



Imagined transformations of bodies: an fMRI investigation

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Abstract

A number of spatial reasoning problems can be solved by performing an imagined transformation of one's egocentric perspective. A series of experiments were carried out to characterize this process behaviorally and in terms of its brain basis, using functional magnetic resonance imaging (fMRI). In a task contrast designed to isolate egocentric perspective transformations, participants were slower to make left-right judgments about a human figure from the figure's perspective than from their own. This transformation led to increased cortical activity around the left parietal-temporal-occipital junction, as well as in other areas including left frontal cortex. In a second task contrast comparing judgments about inverted figures to judgments about upright figures (always from the figure's perspective), participants were slower to make left-right judgments about inverted figures than upright ones. This transformation led to activation in posterior areas near those active in the first experiment, but weaker in the left hemisphere and stronger in the right, and also to substantial left frontal activation. Together, the data support the specialization of areas near the parietal-temporal-occipital junction for egocentric perspective transformations. These results are also suggestive of a dissociation between egocentric perspective transformations and object-based spatial transformations such as mental rotation. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Taking a perspective different from one's own is a skill people demonstrate whenever they shake hands, give directions from place to place, or teach another person to operate a piece of equipment. To do so requires a mental spatial transformation that consists of mentally aligning one's egocentric body orientation with an external perspective. In the case of shaking hands, the imagined transformation is a simple one of reversing left-right orientation, and is probably over-learned early in life. In the case of giving route directions, the transformations are more complex and the task seems to require several such transformations in succession. As the speaker tells the listener 'turn right,' both imagine the corresponding change in egocentric

orientation [32]. We will call such changes in one's imagined position and orientation relative to the surrounding physical environment 'egocentric perspective transformations'.

Neuropsychological evidence suggests there are specialized brain structures that support imagined transformations of egocentric position and orientation. Lesions to areas near the parietal-temporal-occipital (PTO) junction can lead to body-scheme disturbances and difficulties in spatial orientation [12,23]. One line of evidence comes from studies of left-right orientation tasks, which require aligning the egocentric perspective of one's body with that of an external figure. Left posterior lesions are associated with poor performance on such tasks, and on related tasks such as following a path marked on a map [6,25].

Another line of evidence comes from the study of autotopagnosia, a selective deficit in the ability to localize body parts. Autotopagnosia is often associated with left parietal lesions [6,15,16,24,25]. Localizing

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body parts has been dissociated from the ability to point to body parts when identified with arbitrary labels [29], which is consistent with the view that autotopagnosia is a deficit specific to the representation of the body in space.

A small number of functional imaging studies also implicate the left PTO region in mental transformations involving imagined transformations of bodies. Making left-right judgments about visually presented hands has been shown to lead to activity in areas including posterior and inferior parietal cortex, with larger areas of activation in the left hemisphere [18]. Making left-right judgments about hands in various orientations by touch has been associated with activation in the superior parietal lobule bilaterally, and in the intraparietal lobule and medial parietal cortex, with stronger activation in the left hemisphere [1].

Taken together, these behavioral, neuropsychological and functional imaging results suggest there is a system that depends particularly on cortical tissue around the left PTO junction that is responsible for transformations needed to imagine changes in the position and orientation of the body relative to the objects around it.

Egocentric perspective transformations can be distinguished from the mental spatial transformations required to imagine a change in the position, orientation, or shape of an external object, which we will call 'object-based spatial transformations'. A paradigm case of such a transformation is mental rotation [26]. In the typical experimental design, observers judge whether pairs of objects are identical or different. The two objects appear in different orientations, and are either identical or are right-left mirror images. The observer's task is to report whether the objects are identical or different. Times to make these judgments typically increase with the angle of difference in orientation between the objects, as if observers were mentally rotating them into correspondence.

Right posterior cortex has been often associated with object-based spatial transformations. Ratcliff [21], in a study that served as a model for our own, found that patients with right PTO lesions were impaired at making left-right judgments about inverted (upside-down) figures, but not with upright figures. He therefore argued that the right posterior cortex was specialized for mental rotation. Studies using selective presentation to one visual field have confirmed a right-hemisphere advantage for mental rotation, both in normal and brain-injured observers [5,6,8,12].

The view that right posterior regions are specialized for mental rotation has received mixed support from functional imaging. fMRI studies of mental rotation with three-dimensional figures have found activation in posterior parietal areas, the parietal-occipital border, and the middle frontal gyrus [4,22,30]. However, the

activation observed in these studies has been largely bilateral.

Both the neuropsychological literature and limited functional imaging results point to the possible existence of cortical regions that are specialized for the performance of egocentric perspective transformations. This class of process is conceptually distinguishable from object-based spatial transformations, and may be served by different brain structures. However, the evidence on both points is indirect. Based on behavioral measures alone it is difficult to distinguish an imagined perspective transformation from a mental rotation of the external figure, though suggestive patterns have been observed [17]. Neuropsychological studies have drawn primarily on missile wound and epilepsy patients, requiring inferences from large lesions and subject to effects of compensation on the part of the patients. Finally, no functional imaging study has examined egocentric perspective transformations directly, or compared them with object-based spatial transformations. The major goals of this study, then, were first to begin to characterize egocentric perspective transformations behaviorally and neurophysiologically, and second to compare them to object-based spatial transformations.

2. Method

2.1. Participants

Eight right-handed male volunteers, ages 19–34, were recruited from the Stanford community. Each received \$20 for his participation.

One participant was removed from the behavioral and functional analyses because his behavioral data included a large number of errors, which were unusually distributed, indicating that he was performing the tasks in an anomalous fashion (see Results, Scan 2).

2.2. fMRI imaging

Imaging was performed with a 1.5 T whole-body MRI scanner (General Electric Medical Systems Signa, Rev 5.6). A prototype whole-head coil for signal reception was used with five participants. For two participants whose heads were too large for the prototype head-coil, we positioned two 5-inch diameter local receive coils on either sides of their heads to obtain signal. Head movement was minimized using a bite-bar formed with each participant's dental impression. A T2*-sensitive gradient echo spiral pulse sequence [11] was used for functional imaging with parameters of $TR=1080$ ms, $TE=40$ ms, and flip angle = 75° . Four interleaves were obtained for each image, with a total

acquisition time (sampling interval) of 4.32 s per image. T1-weighted, flow compensated spin-warp anatomy images ($TR=500$ ms, minimum TE) were acquired for all sections that received functional scanning. Twelve 6-mm thick slices were acquired in the horizontal plane of the Talairach and Tournoux [31] atlas starting from approximately 24 mm below the anterior commissure (AC)–posterior commissure (PC) plane, with a 1 mm inter-slice interval. In-plane resolution was 2.1 mm. Anatomical images were acquired in the same session, immediately prior to functional imaging.

2.3. Data analysis

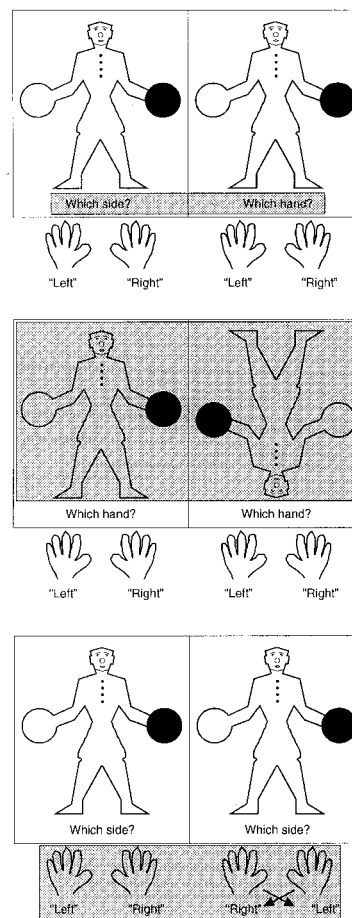
fMRI data were mapped into Cartesian coordinates with a two-dimensional fast Fourier transform. Motion artifacts were corrected using the Woods [35] algorithm, and the data were spatially filtered by convolving with a gaussian filter with a full width at half-maximum of 8.0 mm to reduce high spatial frequency noise. Pixels that were significantly correlated to task performance were identified as described by Friston et al. [10].

To obtain composite maps of activation over all participants, average functional activation maps were created by transforming 11 of the 12 horizontal sections from each participant to a corresponding standardized horizontal section at the same distance above and below the AC/PC plane [7]. (Slice 4, at approximately +4 mm, did not correspond well to slices in the stereotaxic atlas and, as a result, was not used for the composites.) Following transformation, the average z -value for each pixel in a section was computed across participants and pixels that reached a statistical threshold corresponding to $P < 0.005$ or lower were displayed on each map.

2.4. Stimuli

Participants made a series of judgments about schematic pictures of an upright human figure. The figure could be facing toward or away from the observer. Front- and back-facing figures had the same outline, differing only in the rendering of the face and clothing of the figure. On each trial, the picture plane orientation of the figure was perturbed randomly by a rotation of between -50 and 50° (in increments of 10 degrees) in order to discourage participants from simply memorizing associations between particular stimuli and motor responses. The figure's hands were marked such that one hand appeared to be holding a black ball, and the other a white ball. The black ball could appear in either the right or left hand.

Stimuli were presented and responses recorded using the PsyScope software package [3] running on a



Scan 1:

Participants alternated between performing the "Which Hand" and "Which Side" tasks. These two tasks differ in that for the "Which Hand" task, the participant must perform an **egocentric perspective transformation**.

Scan 2:

Participants alternated between performing the "Which Hand" task with inverted and upright figures. For the inverted figures, they performed an **object-based spatial transformation** of the figure to the upright orientation.

Scan 3:

Participants alternated between performing the "Which Side" task with each hand mapped onto the opposite response, or with the normal mapping. These tasks differ only in the incompatibility of the stimulus with the response.

Fig. 1. Schematic representation of the tasks in the three experiments, with examples of the stimuli. For each scan, the control condition is shown on the left and the experimental condition on the right. In each condition, figures could face toward the observer or away from the observer; only front-facing figures are depicted here.

Macintosh computer. During the fMRI experiments, stimuli were displayed on a rear-projection screen mounted in the bore of the scanner, which the participants could view through a mirror. In the pre-scan training sessions, stimuli were displayed on a computer monitor.

2.5. Tasks

2.5.1. Scan 1: egocentric perspective transformations

This experiment was designed to isolate the processes involved in egocentric perspective transformations. The experimental and control conditions differed only in the judgment that was made by the participants. In the experimental condition, participants reported whether the figure's left or right hand held the black ball by pressing a button held in the left or right hand, respectively (henceforth the 'Which Hand' task). Participants were instructed to: 'imagine yourself taking the clown's position, and think which

hand you would be holding the ball in'. In the control condition, participants reported from their own perspective on which side of the screen the black ball appeared, again by pressing a button (the 'Which Side' task). These tasks differed only in that the Which Hand task required participants to make an egocentric perspective transformation, whereas the Which Side task did not require any mental spatial transformation. Thus, the critical processing that differed between the two conditions was the egocentric perspective transformation required to respond from the figure's point of view in the Which Hand task. (See Fig. 1, top panel, for a schematic presentation of this task comparison.)

2.5.2. Scan 2: object-based spatial transformations

This scan compared Which Hand judgments for inverted figures to the same judgments for upright figures. In the experimental condition, the figures were inverted 180° from upright in the picture plane. In the control condition, figures were upright (and so the control condition in this scan corresponded to the experimental condition in Scan 1). As in Scan 1, figures were perturbed by between -50 and 50° from their default orientation (upright or inverted, depending on condition). As in the first functional scan, the two conditions were designed to be equivalent in low-level visual processing demands and in motor output. Additionally, both conditions in this experiment required an egocentric perspective transformation. In the experimental condition, the inversion of the figures was designed to require participants to perform an additional mental transformation. Observers could make judgments about inverted figures either by performing a more difficult egocentric perspective transformation (imagining themselves rotating to the inverted position) or by performing an object-based spatial transformation to rotate the figure to upright. See Fig. 1, middle panel, for a schematic presentation of this task comparison.

2.5.3. Scan 3: stimulus-response compatibility

In the first functional scan, a conflict arises between the response required in the experimental (Which Hand) condition and the control (Which Side) condition. The Which Side task provides a compatible mapping [9,33] between stimulus and response: When the stimulus appears in the right visual field the participant responds with the right hand, and when the stimulus appears in the left visual field the participant responds with the left hand. To perform the Which Hand task, the participant must inhibit this compatible mapping and respond on the basis of the figure's egocentric perspective. (This leads to the same response in half the cases, when the figure's back is to the obser-

ver, and to the opposite response in the other half of cases, when the figure faces the observer.)

We were concerned that some functional activation observed in Scan 1 could have been due to suppression during the Which Hand condition of the prepotent Which Side response. We therefore designed an experiment to examine this suppression directly, without engaging any visuospatial transformations. To do so, we contrasted the Which Side task with a version in which an incompatible stimulus-response mapping was assigned. In both the experimental and control conditions, participants made Which Side judgments about the stimuli. In the experimental condition, participants responded using an incompatible response mapping: They responded with their left hands for 'right' and with their right hands for 'left'. In the control condition, they responded using the normal (compatible) mapping (and so the control condition in Scan 3 was the same as the control condition in Scan 1). Note that neither version of the task requires an egocentric perspective transformation or an object-based spatial manipulation: Participants could respond based solely on the visuospatial location of the marked hand. See Fig. 1, bottom panel, for a schematic presentation of this task comparison.

2.6. Procedure

Before entering the scanner (either earlier in the same day or the day before), participants were trained on all three task comparisons for three alternations of control and experimental blocks, in the same order as in the scanner.

Each functional scan consisted of six alternations by block between the control task and the experimental task and took 514 s. (For one participant, it was 574 s due to a computer problem leading to a slower presentation rate.) Stimuli were presented for 2100 ms, with a 400 ms inter-stimulus interval. Stimuli were presented in blocks of 16 trials, preceded by a two-word on-screen instruction. Within each block, the four possible combinations of marked hand (right or left) and direction facing (forward or backwards) were sampled four times in random order. On each trial, orientation was varied randomly within the -50 to 50° range. In all experiments, there were an equal number of trials in each condition for which right and left responses were correct.

For each participant, Scan 1 was run in the same session as Scans 2 and 3. For all participants, Scan 3 was performed last because a pilot study showed that extensive experience with the incompatible mapping seemed to interfere with performing the Which Hand task. The order of Scans 1 and 2, and conditions within each experiment, was counter-balanced across

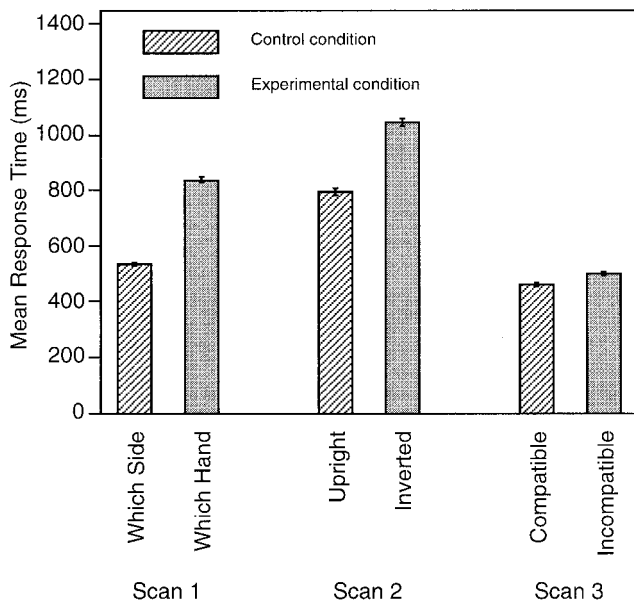


Fig. 2. Response times for each of the three task comparisons. Each panel reports the mean response time for each participant in each of the two conditions. Error bars give 95% confidence intervals.

the participants (with the exception of one error in ordering the conditions).

In the scanner, participants responded by pressing one of two fiber-optic triggers held in each hand and attached to the Macintosh via the PsyScope button box. In the pre-scan practice sessions, participants pressed the right and left arrow keys on the computer keyboard (with their right and left hands, respectively).

3. Results

3.1. Scan 1: egocentric perspective transformations

Error rates were low overall (2.8%). None of the participants had an error rate above 10%.

3.1.1. Response time

We analyzed effects of the experimental task manipulation, the direction the figure faced, and their interaction using an analysis of variance (ANOVA) blocked on participant on the response times for correct responses. (During participant LP's scan, the left hand response trigger failed to function, so for all three experiments only half of his behavioral data could be analyzed.) Responses for the Which Hand task were longer (M 837.6 ms, S.E.M. 8.783 ms) than those for the Which Side task (M 533.6 ms, S.E.M. 10.98 ms), $F(1,1201)=577.3$, $P < 0.001$ (see Fig. 2). This effect was large and robust: it was statistically reliable on a single-participant basis for each of the

seven participants whose data were analyzed; the smallest $T(189)$ was 4.098, $P < 0.001$.

Participants were faster to make right-left judgments about upright figures when the judged figure's back was to the observer, $F(1,1201)=46.55$, $P < 0.001$. This was true only when performing the Which Hand task (Table 1). The interaction between task and direction the figure faced was statistically reliable, $F(1,1201)=38.99$, $P < 0.001$. T -tests showed a reliable difference between front-facing and back-facing figures in the Which Hand task, $T(604)=7.877$, $P < 0.001$, but not in the Which Side task, $T(603)=0.436$, $P = 0.7386$.

3.1.2. fMRI activation

Comparing the Which Hand task to the Which Side control task yielded cortical activation in a number of areas (see Fig. 3 and Table 2). Major foci of activity occurred around the juncture of the parietal, occipital and temporal lobes: bilaterally in the occipital gyri (stronger on the left than on the right), in the lingual gyrus on the left (Brodmann's area (BA) 19), in the cuneus, precuneus (BAs 19 and 7) and strongly lateralized to the left in the superior parietal lobule (BA 7). Activation was also observed bilaterally in middle temporal gyrus (BA 19/39) and in the middle frontal gyrus (BA 9), in the left hemisphere in inferior slices and on the right in the superior-most slice. As Table 2 indicates, activation was strongly lateralized to the left in all areas except the middle temporal gyrus. In all areas except the middle frontal gyrus, as many or more participants showed activation in the left hemisphere as in the right, and when the activation was bilateral it was always stronger on the left.

3.1.3. Discussion

The two conditions studied here were designed to differ only in one regard: In the experimental condition, participants had to perform an egocentric perspective transformation to align their point-of-view with that of the figure. Behaviorally, the addition of

Table 1

Response times in Scan 1. Participants were faster to make Which Side judgments than Which Hand judgments. In the Which Hand task only, they were faster to make judgments about upright figures when the figures faced away from them (top row). Table cells give mean response time in ms for correct responses, with standard errors in parentheses

	Mean response time in ms	
	Back-facing figures (S.E.M.)	Front-facing figures (S.E.M.)
Which hand	752.9 (11.15)	921.1 (16.52)
Which Side	531.8 (11.45)	526.4 (11.66)

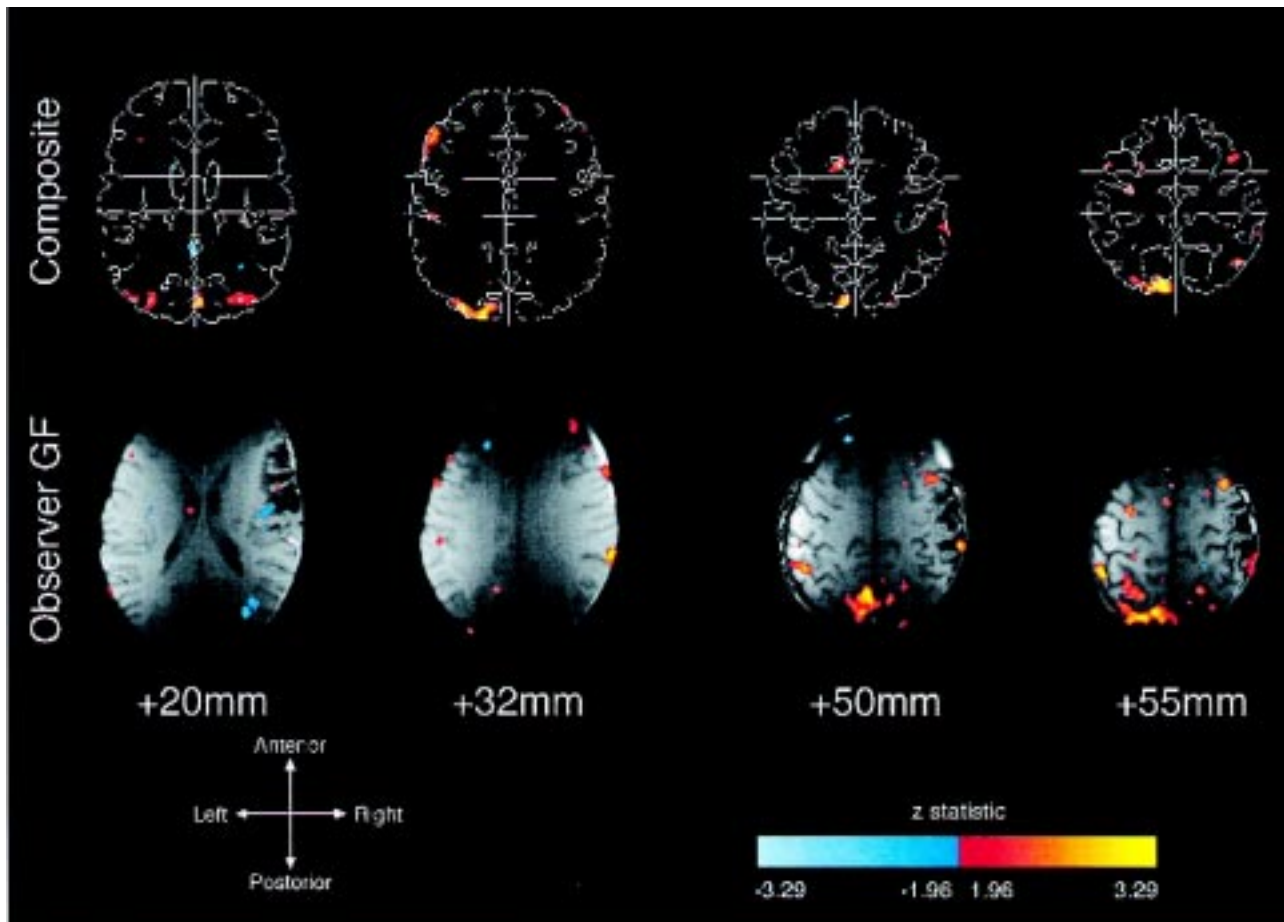


Fig. 3. Functional activation in Scan 1. The top row shows statistically reliable activation in the 7-observer composite in four horizontal slices, superimposed on schematic anatomical images. The bottom row shows statistically reliable activation in a single observer (GF) in the same slices, superimposed on his anatomical images. Red colors indicate areas that were more active during Which Hand judgments; blue colors indicate areas that were more active during Which Side judgments. (Figures were upright in both conditions.)

this mental transformation led to increased response times—especially for front-facing figures, which required a more difficult transformation. Physiologically, it led to the activation of a cortical network with components concentrated around the left PTO junction, and to activation in the left middle frontal gyrus.

The pattern of posterior activation is consistent with

the patient and functional imaging results reviewed earlier, suggesting involvement of cortical tissue around the left PTO junction is important for the computation of changes in egocentric perspective.

3.2. Scan 2: object-based spatial transformations

One participant had reliably more errors in the con-

Table 2

Major foci of cortical activation in Scan 1. Areas listed were significantly more active for Which Hand judgments than for Which Side judgments. The first two columns report which participants showed activation in each major area, and the third column gives the total area corresponding to activation in those regions in the composite analysis, given a threshold of $z = 1.96$

	Participants showing activation		Composite extent (mm ³)	
	Left	Right	Left	Right
Cuneus, precuneus, occipital and lingual gyri	DM, ZP, AS ^a , JH ^a , GF ^a , JG, LP	ZP, AS, JH, GF, JG, LP	4479	1548
Middle temporal gyrus	ZP, JH	JG, LP	301	760
Superior parietal lobule	JH ^a , GF ^a , JG ^a , LP	JH, GF, JG	1383	506
Middle frontal gyrus	JH, GF ^a , LP	JH, GF, JG, LP	1435	464

^a Activation was more extensive on this side.

Table 3

Response times in Scan 2. Participants were faster to make Which Hand judgments about upright figures when the figures faced away from them (top row), but for inverted figures the opposite was true (bottom row). Table cells give mean response time in ms for correct responses, with standard errors in parentheses

	Mean response time in ms	
	Back-facing figures (S.E.M.)	Front-facing figures (S.E.M.)
Upright	736.8 (12.54)	857.4 (15.33)
Inverted	1097 (18.83)	960.0 (19.41)

control condition of Scan 2 than in the experimental condition, (16 errors, compared to 4 in the experimental condition, $\chi^2=6.754$, $P < 0.01$), combined with an unusually high error rate of 10.4%. (No other participants had error rates above 10% in any experiment.) As noted above, we eliminated his data from the beha-

vioral and functional analyses of all scans, as it was not clear he was performing the task properly. Excepting this participant, error rates were again low (3.2%).

3.2.1. Response time

Data were analyzed as in Scan 1. Participants took longer to respond (in the Which Hand task) with inverted figures (M 1043 ms, S.E.M. 14.81 ms) than with upright figures (M 796.6 ms, S.E.M. 10.85 ms), $F(1,1190)=258.5$, $P < 0.001$ (see Fig. 2). This was statistically reliable on a single-participant basis for six of the seven participants whose data were analyzed. For those six, the smallest $T(187)$ was 4.839, $P < 0.001$; $T(94)$ was 0.6837, $P = 0.4959$ for participant LP (for whom only half the data were usable).

Participants were again faster to make judgments about back-facing figures when the figures were upright, but the opposite was true when the figures were inverted, leading to a reliable interaction between

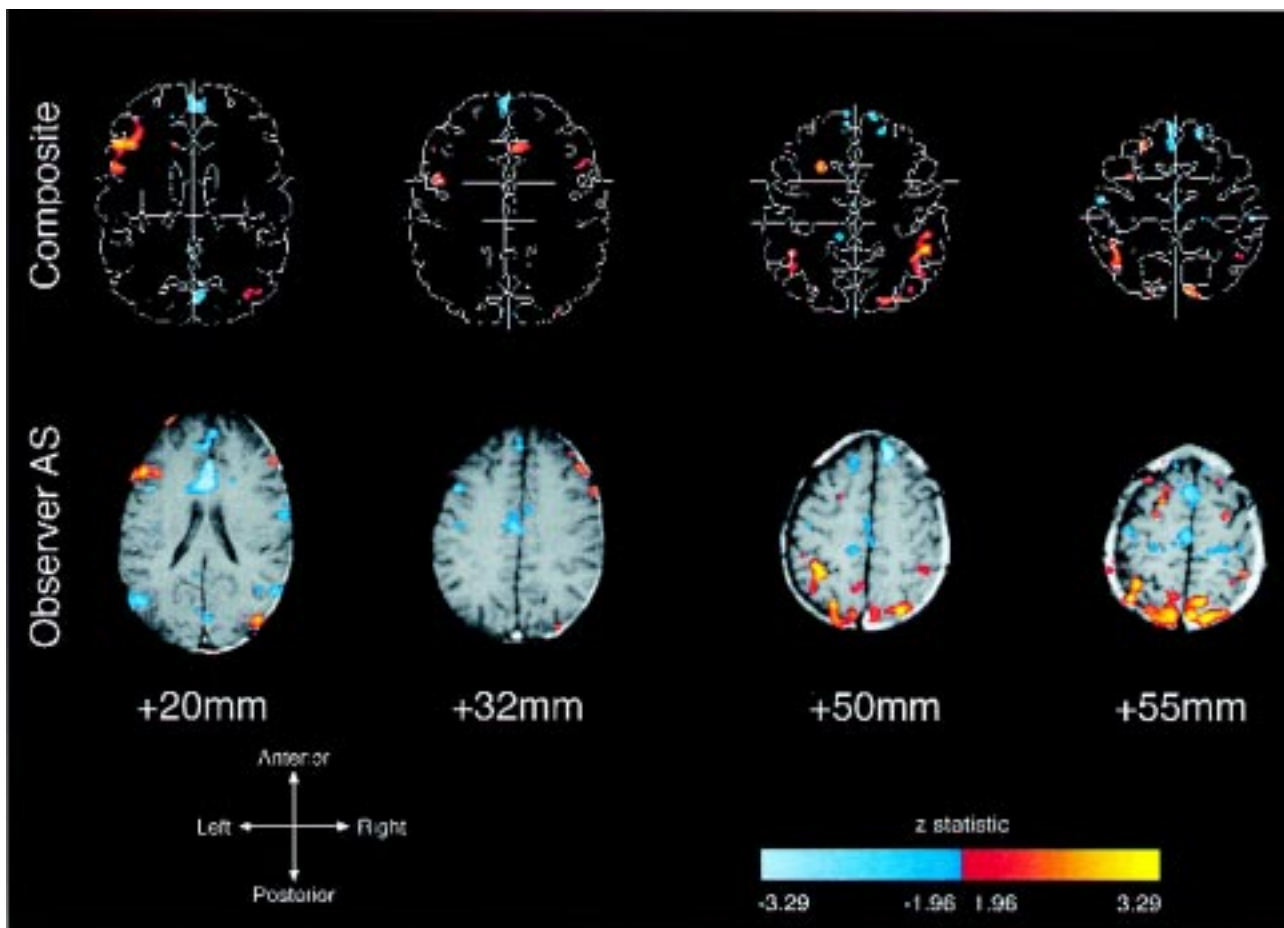


Fig. 4. Functional activation in Scan 2. The top row shows statistically reliable activation in the 7-observer composite in four horizontal slices, superimposed on schematic anatomical images. The bottom row shows statistically reliable activation in a single observer (AS) in the same slices, superimposed on his anatomical images. Red colors indicate areas that were more active during Which Hand judgments about inverted figures; blue colors indicate areas that were more active during Which Hand judgments about upright figures.

Table 4

Major foci of cortical activation in Scan 2. Areas listed were significantly more active for Which Hand judgments of inverted figures than for upright figures. The first two columns report which participants showed activation in each major area, and the third column gives the total area corresponding to activation in those regions in the composite analysis given a threshold of $z = 1.96$

	Participants showing activation		Composite extent (mm ³)	
	Left	Right	Left	Right
Cuneus, precuneus, occipital and lingual gyri	DM ^a , ZP, AS, JG, LP	DM, AS, JH, JG	198	690
Middle temporal gyrus	ZP, JG	ZP, AS, JH, JG	0	306
Superior/inferior parietal lobules	AS, GF, JG	DM, AS, JH, JG	1600	1605
Superior frontal gyrus	ZP, JH, JG	JH, JG, LP	818	1048
Middle/inferior frontal gyrus	DM, AS ^a , JH, JG	AS, JH, JG, LP	3884	308
Pre-central gyrus	DM, JH, JG	JG ^a	444	0
Anterior cingulate	ZP, AS, JH, JG	ZP, AS, JH, JG	0	443
			Midline	
			978	

^a Activation was more extensive on this side.

orientation and direction, $F(1,1190) = 51.86$, $P < 0.001$ (Table 3).

3.2.2. fMRI activation

Performing the Which Hand task with inverted figures yielded greater activation in a number of locations than the same task with upright figures. Little activation was observed in the parts of the cuneus, precuneus, and superior parietal lobule that were active in Scan 1 (see Fig. 4). This result suggests that these areas were being recruited to an equivalent degree during the condition in which the clown was inverted and when it was right-side up. Increased activation during the inverted condition was, however, observed in nearby lingual, occipital, cuneus and precuneus areas (BAs 7, 17, 18 and 19) in more lateral locations. Activation was also observed in left middle temporal gyrus (BA 19/39) and in inferior and superior parietal lobules (BAs 7 and 40). Unlike in Scan 1, activation in posterior cortex was bilateral or slightly stronger on the right, as can be seen in Table 4. In all posterior regions, more participants showed activation in the right hemisphere than the left, and the extent of activation in the composite analysis was greater on the right.

In anterior regions, areas of activation were observed in bilateral superior frontal gyri in inferior slices (BAs 10 and 11). In superior slices, activation was observed in and around premotor cortex: in the left middle and inferior frontal gyri (BAs 6, 9, 10, 44, 45 and 46) and in the precentral gyrus (BA 4/6). Finally, there was activation in the superior part of the anterior cingulate gyrus (BA 32). As can be seen in Table 4, the left middle and inferior frontal activation was strongly left-lateralized.

Out-of-phase activity (i.e. greater activation in the control task than the experimental task) was observed

in the medial portions of the medial and superior frontal gyri (BAs 9/10 and 6), posterior cingulate (BAs 23, 29, 30, 31) and cuneus (BA 18).

3.2.3. Discussion

The two conditions studied here differed only in the orientation of the figures presented: In the experimental condition, a mental transformation was required to orient the figures to upright. Behaviorally, this led to increased response times. Physiologically, it led to a pattern of bilateral or right-lateralized activation in posterior regions, as well as to substantial left frontal activation.

Responses were faster to back-facing figures when the figure was upright, but the opposite was true for inverted figures. This pattern is consistent with either an additional egocentric perspective transformation or an additional object-based spatial transformation. Observers could have performed a 'mental somersault' to imagine themselves in an inverted and front-facing orientation. Alternatively, they may have performed an imagined rotation of the figure through the depth plane (an object-based spatial transformation).

The fMRI data support the object-based spatial transformation interpretation: In contrast to the strongly left-lateralized posterior activation seen in Scan 1, activity in posterior regions in this scan was bilateral or right-lateralized. As can be seen in Table 4, the total area of activation in the occipital, temporal and parietal lobes was 1798 mm³ on the left and 2601 mm³ on the right, as compared to 1435 mm³ and 464 mm³ for the corresponding areas in Scan 1. This pattern is similar to that observed in studies of mental rotation using the Shepard-Metzler [27] paradigm [4,22,30]. It is consistent with the view that participants performed a mental rotation of the inverted figures to transform them to upright. (Functional imaging stu-

dies of mental rotation have also reported premotor activation similar to the left frontal activation observed here; however, the activations reported were bilateral [4,30] or right-hemisphere [22].)

This interpretation is consistent with Ratcliff's [21] interpretation of the deficit of patients with right posterior lesions for inverted figures as reflecting an impairment of mental rotation. However, Parsons [17] has argued, based on an extensive psychophysical study, that viewers make left-right judgments about figures in non-upright orientations by imagining their own body parts in the same orientation as the figure. Both Ratcliff's experiment and the study reported here differed from Parsons's in that the full range of orientation variation was not sampled: Ratcliff employed only perfectly upright and inverted figures, while we employed upright and inverted figures that had been perturbed by up to 50 degrees. It may be that these different designs led to different response strategies. It is also possible that Parsons's data reflect both ego-centric perspective transformations and object-based spatial transformations on the trials in which the figure was far from upright. This possibility cannot be ruled out based solely on the response times; it is for precisely this reason that the fMRI data obtained here are valuable.

Regarding the out-of-phase activity in medial frontal cortex and the cingulate gyrus, Shulman and his colleagues [28] have observed deactivation in these areas across a number of cognitive tasks (though the posterior cingulate/cuneus deactivation they report is inferior to that observed here). They suggest several possible causes: inhibition of task-irrelevant modalities, suspension of basal cognitive activity, and suspension of body-image monitoring (an explanation that seems unlikely in the present case, given the stimuli used). The out-of-phase activity observed here could be such a decrease in activity during the experimental condition, or an increase in activity during the control condition.

To summarize, activity was observed in posterior locations similar to those active in Scan 1, but in the current scan the activity was bilateral or right-lateralized. Robust activation was also observed in the left middle and inferior frontal gyri, and deactivation was observed in the medial frontal cortex and anterior cingulate.

3.3. Scan 3: controlling for response compatibility

As in the two previous scans, error rates were low (2.6%).

3.3.1. Response time

Data were analyzed as in Scans 1 and 2. The Which Side task with an incompatible (switched hands) re-

sponse took slightly longer (M 503.1 ms, S.E.M. 7.266 ms) than with a compatible response (M 458.1 ms, S.E.M. 6.936 ms; see Fig. 2). The effect was statistically reliable overall, $F(1,1200)=27.01$, $P < 0.01$, but it was reliable on an individual participant basis for only three of the seven participants, whose smallest $T(188)$ was 2.754, $P < 0.007$ and marginal for a fourth (LP, for whom only half the responses were recorded), $T(94)=1.983$, $P = 0.0503$. The difference between experimental and control conditions was quite small relative to the effects observed in Scans 1 and 2, and typical for stimulus-response compatibility experiments [13].

3.3.2. fMRI activation

Comparing the Which Side task with a compatible response mapping to the same task with an incompatible mapping led to no activations that were consistent across participants.

In a positron emission tomography study of similar design, Iacobini et al. [13] observed bilateral superior parietal activation associated with an incompatible response mapping. However, that study differed from this one in several regards. First, the stimuli were brief flashes of light in one hemifield, rather than sustained presentations of a figure that filled both hemifields. Second, the trials were more closely spaced, occurring every 1.25 s rather than every 2.5 s. Third, and most important, participants in the Iacobini et al. study were highly practiced, having received 480 practice trials before the functional imaging experiment, and 864 trials during the experiment. In the current study participants performed 192 trials during Scan 3 and received no training on the incompatible mapping. (They did, however, have prior experience with the compatible mapping from Scan 1 and the practice session for Scan 1, a total of 144 trials.) The greater expertise of Iacobini et al.'s participants was reflected in faster response times (means of 287 and 339 ms for the compatible and incompatible conditions respectively, as compared to 458 and 503 ms in the current study). It would be of interest to replicate the compatibility manipulation with extensive practice, performing functional imaging throughout, to investigate how the activation observed by Iacobini et al. may emerge over time. In any case, the lack of functional activation due to stimulus incompatibility in the current paradigm makes it unlikely that the activations in Scans 1 and 2 were due to stimulus-response incompatibility in the experimental conditions.

4. General discussion

When observers were asked to judge in which hand an external figure held a ball, the data indicate they

did so by making an egocentric perspective transformation that aligned their imagined perspective with that of the figure. In Scan 1, participants took longer to judge in which hand the figure held the ball than which side of the screen it was on. When judging which of an upright figure's hands held a ball response times were longer for figures whose orientation in space differed from that of the participant (i.e. front-facing figures). This imagined transformation led to cortical activation at the PTO junction, strongly lateralized to the left, as well as bilateral frontal activation.

Comparing judgments of which hand held the ball when the figure was inverted to judgments for upright figures (Scan 2) led to different patterns of behavior and cortical activity. Behaviorally, participants took longer to respond to inverted figures than upright ones, indicating that additional computation was required. Neurophysiologically, bilateral or right-dominant activity was observed in posterior cortical areas: the lingual gyrus, occipital gyrus, and the cuneus and precuneus. Frontal activation was also observed.

The differences in posterior activation between Scans 1 and 2 suggest two plausible interpretations. They could reflect a dissociation between two different processing systems, one differentially involved with egocentric perspective transformations and the other with object-based spatial transformations. This interpretation is supported by the reversal of posterior lateralization between the two scans. It is also consistent with the neuropsychological data reviewed in the Introduction. Left posterior regions have been associated with disorders of body scheme, personal space and left-right orientation [6,12,15,16,23–25], while lesions to right posterior regions have been tied to deficits in mental rotation [5,6,8,12,21]. (Interestingly, in Ratcliff's [21] study showing patients with right-posterior lesions to be impaired at right-left judgments about inverted figures, left-posterior patients were impaired at left-right judgments about upright figures, though this trend did not reach statistical significance.) Finally, it is consistent with functional imaging studies which have found left posterior activation associated with transformations of body parts [1,18], and bilateral posterior activation associated with mental rotation [4,22,30].

On the other hand, the differences between Scans 1 and 2 could reflect different levels of activity of the same underlying system. As was described previously, the experimental condition in Scan 1 served as the control condition in Scan 2. As expected, response times were longer in Scan 2 than in Scan 1, suggesting that left-right judgments about inverted figures are more demanding than such judgments about upright figures. Thus, the greater right-hemisphere posterior activation observed in Scan 2 could be due to the recruitment of additional cortical tissue to perform a more difficult

transformation of the same type as was performed in the experimental condition of Scan 1, while left posterior regions remained at the same (high) level of activity. There are several ways to arbitrate between these two conflicting explanations. A comparison to a baseline such as fixation would help establish whether left posterior activity was indeed high in both conditions of Scan 2. A direct comparison of the left-right task used here to the typical mental rotation paradigm would also be instructive. Finally, examining stimuli other than bodies, with which egocentric perspective transformations are unlikely, would help discriminate between the two-process and one-process views.

The left PTO activation associated with egocentric perspective transformations (Scan 1) can be interpreted in terms of a distinction between *internal* and *external* spatial frameworks [2]: the Which Hand task can be thought of as isolating the alignment of an internal spatial framework with objects in an external one. This distinction in turn can be related to the neuropsychological dissociation between *personal* and *extrapersonal* spatial tasks [6]. These results may also bear on the current debate over the function of the dorsal visual pathway. The dorsal pathway, which projects primarily to the parietal cortex, has been argued to be a 'where' pathway, responsible for computing information about spatial location and motion [34], or a 'how' pathway, responsible for visual processing in the service of motor coordination [14]. Egocentric perspective transformations to match one's point-of-view with that of an object is particularly important for planning motor actions relative to objects ('how'). Isolation of this component of processing in Scan 1 led to activation in the left hemisphere around the PTO junction. On the other hand, imagined translations and rotations of external objects may reflect spatial processing of a more general nature ('where'). This type of processing may have been isolated in Scan 2, leading to bilateral and right-hemisphere posterior activation. Thus, the answer to the question of whether the dorsal pathway is a 'where' or 'how' pathway may depend on whether one is considering the left or right hemisphere. (We should note that the task employed here differed from those described by Milner and Goodale [14] in that it depended on an explicit spatial judgment. However, the resulting egocentric perspective transformation has exactly the same characteristic of implicit imagined self-motion as the tasks associated with the 'how' pathway.)

The frontal activation observed in Scans 1 and 2 could reflect one of several cognitive processes associated with mental spatial transformations. Functional imaging studies have associated nearby areas with motor planning and imagined motor transformations [18–20]. However, the Which Hand task employed in Scans 1 and 2 was designed to elicit an egocentric per-

spective transformation, but not necessarily a motor plan for executing this change in perspective. In fact, most of the positions assumed by the figure are impossible to achieve by autonomous movements in an environment with gravity. We also observed even greater activation in nearby left frontal cortex in Scan 2, which was designed to isolate the transformation of mental rotation while controlling for the presence of an egocentric perspective transformation. Other investigators have reported activation bilaterally in premotor cortex during mental rotation [4,22,30]. The left frontal activation observed in these two task comparisons could be due to imagined motor movements, or to some computation of a general nature involved in a range of mental spatial transformations. The differences in localization between Scans 1 and 2 could reflect differences in the circuits involved, or recruitment of more tissue for the more difficult experimental condition of Scan 2. (Recall that the control condition in Scan 2 was the same as the experimental condition in Scan 1.)

These data suggest that regions in the left posterior parietal and occipital cortex are important for egocentric perspective transformations. What might be the computations underlying such alignment? On what inputs do they depend, what other processes share the same computational resources, and what other processes depend on their outputs (e.g., motor planning)? Further task manipulations and parametric experimental designs should clarify these issues and extend our understanding of how the brain represents the body.

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