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Neuropsychologia 37 (1999) 1029–1040

NEUROPSYCHOLOGIA

Imagined transformations of bodies: an fMRI investigation

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Received 1 June 1998; accepted 23 November 1998

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.

Keywords: Mental rotation; fMRI; Egocentric; Spatial; Perspective

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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0028-3932/99/$ - see front matter
PII: S0028-3932(99)00012-3

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

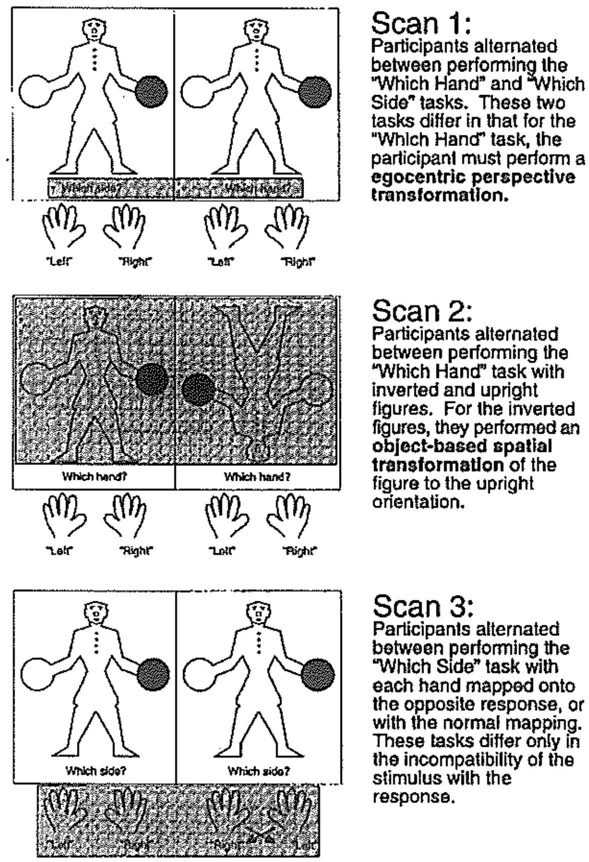

Fig. 1. Schematic representation of the tasks in the three experiments, with examples of the stimuli. For each scan, the control condition is shown on the left and the experimental condition on the right. In each condition, figures could face toward the observer or away from the observer; only front-facing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

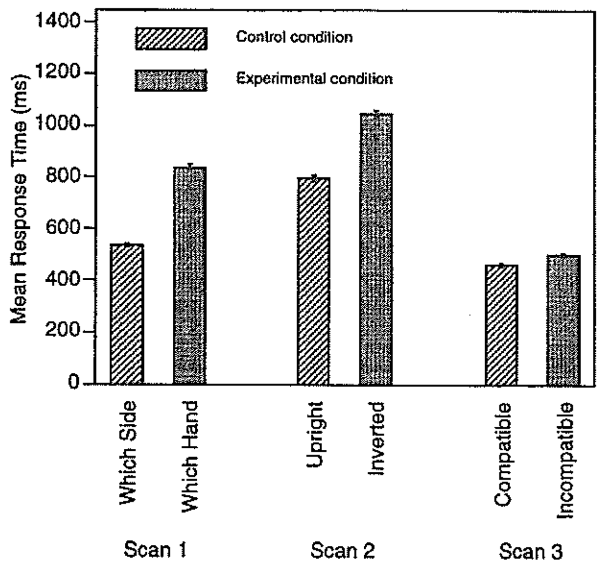

Fig. 2. Response times for each of the three task comparisons. Each panel reports the mean response time for each participant in each of the two conditions. Error bars give 95% confidence intervals.

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)