosslyn et al. (1998) was the absence of Area 7 activation in the Hand rotation condition. The reverse subtraction of baseline–Hand rotation revealed activation in Area 7. In our version of the Hand task, the two hands in a pair had different finger configurations, which may have made the task particularly challenging in some instances. Thus, the participants may have needed to look particularly carefully at the relation of the fingers to the rest of the hand, which required the kind of spatial processing carried out in Area 7. The fact that they would have completed more of these comparisons in the baseline condition than in the rotation condition may explain why this baseline task produced more parietal activation. The Object_{OO} rotation–baseline contrast yielded results similar to the Object task. We found activation in spatial processing, but not motor, areas. In comparison, the Object_{HO} rotation–baseline contrast revealed activation similar to that of the Hand–baseline contrast: Both premotor and spatial processing areas were activated. Thus, analyses of individual conditions support the notion of implicit motor transfer.

Several alternative explanations exist, however. One is that the motor activation we found in the Object_{HO} task may instead indicate that the participants actually moved their hands. This interpretation is unlikely for at least two reasons. First, participants in the Hand–Object group never were given physical practice in the Hand or Object_{HO} rotation tasks; thus, they were not primed to solve the Object_{HO} task by moving their hands. Second, in all conditions their hands were monitored closely by the investigators to ensure that they remained still. Another possibility is that the motor activation we found in Object_{HO} may reflect practice per se (i.e., participation in a second mental rotation task). However, this explanation is untenable because we did not find motor activation in the Object_{OO} task, which was a second mental rotation task for the Object–Object group. Yet another possibility is that the motor activation in the Object_{HO} task was merely residual activation from the previously performed Hand task. This account seems unlikely because of the amount of time (10 min) that elapsed between Hand and Object_{OO} task scans. Finally, participants simply may have been reminded of the Hand task while performing the Object_{HO} task because of the similarity between the two. Thus, the Object_{HO} motor activation might be the result of a residual memory trace from the Hand task. This explanation seems unlikely because the participants would have to sustain such a memory for such a long time that it would probably interfere with their ability to perform the task. In fact, the behavioral results indicate that performance in the Object_{HO} task was just as good as in the Object_{OO} task. Thus, the most plausible account is that the implicit transfer of motor activation from Hand

to Object_{HO} tasks corresponded to a covert egocentric strategy.

The notion of implicit transfer is not new. Researchers have conducted both behavioral and neuroimaging studies to examine the cognitive, perceptual, and motoric characteristics of implicit learning (e.g., Pascual-Leone, Grafman, & Hallett, 1994; Grafton et al., 1998; Reber & Squire, 1994; Willingham, 1997; Willingham, Greeley, & Bardone, 1993). One unresolved issue in the literature is the degree of specificity of implicit learning transfer. Some researchers have proposed that implicit transfer is rigidly context-specific (e.g., Dienes & Berry, 1997), whereas others argue that practice can transfer from one context to another (e.g., Willingham, 1997, 1999). The issue of transfer specificity also can be applied to imaginal movements. For example, although there is some evidence that imaginal rotations of bodies elicit motor activation (Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999), it is unclear whether such motor activation would transfer to subsequent imaginal object rotations. The body-centered egocentric reference frame may not map onto the object-relative frame as readily as does the hand-centered frame.

In summary, we have demonstrated that motor activation can transfer implicitly across different mental rotation tasks. Motor strategies adopted during mental rotation of hands transferred to mental rotations of objects, despite the fact that participants were not instructed to relate the objects to their hands. These findings underscore the flexibility of spatial processing mechanisms within the human brain.

Acknowledgments

This research was supported by Grant REC-0106760 from the National Science Foundation, Grant R01 MH60734-01 from the National Institutes of Health, and Grant F49620-98-1-0334 from the Air Force Office of Scientific Research. We wish to thank Sandy Barrow, Steve Weise, Avis Loring, and the MGH cyclotron staff for their assistance.

References

- Barnes, J., Howard, R. J., Senior, C., Brammer, M., Bullmore, E. T., & Simmons, A., et al. (2000). Cortical activity during rotational and linear transformations. *Neuropsychologia*, 38, 1148–1156.
- Boling, W., Olivier, A., Bittar, R. G., & Reutens, D. (1999). Localization of hand motor activation is localized in Broca's pli de passage moyen. *Journal of Neurosurgery*, 91, 903–910.
- Bonda, E., Petrides, M., Frey, S., & Evans, A. (1995). Neural correlates of mental transformations of the body-in-space. *Proceedings of the National Academy of Sciences of the United States of America*, 92, 11180–11184.
- Bottini, G., Karnath, H. O., Vallar, G., Sterzi, R., Frith, C. D., & Frackowiack, R. S., et al. (2001). Cerebral representations for

- egocentric space: Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain*, 125, 1182–1196.
- 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. *Journal of Cognitive Neuroscience*, 11, 9–24.
- Cohen, M., Kosslyn, S. M., Breiter, H., DiGirolamo, G. J., Thompson, W., & Anderson, A. K., et al. (1996). Changes in cortical activity during mental rotation: A mapping study using functional magnetic resonance imaging. *Brain*, 119, 89–100.
- Costin, D. (1988). MacLab: A Macintosh system for psychological labs. *Behavioral Research Methods, Instruments, and Computers*, 20, 197–200.
- Dienes, Z., & Berry, D. (1997). Implicit learning: Below the subjective threshold. *Psychonomic Bulletin and Review*, 4, 3–23.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189–210.
- 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.
- Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1995). Localization of independent cortical systems in human motor learning. *Journal of Cognitive Neuroscience*, 7, 497–510.
- Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1998). Abstract and effector-specific representations of motor sequences identified with PET. *Journal of Neuroscience*, 18, 9420–9428.
- He, S. Q., Dumm, R. P., & Strick, P. L. (1995). Topographic organization of corticospinal projections from the frontal lobe: Motor areas on the medial surface of the hemisphere. *Journal of Neuroscience*, 15, 3284–3306.
- Howard, I. (1982). *Human visual orientation*. Chichester: Wiley.
- Kops, E. R., Herzog, H. H., Schmid, A., Holte, S., & Feinendegen, L. E. (1990). Performance characteristics of an eight-ring whole body PET scanner. *Journal of Computer Assisted Tomography*, 14, 437–445.
- Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Chabris, C. F., Rausch, S. L., & Anderson, A. K. (1994). Identifying objects seen from different viewpoints: A PET investigation. *Brain*, 117, 1055–1071.
- 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.
- Lamm, C., Windischberger, C., Leodolter, U., Moser, E., & Bauer, H. (2001). Evidence for premotor cortex activity during dynamic visuospatial imagery from single-trial functional magnetic resonance imaging and event-related slow cortical potentials. *NeuroImage*, 14, 268–283.
- Parsons, L. M. (1987). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology*, 19, 178–241.
- Parsons, L. H., Fox, P. T., Downs, J. H., Glass, T., Hirsch, T. B., & Martin, C. G., et al. (1995). Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature*, 375, 54–58.
- Pascual-Leone, A., Grafman, J., & Hallett, M. (1994). Modulation of cortical motor output maps during development of implicit and explicit knowledge. *Science*, 263, 1287–1289.
- Reber, P. J., & Squire, L. R. (1994). Parallel brain systems for learning with and without awareness. *Learning and Memory*, 1, 217–229.
- Richter, W., Somorjai, R., Summers, R., Jarmasz, M., Menon, R. S., & Gati, J. S., et al. (2000). Motor area activity during mental rotation studied by time-resolved single-trial fMRI. *Journal of Cognitive Neuroscience*, 12, 310–320.
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1998). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71, 491–507.
- Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge, MA: MIT Press.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.
- Tagaris, G. A., Kim, S.-G., Strupp, J. P., Andersen, P., Ugurbil, K., & Georgopoulos, A. P. (1997). Mental rotation studied by functional magnetic resonance imaging at high field (4 Tesla): Performance and cortical activation. *Journal of Cognitive Neuroscience*, 9, 429–432.
- Tailairach, J., & Tournoux, D. P. (1988). *Coplanar stereotaxic atlas of the human brain*. New York: Thieme.
- Vingerhoets, G., Santens, P., Van Laere, K., Lahorte, P., Dierckx, R. A., & De Reuck, J. (2001). Regional brain activity during different paradigms of mental rotation in healthy volunteers: A positron emission tomography study. *NeuroImage*, 13, 381–391.
- Willingham, D. B. (1997). Implicit and explicit memory do not differ in flexibility: Comment on Dienes and Berry (1997). *Psychonomic Bulletin and Review*, 4, 587–591.
- Willingham, D. B. (1999). Implicit motor sequence learning is not purely perceptual. *Memory and Cognition*, 27, 561–572.
- Willingham, D. B., Greeley, T., & Bardone, A. (1993). Dissociation in a serial response time task using a recognition measure: Reply to Perruchet and Amorim. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 19, 1424–1430.
- Zacks, J., Rypma, B., Gabrieli, J., Tversky, B., & Glover, G. (1999). Imagined transformations of bodies: An fMRI study. *Neuropsychologia*, 37, 1029–1040.