Selective disturbance of mental rotation by cortical stimulation

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Abstract

In order to plan activity, people must imagine the spatial consequences of potential actions. Two classes of mental spatial transformation can be distinguished: *Object-based spatial transformations* are imagined movements of objects, such as mental rotation. *Egocentric perspective transformations* are imagined changes in one's viewpoint, such as imagining one's self in the position of another person. Here we report a case in which electrical stimulation of the right parietal cortex selectively interfered with performance of a mental rotation task. Interference was selective to this stimulation site, and was task specific. Performance of the perspective transformation task, and a control for visual encoding and responding, were unimpaired by stimulation. This marks the first instance of the use of direct cortical stimulation to investigate mental spatial transformations.
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Keywords: Mental rotation; Cortical stimulation; Imagery; Spatial cognition

1. Introduction

The parietal lobes have been implicated in spatial mental imagery since seminal studies of patients with focal missile wounds and those with seizure disorders in the 1950s and 1960s (Hécaen, Penfield, Bertrand, & Malmo, 1956; Semmes, Weinstein, Ghent, & Teuber, 1955, 1963). These studies showed that brain injured patients could suffer from deficits in spatial cognition despite intact sensory systems. Patients with parietal lesions are disproportionately impaired at tasks such as wayfinding, following simple routes from a diagram, identifying rotated versions of a visually presented figure, and describing a spatial layout from a viewpoint other than one's own (De Renzi, 1982).

An elegant study by Ratcliff (1979) indicated that lesions to right posterior cortex selectively impair mental rotation ability. Participants judged whether a picture of a human body had its right or left arm marked. Patients with right posterior lesions performed normally for upright pictures, but were markedly impaired for inverted pictures. Converging evidence for the importance of the right hemisphere in mental rotation has come from studies of patients whose cor-

pus callosum has been severed to treat intractable epilepsy. In these patients stimuli can be presented selectively to the right or left hemisphere because the left visual field projects exclusively to the right hemisphere and the right visual field to the left hemisphere. In studies with such patients the right hemisphere has been found to be more efficient at performing mental rotation. In neurologically normal participants, the relative contribution of the two hemispheres can be controlled (though less completely) by presenting stimuli briefly, followed by a high-contrast mask, to the left or right visual field. Similar results have been observed with this technique (Corballis, 1997). Electroencephalographic and functional neuroimaging methods have also indicated the importance of parietal cortex in performing mental rotation; in some studies greater activity has been reported in the right hemisphere, but the data are inconclusive (Carpenter & Proffitt, 2001; Cohen et al., 1996; Harris et al., 2000; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Peronnet & Farah, 1989; Pierret, Peronnet, & Thevenet, 1994; Richter et al., 2000; Richter, Ugurbil, Georgopoulos, & Kim, 1997; Rypma et al., 1996; Tagaris et al., 1997; Yoshino, Inoue, & Suzuki, 2000).

One possibility is that the human brain contains a single neural system for performing mental spatial transformations, prominent components of which are located in the right

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parietal cortex. However, an alternative possibility is suggested by the neuropsychological and neurophysiological literatures: There may be multiple spatial transformation subsystems, specialized for particular mental spatial transformations (Zacks, Rypma, Gabrieli, Tversky, & Glover, 1999). On this view *object-based spatial transformations* such as mental rotation are one special case. These transformations, in which an observer imagines an external object moving in space, can be distinguished from imagined movements of the observer's point of view relative to the environment, which we refer to as *egocentric perspective transformations*.[1] Whereas deficits in performing object-based transformations are associated with right hemisphere lesions, several tasks thought to involve egocentric perspective transformations are selectively impaired in patients with left posterior lesions (Zacks et al., 1999). For example, patients with such lesions have been found to be particularly impaired (relative to right posterior lesion patients) at pointing to body parts based on a diagrammed human body and walking simple routes from a map (Semmes et al., 1963). Across the neuropsychological literature, the pattern of evidence indicates a dissociation between a system specialized for object-based spatial transformations with critical components in right parietal cortex, and another system specialized for egocentric perspective transformations with critical components in the left hemisphere.

Until recently, the evidence for such a dissociation was indirect. New behavioral and functional neuroimaging data provide direct evidence for the independence of object-based and perspective transformations. An initial functional MRI (fMRI) study employed the judgment task used by Ratcliff (1979) with neurological patients. Consistent with Ratcliff's report, comparing judgments about inverted figures to judgments about upright figures (thereby isolating the mental rotation component of the task) led to bilateral parieto-occipital activity that was greatest in the right hemisphere. A comparison designed to isolate egocentric perspective transformations led to dissociable parieto-occipital activity, mostly in the left hemisphere.

Zacks, Mires, Tversky, and Hazeltine (2002a) designed a behavioral paradigm to allow direct comparison of object-based spatial transformations to egocentric perspective transformations while controlling stimulus and response properties. Participants made spatial judgments about pictures of human bodies with one arm outstretched (see Fig. 3). In the *same–different task*, similar to a paradigm commonly

used to study mental rotation (Shepard & Metzler, 1971), participants were shown two pictures and asked to report whether they were identical or mirror images by pressing one of two keys. In the *left–right task*, they were asked to identify whether a pictured body had its left or right arm extended; this was expected to give rise to an egocentric perspective transformation (Parsons, 1987). Response time in the two tasks was affected differently by changes in stimulus orientation. Response time increased with increasing stimulus orientation in the same–different task, as is typical for object-based transformation tasks (Shepard & Metzler, 1971), but response time was independent of orientation for the left–right task, paralleling the pattern observed when participants are asked to imagine an egocentric perspective transformation (Parsons, 1987). Also supporting the dissociation, performance in the same–different task was predicted better by a test of mental rotation than by a map-reading test, whereas the opposite was true for the left–right task.

Brain activity during these two tasks has been measured with event-related fMRI (Zacks, Ollinger, Sheridan, & Tversky, 2002b). Although a large network was found to be active during performance of these tasks, a small number of regions were disproportionately active during the same–different task; all were in right parietal, temporal, and occipital cortex, excepting one region in the medial cerebellum.

This pattern of data, and the interpretation that multiple dissociable systems subserve human spatial reasoning, imply that it should be possible to impair performance of object-based spatial transformations with local cortical stimulation while leaving performance of egocentric perspective transformations intact. The fact that object-based transformations have been associated particularly with right parietal cortex suggested that stimulation of this region would be most likely to interfere with these transformations.

We tested this hypothesis by stimulating the right parietal and temporal cortex of a patient, GW, with a chronically implanted electrode array over these areas prior to surgery for intractable epilepsy. Cortical stimulation mapping has elucidated brain function by causing temporary disruption of neural activity by passing current over a focal area of cortex. Restricted to patients undergoing neurosurgical procedures, this technique allows mapping of motor, sensory, and language functions for diagnosis and surgical planning. Information regarding the organization of language function (Ojemann, Ojemann, Lettich, & Berger, 1989), visual system (Lee, Hong, Seo, Tae, & Hong, 2000), and memory (Ojemann & Dodrill, 1985) system has also been explored with these techniques. Studies of spatial systems are rare (Fried, Mateer, Ojemann, Wohns, & Fedio, 1982), with no cortical stimulation studies of mental spatial transformations. Additionally, the function of non-dominant parietal cortex has only been minimally studied with cortical stimulation mapping (Fried et al., 1982).

We presented GW with a task designed to elicit object-based transformations and a task designed to elect egocentric perspective transformations (the same–different

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[1] It is important to distinguish between *transformations* and the *reference frames* on which they operate. Both object-based and perspective transformations involve updating the relationship between three different reference frames: the egocentric reference frame of the body, the intrinsic (or object-based) reference frame of an external object, and the environmental reference frame of the ambient space. Thus the distinction between object-based and perspective transformations does not map onto the venerable distinction in neuropsychology between egocentric and allocentric (intrinsic or environmental) reference frames (for a thoughtful recent discussion of reference frame issues, see McCloskey, 2001).
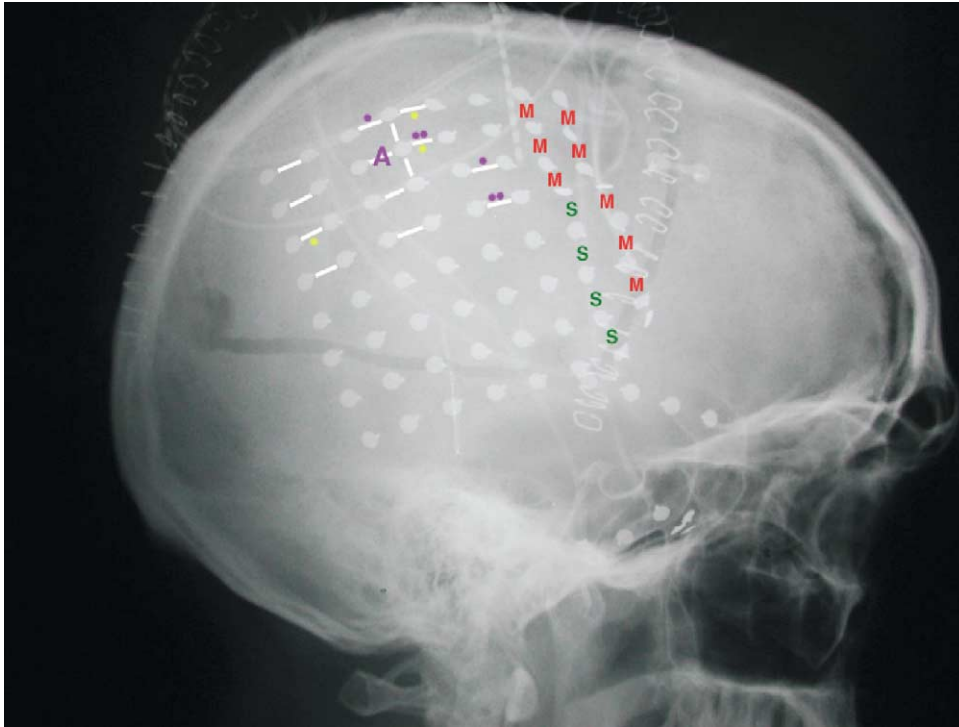
Fig. 1. Errors concurrent with stimulation in the same–different and left–right tasks, superimposed on a lateral skull X-ray showing the implanted electrode array. Electrodes appear as gray circles. White lines connecting the electrode locations indicate all tested sites. At the site marked "A" GW made six errors in 16 stimulated trials of the same–different task. Double purple dots above the lines indicate sites at which GW made two errors during same–different trials concurrent with stimulation. Single purple dots above the lines indicate sites at which GW made single errors during stimulated trials of the same–different task, and single yellow dots below the lines indicate sites at which GW made single errors during stimulated trials of the left–right task. Red M's and Green S's indicate sites at which motor and sensory responses, respectively, were evoked by stimulation.

and left–right tasks, respectively). We also presented a control task designed to allow detection of non-specific impairments of stimulus encoding or response execution. This design allowed us to test the hypothesis that disturbance of right posterior cortex would interfere selectively with performance of object-based transformations.

2. Methods

2.1. Participant

At the time of testing, GW was a 34-year-old with intractable epilepsy who underwent surgery to implant an electrode array in the parietal and temporal regions for localizing the focus of onset of his seizures. The electrodes allowed for both monitoring of seizures and cortical stimulation mapping by passing current through the electrodes onto the cortical surface.

GW presented with a 5-year history of intractable complex partial seizures that followed a head injury suffered in a four-wheeler accident. An MRI of his brain showed bilateral inferior frontal signal changes consistent with prior traumatic injury, but no abnormalities were visible in the parietal lobes. His EEG evaluations showed bilateral temporal discharge, but more frequent right parietal discharges and a right parietal onset. As part of the diagnosis of seizure onset, for later surgical resection, an $8\,cm \times 8\,cm$ electrode array was placed for long-term monitoring and stimulation mapping of essential cortical regions. He underwent a right fronto-parietal craniotomy for subdural implantation of the electrode array. A post-operative lateral skull X-ray allowed for confirmation of the electrode location (Fig. 1). By post-operative day 5, seizure foci had been localized to the right parietal region, just posterior to somatosensory cortex. Sensory and motor cortex were mapped using standard techniques. Additional cortical stimulation mapping was performed to localize cortex involved in spatial processing. This additional mapping was performed separate from clinical mapping and informed consent was obtained in accordance with the Washington University Institutional Review Board. At this post-operative delay, the degree of analgesia required is minimized and the patient is returned to his pre-operative anti-convulsant medication. Thus, medically related impairments in task performance were minimized.

The onset of seizures was localized to the right parietal lobe, including site A in Fig. 1 and cortex under more inferior electrodes. GW underwent a right parietal resection, which included the cortical surface of parietal cortex, posterior to sensory cortex, and extended superiorly and posteriorly to
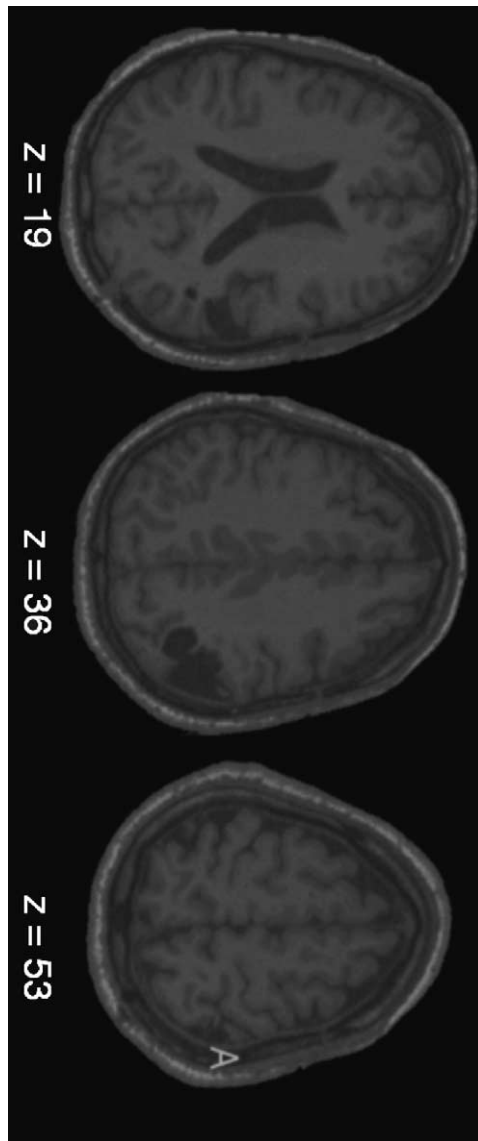
Fig. 2. Structural MRI showing surgical resection. Three axial slices are shown, approximately spanning the lesion from bottom to top the location of each slice in the Talairach and Tournoux (1988) atlas is marked in yellow. The "A" marks the location of the same label in Fig. 1 as estimated from the X-ray of the electrode grid (right is on the right).

the edge of the grid of electrodes. The inferior boundary of the resection was the temporal lobe, or approximately to the fourth row of electrodes in Fig. 1. The extent of resection was confirmed by post-operative MRI (Fig. 2).

2.2. Stimuli and tasks

GW performed three tasks requiring spatial judgments about rendered pictures of human bodies facing the observer with one arm extended (Fig. 3). The same–different task was designed to elicit an object-based transformation, in particular mental rotation of one of the figures to an upright orientation (Shepard & Metzler, 1971). Two figures were presented,
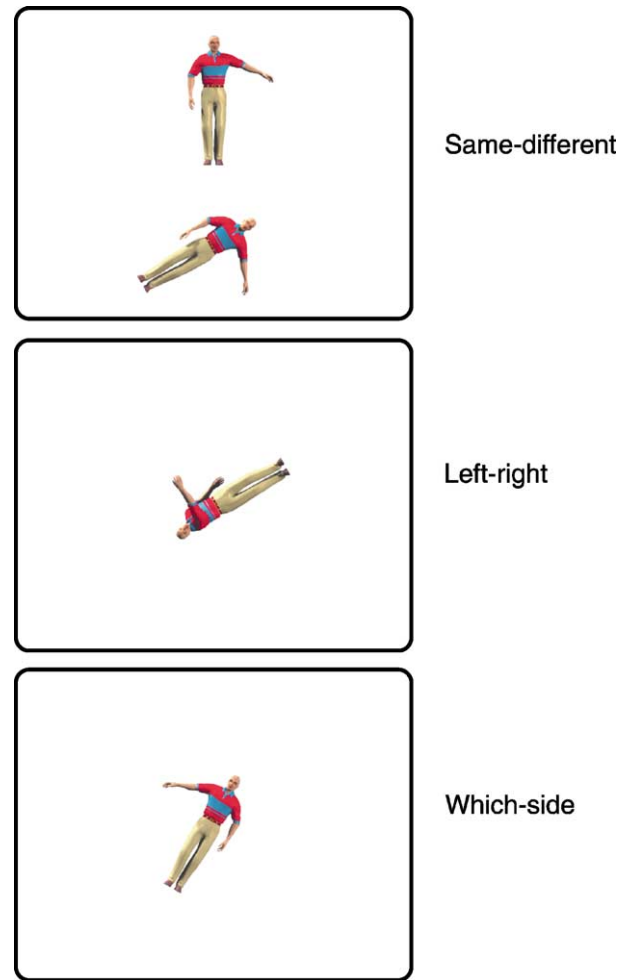

Fig. 3. Stimuli and tasks. The top panel shows an example of the same–different task. In this task, the top figure was always upright, the bottom figure could appear at any orientation, and GW answered whether the two pictures were the same or different (mirror images). On each trial, one of two poses was randomly selected, and both pictures were drawn with the figure in that pose (in this case, posed with an arm extended away from the body). The correct response for this trial was "same" (the "z" key on the keyboard). The middle panel shows an example of the left–right task. In this task only one figure was presented, at any orientation, and GW answered which of the figure's arms was outstretched. In this case, the correct response was "right" (the "/" key). The middle panel also illustrates the second pose used (in all tasks), in which the outstretched arm was crossed over the figure's torso. The bottom panel shows an example of the which-side task. For this task the displays were identical to that for the left–right task, except that only orientations within 30° of 0 or 180° were shown (to avoid ambiguous displays). In the which-side task, GW simply indicated on which side of the *screen* the outstretched arm appeared. In this case, the correct response was "left" (the "z" key").

one above the other, and GW was asked whether the two figures were identical or mirror images. The top figure always appeared at an upright orientation, whereas the bottom figure could appear at any of 12 picture plane orientations (rotated from 0 to 180° clockwise or counter-clockwise, in 30° increments). GW was instructed to press the "z" key if the figures were the same, and the "/" key if they were different.

In prior research, this combination of judgment task and target stimulus led participants to report solving the problem by imagining the bottom figure rotating until upright, and led to monotonic increases in response time with increasing stimulus rotation (Zacks et al., 2002a).

The left–right task was designed to elicit an egocentric perspective transformation using the same stimulus pictures. Stimuli were identical to those for the same–different task, except that the upper (upright) figure was deleted. Orientation of the remaining stimulus was varied randomly as for the same–different task. GW was asked to indicate whether the figure had his left or right arm extended, by pressing the "z" key for left and the "/" key for right. Prior research found this combination of judgment task and target stimulus led participants to report solving the problem by imagining themselves in the position of the figure, and led to response times that were unaffected by changes in stimulus orientation (Zacks et al., 2002a).

The *which-side task* was designed as a control for the visual encoding and response demands of the spatial transformation tasks which would require no spatial transformation. In this task, a single figure was shown as for the left–right task, and its orientation varied from trial to trial. As for the left–right task, GW was instructed to respond by pressing the "z" key for left and the "/" key for right. However, in this task GW was asked to indicate which side of the screen the extended hand occupied, relative to GWs point of view, i.e. no spatial transformation was involved. For this task, the orientations of 60–120 and 240–300° were omitted, to exclude any stimuli for which the judgment was ambiguous.

Testing was administered by a Macintosh PowerBook G3 laptop computer with 15.5 in. diagonal LCD screen (Apple, Cupertino, CA) running PsyScope experimental presentation software (Cohen, MacWhinney, Flatt, Provost & PsyScope, 1993). The computer was placed on a tray mounted over GWs hospital bed at a comfortable distance for viewing and keypresses. GW was seated in an upright position, with his left index finger placed on the computer's "z" key, and his right index finger on the "/" key. For all three tasks, figures were shown in one of two randomly chosen poses (Fig. 3): with the extended arm stretched straight away from the body, or crossed across the chest. For all three tasks, stimulus orientation was varied randomly from trial to trial. For the same–different task, whether the two pictures matched was also determined randomly. GW pressed a key to initiate each block of 12 trials. Each trial began with a chime, to signal the trial's onset to the stimulator operator. After a 500 ms delay, a stimulus was presented and remained on the screen for 4500 ms. When GW responded, one of two sounds was played: a beep for correct responses and a buzz for errors. The next trial began 5000 ms later whether or not a response was made. Trials were presented in blocks of 12. Typically, stimulation at a given site began with a block of the which-side task, followed by the left–right task and then the same–different task. Blocks on which an error occurred during stimulation were generally repeated.

2.3. Procedure

Cortical stimulation mapping was performed by applying current across adjacent electrode pairs (distance = 1 cm), using the Ojemann Cortical Stimulator (Radionics, Burlington, MA). A biphasic 1.0 ms pulse was repeated at 50 ms for the entire duration of the 4 s trial, or until a response was made, whichever occurred first. Currents were progressively increased until after-discharge threshold was reached. Above this threshold, electrical activity persists after stimulation, thus such currents are avoided. All remaining electrodes were monitored during the stimulation sessions to ensure cortical activity had no evidence of after-discharges or of epileptiform activity. The current usually ranged from 6 to 9 mA. No correlation between error rate and stimulation current was seen; in fact, no errors were evoked at the three sites where 9 mA current was applied. At one site where frequent same–different errors were made, an additional session of stimulation was performed at 12 mA current without after-discharge effects.

Eight weeks prior to testing (7 weeks prior to implantation of the electrode array), the overall purpose of the study was explained to GW, and he was trained on the tasks. Before stimulation began, GW was reminded of the task instructions and practiced each task until he felt comfortable. Testing of each electrode pair began with connection of the electrodes and testing for sensory or motor symptoms associated with stimulation. In general, one block of each task was presented, in fixed order: which-side, left–right, same–different. Stimulation was generally administered on the 3rd, 6th, 9th, and 12th trials in each block. When errors were observed, another block of the same task was typically administered. One electrode pair (site A in Fig. 1) was tested a second time for the same–different and left–right tasks at the end of the session, to confirm our initial observation. Following the stimulation session, GW completed five cycles of one block of each of the tasks, to obtain error rate and response time measures in the absence of any stimulation.

One day following GWs resection (2 days after the stimulation study) GW was tested on all three tasks again. He performed five cycles of one block of each of the tasks, plus an extra block of the which-side task.

3. Results

In the absence of cortical stimulation, GW was able to perform all three tasks accurately. During blocks on which stimulation was administered, his error rates on trials without stimulation were 3.3% (5 of 153) for the same–different task, 2.3% (3 of 128) for the left–right task, and 1.0% (1 of 104) for the which-side task. As expected, there were a number of errors during the initial "warm-up" blocks prior to the stimulation session, reflecting relearning of the tasks. GWs error rates during the initial practice blocks were 10.4%

(5 of 48) for the same–different task, 20.8% (5 of 24) for the left–right task, and 0% (0 of 12) for the which-side task. During five blocks of each task at the end of the stimulation session, he made one error out of the 180 trials (this error was made on a same–different trial).

We observed a selective impairment in performance of the same–different task during stimulation of a single location in the superior parietal cortex (site A in Fig. 1). Stimulation at this location was performed at two separate times. In two initial blocks, errors were made on two of eight stimulated trials (one of four in each block) at a current of 7 mA. Stimulation was then performed at 12 mA at a later time. GW made errors on four of eight trials during stimulation at this current for the same–different task (two of four in each of two blocks), thus performing at chance. Error rates for stimulated and unstimulated trials differed reliably ($P = 0.047$ by Fisher's exact test of goodness-of-fit), and GWs performance on stimulated trials did not differ reliably from chance ($P = 0.455$ by a binomial test).

This impairment was specific to the same–different task: GW made no errors when performing the which-side task or left–right task during stimulation of this electrode pair, nor on unstimulated trials during blocks of those tasks on which stimulation was administered (both the which-side and left–right tasks were tested at 7 mA current; the left–right task was retested at 12 mA).

The impairment was also specific to this site of stimulation. During stimulation at one adjacent site, just anterior in the parietal lobe, GW made errors on one of four stimulated trials in two successive blocks of the same–different task. During stimulation at a distant site in temporal–parietal cortex, GW made errors on two of four stimulated trials in an initial block of the same–different task, but made no errors in a following block (these two areas are shown as double purple dots in Fig. 1). At each of two other sites (single purple dots in Fig. 1), GW made a single error on the same–different task during stimulation. For the left–right task, there were three sites at which a single error occurred during stimulation (yellow dots in Fig. 1). At two of those sites we administered a second block of the left–right task, in which no errors occurred during stimulation. For the which-side task, GW made no errors on any of the 52 trials during which stimulation was administered.

There was no evidence that this disturbance depended on stimulus orientation. As can be seen in Table 1, errors during stimulation were just as likely for trials with small orientation disparities as for large-orientation trials.

This site of selective impairment in the same–different task (site A in Fig. 1) corresponded to superior parietal cortex. Based on the lateral skull X-ray, stereotactic methods employing anatomical landmarks visible on the skull X-ray (Fox, Perlmutter, & Raichle, 1985) localized the electrode pair to the stereotactic coordinates of $y = -38$ mm and $z = 53$ mm in the atlas of Talairach and Tournoux (1988). This

Table 1
Pattern of disruption of the same–different task by stimulation of right parietal cortex

Orientation[a]	Correct response	Error	Response time (ms)	Current (mA)
0	Same		1567	12
30	Same		1168	7
30	Different	Yes	1359	7
30	Same	Yes	1587	12
30	Same		1504	7
60	Different	Yes	2349	12
60	Same		1387	7
90	Different		1793	12
90	Different		1883	12
90	Different	Yes	1936	7
120	Same	Yes	2163	12
150	Same		1928	7
150	Different		1826	7
150	Different		1285	12
150	Same		1642	7
180	Same	Yes	2041	12

Shown are the 16 trials on which stimulation was performed at the site marked A in Fig. 1. The data are sorted by orientation. As can be seen in the table, stimulation-induced errors were equally likely for small-rotation trials and for large-rotation trials.

[a] Orientation is collapsed over clockwise and counter-clockwise rotations.

location is in the superior parietal cortex, just posterior to the post-central sulcus, in Brodmann's area 40.

After localizing the onset of seizures to the right parietal lobe, a focal resection of this area was performed, which included site A in its most superior extent (see Fig. 2). On the day following his resection, GWs performance was similar to that previous to the surgery. His error rates were 8.3% (6 of 72) for the same–different task, 8.3% (5 of 60) for the left–right task, and 1.7% (1 of 60) for the which-side task. This was slightly higher than his error rate during the stimulation study but overall better than during his initial warm-up trials prior to stimulation. Note that there was no indication of a selective impairment of the same–different task.

GWs pattern of response time was similar to that of neurologically normal participants performing these tasks (Zacks et al., 2002a). Response times for all nonstimulated trials with correct responses during the stimulation session and post-resection section were analyzed. For the same–different task, GWs response latencies increased with increasing orientation ($r = 0.30$, $t(377) = 6.14$, $P < 0.001$, Fig. 4). For the left–right task, the relationship between orientation and response time was reduced ($r = 0.17$, $t(318) = 3.15$, $P = 0.002$, see Fig. 4). Fisher's z-test for comparing correlations indicated that this difference was statistically reliable, $z = 1.77$, $P = 0.038$. For the which-side task, performance was fast for both near-upright and near-inverted figures (Fig. 4). Response patterns during the post-surgical testing session were similar to those during the warm-up and stimulation blocks for the stimulation session.
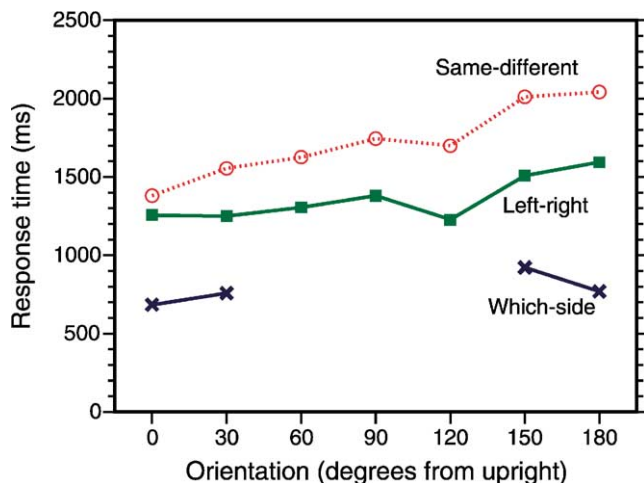
Fig. 4. Mean response time as a function of stimulus orientation for the three spatial judgment tasks. Response time increased more with orientation for the same–different task than the left–right task, replicating previous results with neurologically normal participants (Zacks et al., 2002a). Data from all non-stimulated trials on which a correct response was given during the stimulation session, excepting the initial warm-up blocks.

4. Discussion

Cortical stimulation mapping in this patient demonstrated a selective impairment of object-based spatial transformations during stimulation of a small region of the superior parietal cortex. This converges with findings of functional imaging studies that implicate this, among other, cortical regions in spatial transformation processes. Thus, our findings support a model of distributed systems that support object-based rotations separate, at least in part, from those that support egocentric transformations. In particular, right superior parietal cortex may be preferentially involved in object-based mental transformations.

It is important to emphasize that the two classes of mental spatial transformation studied here do not constitute an exhaustive classification. In particular, behavioral and neuroimaging evidence indicates that imagined motor movements likely constitute an important third class of transformation (Kosslyn et al., 1998; Parsons, 1994; Parsons et al., 1995; Wexler, Kosslyn, & Berthoz, 1998; Wohlschläger & Wohlschläger, 1998). Our working hypothesis is that these three systems interact in everyday problem-solving, and more than one may be brought to bear in any given task. The principal significance of the present results is that they show that at least one spatial transformation system can be selectively disturbed, sparing another.

It is also important to point out that the current results, which constitute a single dissociation, do not speak to the question of whether egocentric perspective transformations require neural substrate not needed for object-based transformations. One possibility is that the network required for egocentric transformations is a strict subset of that required

for object-based transformations; another possibility is that the two systems contain components that doubly dissociate. As noted in Section 1, there is neuropsychological evidence suggesting that perspective transformations can be selectively impaired. However, the paradigms used differed from those testing object-based transformations in components other than the spatial transformation involved, such as stimulus encoding, decision-making, and attention. The best evidence we are aware for the specific involvement of specialized brain regions in perspective transformations comes from recent neuroimaging studies, which have provided greater control over incidental task features. As noted in Section 1, an imaging study using the tasks employed here found right parietal activity that was greater for the same–different task but no region whose response was greater for the left–right task (Zacks et al., 2002b). Imaging studies in which participants imagined themselves in the position of an experimenter (Bonda, Frey, & Petrides, 1996), performing an action on an object shown on a screen (Ruby & Decety, 2001), or rotating in space (Creem et al., 2001) all led to left-lateralized posterior activity. One study has directly contrasted a condition in which participants were directly instructed to imagine their perspective moving in space with a condition in which they were instructed to imagine an array of objects moving. A double dissociation was observed: Object-based transformations led to greater increases in activity in right parietal cortex (and greater decreases in left parietal cortex), whereas perspective transformations led to greater increases in left temporo-occipital cortex (Zacks, Vettel, & Michelon, in press). To test whether object-based and perspective transformations can be doubly dissociated using cortical stimulation, it would be desirable to test patients with left parietal electrode grids in the current paradigm.

An alternative account for the present results is that the same–different task, unlike the other two tasks, requires a comparison between two items. Although we know of no relevant cortical stimulation experiments in the parietal lobe, there are data consistent with this possibility from functional neuroimaging (Faillenot, Decety, & Jeannerod, 1999; Trojano et al., 2000) and studies of behavioral deficits associated with chronic lesions (Warrington & Rabin, 1970). Cortical stimulation data indicate that stimulation of temporal cortex can impair visual matching (Fried et al., 1982). However, none of these studies have directly compared visual matching and image transformations. In the future it would be desirable to test larger numbers of zero rotation trials during stimulation, to test whether matching per se is impaired by stimulation of the right parietal cortex (in the present experiment, on only 1 of the 16 stimulated trials at site A was no rotation required; GW answered correctly on that trial). A related account proposes that the stimulation-induced deficit observed here reflects the fact that the same–different task was more difficult than the left–right or which-side tasks (as evidenced by the response time patterns shown in Fig. 4). Two aspects of the data argue

against this interpretation. First, the deficit was site-specific as well a task-specific. Disrupting posterior cortex in general did not induce errors, as might be expected if the deficit were due to a general disruption of nonspecific processing resources. Second, this account would predict that errors on trials during which site A was stimulated would be more likely for greater rotations. As is shown in Table 1, we did not observe evidence for this (however, the total number of trials was small).

The resection of this region did not cause a permanent deficit, as GWs post-operative performance was quite intact. One possibility is that in GW other tissue is capable of performing the computations required for the same–different task, but that stimulation of this site injects erroneous information into those computations. This is consistent with the view that in neurologically normal adults this region participates in the processing required for the same–different task.

Several nonreproducable errors were observed at areas outside the superior parietal cortex; the significance of these is uncertain. Cortical stimulation just anterior to the site of primary impairment led to a smaller number of errors, suggesting that the area of importance in parietal cortex may not be contained simply between the electrodes at that site. Additionally, the more inferior site of stimulation-related errors, at the temporal–parietal junction, is another area often implicated in object-based transformations (De Renzi, 1982).

In superior parietal cortex, the selectivity of the disruption to object-based spatial transformations persisted even at very high currents. Even at large currents, which reduced same–different performance to chance performance, no effect was seen on left–right or which-side performance.

It is of particular interest that a strong correlation was found between cognitive localization based on fMRI studies of spatial transformation and cortical stimulation mapping of a similar task. The correlation between functional imaging and cortical stimulation mapping is of great interest and, in general, good correlation exists between the two mapping methods, especially for motor, visual and somatosensory function (Jack, 1994; Puce et al., 1995). The correlation for some cognitive functions, especially for language in posterior temporal and parietal regions, has been more difficult to establish (Toga, Ojemann, Ojemann, & Cannestra, 2000). Our findings support the notion that different mapping methods converge, even when studying higher-order cognitive functions.

Acknowledgements

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