

Where is 'where' in the human auditory cortex?

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We examine the functional characteristics of auditory cortical areas that are sensitive to spatial cues in the human brain, and determine whether they can be dissociated from parietal lobe mechanisms. Three positron emission tomography (PET) experiments were conducted using a speaker array permitting quasi free-field sound presentation within the scanner. Posterior auditory cortex responded to sounds that varied in their spatial distribution, but only when multiple complex stimuli were presented simultaneously, implicating this cortical system in disambiguation of overlapping auditory sources. We also found that the right inferior parietal cortex is specifically recruited in localization tasks, and that its activity predicts behavioral performance, consistent with its involvement in sensorimotor integration and spatial transformation. These findings clarify the functional roles of posterior auditory and parietal cortices, and help to reconcile competing models of auditory cortical organization.

A current model of auditory cortical organization¹ holds that separate functional streams exist for identifying the features of sound stimuli (the 'what' pathway) and for localizing their spatial position (the 'where' pathway). According to this view, which draws an analogy to a similar organization in the visual cortices², cortical fields that are sensitive to stimulus features are found anterior and ventral to primary auditory (A1) regions, whereas posterodorsal lateral belt auditory areas have greater sensitivity to spatial position. This hierarchical model is supported by anatomical tracing^{3,4} and neurophysiological studies in animals⁵⁻⁷, as well as by human lesion data⁸. There is considerable evidence, however, that auditory space is coded by the ensemble activity of neurons in widely distributed auditory cortical populations⁹⁻¹¹, rather than primarily in posterior areas. These data, together with the lack of topographic organization in auditory cortices, have led some investigators to question the model¹², and others to propose alternative organizational schemes¹³ in which posterior auditory cortex is sensitive to spectral motion.

Several human neuroimaging studies have sought evidence for a region that is specifically sensitive to spatial position¹⁴⁻¹⁹, but no such response has been found in superior temporal cortex using static stimuli. Such studies do consistently report the engagement of parietal regions during auditory spatial tasks, which has been interpreted as evidence for a 'where' pathway in audition^{17,18}. According to the anatomical and physiological evidence³⁻⁷, however, such a system should engage auditory cortices within the superior temporal gyrus (STG). A more parsimonious explanation of the activity in parietal regions is that it relates to more general aspects of spatial processing that involve sensorimotor integration²⁰, as tasks used in neuroimaging studies often require subjects to use auditory spatial information in conjunction with other sensory and motor systems.

Most neuroimaging studies to date have relied on simulated auditory space to induce the illusion of a spatial position. Although this method is effective when using head-related transfer functions²¹, subtle localization cues from the head and pinnae are slightly different for each individual, and these differences can influence behavioral²² and neural responses²³. Individualized transfer functions have not yet been used in neuroimaging. We sidestepped this problem by designing an apparatus to allow quasi free-field spatial presentation within the PET scanner (Fig. 1a), so that listeners perceive the localization cues with their own ears.

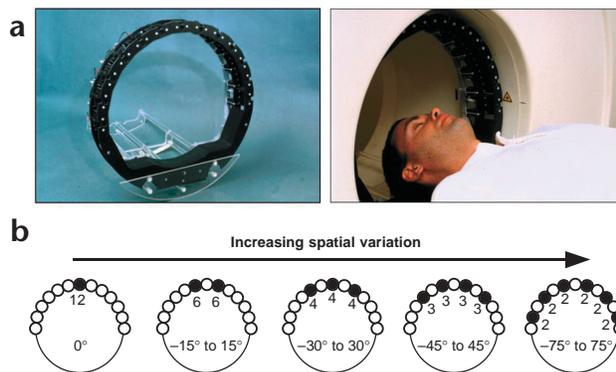
Here we used PET to address three main questions: (i) Are there specialized auditory cortical regions that contain discrete populations of neurons tuned to specific spatial positions? (ii) If so, where are they located and what are their functional characteristics? and (iii) Can the functional roles of such areas be dissociated from those of parietal cortex? First (experiments 1 and 2), we varied the spatial properties of acoustic stimuli systematically, and found that specialized auditory regions are recruited when multiple simultaneous stimuli are presented. Then (experiment 3) we varied the task demands and found recruitment of parietal cortex during active sound localization.

RESULTS

Experiment 1

In experiment 1, we presented a single noise stimulus on each trial, and parametrically varied the number of locations sampled across conditions. This approach avoids problems inherent to choosing a baseline condition, as the variable of interest is systematically manipulated, and areas of covariation with the input variable are sought. A silent baseline condition was also included. We reasoned that if a discrete area containing spatially-tuned neurons exists, then there would be more activity in this area during scan conditions in which the stimulus

Fig. 1. Methods. (a) Stimulus array used for spatial presentation, shown outside the scanner (left) and inside the scanner (right). (b) Design for experiment 2. The circle represents the array, and filled spots indicate speaker positions used in each condition. The number below each position indicates the number of separate, distinct sounds presented simultaneously from that location on each trial. The spatial distribution of the sounds increased across conditions from 0° to 150°, whereas the total number of stimuli presented remained constant at 12.



changed position across trials, because a greater population of putative spatially-tuned neurons would be recruited. In contrast, there should be less activity in scan conditions when the stimulus was in a fixed or less variable position, because that would result in recruitment of only a subset of such neurons. In addition, we chose this method because repeated presentation of a stimulus at one position is expected to result in adaptation effects²⁴.

In searching the image volume for significant covariation with the spatial parameter, we did not find any reliable cerebral blood flow (CBF) changes associated with the increasing variation in spatial position (Fig. 2a). A comparison of the highest spatial variation condition with the fixed condition did not show any significant CBF signal change either. However, contrasting the sum of these conditions with the silent baseline did yield considerable STG activation (Fig. 2a and Table 1) extending across Heschl's gyrus²⁵ and the planum temporale²⁶. This pattern of findings indicates that auditory regions responded strongly to the stimuli, but their responses were not modulated by the spatial distribution of the stimuli.

Experiment 2

The lack of spatially sensitive responses in experiment 1 could result from a number of factors. But one important finding is that many neurons in lateral belt regions are sensitive to both spatial position and spectro-temporal features simultaneously⁷. Therefore, experiment 2 used acoustically distinctive sounds with varying spatial distribution. Unlike experiment 1, the stimuli were presented simultaneously rather than sequentially from different locations, and on each trial, a different mixture of sounds was presented. We predicted that neurons jointly sensitive to spatial and spectrotemporal information would be engaged when these properties interact. To identify neural populations specifically sensitive to space, we held constant the number of distinct sounds played on each trial, and parametrically varied their distribution over the speakers of the array (Fig. 1b).

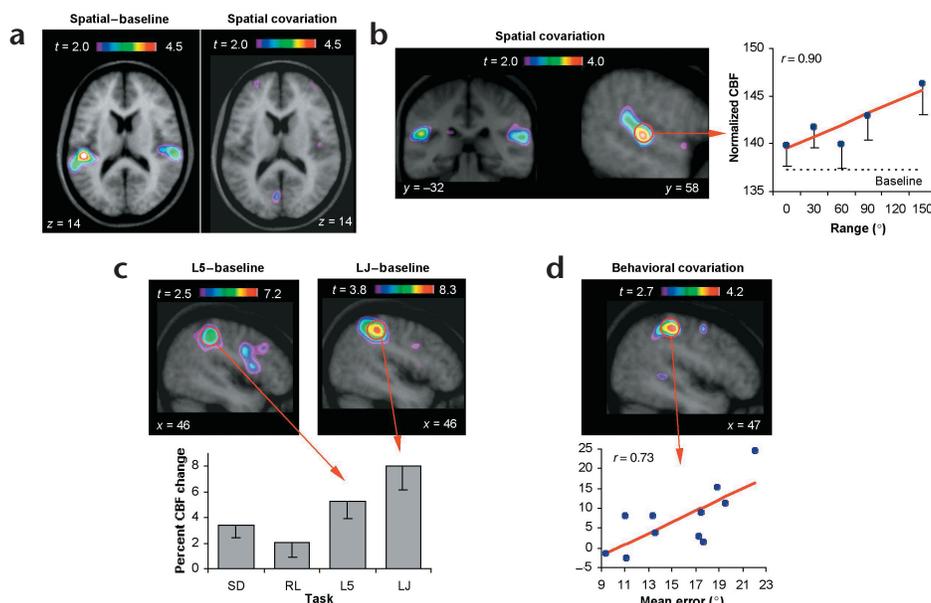


Fig. 2. Neuroimaging results. (a) Experiment 1: left, bilateral activation in the auditory cortices (all conditions minus silent baseline); right, analysis of covariation with spatial distribution—no significant areas of CBF covariation were observed. (b) Experiment 2: coronal and sagittal images showing areas of significant CBF covariation with spatial distribution in auditory cortices within each hemisphere. Right, the correlation ($r = 0.90$, $P < 0.02$) between percent CBF change in right auditory cortex and increasing range of spatial positions; the dashed line indicates baseline CBF. (c) Experiment 3: sagittal slices through CBF activation peaks in right parietal cortex in comparison of five-finger (L5) and joystick (LJ) localization tasks to baseline. Bottom, bar graph shows percent CBF change in this region in each of the four active tasks. Spherical region of interest (5-mm radius); CBF was significantly greater ($P < 0.001$) in localization than discrimination tasks. (d) Sagittal slice through right parietal focus in covariation analysis with behavioral performance for LJ task. Bottom, percent CBF change relative to baseline for each subject at this focus as a function of localization accuracy (absolute error score); the correlation is highly significant ($r = 0.73$, $P = 0.01$).

Table 1. Stereotaxic coordinates and t-values of activation foci.

Condition/Analysis	Region	x	y	z	t-value	
Experiment 1:						
All stimuli minus silence ^a	R STG	60	-28	14	3.59	
	L STG	-48	-30	14	4.95	
		-58	-41	18	3.98	
Experiment 2:						
Covariation with spatial distribution ^a	R STG	58	-21	3	3.97	
	L STG/Par Operc	-48	-35	20	3.51	
Experiment 3:						
5-finger localization (L5) minus baseline ^b	R Inf Parietal	46	-33	45	5.35	
		35	-54	47	4.58	
Joystick localization (LJ) minus baseline ^b	R Inf Parietal	50	-33	47	8.56	
		37	-47	47	7.64	
Experiment 3:						
Covariation with behavioral measure ^b	L5	R Inf Parietal	47	-28	59	2.78
	LJ	R Inf Parietal	47	-28	48	4.14

STG, superior temporal gyrus; Par Operc, parietotemporal operculum.

^aAll significant foci listed.

^bRelevant foci listed; see **Supplementary Table 1** online for complete list. Coordinates refer to standardized stereotaxic space⁴⁴.

An analysis of covariation as a function of spatial distribution yielded two significant CBF foci in posterior auditory cortical areas (Fig. 2b and Table 1): one within the planum temporale²⁶ and the other in a left temporoparietal opercular area²⁷. Thus, the manipulation was successful in identifying auditory cortical regions specifically responsive to spatial position, but only when object-related features were also present in the stimuli.

Experiment 3

In experiment 3, we tested the hypothesis that parietal regions are involved in sensorimotor integration and transformation^{20,28}. We predicted that parietal areas are recruited to the greatest extent when explicit localization is required, and to a lesser extent when localization is unnecessary. We designed four active tasks: the first two required only a relative judgment that did not involve computing the actual spatial position of the sound. In the same-different (SD) task, subjects heard two sounds in either the same place or separated by 30°, and indicated by a key press with the right hand if the sounds were in the same position or not. In the right-left (RL) task, subjects heard sounds that were always separated by 30° and judged whether the first sound was to the right or left of the second. The second pair of tasks

required explicit localization: a target sound was presented at one of five locations, and subjects responded either with a five-finger response box (L5), or by moving a joystick, placed by their side, to indicate the perceived position of the sound (LJ). Behavioral performance on these tasks was similar to that expected from psychophysical studies of discrimination and localization²⁹ (Fig. 3a and b).

Comparing each condition to its matched baseline (Methods) yielded two adjacent foci of significant activation within the right inferior parietal cortex in tasks L5 and LJ, the two localization tasks, but not in SD or RL, the two discrimination tasks (Table 1 and Fig. 2c). A number of other regions were also active in all four task comparisons, particularly motor-related structures and right dorsolateral frontal areas (Supplementary Table 1 online). As a further control for the motor component involved, we tested four new subjects on condition LJ, using a new baseline in which the joystick was simply moved from side to side without regard to sound location. A similar parietal-lobe area was significantly activated in this contrast (Talairach coordinates 43, -50, 48), indicating that the parietal activity seen in the main study did not result from the simple sensorimotor demands of the task.

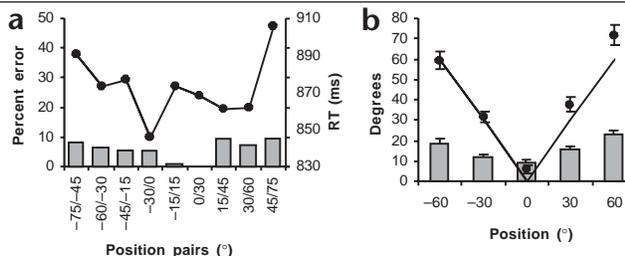
Notably, we found no changes in any STG area in any of these subtractions, presumably because the auditory stimuli in the baseline were similar to those in the active tasks. This finding, together with the data of experiments 1 and 2, suggests that auditory spatial information is computed automatically regardless of how the spatial information will be used in the task.

The data from experiment 3 suggest that right parietal regions are important in relating auditory spatial information to motor, proprioceptive and other systems that are involved in spatial responding. To further test this conclusion, we regressed accuracy of performance on tasks L5 and LJ against CBF. The analysis yielded a highly significant focus for LJ in the right parietal cortex, within 6 mm of the first focus identified in the comparison to baseline (Fig. 2d and Table 1; see Supplementary Table 1 for additional findings). There was a similar, albeit subthreshold, result for L5 (Table 1). These results support the contention that parietal regions are directly involved in localizing a sound stimulus, as opposed to some non-specific aspect of the task.

DISCUSSION

Our findings give partial support to the dual pathway model¹ for audition, but are also consistent with distributed processing. Experiment 1, which used a single noise stimulus, did not show modulation of brain activity as a function of space, in keeping with prior studies using static stimuli¹⁴⁻¹⁹. Experiment 2, on the other hand, did show modulation in posterior STG areas, indi-

Fig. 3. Behavioral results. (a) Performance on RL discrimination task. Bars (referred to left ordinate) indicate mean percent error as a function of position of the pair of stimuli. Solid line (referred to right ordinate) indicates mean latency to respond. (b) Performance on joystick localization (LJ) task. Bars indicate mean absolute error as a function of azimuth. Points indicate mean angle at which the joystick was placed for each of the five positions sampled. Solid line represents veridical localization performance. All measures for both tasks indicate relatively accurate overall performance, but better toward the middle than the periphery, as expected²⁹.



cating that spatial sensitivity is linked to the spectrotemporal features of the stimulus. This result is compatible with the finding that neurons in posterior auditory areas are sensitive jointly to spatial and object-related information⁷, and is consistent with other functions attributed to this region, including spectral motion^{13,30} and the disambiguation of temporal and spatial sound properties³¹. Thus, rather than being strictly segregated, object-related and spatial information may interact within the dorsal pathway¹², similar to the visual pathways³².

This interpretation is also consistent with cognitive studies that point to the integral nature of spatial and spectral processes. For example, responding to the spatial position of a tone is affected by irrelevant variation in its pitch, and vice versa³³. These interactions probably reflect the important role of spatial information in disambiguating overlapping auditory sources, which is facilitated by spatial separation³⁴. We suggest that the STG activity seen in experiment 2 partly reflects such processes, because the stimuli were easier to distinguish when they were more spatially separated.

The anatomical location of the spatially sensitive region is in accord with studies using broad-band moving stimuli^{31,35}, and is compatible with a posterior-directed spatial processing system. An area responsive to spatial features may, however, be compatible with a distributed population code. Neurons throughout many auditory cortical areas are sensitive to binaural cues, and are likely to be involved in localization¹⁰. Evidence from human lesion studies indicates that under some circumstances, anterior STG areas are necessary for localization, because resection of temporal neocortex—even in regions anterior to A1—can disrupt auditory localization^{29,36}. Thus we conclude that a relative concentration of spatially sensitive neurons in posterior regions exists, but that a distributed network encompassing many auditory regions throughout the STG underlies computations relating to spatial position.

This interpretation helps to reconcile the two dominant views of auditory spatial processing. On the one hand, it is likely that the processing of binaural cues relevant to spatial position is accomplished by ensemble coding throughout auditory cortices. This conclusion would explain why most neuroimaging studies, including our experiment 1, have not found differential auditory cortical responses to spatial stimuli: population coding would mean that most neurons would respond to most positions, hence resulting in no net change. It would also explain why anterior STG lesions can disrupt localization performance. On the other hand, posterior STG areas that were identified in prior studies^{7,31,35} and in experiment 2 would integrate spatially relevant information with spectrotemporal features of a sound, and relay this information to parietal-lobe systems via corticocortical connections³⁷ for additional processing.

The data from experiment 3 also indicate that parietal cortex activity is linked to task demands and may be dissociated from that of the posterior temporal cortex. Most neuroimaging studies of auditory spatial processing report similar inferior parietal activation^{16–18}, but the functional relevance of such activity has not been clearly established. Experiment 3 showed that tasks requiring explicit spatial localization elicited the greatest parietal activity, as compared to the discrimination tasks, which require a relative judgment and, in principle, can be done without computing the location itself³⁸. Localization tasks also require a transformation of the spatial coordinate system from a head-centered to a body-centered or world-centered system, to allow for the localization response (for example, joystick). The important role of parietal cortex in such transformation and sensorimotor integration is well estab-

lished²⁰. Moreover, the finding that parietal activity predicts accuracy of localization behavior provides further evidence that the spatial response is specifically and directly linked to computations carried out within this system. The direction of the correlation suggests that those subjects with the least accurate performance made the greatest demands on the parietal system, whereas those who performed better made more efficient use of the same system. The right-hemisphere predominance we observed is also consistent with reports of a relative hemispheric asymmetry in the human brain for auditory spatial tasks^{15,19,29,39} and more generally for global spatial processes²⁸.

METHODS

Apparatus. Stimuli were presented using a circular array (radius 24 cm) containing mini speakers positioned 15° apart (Fig. 1a). The maximal interaural time difference was measured to be 0.78 ms; maximal interaural level differences were on the order of 9.5 dB. These values are consistent with measures of proximal-field cues⁴⁰. No evidence of echoes was detected. Behavioral measures of joystick localization taken in a separate group of six listeners comparing the present array to a more conventional 1-m radius device²⁹ in a quiet room indicated highly correlated performance ($r = 0.99$) and no significant differences in absolute error measures. This indicates that there was no major influence on performance from the proximal location of the sources⁴¹, the background noise or the supine position of the subject.

Experiment 1. Forty-five 500-ms excerpts of environmental sounds, reversed to render them difficult to identify, were added together to produce a single noise stimulus. Each stimulus was band-pass filtered (0–8 kHz; high-pass and low-pass roll-offs of 6 and 12 dB/oct, respectively) to balance for overall spectral range, and equalized for r.m.s. intensity. This single sound was presented every 833 ms from a single speaker on each trial at 66–69 dB SPL; background noise was 56 dB SPL. Across scan conditions, the parameter that we varied was the spatial range of the speakers sampled. In condition 1, the noise always came from the center speaker (0°); in condition 2, the noise came from one of three speakers (–15°, 0° or +15°) chosen randomly per trial; in conditions 3, 4 and 5, these ranges were ±30°, ±45° and ±60°, respectively. Sixty trials were presented to each subject, starting several seconds before the onset of PET scanning. The order of scan conditions was counterbalanced across subjects. Ten healthy right-handed volunteers were tested after they gave written informed consent in accord with guidelines approved by the MNI Ethics and Research Committee; they were instructed to listen attentively with eyes closed, but no response was required. Transmission scans were conducted with the array in place for attenuation correction. Cerebral blood flow (CBF) was measured with a Siemens HR+ scanner and the H₂O¹⁵ bolus method; images were passed through a 14-mm Hann filter and processed using standard techniques¹⁹. Statistical⁴² and covariation⁴³ analyses were done as previously described. Simulations of these sound sequences are available online (www.zlab.mcgill.ca).

Experiment 2. We used the same 45 sounds from experiment 1, but on each trial, 12 different individual sounds were randomly sampled from the set and played simultaneously. Thus, on each trial of all conditions, subjects heard a distinct combination of 12 different sounds. Across conditions, their distribution in space was varied as follows (Fig. 1b): in condition 1, all sounds were played from the center location (0°); in condition 2, six different sounds were played simultaneously from each of two locations (six sounds at position –15°, another six at position +15°); in condition 3, four different sounds were played from three locations (–30°, 0°, +30°); in condition 4, three sounds were played from four locations (–45°, –15°, +15°, +45°); and in condition 5, two sounds were played from six locations (–75°, –45°, –15°, +15°, +45°, +75°). A new group of 12 healthy right-handed volunteers was tested; test conditions were otherwise identical to experiment 1.

Experiment 3. For all four tasks, the stimulus was a 500-ms white noise burst, and the inter-trial interval was 5 s; subjects were familiarized with

each task before testing, which consisted of 72 trials in randomized order. Stimulus intensity was varied randomly over a range of 4 dB on each trial to avoid the use of absolute intensity cues, and to mask any cues related to the individual speakers in the array; subjects were instructed to ignore differences in intensity and judge position. For the two discrimination tasks (RL and SD) the inter-stimulus interval was 500 ms. The baseline for these two conditions consisted of pairs of noise bursts at positions 30° apart (identical to task RL), with no response required. The baseline for the two localization tasks (L5 and LJ) consisted of single noise bursts, presented at locations varying between -60° to +60° on each trial (identical to tasks L5 and LJ), but no response was required. For the behavioral accuracy measure, the absolute value of the difference between the correct position and the response for each trial was taken and averaged across all trials for each subject. This value was entered as a regressor in an analysis seeking significant covariation with CBF change between the task and baseline in the whole brain volume⁴³. Accuracy across tasks (L5 and LJ) was highly correlated in the group of 12 subjects ($r = 0.97$), indicating that error rates are robust and characteristic of each listener, independently of task used. This error score does not capture front-back reversals or other qualitative differences between subjects, although no listener reported hearing the stimuli outside the frontal plane.

Note: Supplementary information is available on the Nature Neuroscience website.

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Competing interests statement

The authors declare that they have no competing financial interests.

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