

The Contribution of the Inferior Parietal Lobe to Auditory Spatial Working Memory

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Abstract

■ There is strong evidence for dissociable “what” and “where” pathways in the auditory system, but considerable debate remains regarding the functional role of these pathways. The sensory–motor account of spatial processing posits that the dorsal brain regions (e.g., inferior parietal lobule, IPL) mediate sensory–motor integration required during “where” responding. An alternative account suggests that the IPL plays an important role in monitoring sound location. To test these two models, we used a mixed-block and event-related functional magnetic resonance imaging (fMRI) design in which participants responded to occasional repetitions in either sound location (“where” task) or semantic category (“what” task). The fMRI data were analyzed with the general linear model using separate regressors for representing sustained and transient activity in both listening

conditions. This analysis revealed more sustained activity in right dorsal brain regions, including the IPL and superior frontal sulcus, during the location than during the category task, after accounting for transient activity related to target detection and the motor response. Conversely, we found greater sustained activity in the left superior temporal gyrus and left inferior frontal gyrus during the category task compared to the location task. Transient target-related activity in both tasks was associated with enhanced signal in the left pre- and postcentral gyrus, prefrontal cortex and bilateral IPL. These results suggest dual roles for the right IPL in auditory working memory—one involved in monitoring and updating sound location independent of motor responding, and another that underlies the integration of sensory and motor functions. ■

INTRODUCTION

Anatomical and neurophysiological studies in nonhuman primates have identified two functionally specialized processing streams that originate from the rostral and caudal parts of the auditory cortex and project to different regions within the prefrontal cortex (Romanski et al., 1999b; Kaas & Hackett, 1998; Rauschecker, Tian, & Hauser, 1995). More specifically, neurons in the anterolateral belt area that respond vigorously to complex sounds, such as vocalization (Rauschecker et al., 1995), also show projections to the anterior portion of the temporal, the inferior prefrontal gyrus, and the dorsolateral prefrontal cortex (Romanski, Bates, & Goldman-Rakic, 1999a; Romanski et al., 1999b). Conversely, neurons from the caudomedial area showing selectivity for sound location and motion have been shown to project to the inferior parietal lobule (IPL), frontal eye fields, superior frontal gyrus, and dorsolateral prefrontal cortex (Romanski et al., 1999a, 1999b). These findings have led to the formulation of the dual-pathway model of auditory processing in which ventral and dorsal processing streams are thought to be analogous to the “what” and “where” processing streams in the visual modality (Rauschecker &

Tian, 2000). Although this model has received considerable support from neuropsychological (Clarke et al., 2002) and neuroimaging studies in humans (Degerman, Rinne, Salmi, Salonen, & Alho, 2006; Arnott, Grady, Hevenor, Graham, & Alain, 2005; Alain, Arnott, Hevenor, Graham, & Grady, 2001; Maeder et al., 2001), the functional role of these pathways in general, and the dorsal pathway in particular, remains a matter of debate in humans (Hall, 2003; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Belin & Zatorre, 2000).

With respect to the dorsal stream, neuroimaging research employing functional magnetic resonance imaging (fMRI) in humans has shown that the caudomedial portion of the superior temporal gyrus is more sensitive to changes in sound location than to changes in pitch (Barrett & Hall, 2006; Krumbholz et al., 2005; Hart, Palmer, & Hall, 2004; Warren & Griffiths, 2003). Using the same stimulus set but varying task instructions, Alain et al. (2001) found greater activity in the IPL and superior parietal and prefrontal regions when listeners were asked to process sound location as opposed to sound identity (for similar findings, see Arnott et al., 2005). Although this effect was bilateral, it tended to be greater in magnitude and extent over the right than the left parietal cortex (for a right hemisphere dominance in processing sound location, see also Degerman et al., 2006; Weeks et al., 1999). These findings are consistent with

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right hemisphere dominance for visual spatial attention (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Corbetta, Miezin, Shulman, & Petersen, 1993) and with neuropsychological studies showing deficits in processing sound source location following right hemisphere damage (Thiran & Clarke, 2003; Griffiths et al., 1997; Cornelisse & Kelly, 1987).

It was originally proposed that the inferior and superior parietal cortex play an important role in localizing and remembering sound source locations (Arnott et al., 2005; Rama et al., 2004; Alain et al., 2001; Martinkauppi, Rama, Aronen, Korvenoja, & Carlson, 2000). Empirical support for this proposal includes an fMRI study, which demonstrated an increase in hemodynamic response in the parietal cortex during the delay period of an auditory spatial working memory (WM) task (Rama et al., 2004). An alternative account emphasizes the requirement for goal-directed action, in which the parietal cortex (Zatorre, Bouffard, Ahad, & Belin, 2002; Iacoboni, Woods, & Mazziotta, 1998) and/or the parietal-temporal boundary (area SPT) (Hickok & Poeppel, 2004; Hickok et al., 2003) would play a role in auditory-motor transformation. Of particular relevance for such a proposal are the findings that activation in the parietal cortex occurs primarily when observers are required to indicate the location of a stimulus (Zatorre et al., 2002; Weeks et al., 1999; Iacoboni et al., 1998) or whether a sound was stationary or moving (Hart et al., 2004). Passive listening (no response required) is usually not sufficient to generate reliable activation in the inferior or superior parietal cortex (Warren & Griffiths, 2003; Zatorre et al., 2002). These findings suggest that goal-directed action is an important determinant for engaging the parietal cortex.

Prior fMRI studies have often used tasks that required a behavioral response on each trial, making it difficult to determine whether the parietal activation in these studies was related to selective processing of sound location or whether it reflected sensory-motor integration and responses. The present study aimed to characterize the functional role of the dorsal stream using a mixed-block/event-related design in which participants responded to occasional repetitions of either sound location ("where" task) or semantic category ("what" task). According to the sensorimotor account, one would expect enhanced signal in parietal regions only when participants are required to make a response to either a location or category target, and that sustained attention to location in the absence of responding should not be sufficient to generate enhanced activation in the parietal cortex relative to that seen when attention is allocated to sound category. On the other hand, if parietal regions are involved in monitoring sound location independently of response demand, then increased activity should be seen during spatial tasks, compared to nonspatial tasks, even when motor responses to the stimuli are not required. We predicted that our results would reflect the latter alternative, thus providing evidence for parietal involve-

ment in monitoring sound source location independent of motor responses.

METHODS

Participants

Sixteen young adults (aged between 21 and 31 years, mean age of 26 ± 3.6 years; 8 men) participated in the study. All participants had normal hearing and were right-handed. Each participant provided informed consent as approved by the University of Toronto and Baycrest Hospital Human Subject Review Committee.

Stimuli and Task

Stimuli consisted of meaningful sounds from three semantic categories: animal (e.g., dog bark, bird chirping), human (e.g., cough, laugh), and musical instruments (e.g., flute, clarinet). In each category, 10 different exemplars were presented. Sounds were chosen from a larger databank and only those that could be unambiguously categorized were included in the study. They were edited to have a duration of 1005 msec. Onsets and offsets were shaped by two halves of an 8-msec Kaiser window, respectively. Stimuli were digitally generated with a 16-bit resolution and a 12.21 kHz sampling rate, passed through a digital-to-analog RP2 converter (Tucker-Davis Technology, Gainesville, FL). Stimuli were delivered to the listener at about 88 dB sound pressure level (root mean square) by means of circumaural, fMRI-compatible headphones (Avotec, Jensen Beach, FL), acoustically padded to suppress scanner noise by 25 dB. Stimuli were presented at three possible azimuth locations relative to straight ahead (-90° , 0° , $+90^\circ$) using head-related transfer functions that replicated the acoustic effects of the head and ears of an average listener (Wenzel, Arruda, Kistler, & Wightman, 1993).

Participants performed a 1-back WM task where sound category or location was occasionally repeated, as there were 10 nonidentical sounds in each of the three categories. Within a block of trials, 15 sounds were presented including 11 nontargets and 4 target sounds (i.e., category or location repeat). The stimulus onset asynchrony was 2 sec and the intertarget intervals varied between 4 and 12 sec. Participants were instructed to press a button as quickly as possible using their right index finger only when a sound category or sound location was repeated. Participants' responses were registered using an fMRI-compatible response pad (Lightwave Technologies, Surrey, BC, Canada). Prior to a block of trials, participants were presented with a visual prompt word (e.g., location or category) on a screen indicating target type. This prompt appeared on the screen 10 sec prior to the first sound and remained on for 35 sec. For instance, when the word "location" was presented, participants were required to press a button as quickly as

possible whenever a stimulus occurred at the same location, regardless of changes or repetition of sound category. In the category task, participants responded whenever a semantic category was repeated, regardless of changes or repetition in sound location. Stimuli were presented in pseudorandom order with each sound category and sound location presented with equal probability. Aside from the prompt, the set of stimuli used was identical in both the category and location tasks. Participants performed each designated task (e.g., location comparisons) for 30 sec followed by a 20-sec rest period in which no stimuli were presented. This on/off sequence was repeated six times in each scanning run for a total duration of 5 min and 10 sec. Participants were presented with six fMRI runs. The tasks alternated throughout the fMRI run and the order of the tasks was counterbalanced across fMRI runs and participants. Participants kept their eyes open throughout all scans.

fMRI Scanning and Data Analysis

Participants were scanned using a research-dedicated whole-body 3.0-T MRI system (Signa 3T94 hardware, VH3M3 software; General Electric Health Care, Waukesha, WI) with a standard quadrature bird-cage head coil. Each scan sequence began with a 20-sec period with no stimuli followed by six alternations between task and rest periods, the latter serving as a baseline. Functional imaging was performed to measure brain activation by means of the blood oxygenation level-dependent (BOLD) effect (Ogawa, Lee, Kay, & Tank, 1990). Twenty-six axial slices, 5 mm thick, were acquired. Functional scans were obtained using a single-shot T2*-weighted pulse sequence with spiral in-out readout, off-line gridding and reconstruction (TR = 2000 msec, TE = 30 msec, flip angle = 70°, 64 by 64 effective acquisition matrix). Structural scans were obtained before fMRI to register brain activation against brain anatomy using standard high-resolution 3-D T1-weighted fast spoiled gradient-echo (FSPGR) images (axial orientation, TR = 7.1 msec, TE = 3.0 msec, inversion-recovery prepared TI = 30 msec, flip angle = 15°, effective acquisition matrix = 256 × 192, number of slices = 124, voxel size = 0.85 × 0.85 × 1.4 mm, FOV = 22 × 16.5 cm). Physiological respiratory and cardiac waveforms were recorded from the bellows and photoplethysmograph peripherals on the scanner, respectively, using LabView (National Instruments, Austin TX). The RETROICOR technique (Glover, Li, & Ress, 2000) was subsequently used to remove these structured noise sources from fMRI time-series data.

Data preprocessing and analyses were performed using Analysis of Functional Neuroimages software (AFNI version 2.56a) (Cox & Hyde, 1997). The first 10 time points in each run, in which transient signal changes occur as brain magnetization reaches a steady state, were excluded from all analyses. In the preprocessing stage, time-series

data were spatially coregistered to correct for head motion using a 3-D Fourier transform interpolation. For each run, images acquired at each point in the series were aligned volumetrically, using the 3dvolreg plugin in AFNI, to a reference image acquired during the scanning session. The alignment parameters were computed by an iterative weighted least squares fit to the reference images. The peak range of head motion was less than 1.5 mm for all participants. The coregistration results were also checked visually for additional quality control. Lastly, the images were de-trended by means of 3dDeconolve from AFNI using a linear fitting.

Block and Event-related Analysis

We analyzed the fMRI data with the GLM using separate regressors for representing the sustained and transient activity during the location and category tasks and by contrasting the activation maps associated with sustained and target-related activity in both listening conditions. This approach allowed us to dissociate sustained task-related activity occurring throughout the block of trials from transient target-related activity elicited by infrequent repetition of either sound category or sound location (Dosenbach et al., 2006; Scheibe et al., 2006; Visscher et al., 2003). For the sustained effect, the shape of the response was modeled as a “gamma” function convolved with a boxcar function of width equal to the duration of the block. For the target-related effect, we also used a gamma function time-locked on stimulus repetition occurring in the attended condition. Only trials where participants responded correctly were included in the event-related analysis. The activation maps created by the GLMs for each condition and each participant were then transformed into stereotaxic space (Cox & Hyde, 1997) and spatially smoothed with a Gaussian filter with a full-width, half-maximum value of 6.0 mm. These last two steps were performed to facilitate the subsequent group analysis, which consisted of a voxelwise, mixed effects (conditions fixed, participants random) analysis of variance with four conditions (sustained-location, target-location, sustained-category, target-category) as within-subject factors.

A spatial cluster extent threshold was used to correct for multiple comparisons using AlphaSim with 1000 Monte Carlo simulations, taking into account the entire spiral matrix. Using an uncorrected *p* value threshold of .005, this procedure yielded a minimum cluster size of 196 μ l (4 voxels in the original acquisition space) with a mapwise false-positive probability of *p* < .03. Moreover, only activations that reflected a true BOLD increase in each task are reported. For example, a voxel coordinate reflecting an apparent increase in location versus category had to meet the additional criterion that the same brain coordinate’s BOLD signal was significantly increased in the location task relative to baseline. Only

significant activations that had a cluster size of 196 μ l (radius of 2 mm) or greater are reported.

RESULTS

Behavior

The hit rate was slightly, but not significantly, higher in the category (mean = 95 \pm 4%) than in the location (mean = 92 \pm 6%) task [$F(1, 15) = 3.75, p = .07$]. However, participants were faster in responding during the location (mean = 829 \pm 215 msec) than in the category (mean = 936 \pm 177 msec) task [$F(1, 15) = 22.22, p < .001$]. Participants also made more false alarms during the location (mean = 5 \pm 4%) than the category task (mean = 3 \pm 3%) [$t(17) = 2.48, p < .05$].

fMRI Results

Figure 1 shows the difference in sustained activity between the category and the location tasks, after accounting for the brain activity elicited by target stimuli. Relative to sound location, WM for sound identity was associated with enhanced BOLD signal in the left Heschl's gyrus and, to a lesser extent, in the medial part of the right Heschl's gyrus, the left superior temporal cortex anterior (including the insula), and posterior to the Heschl's gyrus, the left inferior and middle frontal gyrus (see Table 1). Relative to sound category, WM for sound location was associated with sustained BOLD response in the IPL bilaterally, although the extent of the active area was larger in the right than in the left hemisphere (see Figure 1). Processing sound locations also was asso-

ciated with enhanced sustained BOLD signal in the right inferior and middle frontal gyrus as well as in the right middle temporal gyrus, posterior to the primary auditory cortex, the right superior frontal sulcus, and the right precentral gyrus.

The contrast between sustained activity recorded during the category and location tasks revealed greater activity for location in an extensive region of the right IPL, indicating that WM for sound location, even in the absence of a motor response, is sufficient for eliciting activity in this region of the parietal cortex. More importantly, when participants were presented with the same set of stimuli, but were asked to monitor sound identity rather than location, there was no significant change in BOLD response in the right parietal region (Figure 2, left top panel). Even decreasing the thresholds to a $p < .05$, uncorrected level, did not yield significant activation in the parietal cortex during the category task.

However, when participants were required to respond to infrequent sound repetitions (i.e., targets), we found a significant BOLD signal change relative to baseline in both left and right IPLs (Table 2 and Figure 2), suggesting that the IPL plays a role in guiding the response during auditory WM for both "what" and "where." The transient target-related activity obtained in the right parietal cortex was comparable to the sustained activity obtained during WM for sound location relative to baseline (Figure 2). Increased activity over baseline also was seen for targets in the left pre- and postcentral gyrus, regardless of the target type. This was expected given that participants always responded with their right index finger. In addition, targets generated greater BOLD signal in the medial frontal gyrus, inferior prefrontal cortex, and anterior and posterior portions of the cingulate

Figure 1. Task differences in sustained activity are shown on the average structural images. Warm colors indicate greater activity for category and cool colors indicate greater activity for the location task. All cluster activations contain at least 196 μ l and were significant at $p < .05$, corrected. STG = superior temporal gyrus; IPL = inferior parietal lobule; SPL = superior parietal lobule; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus. Activation maps in this figure, and in subsequent figures, are displayed on the cortical surface using surface mapping (SUMA) (Argall, Saad, & Beauchamp, 2006; Saad, Reynolds, Argall, Japee, & Cox, 2004).

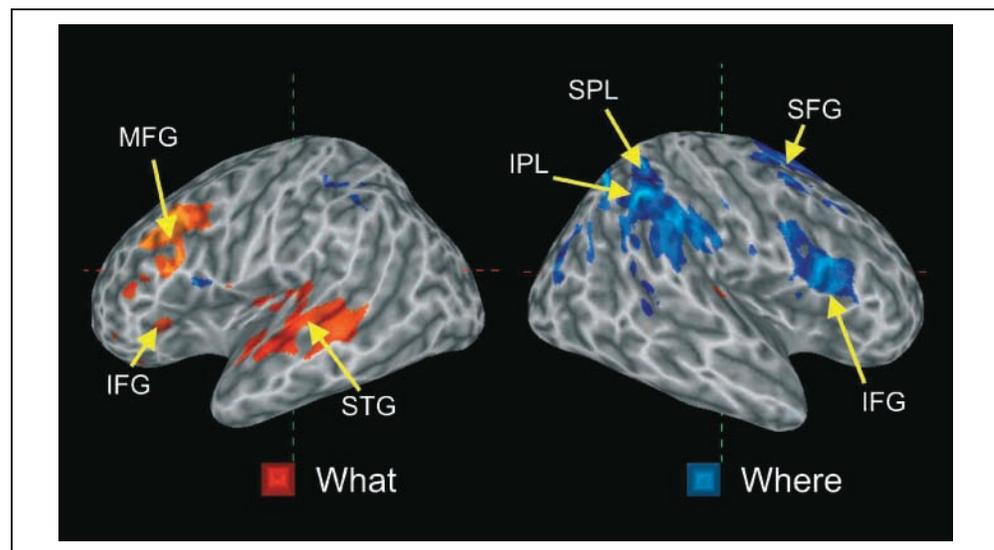


Table 1. Sustained Activity: Location versus Category Activations

Brain Regions	BA	Peak Talairach Coordinate			<i>t</i>		
		<i>x</i>	<i>y</i>	<i>z</i>	<i>C vs. L</i>	<i>C vs. R</i>	<i>L vs. R</i>
<i>Category > Location</i>							
L inferior frontal gyrus	45	-38	28	13	8.25	4.08	1.33
L medial frontal gyrus	6	-3	3	52	6.17	5.66	4.42
Left Heschl's gyrus	42	-40	-28	10	4.89	8.15	7.73
L superior temporal gyrus, anterior	22	-53	-5	0	3.79	5.34	4.41
L superior temporal gyrus, posterior	22	-53	-34	6	5.27	5.67	4.57
Right Heschl's gyrus	41	41	-25	11	3.98	7.17	6.44
R insula	13	44	-2	-3	4.01	5.17	3.74
R cerebellum		5	-63	-28	7.41	6.60	3.49
<i>Location > Category</i>							
L inferior parietal lobule	40	-34	-37	32	-3.49	1.51	3.27
R inferior frontal gyrus	44	45	7	16	-7.58	1.25	5.68
R middle frontal gyrus	10	41	40	22	-4.99	-0.58	3.49
R superior frontal gyrus	6	25	0	63	-5.78	1.68	3.48
R precentral gyrus	4	26	-14	51	-4.98	2.28	4.55
R inferior parietal lobule	40	42	-52	48	-4.20	1.36	5.33

All activations for the category and location contrast are $>196 \mu\text{l}$ and significant at $p < .05$, corrected. BA = Brodmann's area. C vs. L = Category versus Location; C vs. R = Category versus Rest; L vs. R = Location versus Rest.

gyrus (Table 2). A direct contrast between the two target types revealed greater BOLD response for category than location targets in the right middle frontal gyrus, insula, right precentral gyrus, right superior temporal cortex posterior to Heschl's gyrus, and left IPL (Figure 3). There was no difference in the right IPL activity for target location and target identity. In addition, there were no regions where there was greater activity for location targets than for category targets.

In both tasks, the contrast between sustained and transient activity revealed enhanced transient signal in the left pre- and postcentral gyrus, left middle frontal gyrus, left insula, and anterior cingulate (Table 3). During the category task, responding to targets also generated greater activity in the left IPL than when the participants simply monitored the sound identity. For the location task, the target-specific activity was located in the right superior parietal lobule, and activity in the right IPL did not differ from that observed during the monitoring of sound location. In both tasks, transient effects associated with target processing were smaller than sustained activity in auditory cortices and this finding likely reflects some form of adaptation (Altmann, Doehrmann, & Kaiser, 2007; Belin & Zatorre, 2003) because target stimuli consisted of either location or category repetitions. Another possibility is that the sustained activity reflects the summation of responses

to a series of sound stimuli because the BOLD signal integrates over time, whereas the transient response is merely the additional response to the target.

DISCUSSION

Keeping track of sound identity during a 1-back task resulted in enhanced activity in the rostral portion of the superior temporal gyrus and the inferior prefrontal gyrus, whereas monitoring sound location resulted in greater activity in dorsal brain regions, including the IPL and superior frontal cortex. In the present study, the sustained and transient effects were modeled simultaneously in an effort to identify the contribution of each after removing the effect of the other. This combined analysis of sustained and event-related effects revealed greater sustained activity in the right IPL during the location than in the category task. This finding is consistent with results from other auditory fMRI studies that have examined the neural network involved in sound localization (Degerman et al., 2006; Arnott, Binns, Grady, & Alain, 2004; Zatorre et al., 2002; Alain et al., 2001; Weeks et al., 1999). Our findings extend those of prior studies (e.g., Arnott et al., 2004, 2005; Rama et al., 2004; Alain et al., 2001; Maeder et al., 2001) by showing enhanced activity in the IPL

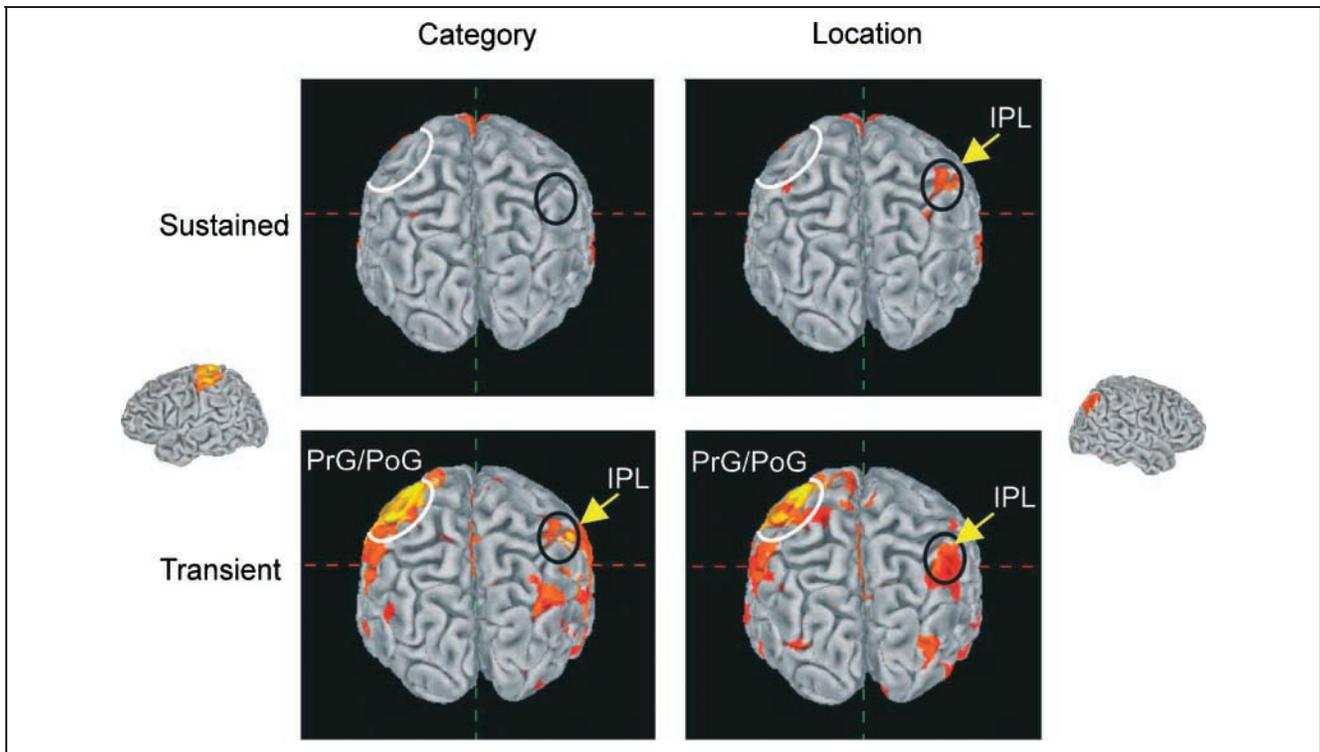


Figure 2. 3-D view from the back of the head revealing greater sustained and transient activities relative to rest (no sound presented). The black circle shows the area of the right inferior parietal lobule with enhanced sustained activity during location working memory and increased transient response-related activity during both tasks. The white circle highlights the enhanced activity in the left motor cortex associated with making a behavioral response. All cluster activations contain at least 196 μ l and were significant at $p < .05$, corrected. PrG = precentral gyrus; PoG = postcentral gyrus; IPL = inferior parietal lobule.

even after taking into account activity related to target processing and motor response. This finding argues against a strict sensorimotor account, and suggests that within the right IPL there is a distinct region that plays an important role in monitoring sound location independently of response demands.

In the present study, the task was designed to place a differential load on monitoring sound attributes and sensorimotor integration by requiring participants to respond only to infrequent repetition (i.e., targets) embedded in a stream of sounds varying in both location and identity. However, one cannot easily rule out the possibility that the requirement not to make a response may also involve some form of integration between sensory and motor information, similar to that performed when a response is required. That is, participants might have been actively inhibiting the motor command, as in a go and no-go experiment. From this view, one would expect additional processing associated with inhibiting the output of the system, rather than expecting the absence of sensorimotor integration processing per se. However, this seems unlikely given that the same requirement to inhibit the motor command would presumably be present during the monitoring of sound category and sound location. As we did not find any sustained IPL activation during the category task,

this would argue against the idea of inhibitory modulation of brain activity in this region.

The enhanced sustained activity in the right IPL during auditory spatial WM suggests that the IPL participates in processing and updating auditory spatial coordinates in memory in order to guide appropriate behavioral responding, and that goal-directed action is not a necessary determinant for engaging the parietal cortex. There is other evidence from the literature that supports this interpretation. For example, findings from a recent fMRI study indicate that the right IPL responds preferentially for sound positions (Zimmer, Lewald, Erb, & Karnath, 2006), consistent with the proposal that this region is part of a network involved in monitoring and updating sound location in memory. Using a passive listening protocol in which no behavioral responses were required from the participants, Brunetti et al. (2005) also found enhanced activity in the right supra-marginal gyrus when sounds were coming from different locations. Moreover, repetitive focal transcranial magnetic stimulation (rTMS) of the right parietal cortex has been shown to induce a systematic shift in sound localization (Lewald, Wienemann, & Boroojerdi, 2004). All of these studies, taken together with the current experiment, provide further evidence that increased activity in the right IPL mediates the processing and/or

Table 2. Target-related Activity

Brain Regions	Peak Talairach				
	BA	x	y	z	t
<i>Category > Baseline</i>					
L precentral gyrus		-35	-20	61	7.82
L postcentral gyrus	3	-30	-30	64	9.21
L inferior parietal lobule	40	-48	-34	49	8.51
L insula	13	-41	-3	16	8.73
L medial frontal gyrus	6	-2	-13	49	6.61
L middle frontal gyrus	10	33	47	11	4.96
L cingulate gyrus	24	-1	-6	43	6.58
L superior parietal lobule	7	-17	-63	52	3.82
R precentral gyrus	44	55	8	6	8.62
R middle temporal gyrus	22	53	-49	3	4.30
R superior temporal gyrus, anterior	22	56	-50	18	4.49
R superior temporal gyrus, posterior	22	52	10	3	5.98
R inferior parietal lobule	40	56	-32	25	7.97
R cingulate gyrus	24	1	1	39	7.55
R superior frontal gyrus	9	21	44	36	5.99
<i>Location > Baseline</i>					
L precentral gyrus		-35	-20	61	6.29
L postcentral gyrus	3	-22	-34	66	10.17
L medial frontal gyrus	6	-1	-14	51	5.44
L inferior frontal gyrus	47	-48	15	1	4.92
L inferior parietal lobule	40	-47	-57	47	3.97
L superior parietal lobule	7	-25	-58	57	4.50
L insula	13	-39	-5	17	6.43
Right superior frontal gyrus	10	12	65	21	6.32
R medial frontal gyrus	8	2	40	41	6.87
Right inferior frontal gyrus	47	54	20	1	4.09
Right middle temporal gyrus	21	56	-24	-12	4.24
R inferior parietal lobule	40	43	-62	43	4.89
R cingulate gyrus	24	2	1	41	6.87

All activations >196 μ l and significant at $p < .05$, corrected for both contrasts.

memory of auditory spatial coordinates, independently of activity necessary for generating stimulus-guided motor responses.

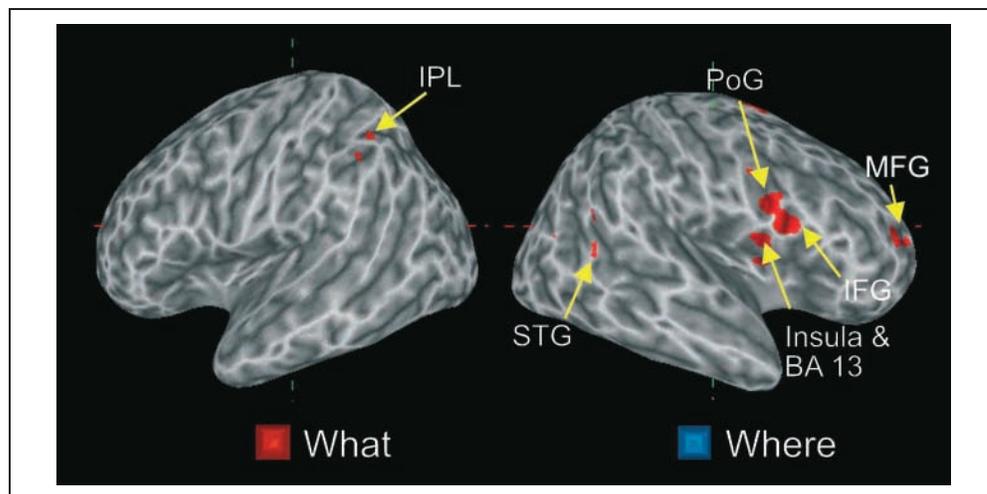
Infrequent responses to either category or location targets were accompanied by activity in the parietal cortex

bilaterally. This finding is consistent with previous studies showing enhanced activity in the parietal cortex during target detection (Stevens, Calhoun, & Kiehl, 2005; Mulert et al., 2004; Muller et al., 2003; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; Stevens, Skudlarski, Gatenby, & Gore, 2000; Linden et al., 1999; Yoshiura et al., 1999). In the present study, the contrast between the two target types, while taking into account task-related sustained activity, yielded greater signal in the left IPL for category than location targets. We also found greater activity for category than location targets in the right middle frontal gyrus, right precentral gyrus, and the rostral portion of the right superior temporal gyrus. These findings seem at odds with the current view that auditory processing is segregated into dorsal and ventral streams. However, there are several possibilities to account for such a pattern. One possibility is that these differences in BOLD signals index task difficulty. For instance, enhanced activity in the left IPL for category relative to location targets may reflect the extra time needed to decide whether the incoming stimulus belonged to the same semantic category or not in order to initiate the appropriate response. This would be consistent with the observed longer reaction times for category than location targets. Another, more likely, possibility is that the enhanced BOLD signals for category relative to location targets reflect differences in stimulus adaptation, which would be greater for location than category repetition particularly in the IPL. Indeed, although in the location task the target was presented at the identical location of the preceding stimulus, in the category task the incoming target differed acoustically (e.g., two different animal sounds).

In the present study, we also found greater sustained activation in the left inferior prefrontal cortex when participants were asked to attend to the semantic category as opposed to when they were asked to focus their attention to sound location. This enhanced activity in the left inferior prefrontal cortex appears to reflect a general process associated with sound identification because similar enhancements have been reported in other studies requiring listeners to make decisions with respect to pitch (e.g., Kiehl et al., 2001; Klein, Zatorre, Milner, & Zhao, 2001; Gandour et al., 2000), or words (Buchanan et al., 2000; Chee, O'Craven, Bergida, Rosen, & Savoy, 1999). There was no difference in target-related activity between the two listening conditions, suggesting that the left inferior prefrontal cortex plays an important role in keeping track of sound identity throughout performance of the category task. This is consistent with prior studies suggesting that the left inferior frontal gyrus plays an important role in semantic processing (Friederici, Opitz, & von Cramon, 2000; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997) and sound categorization (Husain, McKinney, & Horwitz, 2006).

Domain-specific activity also was found in the temporal lobes, where processing sound identity was associated with greater rostral temporal activity relative to

Figure 3. Differences in target-related activity are shown on the average structural images. Category target generated greater activity than location targets as indicated by the warm colors. No areas were found where location targets generated greater activity than category targets. All cluster activations contain at least 196 μ l and were significant at $p < .05$, corrected. PoG = postcentral gyrus; IPL = inferior parietal lobule; STG = superior temporal gyrus; MFG = middle frontal gyrus.



processing sound location. Specifically, this activity was located in the superior temporal gyrus, anterior to the primary auditory cortex. Several nonhuman (Tian, Reser, Durham, Kustov, & Rauschecker, 2001; Romanski et al.,

1999a) as well as human (Alain et al., 2001; for a review, see Barrett & Hall, 2006; Arnott et al., 2004; Zatorre, Bouffard, & Belin, 2004) auditory studies have implicated the anterior temporal area as a locale for the pro-

Table 3. Transient versus Sustained Activity as a Function of Task

Brain Regions	BA	Peak Talairach Coordinate			<i>t</i>		
		<i>x</i>	<i>y</i>	<i>z</i>	<i>T vs. S</i>	<i>T vs. R</i>	<i>S vs. R</i>
<i>Category</i>							
L precentral gyrus	4	-35	-29	61	7.64	8.44	-1.69
L postcentral gyrus	2	-32	-37	58	8.29	8.23	-2.98
L medial frontal gyrus	8	-2	35	38	9.42	5.29	-7.50
L anterior cingulate	32	-7	38	20	7.82	6.60	-6.98
L middle temporal gyrus	21	-57	-9	11	5.93	4.46	-5.49
L insula	13	-40	-4	16	7.55	7.79	-4.39
L inferior parietal lobule	40	-53	-29	43	6.10	6.14	-3.59
L precuneus	31	0	-34	43	8.37	5.32	-6.52
R middle frontal gyrus	46	40	48	16	5.79	4.67	-3.19
R inferior parietal lobule	40	56	-33	43	4.54	5.10	-2.43
<i>Location</i>							
L precentral gyrus	4	-35	-29	61	6.09	6.64	-2.45
L postcentral gyrus	2	-22	-34	68	8.32	8.08	-2.98
L middle temporal gyrus	39	-50	-61	25	8.49	5.60	-5.66
L insula	13	-37	-4	6	7.36	6.80	-3.92
R superior frontal gyrus	6	1	26	60	6.12	5.64	-3.18
R medial frontal gyrus	6	1	-16	50	7.56	4.96	-6.99
R anterior cingulate	32	1	36	10	8.88	4.37	-10.47
R cingulate gyrus	31	1	-41	40	6.92	5.61	-6.29

All activations for the category and location contrast are $>196 \mu$ l and significant at $p < .05$, corrected. BA = Brodmann's area; T vs. S = Transient versus Sustained; T vs. R = Transient versus Rest; S vs. R = Sustained versus Rest.

cessing of nonspatial sound features. A region just anterior and lateral to the primary auditory cortex has also recently been related to listeners' ability to accurately identify auditory stimuli (Binder, Liebenthal, Possing, Medler, & Ward, 2004). However, as mentioned earlier, the sustained effect observed for the category task may also reflect extra processing time needed to segregate the incoming stimuli from the scanner noise such that meaning can be derived from it. Processing sound location was associated with greater activity in the middle temporal gyrus (posterior to the primary auditory cortex near the parietal temporal junction), a finding that is consistent with results from previous fMRI studies (Zatorre et al., 2002; Alain et al., 2001; Martinkauppi et al., 2000; Bushara et al., 1999). Taken together, these findings suggest a segregation of temporal lobe organization in which rostral and caudal regions are more specialized for object-related and spatial-related auditory processing, respectively (Arnott et al., 2004; Rauschecker & Tian, 2000).

In conclusion, the present results support the role of the dorsal stream in sound localization and suggest that the right parietal cortex is important for monitoring auditory space, regardless of whether a motor response is required. This finding is consistent with neuropsychological literature showing that right parietal damage can cause neglect, not only to visual but also to auditory objects (Spierer, Meuli, & Clarke, 2007; Pavani, Husain, Ladavas, & Driver, 2004; Soroker, Calamaro, Glicksohn, & Myslobodsky, 1997; Heilman & Valenstein, 1972). One possible function of the right parietal cortex might be to translate and/or integrate auditory and visual spatial coordinates into a common coordinate system (Cohen & Andersen, 2004). Although there is some evidence suggesting that visual and auditory spatial WM may engage a comparable neural network (Martinkauppi et al., 2000), evidence from other neuroimaging (Bushara et al., 1999) and neuropsychological (Sinnott, Juncadella, Rafal, Azanon, & Soto-Faraco, 2007) studies do not support this hypothesis of a common system underlying auditory and visual spatial WM. Further research using audiovisual stimuli, in conjunction with a parametric manipulation of task difficulty, may help address this issue. In addition to this role of the right IPL in monitoring auditory space, both this region and the left IPL were active for responding to targets. These results suggest dual roles for the right IPL in auditory WM, one that participates in integrating sensory and motor functions, and one that is independent of motor responding.

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