

Perception of Sound-Source Motion by the Human Brain

Jason D. Warren,^{1,2} Brandon A. Zielinski,³
Gary G.R. Green,² Josef P. Rauschecker,³
and Timothy D. Griffiths^{1,2,4}

¹Wellcome Department of Imaging Neuroscience
Institute of Neurology
University College London
12 Queen Square
London WC1N 3BG
United Kingdom

²Auditory Group
Newcastle University Medical School
Framlington Place
Newcastle-upon-Tyne NE2 4HH
United Kingdom

³Georgetown Institute for Cognitive and
Computational Sciences
Georgetown University Medical Center
3970 Reservoir Road
Washington, D.C. 20007

Summary

We assessed the human brain network for sound-motion processing using the same virtual stimulus in three independent functional imaging experiments. All experiments show a bilateral posterior network of activation, including planum temporale (PT) and parieto-temporal operculum (PTO). This was demonstrated in contrasts between sound movement and two control conditions: externalized stationary stimuli (in the midline or to the side of the head) and midline sounds within the head with similar spectro-temporal structure. We suggest specific computational mechanisms in PT for disambiguation of the intrinsic spectro-temporal features of a sound and the spectro-temporal effect of sound movement. The results support the existence of a posteriorly directed temporo-parietal pathway for obligatory perceptual processing of sound-source motion.

Introduction

Sound movement is an important aspect of our perception of the environment and is the only sensory cue available for the perception of movement of objects in the large region of space behind the head. Previous functional imaging studies (Table 1) have demonstrated brain activation during presentation of moving sound stimuli in humans (Baumgart et al., 1999; Griffiths et al., 1994; Griffiths et al., 1998a; Griffiths and Green, 1999; Griffiths et al., 2000; Lewis et al., 2000; Bremmer et al., 2001). Using different stimuli, activation has been shown in bilateral inferior parietal areas, ventral premotor areas, and the frontal eye fields, in addition to right-lateralized areas in the superior posterior parietal cortex. No previous study in which a comparison was made between a

moving stimulus and the appropriate control stimulus (stationary sound) has shown activation of the primary auditory cortex in the region of medial Heschl's gyrus (HG) (Penhune et al., 1996; Rademacher et al., 2001). This argues against the *specific* involvement of the primary auditory cortex (A1) in sound-movement perception. Demonstration of neurons sensitive to cues for auditory motion in primary auditory cortex of cats and monkeys (Ahissar et al., 1992; Toronchuk et al., 1992) does not invalidate this conclusion; such neurons may provide part of the input to movement-specific areas.

Three previous studies have shown activation during sound-movement processing in the planum temporale (PT), the region of the superior temporal plane posterior to HG (Baumgart et al., 1999; Lewis et al., 2000; Bremmer et al., 2001). This raises the possibility of a posterior processing "stream" for analysis of sound movement in space, passing from A1 to PT and, thence, to the inferior parietal lobule (IPL). A similar scheme was first proposed in the macaque, in which spatial information about sound sources is processed in a pathway that runs from primary auditory cortex via adjacent caudal superior temporal areas to the parietal lobe (Rauschecker, 1998; Rauschecker and Tian, 2000). However, Baumgart et al. (1999) used a limited number of slices that did not allow a demonstration of the entire motion analysis system, while Lewis et al. (2000) and Bremmer et al. (2001) used a silent reference condition that does not allow conclusions to be drawn about specific movement analysis mechanisms. Moreover, all three studies used acoustic stimuli that relied on the manipulation of binaural cues to produce the perception of movement of a sound object between the ears, rather than acoustic stimuli that would be produced by actual sounds in space.

The present study uses a virtual acoustic space technique (Wightman and Kistler, 1989) to produce the percept of a single sound source moving around the head. We used whole-brain imaging with positron emission tomography (PET) (Experiment 1) and functional magnetic resonance imaging (fMRI) (Experiment 2) to test the hypothesis that PT is part of a posterior network for the processing of movement in acoustic space. Apart from providing a parallel independent test of the hypothesis regarding PT, the increased spatial resolution of fMRI allows a search for functional subdivisions within this large anatomical area. A secondary aim of Experiments 1 and 2 was to compare first-order sound motion, where the acoustic object moves with a fixed angular velocity, and second-order sound motion, where the acoustic object moves with changing angular velocity. A common example of the latter situation occurs with head movement relative to the acoustic environment. Changing acoustic angular velocity is, therefore, potentially an important cue signaling the position of self relative to the auditory environment. It is a complex sound movement property that might a priori have a different neuroanatomical substrate within or distinct from that responsible for first-order sound-motion processing.

In a third experiment using fMRI (Experiment 3), we sought to identify where brain activation is a neural cor-

⁴Correspondence: t.d.griffiths@ncl.ac.uk

Table 1. Previous Functional Imaging Studies of Sound Movement

Study	Type	Stimulus	Task	Key Contrast	HG	PT	IPL	Insula	SPL	Premotor	
										Dorsal	Ventral
Griffiths et al., 1994	PET	binaural beat	none	movement minus stationary	no	no	no	R	no	no	no
Griffiths et al., 1998	PET	single object from narrow-band sound with interaural phase/intensity variation	none	movement minus stationary	no	no	no	no	R	no	no
	fMRI	single object from narrow-band sound with interaural phase/intensity variation	none	movement minus stationary	no	no	R/L	R	R>L	R/L	R/L
Griffiths and Green, 1999	PET	rotation within a virtual sound field	none	movement minus stationary	no	no	no	no	R	no	R/L
Baumgart et al., 1999	fMRI	single object from interaural intensity variation of FM sound	none	movement minus stationary	no	R	not imaged (limited number of slices)	no	not imaged	not imaged	not imaged
Griffiths et al., 2000	fMRI	single object from narrow-band sound with interaural phase/intensity variation	none	movement minus stationary	no	no	R/L	no	R>L	R/L	R/L
Lewis et al., 2000	fMRI	single object from narrow-band sound with interaural AM	speed discrimination	movement minus silence	R/L	R/L	R/L	R/L	R/L	R/L	R/L
Bremmer et al., 2001	fMRI	binaural beat	none	movement minus silence	R/L	R/L	R/L	R/L	no	no	R/L

AM, amplitude modulation; FM, frequency modulation; fMRI, functional magnetic resonance imaging; HG, Heschl's gyrus; IPL, inferior parietal lobule; PET, positron emission tomography; PT, planum temporale; SPL, superior parietal.

relate of the perception of sound movement (Frith et al., 1999), rather than sensory processing of the stimulus. A priori there are a number of processes necessary for a sound to be perceived as moving in space. One important process is the distinction of movement of the sound object from the localization of a fixed sound object in space. Another is distinction of the spectro-temporal change imposed on moving sounds in space by the dynamic filtering mechanism of the two external ears (Wightman and Kistler, 1989; Hofman et al., 1998) from the intrinsic spectro-temporal structure of the sound. We examined the mechanisms for these processes by comparing the brain activity during movement of a sound object in space with activity due to control stimuli that were either (1) externalized to one location in space but stationary or (2) similar in spectro-temporal structure, but not externalized.

Results

Experiments 1 and 2

PET and fMRI experiments were carried out in two centers using a similar paradigm. Subjects listened to virtual stimuli simulating a single acoustic object in the azimuthal plane.

The stimulus was amplitude-modulated broadband noise convolved with a generic head-related transfer function (HRTF). The use of the HRTF generates a strong percept of a virtual sound object located in external space (Wightman and Kistler, 1989). The sound object either remained stationary in front of the head or rotated around the head with fixed or changing angular velocity. Subjects reliably distinguished the stationary from the moving conditions and the moving conditions with fixed angular velocity from those with changing angular velocity.

Contrasts between activation in the moving and stationary conditions and between the first- and second-order motion conditions were performed using a threshold of $p < 0.05$, corrected for multiple comparisons across the whole-brain volume. Comparison between the moving and stationary (all-motion minus stationary) conditions showed no activation of primary auditory cortex in medial HG in either the PET or fMRI group studies (Table 2; Figures 1 and 2) or in any of the individual subject fMRI data sets (Figure 3). For the all-motion minus stationary sound contrast, both PET and fMRI experiments showed bilateral activation in PT posterior to HG and bilateral activation in the parieto-temporal operculum (PTO), that part of the inferior IPL contiguous with the posterior temporal plane. In both experiments, the significant contrast demonstrated in PT and PTO formed a contiguous cluster bilaterally (Figure 1). In the fMRI data, an additional local maximum was present in left IPL (Figure 1). The fMRI group analysis in Experiment 2 showed activation of the medial part of PT (Figure 2); however, individual analyses showed variation between subjects in the region activated within PT (Figure 3). The PET data showed additional bilateral activation in the premotor cortex (Table 2; Figure 1).

Using a less stringent threshold of $p < 0.001$ without correction for multiple comparisons (not shown in the figure), bilateral posterior parietal activation was ob-

served in the all-motion minus stationary contrast in both experiments. This activation was located at the parieto-occipital junction, anterior to the human visual motion area V5/MT (Watson et al., 1993; Tootell et al., 1995). Activation in the fMRI experiment for all-motion minus stationary contrast occurred at Talairach coordinates 46, -58, 4 and -42, -64, 10 ($Z = 4.30$ and 3.55 , respectively) compared to 45, -76, 3 for V5/MT (Tootell et al., 1995).

Second-order motion processing was assessed by the contrast between sound movement with changing angular velocity and constant angular velocity (with the same mean angular velocity in both cases). Neither the PET nor the fMRI group analyses demonstrated a significant difference in activation.

Experiment 3

In this fMRI experiment, the same fixed-velocity rotating stimulus as in Experiments 1 and 2 was used with two types of control stimulus. Stationary external control sounds were generated where the stimuli were either in the midline as in Experiments 1 and 2 (midline stimuli, azimuth = 0° or 180°) or located to the right or to the left (side stimuli, azimuth = 90° or 270°). A spectro-temporal control sound was also generated by taking the mean of the waveforms at each ear after convolution with the HRTF in the rotation condition and presenting this stimulus diotically. This stimulus has a similar spectro-temporal structure to the rotating stimulus but produces a midline percept within the head without any externalization. The mean waveform, rather than the waveform at either ear alone, was used to avoid monaural cues for movement perception (Zakarauskas and Cynader, 1991). The spectro-temporal control stimulus was perceived by all subjects as a sound with varying intensity over time that did not localize to a point in external space. It was easily distinguishable from the moving and fixed external sounds.

Activation in response to rotating sound was contrasted with the external midline, external side, and spectro-temporal control stimuli. In addition, activation in response to the spectro-temporal control stimulus was contrasted with the external side stimulus. All contrasts were thresholded at $p < 0.05$, corrected for multiple comparisons across the whole-brain volume. The contrast between rotating and external side stimuli showed bilateral activation of PT, extending into PTO (Figure 4A). Although activation spread into HG on the right, all local maxima were posterior to HG on both sides (Table 2). The contrast between rotating and external midline conditions (Figure 4B) demonstrated very similar bilateral involvement of PT and PTO. The contrast between rotating and spectro-temporal control conditions (Figures 4C and 4D) showed more localized activation of posterior medial PT and PTO (Figure 4D). The contrast between spectro-temporal and external side stimuli (Figure 4E) produced bilateral activation in PT and PTO that was more restricted and more laterally distributed than the contrast between the rotating and external side conditions (Table 2; Figures 4A and 4E). No activation was observed in premotor areas in this experiment.

Table 2. Coordinates of Local Maxima and Z Scores for All Experiments

Region	Coordinates (mm)			Z score
	x	y	z	
PET Experiment (1)				
Right planum temporale	60	-36	12	5.78
Left planum temporale	-48	-32	8	6.40
Right premotor	56	10	28	7.09
Left premotor	-54	2	32	4.72
fMRI Experiment (2)				
Right planum temporale	64	-24	12	7.69
Left planum temporale	-42	-34	4	6.33
Left inferior parietal lobule	-46	-40	24	6.22
fMRI Experiment (3)				
Rotation minus external side:				
Right planum temporale	48	-30	12	>8.00
Left planum temporale	-56	-32	12	>8.00
Rotation minus external midline:				
Right planum temporale	64	-24	10	>8.00
Left planum temporale	-56	-30	12	>8.00
Rotation minus spectro-temporal control:				
Right planum temporale	48	-30	12	5.93
Left planum temporale	-46	-28	6	>8.00
Spectro-temporal control minus external side:				
Right planum temporale	62	-8	4	>8.00
Left planum temporale	-56	-14	4	>8.00

Coordinates are in mm according to Talairach and Tournoux (1988), based on spatial normalization to a template provided by the Montreal Neurological Institute. The Z score for Experiments 1 and 2 refers to the contrast between the all-motion and stationary sound conditions. A Z score of 4.5 corresponds to $p < 0.05$ after correction for multiple comparisons.

Discussion

This study made novel use of a virtual acoustic space technique, the convolution of broadband noise with a

generic HRTF, to produce a stable percept of an external sound source moving in azimuth. Using this stimulus and a very conservative criterion for significance that does not take the a priori anatomical hypotheses into

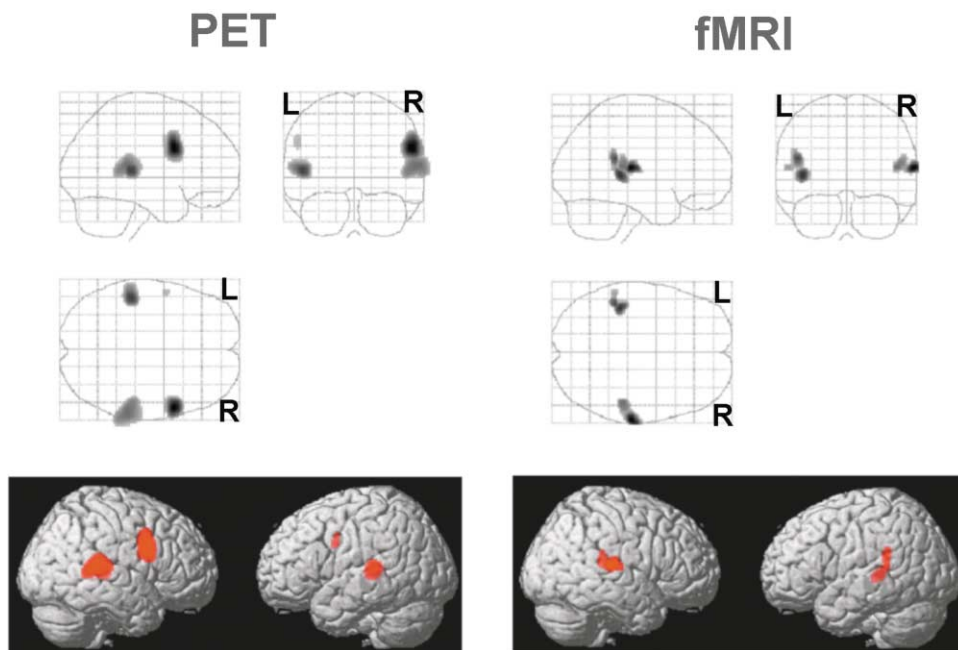


Figure 1. All-Motion Minus Stationary Sound Contrast (Projections and Rendering)

Statistical parametric maps of PET (Experiment 1) and fMRI (Experiment 2) group data are shown as sagittal, coronal, and axial projections (above) and rendered onto a canonical template (below). All voxels significant at the $p < 0.05$ level (corrected for multiple comparisons) are shown.

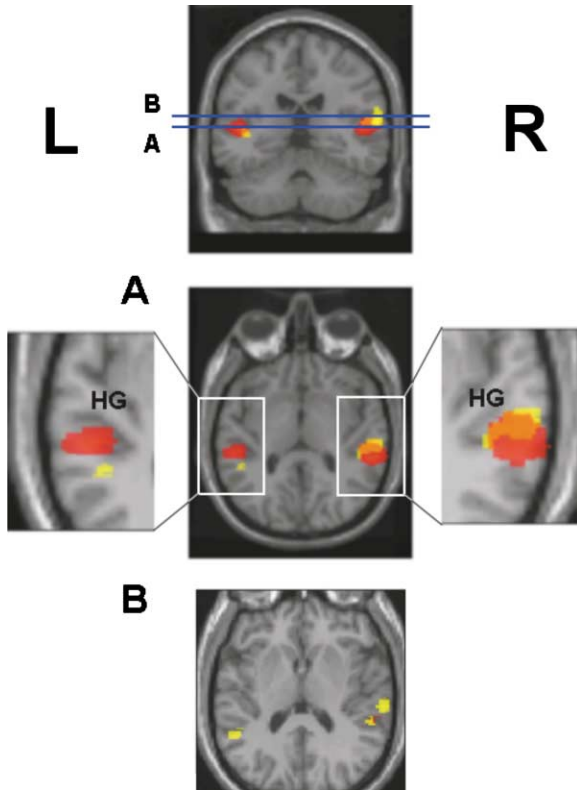


Figure 2. All-Motion Minus Stationary Sound Contrast (Sections)
Statistical parametric maps in Experiments 1 and 2 have been rendered on coronal (top) and axial (below) sections of a canonical structural template. Axial sections have been tilted in the pitch plane to produce axial views parallel to the superior temporal plane at the two levels (A and B) indicated on the coronal view. Insets indicate the relationship of activations to Heschl's gyrus (HG). Both the PET data (red) and the fMRI group data (yellow) show that all activations in the superior temporal plane occur posterior to Heschl's gyrus, in the planum temporale. Voxels activated jointly in both PET and fMRI experiments are indicated in orange. All voxels significant at the $p < 0.05$ level (corrected for multiple comparisons) are shown.

account, we have shown bilateral activation of PT and PTO during sound-movement processing. This has been demonstrated in three separate functional imaging experiments conducted at two institutions. All previous fMRI studies of auditory motion that have imaged IPL have demonstrated bilateral activation of this region (Table 1). The current experiments confirm that IPL is involved in the analysis of actual sound movement in space, with consistent involvement of the parieto-temporal junction.

In addition to specific activation of PTO, the present study also shows that sound movement in external space activates PT. One previous fMRI study showed activation of PT by interaural amplitude modulation (Baumgart et al., 1999), a cue that could be used in the analysis of auditory motion. The absence of PT activation in other studies of sound motion (Table 1) may reflect the stimuli employed. Both the study of Baumgart et al. (1999) and the present study used broadband stimuli with distinct spectro-temporal structures: the stimulus was sawtooth frequency modulation in the study of Baumgart et al. and amplitude-modulated noise here.

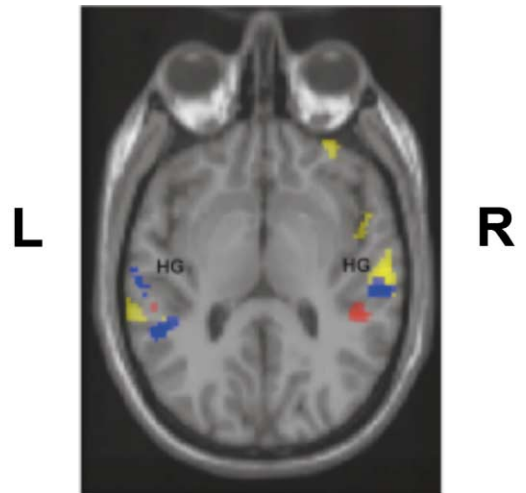
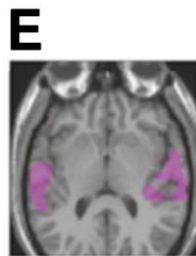
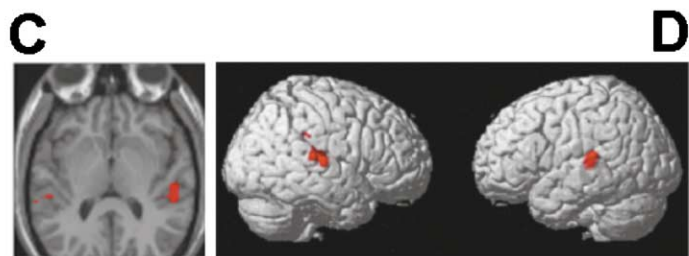
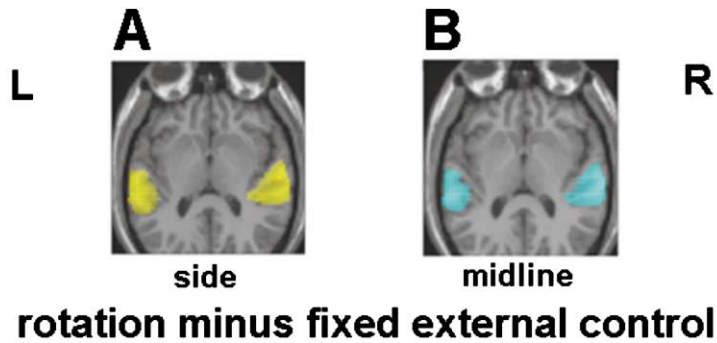


Figure 3. Individual fMRI Data
Individual fMRI data for three subjects (red, yellow, and blue) in Experiment 2 are superimposed on a canonical structural template. Tilted axial sections show the superior temporal plane. The data show absence of activation in Heschl's gyrus (HG) and bilateral activation in the planum temporale for each individual subject and intersubject variation within the planum temporale.

Taken together, the two studies would be consistent with a computational role for PT in the disambiguation of spectro-temporal sound properties due to movement in space from the intrinsic spectro-temporal properties of the sound, to produce a neural correlate of the perception of movement. Such computation might be achieved by a form of independent or dynamic component analysis (Bell and Sejnowski, 1995; Attias and Schreiner, 1998). Although the current experiment does not allow localization of the neural correlate of sound-motion perception to either PT or PTO, the data show that it occurs at or before PTO. The present study does not support a hemispheric asymmetry of sound-movement processing with a preference for right PT, as suggested by Baumgart et al. (1999). However, previous observations in a patient with a lesion involving the posterior right hemisphere are consistent with the right posterior superior temporal cortex being *necessary* for the detection of cues for sound-movement perception (Griffiths et al., 1996). It will be of considerable future interest to assess sound-movement perception in patients with lesions involving left PT.

The combined PT and PTO activation during movement perception suggests a posterior temporo-parietal pathway for processing sound movement in space, extending from PT through PTO into IPL. A potential anatomical substrate for the pathway has been demonstrated in cytoarchitectonic studies of human auditory cortical areas, which show that auditory parakoniocortex extends contiguously from the superior temporal plane into PTO (Galaburda and Sanides, 1980). It appears likely that this pathway represents the human homolog of the posterior/dorsal processing stream for auditory spatial information in the monkey (Rauschecker, 1998). The existence of distinct pathways for spatial processing and recognition of sound is further sup-



spectro-temporal control minus side

Figure 4. Processing of Sound Motion Compared with Fixed-External and Spectro-Temporal Control Sounds

Statistical parametric maps in Experiment 3 have been rendered on axial sections of a canonical structural template (A–C and E) tilted in the superior temporal plane and on a whole brain canonical template (D). Contrasts are indicated below each panel. Activation within planum temporale in (E) occurs more laterally than in (A). All voxels significant at the $p < 0.05$ level (corrected for multiple comparisons) are shown.

ported by functional imaging and neuropsychological studies in normal and brain-damaged human subjects (Clarke et al., 2000; Maeder et al., 2001; Alain et al., 2001).

The involvement of PT in spatial analysis clearly does not represent the sole function of this large anatomical region considered as a whole. In humans, PT is activated bilaterally during the processing of various types of sounds that show complex variation of structure over time, including speech, music, and stimuli with speech-like spectro-temporal structure (Zatorre et al., 1992; Binder et al., 1996; Griffiths et al., 1998; Griffiths et al., 1999; Mummery et al., 1999; Binder et al., 2000; Giraud et al., 2000; Thivard et al., 2000). PT cannot, therefore, be regarded as a dedicated speech area. The present study suggests a specific role for PT in the analysis of spatial sound properties, in addition to its previously demonstrated involvement in the analysis of sounds with complex temporal structure. It is plausible that subregions within PT have different functions, as suggested by the activation of medial PT observed in the fMRI group data in Experiments 2 and 3 here. Comparison of the spectro-temporal minus external side and rotating

minus external side contrasts in Experiment 3 (Figures 4A and 4E) is consistent with a partial segregation of auditory spatial and spectro-temporal processing in medial and lateral PT, respectively. By inspection, a similar locus within right PT was identified in the study of Baumgart et al. (1999); however, coordinates of local maxima were not provided. Local maxima data for acoustic spectro-temporal processing in the present and previous studies are compared with the present data for sound-motion processing in Table 3. Taking the studies as a group, the locus of peak activation within PT produced by processing of intrinsic spectro-temporal structure lies more laterally than the activation produced by sound motion. Although such a comparison is context sensitive and qualitative, it is likely that the disparity would be even more marked were the convex geometry of PT taken into account.

Functional specialization within human PT would be consistent with electrophysiological findings in nonhuman primates. In the macaque, a similarly located area in the posterior supratemporal plane (the caudal belt region) has been implicated in the analysis of sound-source location (Leinonen et al., 1980; Recanzone,

Table 3. Locations of Peak Activations within Planum Temporale (PT) in Studies of Acoustic Spectro-Temporal Processing Compared with Motion Processing in the Present Study

Study	Modality	Key Contrast	Side	Coordinates of PT Peak Activation (mm)		
				x	y	z
Processing of Intrinsic Spectro-Temporal Structure:						
Binder et al., 1996	fMRI	tone sequences minus words	L	-55	-31	17
Griffiths et al., 1998b	PET	interaction between melody and degree of temporal structure	R	72	-40	6
Griffiths et al., 1999	PET	pitch/duration sequences minus silence	L	-58	-42	2
			R	66	-30	6
Griffiths et al., 1999	PET	pitch/duration sequences minus silence	L	-70	-28	4
			R	66	-30	6
Binder et al., 2000	fMRI	tone sequences minus noise	L	-59	-32	14
Giraud et al., 2000	fMRI	Conjunction of different AM rates in temporal envelope processing	R	62	-22	6
Thivard et al., 2000	PET	spectral motion versus stationary stimuli	L	-60	-28	8
			R	62	-30	12
Present study	fMRI	spectro-temporal control minus fixed external sound	L	-66	-16	8
			R	66	-24	12
Present study	fMRI	spectro-temporal control minus fixed external sound	L	-56	-32	12
			R	66	-24	12
Processing of Sound Motion:						
Present study	PET	Sound rotation minus stationary	R	60	-36	12
			L	-48	-32	8
Present study	fMRI	Sound rotation minus stationary	R	64	-24	12
			L	-42	-34	4

2000). More specifically, the caudal belt region (areas CM and CL) has been proposed to be the origin of a processing stream for auditory spatial information (Rauschecker, 1998; Rauschecker and Tian, 2000). The present study supports the role of human PT in auditory spatial analysis, similar to the macaque's caudal belt. However, the electrophysiological data also indicate that functional segregation within PT is not absolute: in addition to being highly selective for the spatial position of a complex sound (like most other caudal belt neurons), a certain subpopulation of neurons in CL also shows specificity for communication sounds (Tian et al., 2001).

It remains uncertain whether an auditory analog of visual area V5/MT exists, specialized for auditory motion processing. Using an uncorrected threshold ($p < 0.001$), we observed a consistent posterior parietal activation anterior to human V5/MT in the all-motion minus stationary sound contrast. However, this activation could not be demonstrated using the more stringent corrected threshold, and its biological significance remains unclear. By analogy with the MT/MST complex in the visual system, it is conceivable that additional cortical areas beyond the temporo-parietal pathway are involved in the perceptual processing of auditory motion.

Activation of frontal and superior parietal areas was inconsistently observed in the present experiments and in previous studies (Table 1). This variability may reflect a spatial attentional or movement preparation function for these areas that differs between techniques and paradigms. Similar activation in studies of visuospatial attention suggests that this activation may not be modality specific (Nobre et al., 1997; Coull and Nobre, 1998; Alain et al., 2001; see, however, Bushara et al., 1999, for modality-specific activation of parietal and frontal areas by virtual auditory space stimuli). The PET data in the current study show bilateral activation of the premotor cor-

tex. One prior imaging study has shown activation in a similar region using a stimulus that creates a sound field surrounding the head (Griffiths and Green, 1999). Potential pathways mediating the frontal activation seen in the PET experiment are suggested by anatomical tracer studies in the macaque, demonstrating both a direct projection (Romanski et al., 1999) and an indirect projection via parietal cortex (Lewis and Van Essen, 2000) from the caudal belt region to prefrontal areas implicated in spatial analysis. Taking these studies together, this activation may be interpreted as reflecting the coding of auditory space in a coordinate system suitable for movement preparation, as may occur in primate area PMv (Graziano et al., 1999).

Finally, we were interested to determine whether the first-order sound-movement property of fixed angular velocity and the second-order property of changing angular velocity might have distinct neuroanatomical substrates, in view of the fact that variable angular velocity relative to a source will be produced by head movements during the exploration of auditory space. The current data do not support this hypothesis. Rather, they show that both first- and second-order sound-movement properties are processed in the posterior temporo-parietal pathway. The current study was designed to address only the simplest scenario of a distinct neuroanatomical substrate; the finding of a shared anatomical framework raises the interesting possibility that the respective neural correlates of these properties may lie in specific patterns of activation or connectivity between PT, PTO, and IPL.

In summary, we have demonstrated a common, bilateral brain network including PT and PTO for the analysis of the sound-movement properties needed to encode the perception of movement in auditory space. Activation of this network is uniform across studies and imaging modalities and cannot be attributed simply to

spectro-temporal processing of complex sound sources nor to externalization of those sources in space. The findings are consistent with a posteriorly directed processing stream comprising PT, PTO, and IPL responsible for the obligatory perceptual processing of the movement of sound objects in space. We propose that the initial disambiguation of binaural and monaural spectro-temporal cues in medial PT enables the subsequent formation of a spatial percept at the level of the parieto-temporal junction.

Experimental Procedures

Subjects

Eight male subjects (seven right-handed, one left-handed) aged 23 to 42 were included in Experiment 1, nine right-handed subjects (five males, four females) aged 19 to 33 in Experiment 2, and twelve subjects (eight males, four females; eleven right-handed, one left-handed) aged 22 to 38 in Experiment 3. No subject had any history of hearing or neurological disorder, and all had normal structural MRI scans. The experiments were carried out with the approval of local ethics committees in London and Washington, D.C., and the PET studies carried out under certification from the Administration of Radioactive Substances Advisory Subcommittee (Department of Health, London, UK).

Stimuli and Task

Stimuli were created digitally at a sample rate of 44.1 kHz. The single-sound object was a fixed-amplitude spectrum, random-phase noise (passband 1 Hz–20 kHz) created in MATLAB 5.3. The noise was sinusoidally amplitude modulated at 80 Hz (modulation depth 80%) to produce an additional cue for spatial location and convolved with a generic HRTF (Wightman and Kistler, 1989) to create a virtual external acoustic stimulus. The generic HRTF used in these experiments does not allow the same spatial acuity as individual HRTFs (Hofman et al., 1998) but, nevertheless, reliably produced the required percept. The use of fixed HRTFs corresponding to one spatial location allowed the simulation of sounds at one point in space, and the use of dynamically updated HRTFs allowed simulation of movement of sounds in azimuth. During PET scanning (Experiment 1), digital recordings of the stimuli were delivered using pneumatic Etymotic insert earphones at a sensation level of 50 dB. During fMRI scanning, digital sound recordings were delivered using a custom pneumatic system for Experiment 2 and a custom electrostatic system for Experiment 3 (<http://www.ihr.mrc.ac.uk/caf/soundsystem/index.shtml>) at a sensation level of 50 dB. Presentation of the moving stimuli by all three delivery systems produced a percept of sound movement around the head at a distance of approximately 0.5 m.

In Experiments 1 and 2, four sound conditions corresponding to four different percepts were used: zero mean angular velocity, no change in angular velocity (object stationary in front of head); zero mean angular velocity, changing angular velocity (object moving from side-to-side in front of head); fixed mean positive angular velocity, no change in angular velocity (object rotating clockwise around head with constant speed); and fixed mean positive angular velocity, changing angular velocity (object rotating clockwise around head with variable speed). Positive mean angular velocity was fixed at 320°/s, and a change in angular velocity was produced by addition of a sinusoidal displacement of peak amplitude 50° and rate 1 Hz. In Experiment 3, four sound conditions corresponding to six different percepts were employed. Midline stimuli were amplitude-modulated broadband noise delivered binaurally in the midline, either at azimuth = 0° (object stationary in front of head) or 180° (object stationary behind head). Side stimuli were amplitude-modulated broadband noise delivered binaurally to the side of the head, either at azimuth = 90° (object stationary opposite right ear) or 270° (object stationary opposite left ear). A moving stimulus was created by convolution of amplitude-modulated noise with dynamically updated HRTFs to simulate a fixed mean positive angular velocity of 320°/s, as in Experiment 1 (object rotating clockwise around head with constant speed). A spectro-temporal control stimulus gener-

ated by taking the mean of the waveforms at each ear after convolving with the HRTF in the rotation condition and presenting this stimulus diotically (a sound with varying intensity over time, not localizing to a point in external space).

Before scanning, subjects were questioned about the stimuli to ensure that the different percepts were reliably experienced by all subjects. During scanning, subjects were required to fixate a cross-piece at the midpoint of the visual axes and listen for any change in the sound stimulus.

PET Paradigm and Analysis

Experiment 1 was conducted at the Wellcome Department of Imaging Neuroscience, London. Regional cerebral blood flow was measured during 12 scans for each subject using the oxygen 15 labeled water bolus technique and a Siemens/CPS ECAT Exact HR+ (962) scanner in 3D mode. Four scans were carried out for each condition. Group analysis for the eight subjects was carried out using statistical parametric mapping implemented in SPM99 software (<http://www.fil.ion.ucl.ac.uk/spm>). Scans were realigned and spatially normalized (Friston et al., 1995) to the standard stereotaxic space of Talairach (Talairach and Tournoux, 1988). Data were smoothed with an isotropic Gaussian kernel of 16 mm full width at half maximum (FWHM). Analysis of covariance was used to correct for differences in global blood flow between scans. Differences in blood flow between conditions were assessed with the *t* statistic at each voxel using a significance threshold of $p < 0.05$ after correction for multiple comparisons using Gaussian random field theory. The effect of sound motion was demonstrated by the contrast between the all-motion and stationary conditions (Table 2; Figures 1 and 2). The effect of second-order motion was assessed by the contrast between the changing and the fixed angular velocity conditions. This represents a “pure” contrast to determine the effect of rotation with changing velocity (second-order motion) compared to an appropriate control condition that still contains first-order motion with the same mean angular velocity. All subjects also underwent structural MRI.

fMRI Paradigm and Analysis

Experiment 2 was conducted at Georgetown University (Washington, D.C.) and Experiment 3 at the Wellcome Department of Imaging Neuroscience (London). In Experiment 2, blood oxygen level dependent (BOLD) contrast image volumes were acquired at 1.5 T (Siemens Vision, Erlangen) with gradient echo planar imaging (TR/TE = 12,000/40 ms). Each volume comprised 35 contiguous 4 mm slices with an in-plane resolution of 3.75 × 3.75 mm. 192 scans were acquired for each subject (48 volumes per condition) in two sessions using a sparse imaging paradigm (Hall et al., 1999) to maximize the difference between the BOLD response to the signal of interest and the response to scanner noise. In Experiment 3, BOLD contrast images were acquired at 2 T (Siemens Vision, Erlangen) with gradient echo planar imaging (TR/TE = 12,000/40 ms). Each volume comprised 48 contiguous 4 mm slices with an in-plane resolution of 3 × 3 mm. 128 scans were acquired for each subject (32 volumes per condition) in two sessions using a sparse paradigm. For both experiments, preprocessing and analysis were carried out using SPM99. Spatial smoothing was carried out using a filter with FWHM of 8 mm. Data were analyzed in each experiment by modeling the evoked hemodynamic response for the different stimuli as boxcar functions in the context of the general linear model. In Experiment 2, a fixed-effects model was used to analyze the same group contrasts as in the PET experiment (between the all-motion and stationary conditions and between the second-order and first-order motion conditions) at the same corrected significance level of $p < 0.05$ (Table 2; Figures 1 and 2). Analyses were also carried out for the individual subjects (Figure 3). In Experiment 3, a fixed-effects model was also used to analyze the contrasts between rotating, external fixed midline and side and spectro-temporal control conditions and analyzed at the same corrected significance level of $p < 0.05$ (Table 2; Figure 4).

Acknowledgments

J.D.W. and T.D.G. are supported by the Wellcome Trust. B.A.Z. and J.P.R. are supported by NIH grants F31-MH-12598 and R01-DC-

03489, respectively. We thank three anonymous reviewers for their valuable suggestions.

Received: August 22, 2001

Revised: January 24, 2002

References

- Ahissar, M., Ahissar, E., Bergman, H., and Vaadia, E. (1992). Encoding of sound source location and movement: activity of single neurons and interactions between adjacent neurons in the monkey auditory cortex. *J. Neurophysiol.* *67*, 203–215.
- Alain, C., Arnott, S.R., Hevenor, S., Graham, S., and Grady, C.L. (2001). 'What' and 'where' in the human auditory system. *Proc. Natl. Acad. Sci. USA* *98*, 12301–12306.
- Attias, H., and Schreiner, C.E. (1998). Blind source separation and deconvolution: the dynamic component analysis algorithm. *Neural Comput.* *10*, 1373–1424.
- Baumgart, F., Gaschler-Markefski, B., Woldorff, M.G., Heinze, H.-J., and Scheich, H. (1999). A movement-sensitive area in auditory cortex. *Nature* *400*, 724–726.
- Bell, A.J., and Sejnowski, T.J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural Comput.* *7*, 1129–1159.
- Binder, J.R., Frost, J.A., Hammeke, T.A., Rao, S.M., and Cox, R.W. (1996). Function of the left planum temporale in auditory and linguistic processing. *Brain* *119*, 1239–1247.
- Binder, J.R., Frost, J.A., Hammeke, T.A., Bellgowan, P.S.F., Springer, J.A., Kaufman, J.N., and Possing, E.T. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cereb. Cortex* *10*, 512–528.
- Bremmer, F., Schlack, A., Shah, N.J., Zafiris, O., Kubischik, M., Hoffmann, K.-P., Zilles, K., and Fink, G.R. (2001). Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron* *29*, 287–296.
- Bushara, K.O., Weeks, R.A., Ishii, K., Catalan, M.J., Tian, B., Rauschecker, J.P., and Hallett, M. (1999). Modality-specific frontal and parietal areas for auditory and visual spatial localization in humans. *Nat. Neurosci.* *2*, 759–766.
- Clarke, S., Bellmann, A., Meuli, R.A., Assal, G., and Steck, A.J. (2000). Auditory agnosia and auditory spatial deficits following left hemisphere lesions: evidence for distinct processing pathways. *Neuropsychologia* *38*, 797–807.
- Coull, J.T., and Nobre, A.C. (1998). Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J. Neurosci.* *18*, 7426–7435.
- Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.-B., Heather, J.D., and Frackowiak, R.S.J. (1995). Spatial registration and normalisation of images. *Hum. Brain Mapp.* *2*, 165–169.
- Frith, C., Perry, R., and Lumer, E. (1999). The neural correlates of conscious experience: an experimental framework. *Trends Cogn. Sci.* *3*, 105–114.
- Galaburda, A., and Sanides, F. (1980). Cytoarchitectonic organization of the human auditory cortex. *J. Comp. Neurol.* *190*, 597–610.
- Giraud, A.L., Lorenzi, C., Ashburner, J., Wable, J., Johnsrude, I., Frackowiak, R.S.J., and Kleinschmidt, A. (2000). Representation of the temporal envelope of sounds in the human brain. *J. Neurophysiol.* *84*, 1588–1598.
- Graziano, M.S.A., Reiss, L.A., and Gross, C.G. (1999). A neuronal representation of the location of nearby sounds. *Nature* *397*, 428–430.
- Griffiths, T.D., and Green, G.G.R. (1999). Cortical activation during perception of a rotating wide-field acoustic stimulus. *Neuroimage* *10*, 84–90.
- Griffiths, T.D., Bench, C.J., and Frackowiak, R.S.J. (1994). Cortical areas in man selectively activated by apparent sound movement. *Curr. Biol.* *4*, 892–895.
- Griffiths, T.D., Rees, A., Witton, C., Shakir, R.A., Henning, G.B., and Green, G.G.R. (1996). Evidence for a sound movement area in the human cerebral cortex. *Nature* *383*, 425–427.
- Griffiths, T.D., Rees, G., Rees, A., Green, G.G.R., Witton, C., Rowe, D., Büchel, C., Turner, R., and Frackowiak, R.S.J. (1998a). Right parietal cortex is involved in the perception of sound movement in humans. *Nat. Neurosci.* *1*, 74–79.
- Griffiths, T.D., Büchel, C., Frackowiak, R.S.J., and Patterson, R.D. (1998b). Analysis of temporal structure in sound by the human brain. *Nat. Neurosci.* *1*, 422–427.
- Griffiths, T.D., Johnsrude, I., Dean, J.L., and Green, G.G.R. (1999). A common neural substrate for the analysis of pitch and duration pattern in segmented sound? *Neuroreport* *18*, 3825–3830.
- Griffiths, T.D., Green, G.G.R., Rees, A., and Rees, G. (2000). Human brain areas involved in the perception of auditory movement. *Hum. Brain Mapp.* *9*, 72–80.
- Hall, D.A., Haggard, M.P., Akeroyd, M.A., Palmer, A.R., Summerfield, A.Q., Elliott, M.R., Gurney, E.M., and Bowtell, R.W. (1999). "Sparse" temporal sampling in auditory fMRI. *Hum. Brain Mapp.* *7*, 213–223.
- Hofman, P.M., Riswick, J.G.A., and van Opstal, A.J. (1998). Relearning sound localisation with new ears. *Nat. Neurosci.* *1*, 417–421.
- Leinonen, L., Hyvärinen, J., and Sovijärvi, A.R.A. (1980). Functional properties of neurons in the temporo-parietal association cortex of awake monkey. *Exp. Brain Res.* *39*, 203–215.
- Lewis, J.W., and Van Essen, D.C. (2000). Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *J. Comp. Neurol.* *428*, 112–137.
- Lewis, J.W., Beauchamp, M.S., and DeYoe, E.A. (2000). A comparison of visual and auditory motion processing in human cerebral cortex. *Cereb. Cortex* *10*, 873–888.
- Maeder, P.P., Meuli, R.A., Adriani, M., Bellmann, A., Fornari, E., Thiran, J.P., Pittet, A., and Clarke, S. (2001). Distinct pathways involved in sound recognition and localization: a human fMRI study. *Neuroimage* *14*, 802–816.
- Mummery, C.J., Ashburner, J., Scott, S.K., and Wise, R.J.S. (1999). Functional neuroimaging of speech perception in six normal and two aphasic subjects. *J. Acoust. Soc. Am.* *106*, 449–457.
- Nobre, A.C., Sebeten, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiak, R.S.J., and Frith, C.D. (1997). Functional localisation of the system for visiospatial attention using positron emission tomography. *Brain* *120*, 515–533.
- Penhune, V.B., Zatorre, R.J., MacDonald, J.D., and Evans, A.C. (1996). Interhemispheric anatomical differences in human primary auditory cortex: probabilistic mapping and volume measurement from magnetic resonance scans. *Cereb. Cortex* *6*, 661–672.
- Rademacher, J., Morosan, P., Schormann, T., Schleicher, A., Werner, C., Freund, H.J., and Zilles, K. (2001). Probabilistic mapping and volume measurement of human primary auditory cortex. *Neuroimage* *13*, 669–683.
- Rauschecker, J.P. (1998). Cortical processing of complex sounds. *Curr. Opin. Neurobiol.* *8*, 516–521.
- Rauschecker, J.P., and Tian, B. (2000). Mechanisms and streams for processing of "what" and "where" in auditory cortex. *Proc. Natl. Acad. Sci. USA* *97*, 11800–11806.
- Recanzone, G.H. (2000). Spatial processing in the auditory cortex of the macaque monkey. *Proc. Natl. Acad. Sci. USA* *97*, 11829–11835.
- Romanski, L.M., Tian, B., Fritz, J., Mishkin, M., Goldman-Rakic, P.S., and Rauschecker, J.P. (1999). Dual streams of auditory afferents target multiple domains in the primate prefrontal cortex. *Nat. Neurosci.* *2*, 1131–1136.
- Talairach, P., and Tournoux, J. (1988). *A Stereotactic Coplanar Atlas of the Human Brain* (Stuttgart: Thieme).
- Thivard, L., Belin, P., Zilbovicius, M., Poline, J.-B., and Samson, Y. (2000). A cortical region sensitive to auditory spectral motion. *Neuroreport* *11*, 2969–2972.
- Tian, B., Reser, D., Durham, A., Kustov, A., and Rauschecker, J.P. (2001). Functional specialization in rhesus monkey auditory cortex. *Science* *292*, 290–293.

Tootell, R.B., Reppas, J.B., Kwong, K.K., Malach, R., Born, R.T., Brady, T.J., Rosen, B.R., and Belliveau, J.W. (1995). Functional analysis of human cortical area MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.* *15*, 3215–3230.

Toronchuk, J.M., Stumpf, E., and Cynader, M.S. (1992). Auditory cortex neurons sensitive to correlates of auditory motion: underlying mechanisms. *Exp. Brain Res.* *88*, 169–180.

Watson, J.D.G., Myers, R., Frackowiak, R.S.J., Hajnal, J.V., Woods, R.P., Mazziotta, J.C., Shipp, S., and Zeki, S. (1993). Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cereb. Cortex* *3*, 79–94.

Wightman, F.L., and Kistler, D.J. (1989). Headphone simulation of free-field listening. I: stimulus synthesis. *J. Acoust. Soc. Am.* *85*, 858–867.

Zakarauskas, P., and Cynader, M.S. (1991). Aural intensity for a moving source. *Hear. Res.* *52*, 233–44.

Zatorre, R.J., Evans, A.C., Meyer, E., and Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science* *256*, 846–849.