Functional reorganization of spatial transformations after a parietal lesion

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Abstract—Background: Mental spatial transformations are ubiquitous and necessary for everyday spatial cognition, such as packing luggage into a car or repairing a broken vase. The posterior parietal cortex is known to be involved in performing such transformations. Objective: To measure reorganization after lesioning of posterior parietal cortex areas subserving spatial transformation. Method: Brain activity in a patient who underwent a resection of right parietal cortex to manage intractable epilepsy was measured using fMRI while he performed a set of spatial transformation tasks. These data were compared with data from a group of healthy control subjects. Results: During spatial transformations, activity in the regions overlapping the resection was reduced in the patient compared with control subjects, but activity in the contralateral cortex was greater than that of control subjects. Conclusions: After a lesion the left hemisphere can adopt components of spatial reasoning normally subserved by the right hemisphere. This converges with evidence that components of language processing normally subserved by the left hemisphere can be taken over by the right hemisphere, suggesting that plasticity of function in the adult human cortex is a general characteristic.

NEUROLOGY 2004;63:287–292

People use transformations of spatial images for spatial navigation, problem solving, and action planning. Neuropsychological studies indicate that these sorts of abilities can be impaired by damage to the posterior cortex.[1,2] Different sorts of image transformations can be distinguished. If one is standing at a table with a map sitting on it, one could imagine viewing the map from a different angle, a perspective transformation. Or, one could imagine that the map were to rotate on its own, an object-based transformation. Object-based transformations, particularly mental rotation of objects, have been associated specifically with the right posterior cortex based on data from lesion studies,[3] EEG,[4] and fMRI,[5] although these data also indicate important left hemisphere involvement.

Motivated by the association between posterior cortex and mental rotation of objects, we recently studied a set of spatial reasoning tasks during cortical stimulation of a surgical patient's right parietal cortex.[6] This patient underwent long-term implantation of a subdural electrode grid before surgery to manage intractable epilepsy. He performed three spatial judgment tasks, which were designed to elicit object-based transformations or perspective transformations or to require no spatial transformation (see Methods). Stimulation of his right parietal cortex selectively impaired the object-based transformation task but had no reliable effect on the other two tasks. The effect was site specific, dominant at one superior parietal location, and task specific, affecting only the object-based transformation task. This site was near the location of the epileptogenic focus and was included in the surgical resection. After surgery, the patient performed all three tasks at a level comparable with his presurgical level, which was well within the normal range. This pattern is suggestive of observations of functional reorganization of language after left temporal or frontal lesions, in which recovery is associated with increased activity in homologous right hemisphere regions.[7,8]

To test the hypothesis that functional reorganization of spatial cognition would be associated with increased activity in contralateral (left hemisphere) regions, we tested the patient and a group of neurologically healthy control participants on the spatial reasoning tasks while measuring local brain activity with fMRI. We also hypothesized that the patient would show reduced activity relative to control subjects in the right parietal cortex because of the lesion.

Additional material related to this article can be found on the Neurology Web site. Go to www.neurology.org and scroll down the Table of Contents for the July 27 issue to find the title link for this article.

Methods. *Case description.* The patient is a right-handed man, aged 34 years at the time of testing, who developed complex partial seizures 5 years previously after a closed head injury.[6] An MRI showed small bilateral inferior frontal signal changes consistent with previous traumatic injury but no abnormalities in the parietal lobes. His EEG evaluations showed bilateral temporal discharge but more frequent right parietal discharges and a right

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Funding was provided in part by the McDonnell Center for Higher Brain Function (J.M.Z. and J.G.O.) and NIH/National Institute of Neurologic Disorders and Stroke NS41272 (J.G.O.).

Received December 9, 2003. Accepted in final form March 17, 2004.

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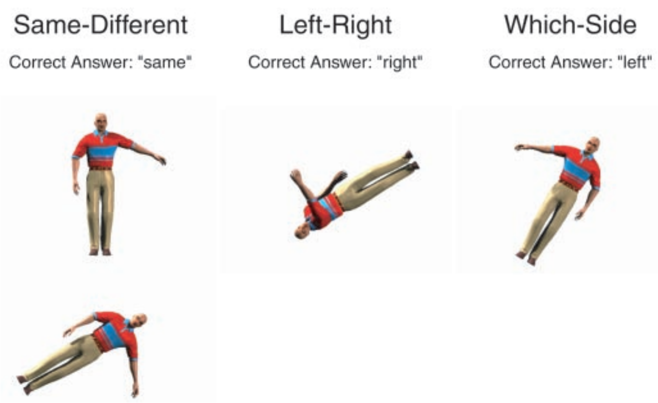

Figure 1. Stimuli and tasks. The left panel shows an example of the same-different task. Participants answered whether the upright top figure and the rotated bottom figure were the same or different (mirror images). The middle panel shows an example of the left-right task. In this task, one rotated figure was presented, and the participant answered which of the figure's arms was outstretched. The right panel shows an example of the which-side task, in which participants simply indicated on which side of the screen the outstretched arm was located.

parietal onset of seizures. His preoperative neuropsychology evaluation demonstrated a verbal IQ of 97 and a performance IQ of 81. After a right parietal craniotomy for subdural electrode placement and video EEG monitoring, a focus in the right parietal postsensory cortex was found. A topectomy was performed, resecting the surface gyri and deep sulcal gray matter of postsensory parietal cortex, involving the superior and inferior parietal lobules. Deep white matter fibers were spared with this technique. Figure 3, which depicts functional activity in the present experiment, also includes a structural MRI of the resected region. Stimulation mapping of the right parietal and posterior frontal cortex did not provide evidence of language impairment, suggesting left lateralization for language. His postoperative recovery was unremarkable with no clinical evidence of visual or somatosensory neglect and no evidence of language impairment. At the time of study, 6 months after surgery, the patient had no seizures except for during one episode of self-initiated discontinuation of his anticonvulsant medication. At the time of study his daily medication included 300 mg oxcarbazepine, 400 mg lamotrigine, and 3 mg lorazepam.

Control participants. Eleven neurologically normal participants (5 women, 6 men) were recruited from the Washington University community. All were right-handed, and they ranged in age from 19 to 28 years. They were paid $25/hour for their participation. An additional participant failed to reach acceptable accuracy during training and therefore was not scanned.

Informed consent was obtained from all control participants as approved by the Human Studies Committee (Institutional Review Board) at Washington University.

Stimuli and tasks. The tasks used here were adapted from those used in conjunction with cortical stimulation during the patient's surgical planning[6] and are similar to tasks we have used with healthy participants in previous behavioral and neuroimaging studies.[9-11] There were three tasks, all involving judgments about pictures of human bodies with one outstretched arm (see figure 1 for examples of the stimuli and tasks.) In the same-different task, participants viewed a pair of bodies presented at different orientations, one above the other, each with one arm outstretched, and indicated whether the two bodies were the same or different. In the left-right task, a single picture was presented, and participants were asked to identify whether the left or right arm was outstretched. The which-side task was designed as a control for the perceptual demands of stimulus encoding and the action demands of responding to the stimuli. In this task, a single body was presented as in the left-right task. However, in this case the participant simply indicated whether the outstretched arm was on the left or right side of the screen. For all tasks, stimulus rotation was varied randomly from trial to trial, and one of two random poses was selected on each trial (see figure 1). For the which-side task, orientations from 60 to 120° were omitted to avoid ambiguous hand locations.

Each scan consisted of 6 blocks of 16 trials each. For each trial, a stimulus was presented at the beginning of a scanner acquisition frame and remained on the screen for the duration of the frame, 2.84 seconds. Participants were instructed to respond as quickly as possible by pressing one of two buttons on a button box with their left or right index finger. For the same-different task, one button was used to indicate "same" and the other to indicate "different." Assignment of buttons was counterbalanced across the control participants; for the patient, right was used for "same." For the left-right and which-side tasks, the left and right buttons represented the left and right sides. Sixteen frames of a fixation cross presented at the center of the screen separated each task block. Participants were instructed to focus their eyes on this cross when present. Each scan began and ended with a fixation block.

Stimuli were presented and responses were collected using a Macintosh computer (Apple, Cupertino, CA) and PsyScope experimental software.[12] In the scanner, stimuli were presented on a screen mounted within the bore of the scanner using a liquid crystal display projector. Stimuli subtended ~12° (horizontal) by 16° (vertical) of visual angle. Responses in the scanner were recorded with a fiberoptic button box. Responses during the prescan training phase were recorded using the same timing mechanism with electrical switch buttons.

Procedure. After providing informed consent, each participant completed a screening for contraindications for MRI and an adaptation of the Edinburgh handedness inventory.[13] They were then trained on the tasks before scanning.

The patient had fairly extensive experience with the tasks used here during the experiment conducted 6 months before the current testing.[6] Therefore, we provided only a brief refresher before beginning the scanning session. He completed one 12-trial block of the which-side task, the left-right task, and the same-different task in that order. Those blocks were presented using the timing with which he was familiar from the previous study: trials of 4,500-ms duration preceded by a 500-ms chime. He made no errors in the which-side block and one error in each of the left-right and same-different blocks.

We developed a training procedure for the control participants designed to mimic the experience of the patient with the tasks. First, the tasks were explained, and participants then completed between 4 and 6 blocks of 12 trials for each of the tasks until they felt comfortable with the task. The which-side task was always run first, and order of the left-right and same-different tasks was counterbalanced across participants. For these initial training blocks, the duration of each trial was 4,500 ms preceded by a 500-ms chime. After these blocks, each participant completed 3 cycles of 12 trials for each of the tasks in the same order as the initial practice blocks. (One participant asked for and was given one extra block of same-different training.) During training, one participant performed at chance in the left-right task (46 of 96 correct); this person was excused before scanning. Excluding this participant, the highest error rate during practice was 6% for the which-side task, 13% for the left-right task, and 16% for the same-different task.

For the patient and each participant, we acquired a structural image series (see below) before functional scanning. Participants completed one run (6 blocks of 16 trials each) of each task. This 3-run cycle was then repeated for a total of 6 runs (12 blocks, or 192 trials of each task).

After scanning, each control participant completed a brief questionnaire that asked how he or she had performed each of the tasks. Previous research indicates that for the same-different task, people generally report performing an object-based transformation, mentally rotating one of the pictures. Conversely, in the left-right task, people typically report performing an egocentric perspective transformation, imagining themselves in the position of the figure, and converging tests indicate that these introspective reports are accurate.[11] In the current study and in previous sessions, the patient reported using these typical strategies. A minority of the control participants (three) reported sometimes imagining the picture moving in the left-right task, consistent

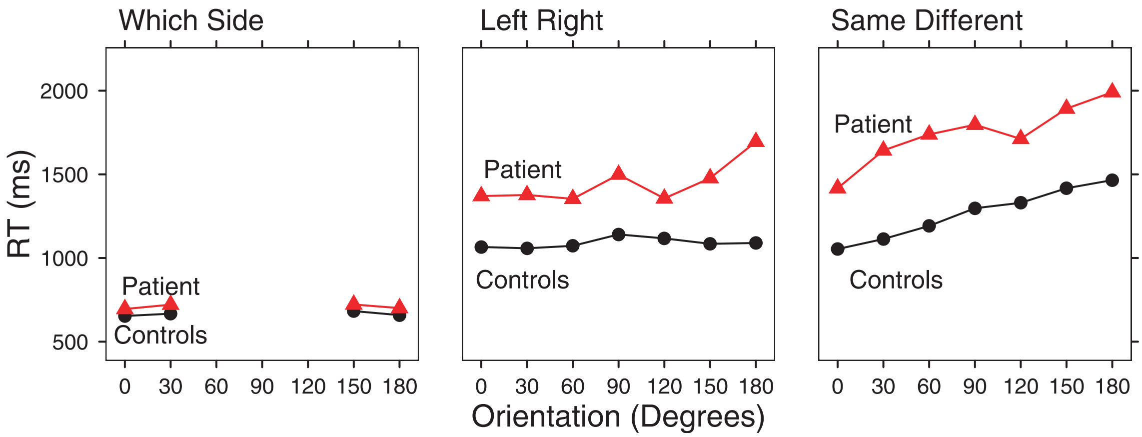

Figure 2. Mean response time as a function of task and orientation for the patient and the control participants.

with previous results. (In addition to the analyses reported here, the data were analyzed with those three participants excluded. All behavioral effects, regional activations, and differences between patients and control subjects reported here were significant with these control participants excluded.)

MRI and analysis. Imaging was performed on a 1.5-T Vision scanner (Siemens, Erlangen, Germany) at the Research Imaging Center of the Mallinckrodt Institute of Radiology at Washington University. Structural images were acquired using a sagittal three-dimensional magnetization prepared rapid acquisition gradient recalled echo (MP-RAGE) T1-weighted sequence with 1-mm^3 isotropic voxels. Functional imaging was performed using an asymmetric spin-echo echo-planar pulse sequence with a flip angle of 90° and a time to echo of 37 ms, optimized for blood oxygen level dependent (BOLD) contrast (T2*).[14] Twenty-one axial slices were acquired with a thickness of 6 mm and in-plane resolution of 3.75 mm. The time to recall (TR) for each slice was 135.2 ms, resulting in a total acquisition time of 2.84 seconds for each functional image. Each functional run took 602 seconds (212 image acquisitions). The first four images were acquired before beginning the task to allow transient signals to diminish. T2-weighted structural images were acquired in the planes of the functional images, with an in-plane resolution of 0.938 mm to facilitate alignment of the functional data to a standard stereotactic space.

Functional data were preprocessed before statistical analysis using methods standard for our laboratory.[10,15-17] First, individual images for each scan were collated into a single four-dimensional array. Second, timing offsets among slices were compensated for using sinc interpolation. Third, systematic odd vs even intensity differences resulting from contiguous interleaved slice acquisition were removed using suitably chosen scale factors. Fourth, head motion was corrected using six-parameter rigid body realignment with three-dimensional cubic spline interpolation. Finally, the MP-RAGE image and functional data were aligned to an atlas conforming to the coordinate scheme of Talairach and Tournoux.[18]

Functional data were analyzed using a blocked fMRI procedure based on the general linear model, treating participant as a random effect. For each participant, a set of three boxcar functions representing the timing of task blocks were convolved with a model hemodynamic response function.[19] The resulting time series were entered as predictor variables in a linear model also including covariates coding for baseline differences from scan to scan and linear trends within each scan.

To identify regions whose activity in control participants changed during performance of the spatial reasoning tasks, we calculated for each voxel in each participant a contrast comparing the three task conditions to the fixation baseline. These contrast values were submitted to t-tests, and the resulting t statistics were converted to Z values. Voxels that were part of a cluster of ≥ 17 adjacent voxels with Z statistics >3.0 were selected for further analysis. This threshold procedure has been shown to control type I error rate at $p = 0.05$.[20] The map of activated voxels was segmented into regions using an automated procedure that identified local maxima in the Z statistic map, subject to a constraint that no two maxima were closer than 25 mm, and clustered each voxel with the peak closest to it. These regions are listed in tables E-2 through E-4 and were used for all subsequent analyses (see tables E-2 through E-4 on the *Neurology* Web site; go to www.neurology.org).

To characterize the activity of each region during the spatial reasoning tasks, mean values were calculated for the contrasts comparing each task to the fixation baseline. These were submitted to t-tests with zero difference as the null hypothesis. To compare the patient with the control participants, t-tests were conducted for each region with his mean contrast value for that region as the null hypothesis.

Results. *Task performance.* The behavioral performance of control participants and the patient is depicted in figure 2. This shows, for control subjects, response time increased with stimulus orientation during the same-different task but not during the left-right task. This pattern replicates that previously reported for these tasks.[6,9] The patient's performance was qualitatively similar, although he performed more slowly and made more errors, especially in the same-different task (see table E-1 on the *Neurology* Web site; detailed analyses of the response time and error patterns also are provided in the supplementary content on the Neurology Web site).

fMRI activity. To identify the brain regions whose activity changed during performance of the three spatial reasoning tasks, we first compared the three task conditions to the low-level fixation baseline. As expected, a large volume of cortex and subcortical structures increased in activity (activated) or decreased (deactivated) relative to fixation during task performance (see tables E-2 through E-4 on the *Neurology* Web site). We identified two foci in right superior parietal cortex that activated during task performance and overlapped the location of the lesion. These are identified in figure 3 as regions A and B. We then projected the lesion volume onto the left hemisphere by mirror reflection and identified two left superior parietal regions that activated during task performance and overlapped the mirror image of the lesion. These are identified as C and D in figure 3. These four regions were selected a priori for analysis and tested with a type I error rate of $p = 0.05$. For all other regions, a Bonferroni correction was used to control the overall false-positive rate.

For each region, we calculated the mean value of the contrast comparing each task with the fixation baseline for each participant. The distributions of these contrasts for the control participants and the values for the patient are

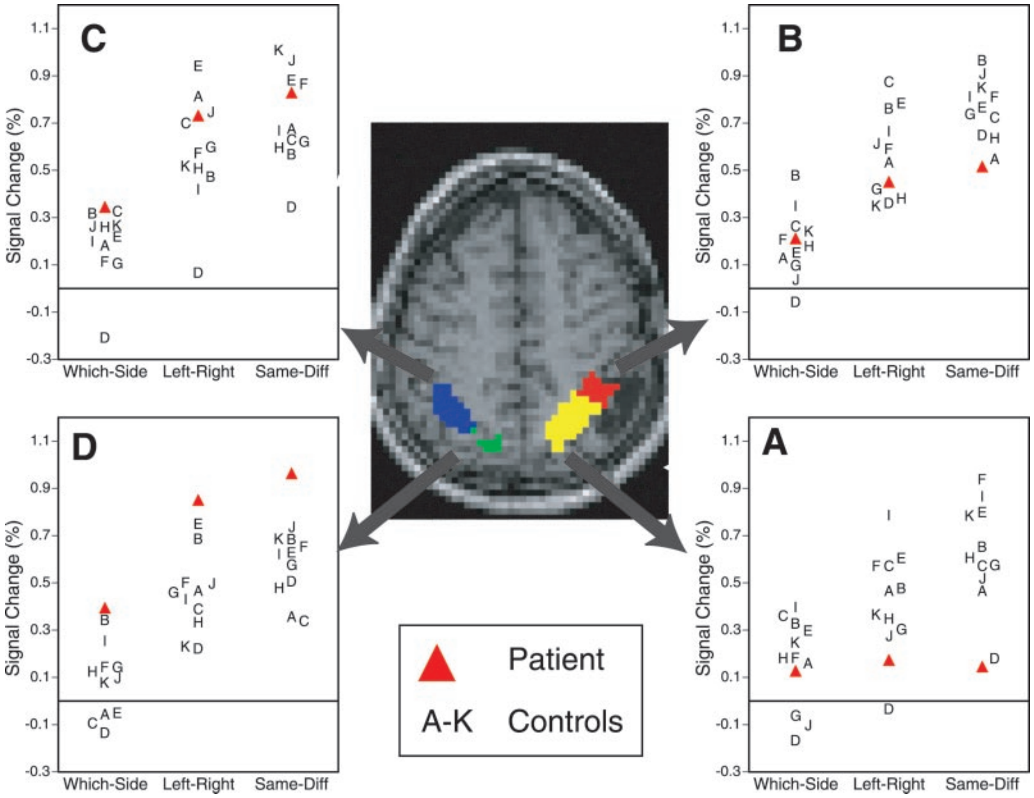

Figure 3. fMRI activity in the patient and control participants during spatial reasoning. The middle panel shows the location of the two regions activated in control subjects that overlapped the patient's lesion, in yellow (A) and red (B), and the regions contralateral to the lesion in blue (C) and green (D). The regions are superimposed on a magnetization prepared rapid acquisition gradient recalled echo (MP-RAGE) image of the lesion at a height of $z = 45$. The graphs plot blood oxygen level dependent (BOLD) signal change for the three tasks, relative to fixation. (Horizontal jitter added to reduce symbol overlap.)

shown in figure 3. We then conducted two sets of one-sample t-tests. The first set tested whether activity in the control participants differed reliably from the fixation baseline for each task. All four regions increased in activity relative to fixation in the same-different and left-right tasks (smallest $t[10] = 6.62$; $p < 0.001$). Three of the four regions also increased in the which-side task compared with fixation, although the changes were smaller (smallest $t[10] = 2.84$; $p = 0.018$) for region D ($t[10] = 1.73$; $p = 0.12$, NS). All four regions showed larger increases for the same-different and left-right tasks compared with the which-side task (smallest $t[10] = 6.62$; $p < 0.001$). Finally, the two right hemisphere regions (A and B) had higher activity in the same-different task than the left-right task (smallest $t[10] = 3.44$; $p = 0.006$). For the left hemisphere region C, this difference also reached significance ($t[10] = 2.32$; $p = 0.043$); for region D it approached, but did not reach, significance ($t[10] = 2.21$; $p = 0.052$).

The second set of analyses tested whether the patient's activation in each task differed from that of the control participants in each region. In the two right parietal regions the patient's evoked fMRI response was reduced relative to the control subjects in the same-different and left-right tasks. For the same-different task, his activation was outside the distribution of the control subjects for both regions, leading to differences (region A: $t[10] = -6.69$, $p < 0.001$; region B: $t[10] = -7.61$, $p < 0.001$). For the left-right task as well, his degree of activation was less than the control subjects, although the difference was less extreme (region A: $t[10] = -2.26$, $p = 0.048$; region B: $t[10] = -3.95$, $p = 0.003$). For the which-side task, which led to minimal activation in the control subjects, the patient did not differ from them (region A: $t[10] = 0.51$, $p = 0.62$; region B: $t[10] = -0.66$, $p = 0.52$). The left parietal regions (C and D) demonstrated a different pattern. In both, the patient had greater activation than the control subjects for all three tasks. For region C, this was significant only for the which-side task ($t[10] = 3.52$; $p = 0.005$). For the left-right and same-different tasks, this difference approached but did not reach significance (left-right: $t[10] = 2.20$, $p = 0.053$; same-different: $t[10] = 1.96$, $p = 0.079$). For region D, the patient's activation was greater than control subjects for all three tasks (smallest $t[10] = 7.05$; $p < 0.001$).

In short, the patient showed reduced activity in regions overlapping his lesion and increased activity in contralateral regions. As can be seen in figure 3, for the left-right and same-different tasks, the patient was the only participant whose activity was below the mean for the group in both right parietal regions and above the mean for both left parietal regions. (For the which-side task, which produced minimal activation in the right parietal cortex, no participant met this criterion.)

Exploratory analyses of other regions indicated other ways in which the patient's BOLD activity differed from control subjects, including increased activity in cortical and subcortical regions, decreased activity in bilateral lateral occipital cortex, and smaller changes in BOLD signal in areas that decreased in the control participants. These are detailed in the supplementary content on the Neurology Web site.

Discussion. The primary conclusions of this study are straightforward: after a right parietal resection, the patient showed greater activity than control participants for all three spatial reasoning tasks in regions contralateral to the lesion. This is consistent with the left hemisphere (and, possibly other right hemisphere regions) taking over spatial cognition functions formerly subserved by the right posterior parietal cortex.

In regions overlapping the resection, the patient showed reduced activity during the two spatial transformation tasks, with the largest difference in the same-different task. This is unsurprising based solely on the reduced tissue volume in the patient in these regions. (The which-side task led only to small increases in the control participants, and for this task the patient's activity in these regions did not differ from that of the control subjects.)

Another potential mechanism of recovery of brain function is the recruitment of ipsilateral regions that are not normally involved in a given task.[21] These may include regions near or distal to the lesion site (see tables E-3 and E-4 on the *Neurology* Web site).

One important consideration is that, before surgery, stimulation of the right parietal cortex adjacent to the tissue that was resected (figure 3) impaired object-based transformations.[6] (The site at which clear impairment was identified was localized to coordinates y = −38 mm, z = 53 mm, on the lateral edge of the resected region, dorsal to the slice shown in figure 3.) One day after surgery, the patient's performance of the tasks reported here was intact—there was no acute loss of spatial transformation ability.[6] This latter observation, plus the fact that the patient performed well before surgery, suggests that reorganization, using left parietal areas, occurred before the surgery. How then to reconcile the finding of a stimulation site that disrupted spatial transformations with preserved postsurgical function and the present evidence for left hemisphere compensatory activity?

One possibility is reorganization occurred before the resection but that stimulation interfered with performance by activating competing networks (a form of noise) that were not used in his normal approach to object-based transformations. Another possibility is that after surgery the patient adopted an alternative strategy, one that used left parietal centers instead of right. The argument of differing strategies has been raised to explain recovery from aphasia after left frontal injury, but evidence from patients with aphasia argues against it, at least for language function.[22] Moreover, in this case this account requires that his strategy for performing object-based transformations changed during the 2-day interval between the presurgical and postsurgical tests but did not change trial by trial during the stimulation session.

Another important consideration is that the region contralateral to the patient's lesion was more active than control subjects for the left-right and which-side tasks and for the same-different task. This is consistent with graded differences in activation between object-based and perspective transformations, which have been observed in previous neuroimaging studies.[10,17] However, it is at odds with the selective, all-or-none effect of cortical stimulation on performance in the same-different task. One possibility is that the apparently graded effects in the neuroimaging data reflect the limitations of the spatial resolution of this technique; different functional units may be blurred together.

The present results extend previous behavioral and neuroimaging studies in neurologically healthy adults, replicating previously observed behavioral patterns[9] and greater activity in the right posterior cortex during object-based transformations.[10] However, we would like to emphasize that the current study was not designed to directly compare object-based and perspective transformations. The two transformation tasks used here differ in overall difficulty, as indexed by error rate and response time. Therefore, greater activity in the object-based transformation task may reflect an increase in amount of processing rather than a difference in the kind of processing performed.

These results complement observations of cortical reorganization of language function after brain injury.[7] Few studies have examined recovery from nondominant hemisphere injury in the realm of spatial cognition.[23,24] Just as the right hemisphere can compensate for lesions to left-hemisphere language areas, so it appears that the left hemisphere can compensate for the loss of a right hemisphere region that is critical for some spatial transformations. More broadly, this finding converges with studies in humans and other animals showing that brain structures including the neocortex and subcortical structures can adapt to changes in other brain regions, in their inputs, or in the types of processing habitually required by an organism's activity.[25,26] Together, these findings suggest that the mammalian brain retains considerable plasticity into adulthood.

Acknowledgment

The authors thank the patient for his cooperation.

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