



# Role of motor processes in extrinsically encoding mental transformations

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## ABSTRACT

Previous research has shown that imagined perspective rotations elicit spatial and low-level cortical motor areas of the brain when participants rely on knowledge of their physical body, or body percept (Wraga, Flynn, Boyle, & Evans, 2010). The current study used functional magnetic resonance imaging (fMRI) to investigate whether recruitment of the body percept would activate low-level cortical motor areas of the brain within other classes of mental transformations. Participants performed imagined object and perspective rotations of three-dimensional Shepard-Metzler (1971) stimuli. For each task, participants used button presses serving as virtual pointers to locate a prescribed portion of the stimuli with respect to their “right” and “left.” We found low-level cortical motor activation (M1) for both mental transformations; however, the degree to which such activation related to participants’ performance differed, as well as the recruitment of additional nonmotoric strategies. The results are discussed in terms of recent hypotheses regarding the role of the body percept in extrinsically encoded mental transformations.

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## 1. Introduction

The ability to create and manipulate mental images is an important function of human cognition. Mental rotation allows us to perform a variety of everyday cognitive tasks, such as extrapolating spatial layout from a GPS system, learning a sports play, or packing a suitcase. Shepard and Metzler (1971) introduced the paradigmatic approach used to study mental rotation. In their experiments, subjects were required to compare pairs of three-dimensional objects presented at different degrees of rotation within the picture plane and to judge as quickly as possible whether the objects were identical or mirror images. The results showed a linear relationship between the degree of angular disparity of the objects and response time (RT) for rotations up to 180°. This finding suggests that mental manipulation of objects follows laws akin to those for real manipulation of physical objects. In the last few decades the mental rotation paradigm has been extended to include imagined transformations of space such as mental rotation of one’s body, or imagined perspective rotations, as well as mental transformations of body parts such as hands and feet (Presson, 1982; Wraga, Creem, & Proffitt, 2000; Zacks, Vettel, & Michelon, 2003).

A useful way to distinguish different classes of mental rotation is to consider the spatial frames of reference that underlie each transformation. Spatial frames of reference provide an inherent

structure for identifying an object’s location and orientation. For example, imagined object rotations require transformation of the object-relative reference frame, which specifies the location and orientation of an object’s internal configuration, or of one object with respect to another (Easton & Scholl, 1995). The object-relative frame is composed of the up/down, right/left, and front/back orientations belonging to the object. Imagined perspective transformations involve the egocentric reference frame, which specifies an object’s location and orientation with respect to the major axes of the observer’s body (Howard, 1982). The egocentric reference frame is comprised of the up/down, right/left, and front/back positions of the observer. The egocentric frame also can be accessed on smaller scales relating objects to specific body parts of the observer such as the head, hand, or foot. Recently, a further distinction has been made, involving the updating component of the mental transformation (e.g., Buxbaum & Saffran, 2002; Creem-Regehr, Yeh, & Neil, 2007). Extrinsic encoding specifies an object relative to the egocentric frame, creating an object-to-body relationship (Creem-Regehr et al., 2007). In contrast intrinsic encoding specifies a body or body part relative to the egocentric frame, creating a body-to-body relationship (Buxbaum & Saffran, 2002).

Several studies comparing performance of imagined perspective and object rotation tasks have found a consistent advantage for imagined perspective rotations, for both speed and accuracy (e.g., Creem, Wraga, & Proffitt, 2001b; Presson, 1982; Wraga et al. 2000; Wraga, Creem-Regehr, & Proffitt, 2004). Moreover, the traditional monotonic RT function found with mental rotation of objects usually does not apply to its imagined perspective rotation counterpart. RTs for imagined perspective rotations usually are

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independent of angular disparities beyond 0°, particularly for angles that correspond to the major axes of the body (Wraga, 2003; Wraga et al. 2000; Wraga, Shephard, Church, Inati, & Kosslyn, 2005).

In recent years, researchers have begun to examine the brain regions and circuits involved in different classes of mental rotation. Several regions shared by many types of rotation include spatial processing regions of the inferior and superior parietal lobules (e.g., Creem et al., 2001a; for a recent review, see Zacks, 2008) as well as primary and/or secondary visual processing regions (e.g., Alivisatos & Petrides, 1997; Cohen et al., 1996; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998). However, there have been conflicting results as to whether mental rotation tasks lead to recruitment of lower-level cortical motor activation, such as premotor cortex (PMC) and primary motor cortex (M1). Lower-level cortical motor activation has been found in classical mental rotation tasks involving transformations of the object-relative reference frame (e.g., Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Kosslyn, Thompson, Wraga, & Alpert, 2001; Tomasino, Boironi, Rumiat, & Isaja, 2005). One interpretation of this finding is that observers may use motor strategies involving hand movement in mental rotation of objects. Using positron emission tomography (PET), Kosslyn et al. (2001) compared differences in neuronal activation for mental rotation of objects when participants employed either an internal strategy, in which they imagined rotating the object with their dominant hand; or an external strategy, in which they imagined the object being rotated by a motor. The results revealed M1 activation only for the internal strategy. Converging evidence for the role of M1 in imagined object rotations comes from a single case study. Tomasino et al. (2005) administered direct cortical stimulation to a patient with an electrode grid implemented into his primary motor cortex (M1). The patient exhibited relatively poor mental rotation performance when instructed to use a motor strategy similar to Kosslyn and colleagues' (2001) internal strategy, but not when using a visual strategy comparable to Kosslyn et al.'s external strategy.

For imagined transformations involving the egocentric reference frame, motor activation mostly has been limited to self-congruence tasks involving individual body parts such as hands (e.g., Creem-Regehr et al., 2007; Parsons, 1994). In such tasks, participants typically decide whether an individual hand stimulus is of a right or left hand by imagining rotating their own hand into that stimulus. This task has been known to produce monotonic RT functions and corresponding low-level motor activation (Creem-Regehr et al., 2007). Low-level 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 (Kosslyn et al., 2001; Wraga, Thompson, Alpert, & Kosslyn, 2003). These findings suggest that areas of the cortex used in movement control also play a part in mental transformations of body parts.

However, low-level cortical motor activation is not observed in all types of egocentric transformations. Studies examining the neural substrate of imagined perspective rotations have shown little or no low-level cortical motor involvement (Creem et al., 2001a; Creem-Regehr et al., 2007; Keehner, Guerin, Miller, Turk, & Hegarty, 2006; Wraga et al., 2005; Zacks, Ollinger, Sheridan, & Tversky, 2002; Zacks et al., 2003). For example, Creem et al. (2001a) used fMRI to examine the neural mechanisms involved in imagined perspective rotations. Participants were asked to update the locations of objects in a memorized array configuration after they had performed an imagined "log-roll" transformation of their body about the array's center. Activation in the perspective rotation condition was compared to that of a control condition in which participants merely located the objects' position in the array without imagining a change in viewpoint. This contrast yielded greater left supplementary motor area (SMA) and PMC

activation for the imagined perspective-rotation task, but this was only seen in half of their participants. M1 activation was not found in any participants.

Wraga et al. (2005) directly compared neural activation found in imagined object and perspective-rotation tasks using fMRI. This study found a dissociation of motor activation between two types of spatial transformations. In the object rotation task, participants imagined rotating versions of individual Shepard-Metzler objects and judged whether a prescribed part of the object would be visible in its new orientation. In the perspective-rotation task, participants imagined rotating themselves around the object and then judged whether a part of the object would be visible from the new perspective. A direct comparison of the two tasks revealed left M1 activation for the object rotation task that was consistent with hand movements. However, in the imagined perspective-rotation task, no low-level motor activation was found. The imagined perspective-rotation task was associated with weak activation of the left SMA and the left middle occipital gyrus bordering the fusiform gyrus. This area is very close to the parietal-temporal-occipital (PTO) region, which has been activated in other studies of imagined perspective rotations (Zacks et al., 2003) and is also referred to as the extrastriate body area, or EBA (e.g., Downing, Jiang, Shuman, & Kanwisher, 2001).

Creem-Regehr et al. (2007) recently hypothesized that the presence of intrinsic versus extrinsic encoding, mentioned previously, may be a factor in determining whether motor activation is involved in mental rotation tasks. For example, a typical imagined perspective-rotation task requires extrinsic encoding, where an object is updated with respect to the persons' newly transformed viewpoint. In contrast, most tasks involving mental rotation of body parts require intrinsic encoding, where a body part is updated with respect to the person's newly transformed body part. According to Creem-Regehr and colleagues, intrinsic tasks, which necessarily involve body part-to-body part encoding, may employ the dynamic representation of one's body to a greater extent than tasks involving extrinsic encoding. Intrinsic tasks are thus predicted to recruit more regions associated with motor control, such as low-level cortical motor areas. Creem-Regehr et al. (2007) tested this hypothesis by comparing the neural activation of two different egocentric tasks: an imagined hand task and an imagined perspective-rotation task. In the hand-rotation task, participants imagined rotating their own hand into a hand stimulus and then judged whether the stimulus was a right or left hand (intrinsic encoding). In the perspective-rotation task, participants imagined rotating themselves around a hand stimulus and then decided whether a particular component of the stimulus was on the right or left of their new viewpoint (extrinsic encoding). The results supported the hypotheses. Creem-Regehr and colleagues found greater PMC activation in the hand-rotation task, which increased as a function of RT. The hand-rotation task also yielded greater activation in the left parietal lobe, a region that Creem-Regehr et al. also attributed to intrinsic encoding. In contrast, the perspective-rotation task yielded greater activation in visuospatial areas such as the occipital gyrus and the right superior and inferior parietal lobes, but no low-level motor or left parietal activation.

Although the dissociation of motor activation within hand- and perspective-rotation tasks was clear in Creem-Regehr et al.'s (2007) study, several contradictory findings regarding the general intrinsic/extrinsic hypothesis exist in the literature. For example, as previously mentioned, low-level motor activation has been found for hand-rotation tasks involving pairs of hand stimuli, in which one hand stimulus is rotated into another (Kosslyn et al., 1998; Kosslyn et al., 2001). However, it is questionable as to whether this task should be considered as recruiting intrinsic encoding, given that the two stimuli may be treated as two external objects (i.e., object-to-object) rotated independently of

the participant's egocentric reference frame.<sup>1</sup> Moreover, regarding the hypothesis that limits intrinsic encoding to processing in the left parietal lobule, there is ample evidence indicating that this region is activated in imagined perspective-rotation tasks, all of which have required extrinsic encoding (e.g., Wraga et al., 2005; Zacks et al., 2003; for a review, see Parsons, 2003).

Wraga, Flynn, Boyle, and Evans (2010) tested for a more general phenomenon that may recruit low-level motor activation in mental transformations. Using fMRI they compared brain activation in two imagined perspective-rotation tasks that varied only by the degree to which the participants' body percept was emphasized. In the task that minimized awareness of the body percept, participants imagined rotating themselves around an object and then used button presses to decide ("yes, no") whether a part of the object was visible from the new viewpoint. In the task that maximized awareness of the body percept, participants performed an identical egocentric transformation but used the button presses to locate the object part with respect to their body midline ("left, right") at the new viewpoint. In the latter task, the participants were instructed to imagine the button presses as spatial indicators to their right or left. Thus, the button presses served as virtual pointers that anchored the participants to their physical body during the perspective transformation. However, both tasks required extrinsic, object-to-body encoding. A direct comparison of activation in both conditions showed greater recruitment of non-motor regions in the Body Minimize condition; in contrast, the Body-Maximize condition showed greater low-level cortical motor activation from both the PMC and M1. These findings suggest that one critical variable driving the motor dissociation in imagined egocentric transformations is the degree to which the body percept is elicited during the imagined rotation task. A logical question that follows from these findings is whether recruitment of the body percept modulates motor activation within other classes of mental transformations requiring extrinsic encoding.

In the present study we attempted to extend the findings of Wraga et al. (2010) by examining low-level cortical motor involvement in two different classes of mental rotation involving extrinsic encoding: an imagined perspective-rotation task and an imagined object rotation task. Our object task, which we refer to as Object-in-Hand, was based on the internal strategy of Kosslyn et al. (2001), but only involved one object stimulus. Participants imagined rotating an object in their hand and decided if a portion of the object in its new orientation would be to the right or left of their body midline. The Object-in-Hand task involved transformation of the object-relative reference frame; however it also required extrinsic (i.e. object-to-body) encoding. The perspective-rotation task was identical to that of Wraga et al.'s (2010) body-maximize condition. It involved transformation of the egocentric reference frame but also extrinsic encoding. Both tasks used a virtual pointing response measure, which served to anchor participants to their physical body and in turn emphasize their body percept. We predicted that, although both tasks required extrinsic encoding, they both also engaged the body percept, which would elicit low-level cortical motor activation.

## 2. Methods

### 2.1. Participants

We recruited eighteen right-handed individuals (10F, 8 M; 18–30 years of age; mean age: 22) from the Dartmouth College community. The data of eleven additional participants were eliminated

from analysis: ten for performing at chance on at least one of the tasks and one for technical difficulties with the scanner. In addition, the behavioral data of two of the participants were lost due to technical difficulties of the scanner. However, these participants' fMRI data were retained. Thus, in this experiment,  $n = 18$  for the functional analysis and  $n = 16$  for the behavioral analysis. Before participating in the study, all participants filled out consent forms of the protocol from both Smith College and Dartmouth College and completed the Edinburgh handedness scale (Oldfield, 1971). Each participant was paid \$20 for his/her participation.

### 2.2. Materials

The experiment utilized stimuli that were three-dimensional depictions of the multi-armed cube figures used by Shepard and Metzler (1971) (see Fig. 1). Versions of these stimuli were previously used by Wraga et al. (2005) and Wraga et al. (2010). For each stimulus, a single object was situated within a semi-transparent sphere in the middle of the viewing screen. One of the inner cubes of the object was textured. For the hand-rotation task, a three-dimensional T-shaped prompt appeared on the end of one arm of the object; a second T-prompt appeared somewhere outside of the sphere (see Fig. 1a). For the perspective-rotation task, one T-prompt appeared outside of the sphere only (see Fig. 1b).

Stimuli for fMRI scanning were displayed on a Dell Latitude D830 computer using E-prime (Psychology Software Tools, Inc., Pittsburgh, PA) software, which also recorded responses and response time (RT) values. During scanning, the stimuli were presented on an Epson (model ELP-700) projector at the rear of the scanner, which forward-projected the images a distance of 3.5 feet to a mirror approximately 6 in. in front of the (recumbent) participant's eyes. The screen was centered on the participant's nose. Stimuli for the pre-scan training session were displayed on a Macintosh MacBook Pro computer using PsyScope (New Micros, Dallas, TX) software.

### 2.3. Tasks

#### 2.3.1. Object-in-Hand rotation

In the Object-in-Hand task, participants were asked to imagine holding the object in their right (i.e., dominant) hand and mentally rotate the object so that the T-prompt attached to it lined up with the T-prompt located outside of the sphere. Participants were informed that the two T-prompts would not touch, but that the T-prompts had to line up in terms of orientation. The participants then made a "right" or "left" decision with respect to the body midline of where the textured part of the object would be visible in its new orientation.

#### 2.3.2. Perspective rotation

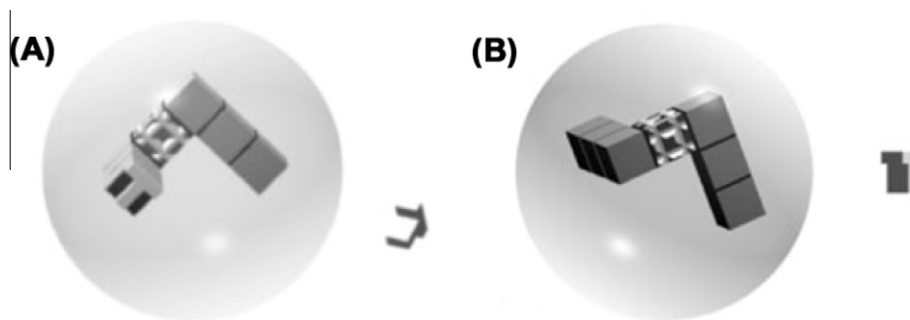
Participants were asked to imagine rotating their bodies around the sphere until their eyes were aligned behind the horizontal line of the floating T-prompt and their noses were aligned behind the vertical line of the floating T-prompt. They then made a "right" or "left" decision of where the textured part of the object would be located with respect to the participants' new viewpoint.

### 2.4. Procedure

Participants were tested at Dartmouth College's Brain Imaging Center (DBIC) fMRI facility. Participants first were trained outside of the scanner on the two tasks in the same order in which they performed them in the scanner.

The participants were presented with a detailed set of visual instructions for each task, which they read through at their own pace. Participants were asked to summarize each instruction

<sup>1</sup> For a similar argument involving pairs of body stimuli, see Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999; Zacks et al., 2002.



**Fig. 1.** The stimuli used in the experiment. (A) In the hand task, participants were asked to imagine holding the object in their dominant hand and rotating it until the T-prompt on the object became aligned with the T-prompt outside of the sphere. They then judged whether the object's textured cube in its new orientation was to the left or right of their body midline. The correct answer for this trial is "right." (B) In the Perspective task, participants were asked to imagine rotating themselves to the location of the T-prompt. From this new perspective, they then judged whether the textured cube of the object was on their right or the left. The correct answer for this trial is "left".

screen out loud to ensure that they understood the task. The experimenter gave additional verbal instruction when more information was needed to ensure comprehension of the task; fewer than 10% of participants required this. Next, participants performed six practice trials with feedback: one for each rotation and axis of rotation using stimuli that did not appear in the test trials. After each practice trial of each task, participants received feedback on the correct answers in the form of a depiction of the stimulus in its final orientation/viewpoint. After the practice trials were completed, the participants were asked about their comprehension of the tasks and were given the opportunity to repeat the practice session to increase their performance level if necessary. Upon completion of the instructions and practice trials for the first task, participants viewed the instructions for the second task directly afterwards in the same manner, followed by performance of six practice trials. Ten percent of participants chose to repeat the practice session for one or both of the tasks prior to entering the fMRI scanner.

Participants next entered the scanner for preliminary scans. Prior to the two runs of each task, the experimenter reviewed the instructions for each upcoming task over the scanning room intercom. A total of four runs were performed (2 per task). Each scan lasted for 7 min, 40 s. After the runs were completed, the participant rested in the scanner while high-resolution anatomical scans were performed. Total time in the scanner was approximately 50 min.

Each run (i.e., one set of trials) began with a fixation star that remained on the screen for 12 s. This was followed by a stimulus that remained on the screen for 14 s regardless of the speed of the participant's response. Most subsequent stimuli preceded (and followed) a single fixation star that was presented for durations varying between 3 and 24 s; several of the stimuli occurred with no fixation star. The varying durations of the fixations added jitter into the experiment to increase the power of the acquisition of each trial by preventing boredom, over-saturation of activated areas, and to shield against predictability.

Participants responded in the scanner by pressing one of two buttons on fiber-optic key presses that were connected to the Dell computer. The participant held one key press in each hand. Participants were instructed to keep their hands at their sides for the duration of the experiment. The participants pressed the right button press for "right" responses and the left button for "left" responses. In both conditions participants were instructed to treat the button presses as virtual pointers to indicate right and left directions with respect to the body midline. After completion of the study, participants filled out debriefing forms that asked about the participants' mental strategies, ideas about the purpose of the study, as well as compliance and difficulties performing the tasks.

## 2.5. Design

The experiment used a within-subjects design in which each participant was tested in both conditions of the study. Task order (Object-in-Hand, Perspective) was counterbalanced across subjects.

For each task, four different objects were rotated 65°, 100°, or 135° with respect to the T-prompt, along either the X (frontal) or Y (transverse) planes, for a total of 24 stimuli (4 stimuli × 2 planes of rotation × 3 rotation angles). Two pseudo-random orders of the 24-trial sets were created for each task: within each individual trial set, the full range of rotation angles had to appear before any degree of rotation was repeated, and no more than three trials of a given response appeared in a row. In addition, all trials sets had an equal number of "right" and "left" responses.

For the behavioral analysis, only RTs for correct trials were used to calculate individual and group means.

## 2.6. fMRI acquisition

Event-related functional MR imaging was performed on a 3.0 T Phillips Intera scanner with an eight-channel phase arrayed coil. Four functional runs of volumes (227 scans each) were obtained from each participant. At the beginning of each run, four scans were discarded to ensure steady-state conditions of tissue magnetization. A standard head coil was used with foam pillows and padding to restrict head motion. The participant was also instructed to remain still during the scanning. Functional images were acquired with a single-shot gradient echo EPI sequence, with parameters TR = 2000 ms, TE = 35 ms, flip angle = 90°, 27 contiguous 4.5 mm thick axial slices with 1 mm gap and an in-plane resolution of 64 × 64 in a FOV of 240 mm. Immediately following the functional scans, high-resolution, 3D T1-weighted structural images were acquired.

## 2.7. Imaging data analysis

The data were analyzed using Statistical Parametric Mapping (SPM2) preprocessing software (Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997). Functional data first were corrected for differences in slice acquisition time using sinc 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 International Consortium of Brain Mapping 152-brain template (Montréal Neurological Institute). Data were smoothed using a Gaussian filter of 6 mm full-width half maximum (FWHM) to counteract anatomical differences among participants.

The images were analyzed using a two-stage, random effects analysis. First a within-subject, whole-brain analysis was performed using a fixed-effect model under the assumption 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). A second group-level analysis was then performed for each contrast, in which the subject was treated as a random effect. Based on the parameters of our previous studies (Wraga, Helt, Jacobs, & Sullivan K., 2007; Wraga et al., 2005), the *t*-tests of the group-level analysis were thresholded at  $p < 0.005$  (uncorrected for multiple comparisons) with an extent threshold of five contiguous voxels.<sup>2</sup> The resulting coordinates of activated clusters were converted from MNI to Talairach-Toutnoux space (Brett, 2002).

### 3. Results

#### 3.1. Behavioral results

##### 3.1.1. Response times

In line with previous studies (e.g., Creem-Regehr et al., 2007), participants were faster at performing the Perspective task ( $M = 3825.78$  msec;  $SE = \pm 268.28$ ) than the Object-in-Hand task ( $M = 5616.49$  msec;  $SE = \pm 407.54$ ) (see Fig. 2A). A 2 (task)  $\times$  3 (rotation magnitude) repeated-measures analysis of variance (ANOVA) yielded a main effect of task,  $F(1, 15) = 65.90$ ,  $p < .0001$ . We also found a main effect of rotation magnitude,  $F(2, 28) = 3.25$ ,  $p < .05$ . Posthoc linear analyses revealed a trend for an increase in RTs from 65° to 100°, although the increase did not reach significance,  $t(15) = -1.732$ ,  $p = .104$ . RTs from 100° to 135° did not show a significant difference ( $p = .357$ ).<sup>3</sup> No other main effects or interactions reached significance.

##### 3.1.2. Accuracy

As predicted, participants made significantly fewer errors in the Perspective task ( $M = 17\%$ ;  $SE = \pm 0.142$ ) than in the Object-in-Hand task ( $M = 31\%$ ,  $SE = \pm 0.151$ ) (see Fig. 2B). A 2 (task)  $\times$  3 (rotation magnitude) repeated-measures ANOVA performed on mean error rates revealed a main effect of task,  $F(1, 15) = 24.38$ ,  $p < .0001$ . We also found a significant Condition  $\times$  Rotation Magnitude interaction,  $F(2, 28) = 3.44$ ,  $p < .045$ . Posthoc linear comparisons revealed that this interaction was not driven by differences in error patterns within tasks (Perspective: 65° vs. 100°,  $p > .05$ ; 100° vs. 135°,  $p > .05$ ; Object-in-Hand: 65° vs. 100°,  $p > .05$ ; 100° vs. 135°,  $p > .05$ ), but rather by significant differences across tasks for 65° rotations,  $t(15) = 4.719$ ,  $p < .0001$ , and 100° rotations,

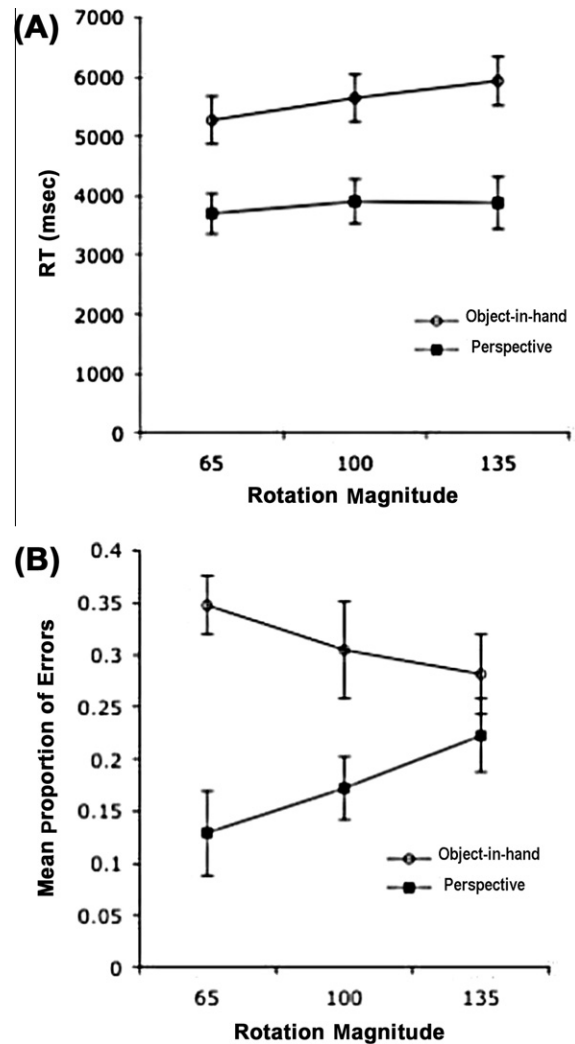


Fig. 2. (A) Mean RT and standard errors for the two tasks, as a function of rotation magnitude. (B) Mean proportion error and standard errors for the two tasks as a function of rotation magnitude.

$t(15) = 2.874$ ,  $p < .05$ , but not for 135° rotations ( $p = .177$ ). No other main effects or interactions reached significance.

##### 3.1.3. fMRI Results

The purpose of this study was to examine the neural correlates underlying two mental rotation tasks, both involving extrinsic encoding. To achieve this, we first performed whole-brain analyses contrasting each task with low-level fixation and then directly compared the activation in each task. We considered the latter to be the main test for differences between neural regions across tasks; these findings are presented first.

#### 3.2. Direct contrasts

Table 1 and Figs. 3 and 4 show the results of the direct comparisons between tasks. The Perspective – Object-in-Hand contrast yielded strong amounts of activation (see Fig. 3). We found activation in the secondary visual areas (BAs 18, 19) bilaterally and activation in the left precuneus (BA 7) and inferior parietal lobule (BA 40) spatial processing regions (Harris et al., 2000). Most significantly, we found activation in the left premotor cortex (PMC: BA 6) extending to primary motor cortex (M1: BA 4), as well as right M1 activation. Other areas of activation included the right cingulate gyrus (BA 32).

<sup>2</sup> In our most recent study (Wraga et al., 2010), we chose a more stringent cluster threshold of  $k = 12$ ; however, preliminary analysis of the present data did not replicate any low-level cortical motor activation for either task at that threshold in the direct comparisons between tasks, perhaps because of the strong similarity between tasks. Given the relatively consistent finding of low-level cortical motor regions in previous hand-rotation tasks (e.g., Creem-Regehr et al., 2007; Kosslyn et al., 2001; Parsons, 1994), we reverted to our previously used cluster threshold of  $k = 5$ , which revealed low-level cortical activation in both tasks of a size just below the more stringent cluster threshold.

<sup>3</sup> For the Perspective task, this pattern of RTs differs from that of the corresponding body-maximize condition of Wraga et al. (2010), which showed significantly higher RTs for 100° rotations. However, the RT function of the present study is more in line with previous studies of perspective rotations (e.g., Wraga et al., 2001), which indicates that the Body Maximize results of Wraga et al. (2010) may be attributable to individual differences in performance.

**Table 1**

Areas of activation in the Perspective task compared to the Object-in-Hand task, and vice versa.

	Brodman area (s)	X	Y	Z	t-Value	Clust. size (mm <sup>3</sup> )
<i>Perspective – Object-in-Hand</i>						
Cerebellum		42	–57	–35	6.43	222
Superior temporal gyrus	22/42	59	–20	12	5.99	53
Secondary visual cortex	19	30	–81	7	5.93	87
Inferior parietal lobe	40	–39	–45	38	5.67	314
Cingulate gyrus	32	12	22	32	5.15	394
Superior frontal gyrus	10	–39	43	–5	4.95	15
Inferior parietal lobe	40	45	–54	44	4.76	83
Secondary visual cortex	18/19	–36	–76	–1	4.76	154
Inferior frontal gyrus	47	–41	14	–8	4.70	101
Superior temporal gyrus	22	41	–6	3	4.50	109
Inferior frontal gyrus	44	–33	13	19	4.48	73
Cerebellum		–21	–45	–31	4.12	28
Medial frontal gyrus	8/9	–39	8	38	3.54	17
Medial frontal gyrus	10/46	–39	44	14	3.98	26
Secondary Visual Cortex	19	–27	–80	29	3.76	17
Inferior parietal lobe	40	–62	–48	30	3.64	5
Superior temporal gyrus	22	–45	0	3	3.64	12
Cerebellum		15	–37	–33	3.63	10
M1	4	–36	–23	65	3.60	6
M1/PMC	4/6	39	–23	65	3.59	9
Inferior parietal lobe	40	65	–42	33	3.50	12
Cerebellum		–15	–74	–22	3.37	6
Cerebellum		–30	–71	–22	3.36	46
Precuneus	7	–3	–64	53	3.36	5
Inferior parietal lobe	39	–56	–36	27	3.26	9
<i>Object-in-Hand – Perspective</i>						
Medial frontal gyrus	10	0	52	–8	4.49	108
Primary/secondary visual cortex	17/18	12	–100	–10	4.38	38
Medial temporal gyrus	21/22	62	–9	–15	4.00	25
Superior frontal gyrus	9/10	12	50	17	3.82	10
M1	4	–3	–29	62	3.77	11
Medial frontal gyrus	8	21	–22	38	3.71	6
Posterior cingulate gyrus	31	3	–60	17	3.61	29
Cingulate/precuneus	31/7	15	–45	33	3.51	43
Superior frontal gyrus	9/10	–6	62	19	3.45	6
Medial frontal gyrus	8	21	34	39	3.44	18
Medial frontal gyrus	8	24	37	48	3.29	6
Superior parietal lobe	40	48	–71	28	3.19	11

The opposite contrast of Object-in-Hand – Perspective revealed a network of neural regions generally consistent with those of previous studies (see Table 1 and Fig. 4). We found activation in right primary and secondary visual cortex (BAs 17, 18), as well as the right anterior prefrontal cortex (PFC: BA 10). The Object-in-Hand – Perspective contrast also yielded activation in the right precuneus (BA 7) spatial processing region, as well as the cingulate gyrus (BA 31). Most significantly, we found activation in the medial region of left M1. This region overlaps M1 activation found in a previous study comparing object and perspective rotation activations (Wraga et al., 2005).

### 3.3. Region-of-interest analysis

To further examine the brain activation found in the direct contrasts, we computed the averaged adjusted beta estimates (across all voxels) for all regions of interest (ROIs) resulting from the two direct contrasts (Perspective – Object-in-Hand; Object-in-Hand – Perspective). We considered ROIs to be the regions discussed in the previous direct-comparison sections. A recent ROI analysis performed in our lab, involving the assessment of rotation magnitude effects in a similar paradigm, revealed nonsignificant findings for all ROIs (Wraga et al., 2010). For the present study we therefore chose an alternate method of assessing these data, one more sensitive to the nature of the relationship between brain activation

and participants' actual behavior. We correlated ROI beta estimates with participants' mean RT and mean percent error (e.g., Richter et al., 2000; Wraga et al., 2007). The resulting *R* values appear in Table 2.

For Perspective – Object-in-Hand ROIs, activations in M1 and PMC were positively correlated with mean error ( $r = .595$ ,  $p < .05$ ;  $r = .566$ ,  $p < .05$  respectively) and mean RT ( $r = .534$ ,  $p < .05$ ;  $r = .513$ ,  $p < .05$ , respectively). For Perspective – Object-in-Hand ROIs, we also found a positive correlation between activation in the precuneus (BA 7) and mean RT ( $r = .534$ ,  $p < .05$ ).

For Object-in-Hand – Perspective ROIs, activation in anterior PFC (BA 10) was positively correlated with mean error ( $r = .552$ ,  $p < .05$ ). We also found a negative correlation between activation in the primary/secondary visual cortex (BA 17/18) and mean RT ( $r = -.497$ ,  $p < .05$ ); however, the correlation between M1 beta estimates and either error ( $r = .227$ ,  $p > .05$ ) or RT ( $r = -.116$ ,  $p > .05$ ) did not reach significance.

The absence of a significant correlation between low-level motor activation and behavior data for Object-in-Hand – Perspective was unexpected. To examine this finding further, we separated Object-in-Hand – Perspective beta estimates as a function of rotation magnitude and looked for relationships between M1 and other Object-in-Hand – Perspective ROIs that had shown significant correlations with the behavioral data. Beta estimates for anterior PFC were not significantly correlated with M1 for any of the rotation magnitudes (65°:  $r = .506$ ,  $p > .05$ ; 100°:  $r = .318$ ,  $p > .05$ ; 135°:  $r = .003$ ,  $p > .05$ ). Beta estimates for primary/secondary visual cortex were significantly correlated with M1 for the 100° ( $r = .542$ ,  $p < .05$ ) and the 135° rotations ( $r = .680$ ,  $p < .05$ ) values; however, the relationship between M1 and the primary/secondary visual cortex for 65° rotations did not reach significance ( $r = .131$ ,  $p > .05$ ). This finding suggests that, for Object-in-Hand rotations beyond 65°, participants may have relied more on visual (i.e., nonmotoric) strategies than motor strategies, possibly because of the increased difficulty of these greater rotation magnitudes.

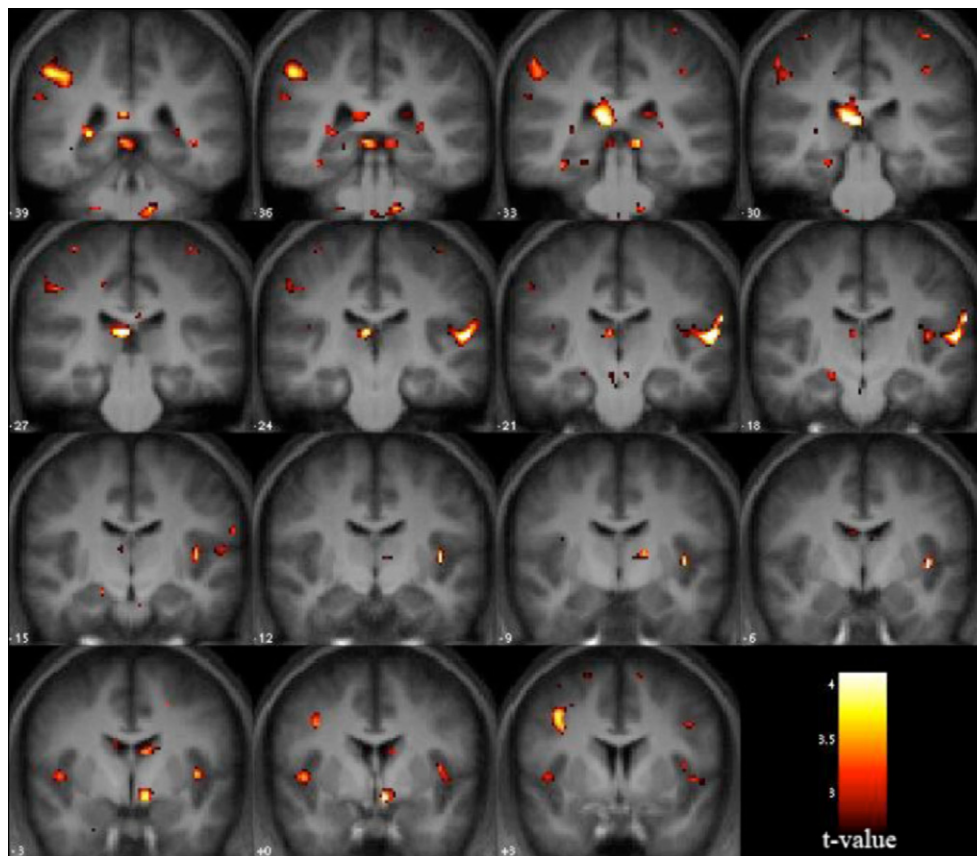
### 3.4. Contrasts with fixation

We also performed contrasts of each task with fixation (see Table 3). The resulting activations generally support those of the direct contrasts. The Perspective – Fixation contrast revealed a large region of activation peaking in the junction between middle and anterior cingulate gyrus (BAs 23/24). Within this cluster we also found activation in the left M1 and right PMC. Other regions of activation included the right medial frontal gyrus (BA 8/9) and right primary visual cortex (BA 17), as well as the posterior cingulate (BA 31).

The Object-in-Hand – Fixation contrast also revealed a large region of activation, peaking in the left inferior temporal gyrus (BA 37). Within this region we found clusters of activation extending to PMC and lateral regions of left M1. The Object-in-Hand – Fixation contrast also yielded activation in the left superior temporal gyrus (BA 38) and the right medial temporal gyrus (BA 21). Other areas of activation included the right primary and secondary visual association areas (BA 17/18) and the right dorsolateral prefrontal cortex (DLPFC; BA 9).

## 4. Discussion

In this study we examined low-level cortical motor recruitment for two mental rotation tasks: an imagined object rotation task and an imagined perspective-rotation task. In the Object-in-Hand task, participants imagined holding an object and rotating it in their hand to determine the location of a prescribed portion of the object in its new orientation. In the Perspective task, participants



**Fig. 3.** Coronal images ( $y = -39 \pm 3$ ) depict activation resulting from the Perspective – Object-in-Hand contrast. Areas include left M1 activation and left inferior parietal lobe activation. Activation appears on an anatomical image created from the average of all participants.

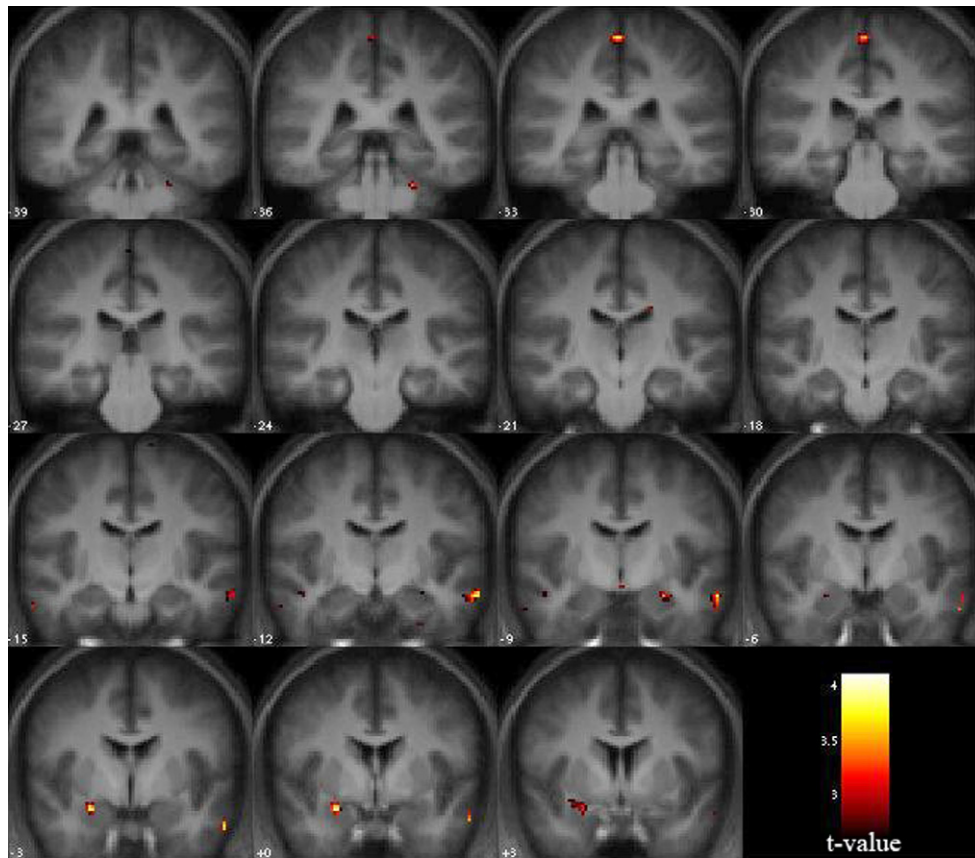
imagined rotating themselves around an object and determined the location of a prescribed part of the object from their new perspective. In both tasks, participants responded by pressing buttons serving as virtual pointers to indicate “right” and “left” locations. Thus, although each task required extrinsic, object-to-body encoding, they each also engaged the participants’ physical body, or body percept. Wraga and colleagues (2003, 2010) have argued that the virtual pointer response measure acts to ground observers to their body percept, and thus may elicit motor strategies more readily than more abstract, nonpointing measures. The results of the present study provide additional support for this hypothesis. We replicated Wraga et al.’s (2010) finding of low-level cortical motor activation for an imagined perspective-rotation task involving extrinsic encoding. We also found low-level cortical motor activation in an imagined object rotation task involving extrinsic encoding. These findings indicate that level of embodiment plays a more critical role in recruiting motor activation in mental transformations than the type of encoding per se (c.f. Creem-Regehr et al., 2007). More generally, these findings also demonstrate that individual classes of mental rotation may recruit multiple neural mechanisms, depending on the strategy used to perform them (Creem-Regehr et al., 2007; Kosslyn et al., 2001; Wraga, 2001; Wraga et al., 2010).

Evidence for the influence of the body percept on egocentric transformations was found in the direct comparison of the two egocentric tasks. The Perspective – Object-in-Hand contrast revealed relatively stronger activations, despite the fact that the Perspective task was performed more quickly and accurately than the Object-in-Hand task. Therefore, potential confounds associated with increases in task difficulty such as time on task or higher working memory load cannot account for the findings. Perspective

– Object-in-Hand revealed activation typical of the mental rotation network, including bilateral activation of secondary visual areas, left activation of the inferior and superior parietal lobules, and the right cingulate gyrus. However, in contrast to most studies of perspective transformations, we also found left PMC and bilateral M1 activation. This low-level cortical activation was similar in location to, but somewhat smaller in extent than the activation Wraga et al. (2010) found for a similar imagined perspective-rotation task.

The opposite contrast of Object-in-Hand – Perspective revealed some regions of activation in common with the previous contrast, and in keeping with the typical neural circuit of mental rotation, including right primary and secondary visual areas, right activation of the superior parietal lobule, and the cingulate gyrus. This contrast also yielded greater activation of anterior PFC (BA 10) working memory region. Most significantly, we found activation in left M1. The peak of this activation corresponded to that found in a previous study for a similar Object rotation task not explicitly requiring hand movements (Wraga et al., 2005); however, M1 activation for that task was much larger and, in accord with the hypothesis that imagined object rotation tasks may involve implicit hand-movement strategies, extended laterally into the hand region of the M1 motor strip (Rao et al., 1995). For the Object-in-Hand task of the current study, which required explicit hand-movement strategies, the absence of laterally spreading activation along the motor strip was unexpected. One possibility is that the hand region of M1 did not play a major role in eliciting body awareness within the Object-in-Hand task. However, we did find M1 activation extending laterally in the Object-in-Hand – Fixation contrast, which suggests the contrary. In future research it will be important to pinpoint more accurately the nature of embodiment





**Fig. 4.** Coronal images ( $y = -39 \pm 3$ ) depict activation resulting from the Object-in-Hand – Perspective contrast. Areas include left M1 activation and left precuneus and cingulate activation. Prominent activation not shown is BA 18. Activation appears on an anatomical image created from the average of all participants.

**Table 2**  
Results of region of interest (ROI) analyses.

	Brodman area (s)	R with M% error	R with M% RT
<i>Perspective – Object-in-Hand</i>			
Secondary visual cortex	19	.357	.232
Cingulate gyrus	32	.044	.048
Superior temporal lobe	21/22	.198	.413
M1	4	.595*	.534*
M1/PMC	4/6	.566*	.513*
Precuneus	7	.464	.534*
Inferior parietal lobe	39	.319	.266
<i>Object-in-Hand – perspective</i>			
Medial frontal gyrus	10	.552*	–.154
Primary/secondary cortex	17/18	–.032	–.497*
M1	4	.227	–.116
Posterior cingulate gyrus	31	–.043	–.471
Medial frontal gyrus	8	.150	.411
Superior parietal lobe	40	.419	.225

\* Pearson correlation significant at  $p < .05$  (2-tailed).

within the Object-in-Hand task. This could be accomplished by directly comparing activation in imagined object rotation tasks that required differing levels of emphasis of the hands and body, or both. Another approach would be to examine neural differences within different phases of the Object-in-Hand task itself, by separating out the spatial transformation of the stimuli from the categorical “right/left” judgment with respect to participants’ body midline.

The results of the ROI analysis we performed shed some light on the role of M1 in our two rotation tasks. For the Perspective task, we found significant positive correlations between M1/PMC

**Table 3**  
Areas of activation in each rotation task compared to fixation.

	Brodman area (s)	X	Y	Z	t-Value	Clust. size (mm <sup>3</sup> )
<i>Perspective – Fixation</i>						
Junction of Mid./ant. cingulate gyrus	23/24	6	–22	26	14.3	17,660
M1	4	–12	–34	58		
PMC	6	4	–18	64		
Medial frontal gyrus	8/9	33	36	20	4.28	58
Primary visual cortex	17	9	–99	0	3.91	17
Posterior cingulate	31	18	–29	37	3.78	28
<i>Object-in-Hand – Fixation</i>						
Inferior temporal Gyrus	37	–30	–53	–10	13.65	14,314
M1	4	–12	–34	58		
PMC	6	–6	–20	67		
Medial temporal gyrus	21	56	5	–18	5.28	38
Superior temporal gyrus	38	–33	13	–31	3.77	5
Primary/secondary visual cortex	17/18	12	–100	–1	3.71	12
DLPFC	9	33	45	36	3.35	7

beta estimates and mean error rates and RT values. This tight coupling between low-level cortical motor activation and performance of the Perspective task suggests that the motor activation we found was not merely epiphenomenal or an artifact of the button presses per se. Rather, it demonstrates the invocation of the body percept through the virtual pointing response measure, which required participants to remain attuned to the egocentric reference frame of their physical bodies during the imagined rotation.



Based on the ROI results, another unexpected finding of the present study was that the Object-in-Hand task did not show a tight coupling between low-level cortical motor activation and participants' performance. One possible explanation is that in comparison to several other studies, the task we used was relatively more difficult task to perform.<sup>4</sup> For example, the stimuli used in Kosslyn et al. (2001) were always oriented perpendicular to the gravitational vertical, whereas in the present study, the majority of the stimuli were in an orientation oblique to the gravitational vertical. Rotations of objects on the oblique are known to be more different than those aligned with the gravitational vertical (e.g., Pani & Dupree, 1994). This increase in task difficulty may have resulted in participants relying on additional strategies to boost the motor strategy typically associated with imagined object rotations. The results of our ROI analysis support this claim. One likely candidate is an increased reliance on visual strategies, as evidenced in the significant negative correlation found between RTs and activation of the primary/secondary visual cortices in the Object-in-Hand task: the faster the response, the greater the visual activation. To explore this possibility further, we correlated beta estimates of visual areas with those of M1, as a function of rotation magnitude. We found significant relationships between the two regions for 100° and 135° rotations, but not for those of 65°. This finding suggests that participants relied increasingly on supplementary visual strategies to perform the Object-in-Hand task with increasing degrees of rotation.

The Object-in-Hand task also yielded a significant correlation between activation of the anterior PFC (BA 10) and mean error; however, the direction of the correlation indicates that reliance on this region reflects an unsuccessful performance strategy. Anterior PFC has been implicated in high-level processing within working memory. For example, greater anterior PFC activation is associated with the coordination of multiple cognitive inputs for a common behavioral goal (Ramnani & Owen, 2004), as well as distinguishing between target and nontarget stimuli during the recognition phase of a spatial working memory task (Leung, Gore, & Goldman-Rakic, 2005). Either or both of these functions could supplement a motor strategy for the Object-in-Hand task. However, it is interesting to note that we found no significant correlations between anterior PFC and M1 beta values. Thus, the anterior PFC activation recruited in this task suggests reliance on a strategy independent of the motor strategy, one that was not successful in improving performance of the Object-in-Hand task.

Finally, one region we did not find activated in the Perspective task that has played a prominent role in previous studies of egocentric transformations is the parieto-temporal-occipital (PTO) junction (e.g., Wraga et al., 2005, 2010; Zacks et al., 2003), also known as the extrastriate body area, or EBA (e.g., Downing et al., 2001). Wraga et al. (2010) found activation near the PTO junction for their Body-Maximize condition, which employed the same virtual pointing response measure as the present study. Although in the present study we found activation in secondary visual areas for in the Perspective – Object-in-Hand and Object-in-Hand – Perspective contrasts, both regions were substantially posterior to the PTO junction. Given that both tasks required an equivalent level of embodiment, it is most likely that this activation was cancelled out in both contrasts. This issue warrants further empirical investigation.

In summary, our findings help clarify the conditions under which low-level cortical motor activation is recruited in mental transformations. Imagined object and perspective-rotation tasks that required the participant to associate the stimuli with their physical bodies both yielded low-level cortical motor activation,

despite both requiring extrinsic encoding. These findings suggest that level of embodiment plays a more critical role than type of encoding in eliciting motor processes in mental transformations.

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<sup>4</sup> The level of difficulty of the Object-in-Hand task of the present study was similar to the Object task of Wraga et al. (2005); however, ROI data were not analyzed in that study so comparisons are not possible.

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