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Effects of a Body-Oriented Response Measure on the Neural Substrate of Imagined Perspective Rotations

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Abstract

■ Previous behavioral studies suggest that response measures related to the body, such as pointing, serve to anchor participants to their physical body during mental rotation tasks in which their perspective must be shifted elsewhere. This study investigated whether such measures engage spatial and low-level cortical motor areas of the brain more readily than non-body-related measures. We directly compared activation found in two imagined perspective rotation tasks, using responses that varied in the degree to which they emphasized the human body. In the body minimize condition, participants imagined rotating themselves around an object and judged whether a prescribed part of the object would be visible from the imagined viewpoint. In the body maximize condition, participants imagined rotating around the object and then located the prescribed object part with respect to their bodies. A direct comparison of neural activation in both conditions revealed distinct yet overlapping neural regions. The body maximize condition yielded activation in low-level cortical motor areas such as premotor cortex and primary motor cortex, as well as bilateral spatial processing areas. The body minimize condition yielded activation in nonmotoric egocentric processing regions. However, both conditions showed activation in the parietal–occipital region that is thought to be involved in egocentric transformations. These findings are discussed in the context of recent hypotheses regarding the role of the body percept in imagined egocentric transformations. ■

INTRODUCTION

Mental rotation allows us to perform a variety of everyday spatial reasoning tasks, from solving geometry problems to following a dance instructor to assembling our children's toys. Beginning with the classical studies of Shepard and Metzler (1971), much of the empirical work in the literature has focused on mental rotation of objects. More recently, researchers have examined other classes of mental rotation, including mental rotation of body parts such as hands and feet (Parsons, 1987, 1994) and mental rotation of one's body (Wraga, Creem, & Proffitt, 2000; Presson, 1982), which we will call "imagined perspective rotations."

A useful way to delineate these rotation events is to compare the major spatial reference frames involved in each (e.g., Wraga et al., 2000). Imagined object rotations require transformation of the object-relative reference frame, which specifies the location and orientation of an object's parts to each other, or of two objects with respect to each other (Easton & Sholl, 1995). Imagined perspective rotations require transformation of the egocentric reference frame, which specifies an object's location and orientation with respect to the major axes of the human body

(Howard, 1982). The egocentric frame also can be specified at smaller scales that relate objects to individual body parts such as the hand or foot.

Behavioral studies of mental rotation suggest qualitative differences in the way the human brain transforms the object-relative and egocentric reference frames. Roger Shepard and colleagues were the first to demonstrate that mental rotation of the object-relative frame occurs incrementally. When participants were asked to compare whether two misoriented objects were similar in shape, they mentally rotated the objects into alignment with each other (Shepard & Metzler, 1971). Moreover, time to respond (RT) increased monotonically with increasing angular disparity between objects. This finding implies that people mentally transform representations of objects similarly to the way they manipulate physical objects, despite the fact that mental space need not conform to the physical constraints of the environment.

The cognitive processes underlying imagined perspective rotations appear to be uniquely different. Behavioral studies comparing mental rotation of an array of objects to mental rotation of the self around the array were the first to shed light on this distinction (e.g., Wraga, Creem-Regehr, & Proffitt, 2004; Creem, Wraga, & Proffitt, 2001; Wraga et al., 2000; Amorim & Stucchi, 1997; Huttenlocher & Presson, 1997; Presson, 1982). Researchers consistently

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have found faster and more accurate performance during mental rotation of the body than during mental rotation of the array. Moreover, the RT functions corresponding to imagined perspective transformations often show unique characteristics. Unlike the monotonic RT functions of imagined array and object rotations, RTs for imagined perspective rotations usually are independent of angular disparities beyond 0°, particularly for angles aligned with the major axes of the body (Wraga, Shephard, Church, Inati, & Kosslyn, 2005; Wraga, 2003; Wraga et al., 2000). Imagined perspective rotations also have been shown to transcend other laws of physics. Creem, Wraga, et al. (2001) found that performance of imagined self-rotations about an array was not affected when the array appeared in a physically impossible position, such as parallel to a wall. Nor was performance affected when participants' bodies were lying supine on the ground, in a position prohibitive to physical self-movement. Wraga et al. (2000) have argued that the mental agility reflected in imagined perspective rotations may be due to the relative ease with which the human brain transforms the egocentric reference frame.

To date, these behavioral findings suggest that transformations of the egocentric and object-relative reference frames are subserved by distinct neural mechanisms. There is growing support for this hypothesis in the neuroimaging literature, both from studies of individual classes of mental rotation (e.g., Creem, Hirsch Downs, et al., 2001; Cohen et al., 1996) and comparisons of multiple classes of rotation (e.g., Wraga et al., 2005; Zacks, Vettel, & Michelon, 2003; Kosslyn, Thompson, Wraga, & Alpert, 2001). One contentious issue arising from such research is the role that motor processing may play in mental rotation. For tasks involving rotations of the object-relative reference frame, many studies have found activation of low-level cortical motor regions such as primary motor cortex (M1) and premotor cortex (PMC) (e.g., Harris & Miniussi, 2003; Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Vingerhoets et al., 2001; Barnes et al., 2000; Richter et al., 2000; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Tagaris et al., 1997; Cohen et al., 1996). For example, Vingerhoets et al. (2001) found M1 activation in a positron emission tomography study involving mental rotation of alphanumeric characters. Using time-resolved fMRI on a task involving mental rotation of Shepard–Metzler objects, Richter et al. (2000) reported that the duration of the hemodynamic response in PMC increased monotonically with participants' RT, which suggests that PMC is intrinsically involved in the mental rotation process per se.

Low-level cortical motor activation also has been found for transformations of the egocentric reference frame, but thus far the presence of such activation has been limited to self-congruence tasks involving individual body parts such as hands. In these tasks, participants typically judge the handedness of individual hands by imagining rotating their own hand into the stimulus (Parsons, 1994). This task has been known to produce monotonic RT func-

tions and corresponding low-level cortical motor activation (Creem-Regehr, Neil, & Yeh, 2007). Low-level cortical motor activation also has been found for tasks involving pairs of misoriented hands, for which the participant must imagine rotating one external hand into another (Wraga, Thompson, Alpert, & Kosslyn, 2003; Kosslyn et al., 2001).

In contrast, studies examining the neural substrate of imagined perspective rotations have shown little or no motor involvement (Creem-Regehr et al., 2007; Keehner, Guerin, Miller, Turk, & Hegarty, 2006; Wraga et al., 2005; Zacks et al., 2003; Zacks, Ollinger, Sheridan, & Tversky, 2002; Creem, Hirsch Downs, et al., 2001). For example, Creem, Hirsch Downs, et al. (2001) used fMRI to examine the neural substrate of a task in which participants updated the locations of objects in a memorized array configuration while imagining rotating their bodies in a "log roll" about the array's center. Activation in the perspective rotation condition was compared to that of a control task in which participants made an identical discrimination for a 0° rotation. The researchers found left SMA and PMC activation in only half of their participants, and M1 activation in none. Using a more comprehensive approach, Zacks et al. (2003) directly compared neural activation involved in imagined object and perspective rotation tasks. For the object task trials, participants imagined an array of objects rotating a prescribed amount and then either updated the location of one individual object in the array or updated which object would be present at a particular location in the array. For the corresponding versions of the perspective rotation task, participants answered the questions by imagined rotating themselves around the array. The researchers found two distinctive regions across the two types of mental transformation. The object tasks yielded activation in right intraparietal sulcus, whereas the perspective rotation tasks yielded activation in the left parietal–temporal–occipital (PTO) region. A more recent study found a dissociation of motor activation across object and perspective rotation tasks (Wraga et al., 2005). In the object rotation task, participants imagined rotating a Shepard–Metzler object and then judged whether a prescribed part of the object would be visible. In the perspective rotation task, participants imagined rotating themselves around the object, and then judged whether a prescribed part of the object would be visible from the new perspective. A direct comparison of the two tasks revealed activation in left PMC extending to M1 for imagined object rotations. In contrast, although the perspective rotation task yielded weak activation in SMA, no low-level cortical motor activation was found. The self-rotation task did activate a region in left middle occipital gyrus bordering fusiform gyrus, close to the PTO region reported by Zacks et al., providing additional support for this region's role in egocentric perspective transformations.

Taken together, the findings of neuroimaging studies implicate low-level cortical motor activation for egocentric transformations involving imagined rotation of body

parts, but not for imagined rotations of one's perspective. The present study is designed to address this issue further. One explanation for motor differences within egocentric transformations is that imagined perspective and body-part rotation tasks usually require different types of spatial encoding. In perspective rotations, participants imagine rotating their bodies to a location in space and then locate some aspect of the environment (e.g., part of an object or a display) with respect to the body. This object-to-body relationship is referred to as extrinsic encoding (e.g., Creem-Regehr et al., 2007; Buxbaum & Saffrana, 2002). In contrast, imagined rotations of individual body parts require participants to imagine rotating one of their own body parts (e.g., a hand) into a misaligned body-part stimulus. This body-part-to-body-part relationship is referred to as intrinsic encoding (e.g., Creem-Regehr et al., 2007; Buxbaum & Saffrana, 2002). Creem-Regehr et al. (2007) have postulated that intrinsic encoding necessarily involves a greater role of the dynamic representation of one's body, or body percept,[1] than extrinsic encoding; intrinsic encoding thus recruits more regions associated with motor control, such as low-level cortical motor areas. A second hypothesis mapped intrinsic and extrinsic encoding to left and right parietal regions, respectively, on the basis of similar dissociations found in the motor control literature (e.g., Buxbaum, Kyle, & Menon, 2005). Creem-Regehr et al. tested these hypotheses by directly comparing activation in two egocentric tasks using fMRI technology. In the hand rotation task (intrinsic encoding), participants imagined rotating their own hand into a misoriented hand stimulus in order to judge whether it was a right or left hand. In the perspective rotation task (extrinsic encoding), participants imagined rotating themselves around a misoriented hand stimulus in order to judge whether a prescribed component of the stimulus was on their right or left. The results supported the hypotheses. Creem-Regehr et al. found PMC activation in the hand rotation task, which increased as a function of rotation magnitude. The hand rotation task also yielded greater activation in left parietal regions. In contrast, the perspective rotation task yielded activation in visuospatial areas such as occipital gyrus and right superior and inferior parietal lobules, none of which increased with rotation magnitude.

From these results, it is tempting to conclude that differences in spatial encoding are the critical factor in dissociating low-level motor activation within multiple egocentric reference frames. However, several contradictory findings exist in the literature. As previously mentioned, low-level cortical motor activation has been found for hand rotation tasks that require "same–different" judgments involving the rotation of one hand stimulus into another hand stimulus (Kosslyn et al., 2001; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998). However, this task may be difficult to construe as requiring intrinsic encoding because the two stimuli may be treated as two external objects that are rotated independently of one's egocentric reference frame. In fact, researchers have de-

scribed a similar paradigm, involving the rotation of one body into another body, as more akin to rotation of the object-relative reference frame (Zacks et al., 2002; Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999). Moreover, regarding the hypothesis that maps intrinsic encoding to left-lateralized parietal processing, there is ample evidence indicating that the left parietal lobule is activated in imagined perspective rotation tasks, all of which, to date, have required extrinsic encoding (e.g., Wraga et al., 2005; Zacks et al., 2003; for a review, see Parsons, 2003).

Hints that a more general process than spatial encoding may influence motor activity come from the behavioral literature (Avraamides, Klatzky, Loomis, & Gollege, 2004; Wraga, 2003). For example, Wraga (2003) found that altering the response measure of an imagined perspective rotation task from a verbal response to a pointing response significantly altered performance, although both tasks involved identical extrinsic encoding. Wraga hypothesized that the pointing response measure, which required judgments with respect to participants' "right" or "left," served to "anchor" participants to their physical body. This anchoring effect tends to emphasize the spatial conflict between the physical egocentric frame pertaining to the body percept and the projected egocentric frame of the new viewpoint. The conflict thus interferes with people's ability to adopt the projected egocentric frame during imagined perspective rotation. On the other hand, an imagined perspective rotation task involving a response measure that minimizes this conflict, such as a "yes, no" verbal response, consequently de-emphasizes the body percept (Keehner et al., 2006; Wraga, 2003). By this account, one critical variable for driving egocentric motor differences in imagined perspective rotations may be the degree to which a person's body percept is minimized or maximized during imagined rotation, independently of what aspect of the environment (e.g., object or body part) is being updated per se.

We designed the current study to address these issues. We used the egocentric paradigm of Wraga et al. (2005) to compare the neural activation of two imagined perspective rotation tasks. The body minimize condition was identical to the imagined perspective rotation task of Wraga et al., in which participants imagined rotating around depictions of a cubed figure and pressed buttons to indicate ("yes" or "no") whether a prescribed component of the object was visible from the new perspective. In the body maximize condition, participants made identical imagined rotations of perspective, but used the buttons as "right" or "left" pointers to locate the prescribed object part with respect to their new perspective.[2] As in Wraga (2003), the pointer manipulation was intended to emphasize the participant's body percept. In both tasks, the object was updated with respect to the participant's new perspective, which required extrinsic encoding. However, we predicted that low-level cortical motor activation would be evidenced more in the body maximize condition than in the body minimize condition.

METHODS

Participants

We recruited 13 right-handed individuals (6 women, 7 men; mean age = 22 years; range = 19–28 years) from the Dartmouth College community. The data of eight additional participants were excluded; four for performing at chance levels in at least one task and four for technical difficulties with the scanner. Handedness was determined with the Edinburgh Handedness Scale (Oldfield, 1971). Prior to the study, all participants gave written consent to the protocol as approved by Smith College and Dartmouth College. Participants were paid $20 for their participation.

Materials

The stimuli were versions of those used previously by Wraga et al. (2005). They consisted of depictions of the multiarmed cube figures originally used by Shepard and Metzler (1971), rendered with Bryce 3-D software (Metacreations, New York, NY). Each object was depicted within a sphere. One of the inner cubes of each object was textured. Each stimulus contained a three-dimensional T-shaped prompt that appeared somewhere outside of the sphere (see Figure 1A). For each task, we used four different objects, which were rotated in increments of 65°, 100°, and 135° in either the x (frontal) or y (transverse) planes of rotation for a total of 24 stimuli. We created two orders of the 24-trial sets for each task.

Stimuli were displayed on a Macintosh PowerBook G4 computer using PsyScope software (Cohen, MacWhinney, Flatt, & Provost, 1993), which also recorded responses and RTs. During fMRI scanning, an Epson (model ELP-7000) projector at the rear of the scanner forward-projected the stimuli to a mirror approximately 6 inches directly above the participant's eyes. The distance from the mirror to the projector was approximately 3.5 feet. During the prescan training session, stimuli were displayed on the computer monitor.

Conditions

Body Minimize

For each trial, participants imagined rotating their bodies about the sphere until their eyes were behind and aligned with the horizontal line of the T prompt. They then judged ("yes" or "no") whether the textured part of the object would be visible from their new perspective.

Body Maximize

For each trial, participants imagined rotating their bodies about the sphere until their eyes were behind and aligned with the horizontal line of the T prompt. They then judged
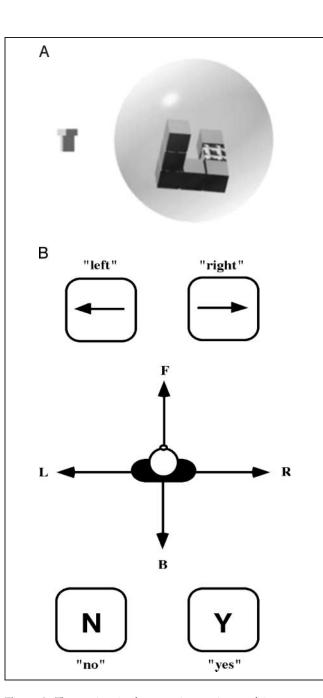

Figure 1. The two imagined perspective rotation conditions. (A) Sample stimulus, originally used in Wraga et al. (2005). In the body minimize condition, participants imagined rotating themselves to the location of the T prompt floating outside the sphere and then pressed "no" or "yes" buttons to indicate whether the textured portion of the object was visible. The correct answer for this trial is "yes." In the body maximize condition, participants performed the same imagined transformation, but pressed "left" or "right" buttons, which served as virtual pointers, to indicate whether the textured portion of the object was to their right or left. The correct answer for this trial is "left." (B) Response buttons for each condition, and their relationship to the egocentric reference frame. The "left" and "right" buttons of the body maximize task are aligned with the left/right axis of the human body. The same buttons, construed as "no" and "yes" responses in the body minimize condition, are arbitrarily mapped to the body.

the location ("right" or "left") of the textured part of the object with respect to their new perspective.

Procedure and Design

Participants were trained first on the two task conditions outside the scanner, in the same order they performed them in the scanner. After reading the instructions for each condition, participants performed six practice trials with feedback, one trial for each rotation and axis of rotation, using stimuli that did not appear during testing.

Body minimize and body maximize conditions were blocked across runs, with two consecutive runs for each condition. For the body minimize condition, there was an equal number of "yes" and "no" trials in each run, and for the body maximize condition, there were an equal number of "right" and "left" trials in each run. Each run began with a fixation point that remained on the screen for 30 sec. This was followed by the test trials, each of which remained on the screen for 12 sec irrespective of the speed of the participant's response. Participants were instructed to continue to look at the stimulus if they responded before it disappeared from view. If a participant did not respond within 12 sec, the next stimulus came up automatically, and the trial was counted as an error. A fixation point appeared for varying durations between each test trial, which induced "jitter" into the experiment. Jitter was added to increase the power of acquisition of each trial by helping to prevent predictability of trials, boredom, and oversaturation of activated areas. The fixation durations ranged between 3 and 24 sec in 3-sec intervals. The total duration for each run was 444 sec.

Participants responded in the scanner by pressing one of two buttons on a fiber-optic keypress, which were connected to the Macintosh computer via the PsyScope button box (New Micros, Dallas, TX). The keypress was separable so that participants held one button response in each hand. Their hands were placed on the sides of their body. Participants depressed the left button for "no" (body minimize) and "left" (body maximize) responses; they depressed the right button for "yes" (body minimize) and "right" (body maximize) responses. For the body maximize condition, they were instructed to treat the button presses as virtual pointers. After participants completed the first task, they paused to review the instructions for the next task, and scanning began again after the experimenter was satisfied that they understood the task.

Order of condition (body maximize, body minimize) was counterbalanced across participants. Trials in each run were presented in a pseudorandom order with the following restrictions: The same response could not occur three times in succession, and the same rotation magnitude could not be repeated until all variations had appeared once. Order of trials within each run was kept constant across participants.

For the behavioral analysis, only RTs for correct trials were used.

fMRI Acquisition

Imaging was performed on a 3.0-T Phillips Intera scanner with an eight-channel phase arrayed coil. We obtained four functional runs of volumes (222 scans each) in a single experimental session for each participant. Four additional scans at the beginning of each run were discarded to ensure steady-state conditions. A standard head coil with foam padding for head stabilization was used. Functional images were acquired with a single-shot, gradient-echo EPI sequence, with parameters TR = 2000 msec, TE = 35 msec, flip angle = 90°, 27 contiguous 4.5-mm-thick axial slices with 1 mm gap, and an in-plane resolution of 64 × 64 in an FOV of 240 mm. Immediately following the functional scans, high-resolution, 3-D T1-weighted structural images were acquired.

Imaging Analysis

The data were analyzed using Statistical Parametric Mapping (SPM2) (Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997). Functional data first were corrected for different slice acquisition time using sync interpolation. Each image was then realigned to the first image collected to correct for motion artifacts. The 27-slice structural image was then coregistered to the high-resolution structural image by first coregistering the 27-slice image to the high-resolution image and then applying those parameters to the functional images. The functional images were then directly coregistered to the high-resolution structural image via mutual-information coregistration. The images were spatially normalized to the MNI template (which averages over 152 brains) and then smoothed with a Gaussian filter of 6 mm full-width half-maximum to compensate for anatomical differences among participants.

We analyzed images using a two-stage, random effects analysis. First, we conducted within-subject, whole-brain analyses using a fixed-effects model under assumptions of the General Linear Model. A regressor was included in the model for each rotation magnitude (across runs) within each task, convolved with a standard hemodynamic response function (Frackowiak et al., 1997). We then performed a second group-level analysis for each contrast, in which subject was treated as a random effect. The t tests of the group-level analysis were thresholded at $p < .005$ (uncorrected for multiple comparisons) with an extent threshold of 12 contiguous voxels. We chose this combination of intensity and extent threshold to survive a corrected probability criterion for clusters, on the basis of previously published recommendations (Hayasaka & Nichols, 2003; Forman et al., 1995; Xiong, Gao, Lancaster, & Fox, 1995). As a final step, we converted coordinates of all clusters of activation from MNI to Talairach–Tournoux space (Brett, 2002).

RESULTS

Behavioral Results

Response Times

Figure 2A shows mean RTs and standard errors for both conditions as a function of rotation magnitude. As expected, participants were faster at updating in the body maximize condition (M = 3087 msec) than in the body minimize condition (M = 3679 msec). A 2 (condition order) × 2 (condition) × 3 (rotation magnitude) mixed-design analysis of variance (ANOVA) performed on mean scores yielded main effects of condition [$F(1, 11)$ = 9.30, p < .011] and rotation magnitude [$F(2, 22)$ = 7.22, p < .004], and a significant Condition × Rotation magnitude interaction [$F(2, 22)$ = 20.20, p < .0001]. Linear contrasts performed for each rotation condition yielded the following
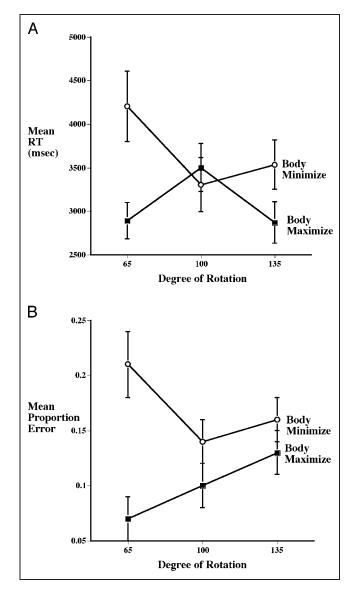

Figure 2. (A) Mean response times and (B) mean proportion error for trials in the minimize and maximize conditions, as a function of rotation magnitude.

patterns. For the body minimize condition, RTs revealed a typical V-shaped pattern found in other imagined perspective rotation studies (e.g., Wraga et al., 2005). RTs decreased from 65° to 100° [$t(12)$ = 4.87, p < .0001], and tended to increase from 100° to 135°, although this increase did not reach significance (p = .143). For the body maximize condition, RTs showed an inverted V-shaped pattern, with increases from 65° to 100° [$t(12)$ = −4.98, p < .0001], and decreases between 100° and 135° [$t(12)$ = 4.86, p < .0001]. No other effects or interactions reached significance.

Accuracy

Figure 2B shows mean percent error and standard errors for each condition as a function of rotation magnitude. As predicted, participants made significantly fewer errors in the body maximize condition (M = 10% error) than in the body minimize condition (M = 17% error). A 2 (condition order) × 2 (condition) × 3 (rotation magnitude) mixed-design ANOVA performed on mean percent error scores produced main effects of condition [$F(1, 11)$ = 12.98, p < .004], and a significant Condition × Rotation magnitude interaction [$F(2, 22)$ = 5.39, p < .012]. Linear contrasts performed for each condition yielded the following patterns. For the body minimize condition, errors decreased between 65° and 100° [$t(12)$ = 2.92, p < .013], but remained invariant between 65° and 100° (p = .488). For the body maximize condition, errors tended to increase from 65° to 100°, and from 100° to 135°, although the differences were not significant (p = .247 and p = .382, respectively). No other effects or interactions reached significance.

fMRI Results

The purpose of this study was to compare the neural activation underlying two versions of an imagined perspective rotation task. We achieved this by performing whole-brain analyses directly comparing the activation in each condition. We also performed supplementary analyses comparing the activation of each task with that of baseline.

Table 1 and Figure 3 present the results of the direct comparisons between the two perspective rotation conditions. In general, our findings are consistent with those of previous studies. For the maximize > minimize contrast, we found activation in left extrastriate visual areas (BA 18); bilateral activation in the inferior (BA 40) spatial processing areas bilaterally; activation in the left superior (BA 7) spatial processing area; and activation in left inferior temporal gyrus (BA 37). The latter region was somewhat more ventral and posterior to the PTO junction activation found in previous studies of imagined perspective rotations (Wraga et al., 2005; Zacks et al., 2003). In contrast to previous studies, the maximize > minimize contrast also yielded right SMA (BA 6) activation, and bilateral PMC activation extending to M1, with the strongest activation in the

Table 1. Areas of Activation in the Body Maximize Condition Compared to the Body Maximize Condition

Contrast	Brodmann's Area(s)	x	y	z	t	Cluster Size (Voxels)	p Value Rotation Effect
Maximize–Minimize							
Cuneus	18	−15	−102	8	7.04	93	.30
Cuneus	18	0	−96	8	5.16		
Middle occipital gyrus	18	−23	−99	8	4.87		
Inferior parietal lobule	40	−30	−48	38	5.16	57	.85
Inferior temporal gyrus	37	−42	−50	−8	5.11	23	.03
SMA	6	15	0	64	4.97	12	.79
Medial frontal gyrus	9	33	36	26	4.73	49	.92
Medial frontal gyrus	8	30	43	37	3.60		
Superior temporal gyrus	22	36	−11	3	4.65	31	.53
PMC/M1	6/4	−42	1	11	4.63	33	.76
Inferior parietal lobule	40	42	−47	47	4.45	58	.89
Inferior parietal lobule	40	51	−38	49	4.02		
Inferior parietal lobule	40	45	−36	46	3.58		
Inferior parietal lobule	40	−50	−36	29	4.17	13	.64
Cingulate gyrus	31	−12	−57	30	4.03	14	.65
PMC/M1	6/4	39	−4	36	3.99	19	.70
Anterior cingulate gyrus	24	3	38	4	3.63	14	.48
Superior parietal lobule	7	−9	−55	61	3.54	17	.55
Superior parietal lobule	7	−12	−50	55	3.39		

Talairach and Tournoux (1988) coordinates for activation peaks and maxima *t* values are provided. Also included are *p* values for effects of rotation magnitude.
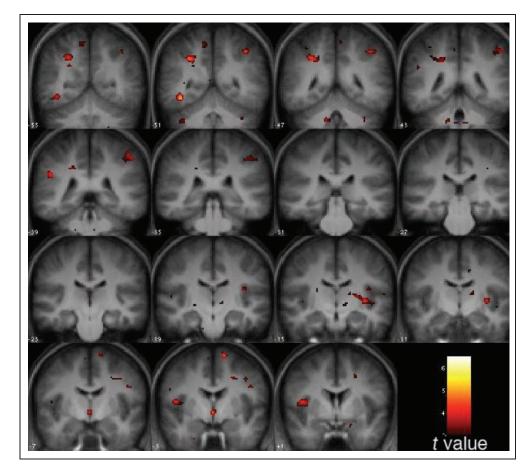
left hemisphere. Other regions included right anterior cingulate cortex (BA 24), as well as superior temporal gyrus (BA 22). The opposite contrast of minimize > maximize yielded no suprathreshold activations.

In order to assess effects of rotation magnitude, we computed the average adjusted beta estimate (across all voxels) for all regions of interest (ROIs) resulting from the maximize > minimize contrast. These values then were submitted to a one-way repeated measures ANOVA with rotation magnitude as a within-subject factor. The resulting *p* values for each ROI appear in Table 1. We found a trend (*p* = .03) for a rotation magnitude effect for one cluster only, left inferior temporal gyrus (BA 37). Post hoc linear comparisons revealed that activation in this region increased in the body maximize condition from 65° to 100° (*p* < .038) but remained stable between 100° and 135° (*p* = .785). However, the general rotation magnitude effect for this region did not survive a Bonferroni correction for multiple comparisons (*p* = .002).

The analyses comparing activation of each condition to baseline provided complementary findings to the direct contrasts. Table 2 presents the results of the body

maximize–fixation contrast. Major regions of activation in common with those of previous imagined perspective rotation studies included left primary visual cortex (BA 17), bilateral inferior temporal gyrus (BA 20), and right middle temporal gyrus (BA 21). We also found activation in left middle occipital gyrus (BA 19), in a region more medial to the PTO junction activation found in previous studies of imagined perspective rotations (Wraga et al., 2005; Zacks et al., 2003). However, the largest area of activation we found was unique to the body maximize condition. This activation peaked in the low-level cortical motor region of left PMC and extended to left M1 (BAs 6/4).

Table 3 presents the results of the body minimize–fixation contrast. We found a large region of activation bilaterally in the occipital–temporal region of the brain with peak activation in left fusiform gyrus (BA 37) extending to a subcluster of activation within right middle occipital gyrus (BA 37). These regions are somewhat more ventral to the PTO junction activation found in previous studies of imagined perspective rotations (Wraga et al., 2005; Zacks et al., 2003). We also found left mid/anterior cingulate (BAs 23/24) activation in a region slightly posterior to that found by

Figure 3. Coronal images ($y = -55 - +1$) depicting activation resulting from the maximize > minimize contrast. Areas depicted include PMC/M1 bilaterally, and inferior and superior parietal lobules bilaterally. Activation is superimposed onto an anatomical image created from the average of all participants.

Wraga et al. (2005), as well as left primary visual cortex (BA 17).

DISCUSSION

In this study, we examined the effect of a body-oriented response measure on the neural regions associated with egocentric mental rotation by comparing two versions of an imagined perspective rotation task. In the body minimize task, participants imagined rotating themselves around an object and determined whether a part of the object was visible from the new perspective by pressing buttons indicating "yes" or "no." In the body maximize task, participants performed an identical imagined movement, but determined whether the object part was to their "right" or "left" by pressing buttons serving as virtual pointers for

Table 2. Areas of Activation in the Body Maximize Condition Compared to Fixation

Body Maximize–Fixation	Brodmann's Area(s)	x	y	z	t	Cluster Size (Voxels)
PMC/M1	6/4	−24	−3	50	14.33	17,074
Occipital gyrus	19	−36	−83	24	12.60	
Medial frontal gyrus	9/46	−30	39	23	8.28	71
Inferior temporal gyrus	20	−42	−13	−25	6.07	22
Cuneus	17	−12	−78	15	5.10	64
Cuneus	17	0	−72	15	3.61	
Inferior temporal gyrus	20	36	−10	−35	4.68	13
Middle temporal gyrus	21	30	1	−33	4.12	

Talairach and Tournoux (1988) coordinates for activation peaks and maxima t values are provided.

Table 3. Areas of Activation in the Body Minimize Condition Compared to Fixation

Body Minimize–Fixation	Brodmann's Area(s)	x	y	z	t	Cluster Size (Voxels)
Fusiform gyrus	37	−30	−47	−13	17.20	15,182
Middle occipital gyrus	37	33	−59	−7	16.39	
Junction of mid./ant. cingulate gyrus	23/24	−6	−22	27	15.08	
Cuneus	17	−15	−75	15	3.84	13
Cuneus	17	−15	−81	10	3.48	

Talairach and Tournoux (1988) coordinates for activation peaks and maxima *t* values are provided.

those directions. Our results confirmed the existence of several different regions of brain activation between the two imagined perspective rotations. As predicted, one of the largest and most significant involved low-level cortical motor activation, including PMC and M1, which we found more of in the body maximize condition compared to the body minimize condition. To the best of our knowledge, this is the first instance of M1 activation being reported in an imagined perspective rotation task. It also is the first instance of activation differences being found within two versions of one imagined perspective rotation task. These findings lend support to the hypothesis that individual classes of mental rotation may be subserved by distinct neural mechanisms, depending on the strategy used to perform them (Creem-Regehr et al., 2007; Kosslyn et al., 2001; Wraga, 2003).

Evidence for different mechanisms was found in the direct comparison of body maximize and body minimize conditions. The maximize–minimize contrast revealed a relatively large number of stronger activations, despite the fact that the body maximize condition was performed more quickly and accurately than the body minimize condition. Therefore, potential confounds such as time on task or higher working memory load associated with relative task difficulty cannot account for the findings. The maximize condition yielded greater activation in right SMA, a higher-level motor planning region (Picard & Strick, 1996). More importantly, it yielded greater bilateral activation in PMC extending to area M1. The presence of this low-level cortical activation is in line with previous research highlighting the role of motor processing in other egocentric tasks involving imagined hand rotations, which has been interpreted as evidence for recruitment of the body percept (Creem-Regehr et al., 2007). However, the fact that our task involved extrinsic encoding does not support Creem-Regehr et al.'s (2007) hypothesis that activation of the body percept is associated only with intrinsic, or body-to-body spatial transformations. Moreover, unlike the findings for imagined hand rotations, low-level cortical motor activation in the body maximize condition was not related to rotation magnitude, which suggests a more tangential relationship between motor control recruitment and egocentric transformations in the latter task. Thus motor processing may play a func-

tionally different role in imagined hand rotations than in imagined perspective rotations that engage the body percept. This issue warrants further empirical investigation.

The body maximize condition also yielded greater activation in extrastriate visual areas, and activation in spatial processing areas of the superior and inferior parietal lobules. Activation in the parietal regions is particularly significant for two reasons. First, we found no support for the hypothesis that egocentric tasks involving extrinsic encoding elicit right-lateralized parietal processing only (Creem-Regehr et al., 2007). The body maximize task of the present study, which required extrinsic encoding, elicited bilateral activation of the inferior parietal regions and left activation of the superior parietal region. This finding is in line with previous studies of imagined perspective rotations requiring extrinsic encoding (e.g., Wraga et al., 2005; Zacks et al., 2003). Second, the inferior parietal lobule may play a role in the engagement (or not) of the body percept during perspective taking (e.g., Keehner et al., 2006; Vogeley & Fink, 2003; Ruby & Decety, 2001). Keehner et al. (2006) found activation in right superior parietal cortex that increased with rotation magnitude for an imagined object rotation task. They attributed this finding to continual spatial updating of the object with respect to the body. However, in the imagined perspective rotation version of the task, activation in the same parietal region decreased as a function of rotation magnitude. Keehner et al. interpreted this finding as evidence of body percept suppression per se, where decreased activation corresponds to a de-emphasis or ignoring of one's physical body position. Although we did not find significant rotation magnitude effects for any of the parietal regions resulting from the maximize > minimize contrast, the fact that this contrast resulted in greater superior and inferior parietal activation overall lends support to the idea that the posterior parietal activation corresponds to an enhanced role of the body percept in egocentric transformations.

The maximum–minimum contrast also revealed greater activation within the left parietal–occipital region, near an area implicated in other studies involving imagined perspective movement (e.g., Wraga et al., 2005; Zacks et al., 1999, 2003). This region also has been referred to as the extrastriate body area (e.g., Downing, Jiang, Shuman, &

Kanwisher, 2001). The results of the ROI analysis of this region showed a trend for a rotation magnitude effect, which suggests that the left parietal–occipital region is intrinsically involved in processing embodied egocentric transformations. Further research is required to address this issue.

The reverse comparison of minimize–maximize revealed no suprathreshold activations—motor or otherwise—however, this finding is not inconsistent with some previous studies comparing imagined perspective rotations to other classes of mental rotation (e.g., Keehner et al., 2006; Zacks et al., 2002). As previously mentioned, studies in our own lab have found suprathreshold activation using a similar perspective rotation task (Wraga, Helt, & Jacobs, 2007; Wraga et al., 2003); however, in those studies, we used a more lenient statistical threshold and also directly compared perspective-taking activation to qualitatively different classes of rotation, such as those involving imagined object movement.

The contrasts comparing each condition to fixation did reveal robust activations, in patterns supportive of the direct comparisons. The body maximize–fixation contrast yielded several regions found with previous imagined perspective rotation tasks (e.g., Wraga et al., 2005, 2007), including left primary visual cortex, a region associated generally with mental imagery, and right middle temporal gyrus (BA 21), a region involved in egocentric encoding (Bottini et al., 2001). This contrast also yielded activation in left middle occipital gyrus (BA 19) near the PTO region found in previous studies of imagined perspective rotations (Wraga et al., 2005; Zacks et al., 2003). However, in line with the results of the direct contrasts for the body maximize task, a major area of distinction found in this contrast was greater activation of left PMC extending to M1.

In contrast, body minimize–fixation showed greater activation for nonmotoric regions, including one that overlapped with those of the body maximize condition: left primary visual cortex. This contrast also yielded activation in the mid/anterior cingulate, which has been found in previous studies involving imagined perspective rotations (Wraga et al., 2005). It also yielded a large region of activation bilaterally in the left occipital–temporal region of the brain extending to right middle occipital gyrus, which is close to the PTO activation found in previous studies of imagined perspective rotations that is thought to be involved in egocentric transformations (Wraga et al., 2005; Zacks et al., 2003).

Differences in the presence of motor activation across the two conditions are supported by their corresponding behavioral findings. As anticipated, participants were faster and more accurate in the body maximize condition than in the body minimize condition; however, the two conditions also revealed interesting differences in RT functions. The body minimize task exhibited the typical V-shaped function found previously in similar imagined perspective rotation tasks, with fastest performance for 100° rotations, which are most closely aligned with the orthogonal axes of the human body (e.g., Wraga et al., 2004, 2005). In contrast,

performance in the body maximize condition showed the opposite effect, with slowest performance occurring for 100° rotations. In line with our hypothesis regarding recruitment of the body percept, this finding suggests a type of interference between physical and projected egocentric reference frames.

In summary, our findings help clarify the conditions under which the body percept, the representation of one's physical body, is recruited in imagined egocentric transformations. Imagined perspective rotations that required participants to relate aspects of the stimulus to their bodies yielded greater low-level cortical motor and posterior parietal activation, the combination of which may contribute to embodiment. In contrast, imagined perspective rotations requiring a non-body-related response showed little evidence of low-level cortical motor activation. This finding suggests a type of interference between physical and projected egocentric reference frames; however, further replication of this effect is warranted before strong conclusions may be drawn.

Notes

1. In their description of intrinsic encoding, Creem-Regehr et al. (2007) actually used the phrase "body schema" rather than "body percept." However, we prefer to adhere to the nomenclature proposed by Reed (2002), who distinguished between the "body percept," the immediate, dynamic representation of the spatial relations among body parts of one's own physical body; and the more general "body schema," which represents a long-term representation of the relationship among body parts that also may be applied to another person.

2. Previous research has shown that participants typically perform better on mental rotation trials in which the pre- and postrotation event match (i.e., "same" trials of the traditional self-congruence paradigm), compared to trials in which participants must discriminate between discrepant pre- and postrotation events (i.e., "different" trials) (Kerkman, Wise, & Harwood, 2000). In our study, the body maximize condition was more similar to the former category, in that its pre- and postrotation events always contained a textured cube. Therefore, we expected participants' performance in the body maximize condition to be superior to that of the body minimize condition.

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