

Assessing the auditory dual-pathway model in humans

Stephen R. Arnott,^{a,b,*} Malcolm A. Binns,^a Cheryl L. Grady,^{a,b,c} and Claude Alain^{a,b}

^aRotman Research Institute, Baycrest Centre for Geriatric Care, Toronto, ON, Canada M6A 2E1

^bDepartment of Psychology, University of Toronto, Toronto, ON, Canada M8V 2S4

^cFaculty of Medicine (Psychiatry), University of Toronto, Toronto, ON, Canada M5S 1A8

Received 16 October 2003; revised 14 January 2004; accepted 14 January 2004

Evidence from anatomical and neurophysiological studies in nonhuman primates suggests a dual-pathway model of auditory processing wherein sound identity and sound location information are segregated along ventral and dorsal streams, respectively. The present meta-analysis reviewed evidence from auditory functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies to determine the reliability of this model in humans. Activation coordinates from 11 “spatial” studies (i.e., listeners made localization judgements on sounds that could occur at two or more perceptually different positions) and 27 “nonspatial” studies (i.e., listeners completed nonspatial tasks involving sounds presented from the same location) were entered into the analysis. All but one of the spatial studies reported activation within the inferior parietal lobule as opposed to only 41% of the nonspatial studies. In addition, 55% of spatial studies reported activity around the superior frontal sulcus as opposed to only 7% of the nonspatial studies. In comparison, inferior frontal activity (Brodmann’s areas 45 and 47) was reported in only 9% of the spatial studies, but in 56% of the nonspatial studies. Finally, almost all temporal lobe activity observed during spatial tasks was confined to posterior areas, whereas nonspatial activity was distributed throughout the temporal lobe. These results support an auditory dual-pathway model in humans in which nonspatial sound information (e.g., sound identity) is processed primarily along the ventral stream whereas sound location is processed along the dorsal stream and areas posterior to primary auditory cortex.

Published by Elsevier Inc.

Keywords: Auditory scene analysis; fMRI; Meta-analysis; Nonspatial; PET; Spatial

Over the past decade, animal studies provided shed insight into the functional organization of the auditory system. Single-cell recordings and neuroanatomical tracer studies on nonhuman primates have described a primary auditory cortex that is surrounded by a ‘belt’ area, which is in turn bordered laterally by a ‘parabelt’ region (Hackett et al., 1998; Kosaki et al., 1997; Morel et al., 1993; Rauschecker et al., 1995, 1997). Whereas the core area responds

best to simple auditory stimuli, neurons in the belt and parabelt regions respond best to more complex sounds (e.g., vocalizations and bands of noise) (Rauschecker et al., 1995). Interestingly, beginning at the level of the belt area, rostral and caudal regions are functionally distinct with caudal but not rostral neurons being sensitive to locations of sounds (Benson et al., 1981; Hackett et al., 1998; Kaas and Hackett, 2000; Leinonen et al., 1980; Morel et al., 1993; Rauschecker, 1998; Rauschecker et al., 1995; Tian et al., 2001; Vaadia et al., 1986).

Elegant studies by Romanski et al. (1999a,b) as well as Hackett et al. (1999) have extended this knowledge, revealing reciprocal connections from the caudal parabelt regions, out to the posterior parietal cortex as well as forward into the caudal principal sulcus (area 46) and frontal eye fields (area 8a). By comparison, the rostral belt region has connections with the frontal pole (area 10), rostral principal sulcus (area 46), and ventral prefrontal areas (areas 12 and 45) (Romanski and Goldman-Rakic, 2002). Together, these results detail a domain-specific model of auditory processing whereby auditory spatial (i.e., “where”) and nonspatial (i.e., “what”) information are processed by dorsal and ventral brain areas, respectively (Rauschecker and Tian, 2000).

One question that emerges from this research is whether this auditory model is applicable to humans. Several positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies support such a model (Alain et al., 2001; Belin and Zatorre, 2000; Belin et al., 2000; Bushara et al., 1999; Maeder et al., 2001; Weeks et al., 1999; Zatorre et al., 2002). For example, in a previous study (Alain et al., 2001), processing the location of noise bursts elicited relatively greater parietal and superior prefrontal activity than did processing the pitch of the noise bursts. In contrast, pitch processing resulted in relatively greater superior temporal and inferior frontal activity. Such results, in conjunction with human lesion data (Clarke et al., 2000; Thiran and Clarke, 2003), are consistent with the proposal that the human auditory system can be functionally segregated into “what” and “where” pathways.

In the present meta-analysis, we analyzed the findings from the last 10 years of human auditory PET and fMRI imaging studies to further evaluate the dual-pathway model in humans. We focused on the five brain regions of interest as described by the Rauschecker model (Rauschecker and Tian, 2000): the inferior parietal lobe, the anterior and posterior regions of the temporal lobes, the inferior frontal lobe, and the dorsal frontal lobe around the region of the superior frontal sulcus.

* Corresponding author. Rotman Research Institute, Baycrest Centre for Geriatric Care, 3560 Bathurst Street, Toronto, ON, Canada M6A 2E1. Fax: +1-416-785-2862.

E-mail address: sarnott@rotman-baycrest.on.ca (S.R. Arnott).

Available online on ScienceDirect (www.sciencedirect.com).

Materials and methods

We searched peer-reviewed articles for auditory studies that incorporated either PET or fMRI recordings. With the exception of one spatial study on congenitally blind adults (Weeks et al., 2000), only studies that used normal, healthy adults and reported coordinates in Talairach space (Talairach and Tournoux, 1988) were included in the meta-analysis. In an attempt to reduce the influence of publication biases where spatial and nonspatial hypotheses motivate the research, only studies that imaged the entire brain were included. All studies were then categorized as either spatial or nonspatial. Nonspatial studies were those that presented sounds from only one location while listeners actively assessed the stimuli for nonspatial features. Spatial studies were those that presented sounds at multiple locations and the listener's task involved making relative spatial judgments. Studies presenting sounds at multiple locations, but involving tasks that required nonspatial judgements, were considered ambiguous and were not analyzed. Accordingly, 36 studies spanning January 1993 to August 2003 were used. Including the two studies that contained both spatial and nonspatial data, the total number of spatial and nonspatial studies was 11 and 27, respectively (see Table 1). Despite differences in methodology, statistical analysis, and threshold cutoff adopted by each study, all reported foci were entered in the meta-analysis so long as the foci reflected a significant increase in activation relative to a reference task.

Coregistering data points

One difficulty with any meta-analysis of neuroimaging data is that different software packages use different sized brain templates. As a result, the same brain coordinate may correspond to physically different brain locations in different studies. Among the two most commonly used templates, the Talairach and the Montreal Neurological Institute (MNI) templates, discrepancies as large as 10 mm can exist (Brett et al., 2002). For this reason, any study that used image-processing software based on the MNI template (e.g., SPM96 and SPM99; Friston et al., 1995) and did not explicitly report transforming the data to a Talairach template (Talairach and Tournoux, 1988) were subjected to a linear MNI-to-Talairach transformation (Brett et al., 2002; Brett, <http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml>). For x (left to right), y (anterior to posterior), and z (superior to inferior) coordinates located at or above the anterior commissure (i.e., $z \geq 0$), the transformation was as follows: $x' = 0.9900x$; $y' = 0.9688y + 0.0460z$; $z' = -0.0485y + 0.9189z$ (where ' denotes the transformed variable). For coordinates located below the anterior commissure (i.e., $z < 0$), the transformation was as follows: $x' = 0.9900x$; $y' = 0.9688y + 0.0420z$; $z' = -0.0485y + 0.8390z$. When applied to a superior temporal gyrus location of (64, -18, -2), for example, the resulting transformed coordinates would be (63.4, -17.5, -0.8).

Defining brain regions

The boundaries of brain regions of interest (i.e., inferior parietal lobe; temporal lobe including the superior temporal gyrus, middle temporal gyrus, inferior temporal gyrus, and transverse temporal gyrus; and inferior frontal lobe including BAs 44, 45, and 47) were determined using the Talairach Daemon atlas

function (Talairach and Tournoux, 1988) included in the Analysis of Functional NeuroImages software (AFNI version 2.50; Cox and Hyde, 1997). This AFNI option approximates three-dimensional brain regions called 'masks' based on the San Antonio Talairach Daemon database provided by J. Lancaster and P. Fox of RIC UTHSCSA (for more detail, see <http://afni.nimh.nih.gov/afni/TT/>). To compensate for errors in localization, measurement, and the possibility of double transformations, each activation coordinate was enlarged 1 mm radially so that it covered a 27-mm³ volume. All coordinates were then filtered through the masks using AFNI's '3Ddump98' function. A coordinate was considered to be located within a brain region of interest as long as the intersection of the enlarged activation volume and the region of interest was at least 1 mm³.

Data analysis

Our method of analysis was similar to that adopted by others (e.g., D'Esposito et al., 1998; Phan et al., 2002; Schacter and Wagner, 1999). A study that reported at least one coordinate of activity within a given region of interest was counted as one observation, irrespective of the brain label that had been assigned to that activation, the number of participants in the study, the significance level, or the extent of the activation. To investigate whether the proportion of spatial tasks in a given region was different from the proportion of nonspatial tasks within that same region, we calculated a Fisher exact test on the 2 × 2 contingency table.

Results and discussion

Table 1 and Fig. 1 summarize the data used in the meta-analysis. Fig. 2 summarizes the findings.

Inferior parietal lobe

The human parietal lobe is a functionally heterogeneous region, subserving a wide range of functions related to attention, motion processing, stereo vision, and spatial and nonspatial working memory (Culham and Kanwisher, 2001). Single-unit research in monkeys suggests that the lateral inferior parietal lobe (IPL) is particularly important during auditory spatial working memory tasks (Mazzoni et al., 1996; Stricanne et al., 1996) and the same may be true for humans (Hall et al., 2003).

In our analysis, 10 of the 11 spatial studies (but only 11 of the 27 nonspatial studies) reported Talairach coordinates within the IPL. Fisher's exact test ($P = 0.01$) confirmed that the spatial tasks had significantly more studies reporting IPL activity. This suggests that the IPL, while not being exclusively related to spatial processing, is a necessary component for human auditory spatial processing. The one spatial study that did not report IPL activity (Zatorre et al., 1999) did report a nearby coordinate in the superior parietal lobule (see Fig. 1).

There did not appear to be any hemispheric lateralization in these spatial processing tasks. Of the 10 spatial studies that reported inferior parietal activity, 50.0%, 20.0%, and 30.0% reported bilateral, right hemisphere only, and left hemisphere activity only, respectively. For the 11 nonspatial studies, the proportions were 81.8%, 9.1%, and 9.1%, respectively.

Table 1
Summary of studies

Study	<i>N</i>	Task	Contrast task	Type	IPL	SFS	aT	pT	IFG
Alain (2001)	fMRI	12	delay match location comparison	silence or pitch comparisons	SP	✓	✓	✓	
Bushara et al. (1999)	PET	9	count and indicate noise burst locations	passive listening to noise burst locations	SP	✓		✓	
Griffiths et al. (1998)	fMRI	3	indicate direction of moving broadband noise	stationary noise (in phase)	SP	✓	✓		
Griffiths and Green (1999)	PET	6	report “changes” (i.e., movement) of noise	stationary noise (in phase)	SP	✓		✓	
Lipschutz et al. (2002)	PET	10	repeat syllables occurring in specific ear	repeat binaurally presented sounds	SP	✓	✓		✓
Maeder et al. (2001)	fMRI	18	detect location differences in noise bursts	respond to ‘animals’ among natural sounds	SP	✓			
Martinkauppi et al. (2000)	fMRI	10	sound location 3—back task	sound location 1—back task	SP	✓	✓		✓
Weeks et al. (2000)	PET	9	same or different location judgement	silence	SP	✓	✓		
Weeks et al. (1999)	PET	9	same or different location judgement (Exp. 1)	silence or passive listening	SP	✓			✓
Zatorre et al. (2002)	PET	12	indicate sound location (Exp. 3)	passive listening	SP	✓	✓		✓
Zatorre et al. (1999)	PET	8	respond to any sound at a specific location	silence	SP			✓	
Becker et al. (1994)	PET	12	repeat words aloud	silence	NS			✓	✓
Benedict et al. (1998)	PET	7	active listening to syllables	silence or passive listening to syllables	NS				
Benedict et al. (2002)	PET	12	actively discriminating vowels	passive listening	NS			✓	
Buchanan et al. (2000)	fMRI	10	respond to target words spoken with emotion	respond to phonetic target words	NS			✓	✓
Burton et al. (2003)	fMRI	8	identify semantic or phonetic target words	identify phonetic or semantic target words	NS			✓	✓
Caplan et al. (1999)	PET	16	indicate sentence’s syntactic structure	easier version of syntactic structure task	NS				
Chee et al. (1999)	fMRI	8	semantic or nonsemantic word task	silence	NS	✓		✓	
Frey et al. (2000)	PET	11	rate pleasantness of unpleasant sounds	rate pleasantness of pleasant sounds	NS			✓	✓
Gandour et al. (2000)	PET	5	discriminate pitch or patterns	silence or pattern or pitch discriminations	NS			✓	
Gandour et al. (2002)	fMRI	10	pitch and duration discriminations	passive listening	NS	✓		✓	
Grasby et al. (1993)	PET	18	recall words previously read aloud	silence	NS				
Kiehl et al. (2001)	fMRI	10	respond to frequency target tone sweeps	listening to nontarget tones	NS	✓		✓	✓
Klein et al. (2001)	PET	12	word discrimination	silence	NS	✓		✓	✓
Linden et al. (1999)	fMRI	5	count or button press to frequency deviants	nondeviant stimuli	NS	✓		✓	✓
Maddock et al. (2003)	fMRI	8	evaluate the valence of emotional words	evaluate the valence of nonemotional words	NS			✓	✓
Maeder et al. (2001)	fMRI	18	respond to ‘animals’ among natural sounds	detect location differences in noise bursts	NS	✓		✓	✓
Muller et al. (2001)	fMRI	7	detect tones with rising frequency	detect white noise	NS			✓	✓
Opitz et al. (2000)	fMRI	20	encoding or recognition of verbal information	encoding or recognition of nonverbal information	NS				
Pedersen et al. (2000)	PET	5	duration and word discriminations	silence	NS	✓			✓
Platel et al. (1997)	PET	6	semantic/timbre/duration judgements	pitch or rhythm judgements	NS			✓	✓
Salvi et al. (2002)	PET	10	repeat last word of sentence	silence	NS			✓	
Stevens et al. (2000)	fMRI	10	detect frequency deviants of tones	(visual) detect letter deviants; silence	NS	✓		✓	✓
Tranel et al. (2003)	PET	10	identifying animal sounds	identifying tonal sounds	NS	✓			✓
Weeks et al. (1999)	PET	8	delay match frequency comparison (Experiment 2)	silence	NS				
Zald and Pardo (2002)	PET	8	listen to aversive sounds	listen to white noise	NS			✓	✓
Zatorre et al. (1994)	PET	12	pitch comparisons	passively listen to melodies	NS	✓	✓		✓
Zatorre et al. (1998)	PET	20	indicate musical interval between sound pairs	button press to noise bursts	NS	✓	✓		✓

N = number of participants; NS = nonspatial task; SP = spatial task; IPL = inferior parietal lobule; SFS = superior frontal sulcus; aT = anterior temporal lobe ($y > -10$ mm); pT = posterior temporal lobe ($y < -30$ mm); IFG = inferior frontal gyrus (Brodmann’s areas 45 and 47).

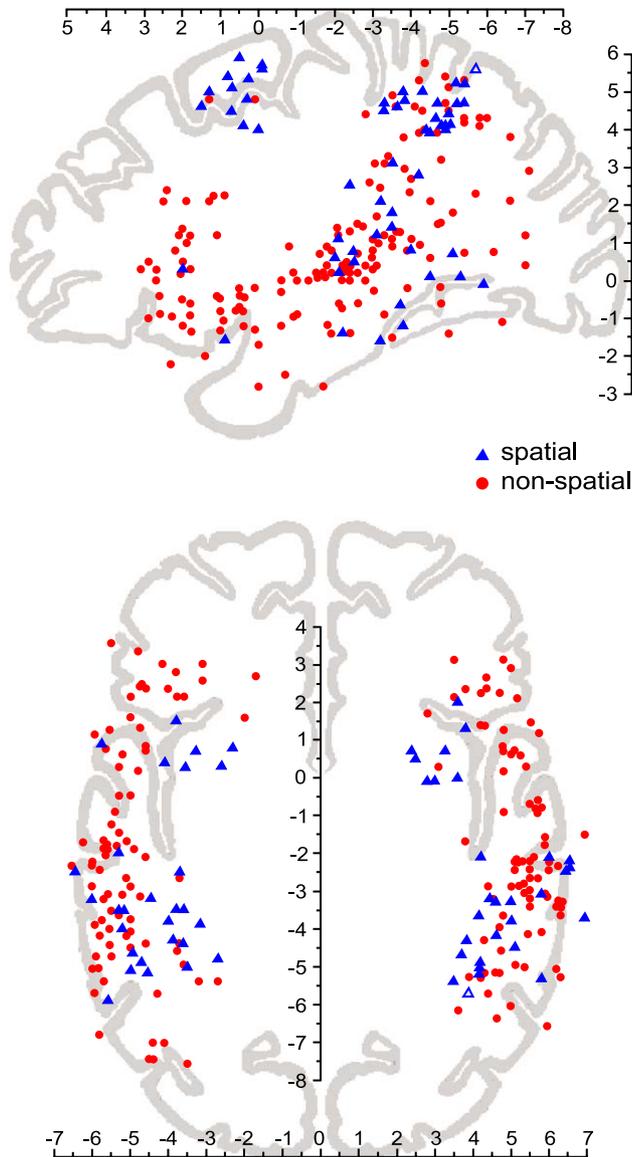


Fig. 1. Sagittal and axial views of all spatial (blue triangles) and nonspatial (red spheres) data plotted in Talairach space within each of the five brain regions. Sagittal ($x = +29$ mm) and axial ($z = -4$ mm) Talairach images are displayed for reference. The open blue triangle represents the superior parietal lobule data from Zatorre et al. (1999).

Superior frontal sulcus

Monkey research has revealed dorsofrontal neurons around the periarculate area that are sensitive to variations in sound location (Azuma and Suzuki, 1984; Vaadia et al., 1986) and visual object location (Funahashi et al., 1989). Based on anatomical landmarks, Courtney et al. (1998) have hypothesized that the human correlate to the monkey spatial area lies within area 6, near the superior frontal sulcus (SFS). In support of this, these authors have demonstrated that a visual spatial working memory task elicits delay-dependent activity within the SFS that is independent from eye-movement-related activity. Other human visual studies involving spatial working memory have reported similar activity (Haxby et al., 1994; Jonides et al., 1993), and our previous results suggest

that this may also be the case for auditory localization tasks (Alain et al., 2001).

Based on the results of Courtney et al. (1998), we defined our second region of interest to be anterior to the frontal eye fields (FEF), encompassing the SFS. Because none of the auditory spatial studies that we reviewed localized the FEF, we estimated the FEF boundary based on a previous meta-analysis of FEF research (Paus, 1996). In that review, the human FEF were found to be consistently located within the region of the precentral sulcus and/or in the caudal-most part of the superior frontal sulcus (within a rostral-caudal boundary of -6 to 1 mm, a dorsoventral boundary of 44 to 51 mm, and a mediolateral boundary of about -21 to -40 mm). Accordingly, we defined our spatial frontal region as $x = -40$ to -20 mm or 20 to 40 mm, $y = 0$ to 20 mm, and $z = 40$ to 60 mm. These boundaries encompassed the caudal portion of the superior frontal sulcus while excluding most of the FEF.

Within this region, 6 of the 11 spatial but only 2 of the 27 nonspatial studies reported significant activity. Fisher's test ($P < 0.01$) confirmed that there was significantly greater proportion of spatial-related activations in this area. Of note was the observation that all of the studies that reported SFS activity including the two nonspatial studies also reported IPL activity.

As was the case for the IPL activity, there did not appear to be any hemispheric bias associated with the SFS activity. Bilateral, only right hemisphere, and only left hemisphere activity were present in 50.0%, 33.3%, and 16.7% of the spatial studies, respectively. In terms of the two nonspatial studies, one reported only left hemisphere activity and the other reported only right hemisphere activity.

Inferior frontal lobe

We next examined the inferior frontal lobe, which according to the animal model (Rauschecker and Tian, 2000) is part of the nonspatial processing network. Specifically, we examined Brodmann's areas 45 and 47 (note that with the exception of one data point that lay on the border of BAs 44 and 45, there were no BA 44 activations). In support of the model, Fisher's test revealed

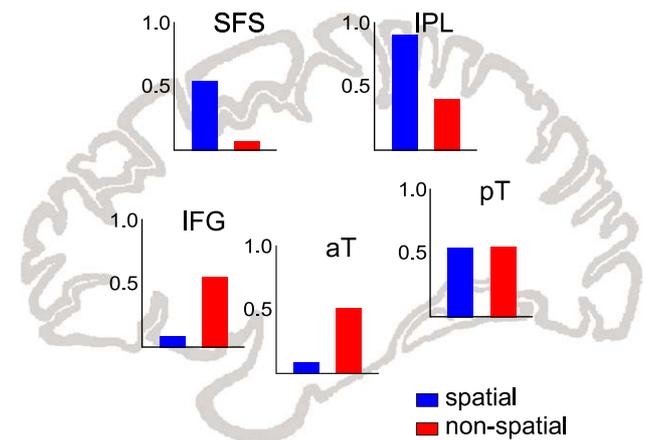


Fig. 2. Proportion of spatial and nonspatial auditory studies reporting activity in each of the five brain regions: SFS= superior frontal sulcus; IPL = inferior parietal lobule; aT = anterior temporal lobe ($y > -10$ mm); pT = posterior temporal lobe ($y < -30$ mm); IFG= inferior frontal gyrus (Brodmann's areas 45 and 47).

significantly more nonspatial than spatial activations in this region ($P = 0.01$). Only 1 of the 11 spatial studies reported activity in the inferior frontal lobe, whereas 15 of the 27 nonspatial studies reported such activity.

The inferior frontal activity that was reported in the lone spatial study was in the right hemisphere. Of the 15 nonspatial studies that reported activity in the inferior frontal cortex, 33.3% reported bilateral activity, 26.7% reported only right hemisphere activity, and 40.0% reported only left hemisphere activity.

Temporal lobe

As described earlier, the lateral belt of the monkey auditory cortex appears to be functionally organized such that rostral areas are more specialized for processing sound identities (e.g., differentiating species-specific vocalizations) whereas the caudal portion seems specialized for processing the location of a sound (Rauschecker and Tian, 2000; Tian et al., 2001). Recent fMRI data of the area along the superior temporal plane posterior to Heschl's gyrus (i.e., the planum temporale) support a similar dissociation in humans, though the segregation appears to be better described as rostralateral–caudomedial (Warren and Griffiths, 2003). It is not yet clear what specific role posterior temporal areas play in auditory spatial processing. For example, posterior temporal area activity has been found to covary with the amount of variation in sound location but only when complex sounds are played simultaneously (i.e., overlapping in time) and not when they are played sequentially (Zatorre et al., 2002). One recent hypothesis suggests that the planum temporale acts as a 'computational hub' where spatial information is disambiguated from object information (Griffiths and Warren, 2002).

We first examined temporal areas anterior to the primary auditory cortex (i.e., $y > -10$ mm). In that region, activity was reported in only 1 of the 11 spatial studies. In contrast, half (13 of 27) of the nonspatial studies reported anterior temporal activity. Fisher's test supported the claim that this area does not seem to be important for spatial processing ($P < 0.05$). This is consistent with reports that auditory spatial function in humans is not compromised by anterior temporal lesions (Clarke et al., 2000). On the other hand, temporal regions posterior to the primary auditory cortex (i.e., $y < -30$ mm) were active in both types of studies. In that case, roughly half of each type of group reported posterior temporal activity: 6 of 11 spatial studies and 15 of 27 nonspatial studies (see Fig. 2). Note also that the results remained similar when only the superior temporal gyrus was examined. In that case, only 1 of the 11 spatial studies but 11 of the 27 nonspatial studies reported anterior temporal activity whereas an equal proportion of spatial and nonspatial studies reported posterior temporal activity (36% and 37%, respectively). Whereas superior temporal spatial activity was confined to a relatively narrow anterior–posterior range of cortex (85% of the spatial data were confined to y values between -20 and -35 mm), nonspatial activity was found throughout the length of the superior temporal gyrus (85% of the nonspatial activations occurred between y values of 6 and -40 mm).

Among the nonspatial studies that reported anterior temporal activity, 53.8% reported bilateral, 38.5% reported only right hemisphere, and 7.7% reported only left hemisphere activity. The activation from the lone spatial study was in the left hemisphere. With regard to laterality effects in posterior temporal areas, the proportion of nonspatial studies reporting bilateral, right-side only, and left-side only posterior temporal activity was 46.6%, 26.7%,

and 26.7%, respectively. The corresponding proportions of posterior temporal spatial activations were 83.3% bilateral and 16.7% right hemisphere only. No spatial studies reported activity in the left hemisphere only.

We were also interested in examining the hypothesis that a caudomedial (spatial)–rostralateral (nonspatial) functional dissociation exists within the planum temporale of the posterior superior temporal gyrus (Warren and Griffiths, 2003). Although there is a lack of consistency concerning the precise boundary of the planum temporale, quantitative analysis indicates that the region is more anterior in the right hemisphere as compared to the left (Westbury et al., 1999). Based on Westbury's findings, we defined our area to be located within the superior temporal gyrus, along a y -axis range of -10 to -55 mm (left hemisphere) and -5 to -40 mm (right hemisphere). We then ran separate left and right hemispheric t tests, comparing spatial and nonspatial activations along the x -, y -, and z -axes. To ensure that no one study had any undue influence on the results, each data point was weighted according to the number of left or right planum temporale coordinates reported in each study. Results showed that neither hemisphere demonstrated significant spatial versus nonspatial differences along the y -axis (P 's > 0.40) or z -axis (superior–inferior; P 's > 0.10). However, significant medial–lateral differences were found within the left hemisphere ($P < 0.005$) with spatial tasks eliciting more medial activations (mean $x = -46.4$ mm) than nonspatial (mean $x = -56.6$ mm). No such difference was found in the right hemisphere ($P > 0.80$).

Baseline and linguistic effects

As a final consideration, we limited our analysis to studies that used an auditory control task rather than a silent baseline. We also reanalyzed the data according to whether nonlinguistic stimuli were used. The former analysis allowed us to rule out the possibility that simple auditory (sensory) processing influenced our results as oppose to auditory spatial or nonspatial processing per se. The latter analysis investigated whether the nonspatial and spatial differences that we found could be accounted for by the fact that there were disproportionately more nonspatial tasks using linguistic stimuli.

Except for two of the temporal region analyses, the results remained largely the same for the baseline analysis. Nine of the 11 spatial studies contained auditory stimuli in their baseline tasks, and the resulting analysis revealed that 8 (88.9%), 5 (55.6%), 1 (11.1%), 1 (11.1%), and 4 (44.4%) of those studies demonstrated IPL, SFS, IFG, anterior temporal, and posterior temporal areas, respectively. Of the 17 nonspatial studies that controlled for sound stimulation in their baseline condition, the proportions were 6 (35.3%), 2 (11.8%), 10 (58.8%), 6 (35.3%), and 9 (52.9%) for areas IPL, SFS, IFG, anterior temporal, and posterior temporal, respectively. Thus, relative to the previous analyses, the only changes that were greater than 10 percentage points occurred in the spatial posterior temporal analysis (the proportion of activity decreased when sound stimulation was controlled for) and the nonspatial anterior temporal analysis (the proportion of activity decreased when sound stimulation was controlled for).

Examining the experimental tasks in each of the experiments (Table 1) reveals a potential confound in the data. While only 1 of the 11 spatial studies presented linguistic stimuli, approximately half of the nonspatial studies used linguistic stimuli in their experimental paradigms. Accordingly, our findings could reflect

differences between nonlinguistic and linguistic processing rather than spatial and nonspatial auditory processing. However, upon further analysis, this does not appear to be the case. Examining the 14 nonspatial studies that presented nonlinguistic sounds to listeners (i.e., nonspatial studies that did not involve language processing) revealed similar proportions found in the overall nonspatial analysis: 50.0% in the anterior and posterior temporal areas, 57.1% in the IFG and IPL, and 14.3% in the SFS. We conclude from this analysis that language processing cannot account for our observed nonspatial auditory findings given that the pattern is still present when only nonlinguistic tasks are analyzed.

General discussion

The results of this meta-analysis are consistent with a domain-specific model of auditory organization in humans. In keeping with the animal auditory dual-pathway model (Rauschecker and Tian, 2000), it was found that human IPL activity is ubiquitous among tasks that require listeners to compare or evaluate the location of a sound source. Furthermore, spatially processing sounds was also associated with activity around the SFS, as well as in posterior, but not anterior, areas of the temporal cortex.

The IPL finding is consistent with a recent transcranial magnetic stimulation study demonstrating the importance of the posterior parietal cortex in spatial hearing (Lewald et al., 2002). Similarly, SFS activity has also been observed during nonauditory spatial working memory tasks (Courtney et al., 1998). Unlike the IPL however, SFS activity in the current meta-analysis was not reported in every spatial study indicating that perhaps the activity is difficult to record or that the SFS may only be involved in specific types of spatial tasks. It is noteworthy that every study that reported activity around the SFS area, including the two nonspatial studies, also reported activity in the IPL. This may suggest a connectivity between the two brain regions and would be in keeping with neuroanatomical reports of an archicortical trend that projects from the medial preisocortical region towards the dorsolateral cortex covering areas Pro (24, 25, and 32) 9, dorsal 10, dorsal 46, and dorsal 8 (Barbas and Pandya, 1989; Pandya and Yeterian, 1990; Petrides and Pandya, 1984).

In addition to the SFS, posterior temporal activity was not reported in every spatial study either. One interpretation of this inconsistency is that the putative 'spatial network' is not an all-or-none serial circuit. In other words, performing a spatial task necessarily invokes inferior parietal activity but does not always recruit SFS or posterior temporal areas. However, before considering this functional interpretation, one should also consider other factors including the ease with which hemodynamic activity can be recorded from different brain areas (Harrison et al., 2002), as well as publication biases (i.e., certain brain regions may not be of relevance to a given study's hypothesis and corresponding activity in those regions may not be reported). Similarly, one should also be aware of the extent to which baseline contrasts affect the proportion of activity in these regions. For example, among the spatial studies in Table 1, SFS activity is often observed when a silent baseline condition is used (Alain et al., 2001; Weeks et al., 2000; but see Weeks et al., 1999; Zatorre et al., 2002) or when the spatial variance of the sounds is removed in the baseline task (but see Griffiths and Green, 1999; Griffiths et al., 1998; Lipschutz et al., 2002). However, when passive

listening to moving sounds is used as a baseline condition, SFS activity may not be observed (Bushara et al., 1999; but see Zatorre et al., 1999, 2002). Behavioral evidence points to a relationship between auditory localization and visual saccades (Rorden and Driver, 1999), so it may be that the SFS is automatically involved whenever sounds are heard at more than one location, reflecting an automatic or very low-level saccadic prime. In studies where contrasts are made between active and passive auditory conditions, SFS activity may be removed. In contrast, the IPL may be more sensitive to attentional demands and may therefore be active to a greater degree when spatial attention increases. Certainly, there are many reports that point to the sensitivity of the parietal lobe to attentional demands (Colby and Goldberg, 1999; Hugdahl et al., 2000; Rushworth et al., 2001; Wojciulik and Kanwisher, 1999).

An important finding in the current study was that while the anterior temporal lobe was found to be almost exclusively involved in nonspatial processing, the proportion of nonspatial and spatial studies reporting posterior temporal activity was approximately equal. These results did not change when the analyses were restricted to the superior temporal gyrus, nor when the potential confounds of baseline effects and language processing were removed. Such findings are in agreement with results from animal studies demonstrating neuronal sensitivity in rostral and caudal superior temporal areas for sound identity (e.g., species-specific calls) but only caudal sensitivity for sound location processing (Rauschecker and Tian, 2000; Tian et al., 2001). Moreover, and consistent with Warren and Griffiths' (2003) findings, the nonspatial activity that occurred in the posterior temporal area tended to be located more anterolaterally than the spatial activity. Accordingly, our findings suggest that an anterior boundary exists within the temporal lobe for auditory spatial processing. This result sheds light on the recent controversy concerning whether human auditory spatial processing is confined to a particular region or is evenly distributed throughout the auditory cortex (see Middlebrooks, 2002). The results from our analysis do not support the latter.

In contrast to the aforementioned areas, anterior temporal and inferior frontal regions in the current review appear to have little involvement with human auditory spatial processing. Rather, these areas are often invoked during nonspatial auditory processing. This finding strongly supports predictions derived from animal research for a secondary nonspatial auditory pathway involving the rostral temporal and ventral prefrontal areas (Deacon, 1992; Hackett et al., 1999; Rauschecker and Tian, 2000; Romanski and Goldman-Rakic, 2002; Romanski et al., 1999a,b).

Taken together, the present review of auditory neuroimaging data supports the idea that specialized spatial and nonspatial auditory processing networks exist in the human brain. Specifically, actively comparing the locations of sounds in the environment almost always results in a BOLD increase in the inferior parietal lobe and quite often elicits increases around the SFS and posterior temporal regions as well. In contrast, activity is often observed in the anterior temporal regions and the inferior frontal gyrus during nonspatial tasks but not during spatial tasks. Primary sensory processing areas aside, the two networks share many commonalities with the human spatial and nonspatial visual processing findings (Ungerleider and Haxby, 1994). The fact that such a similar organization is observed between these different modalities suggests a fundamental principle of functional organization in the human brain.

Acknowledgments

This research was supported by the Canadian Institutes of Health Research and the Natural Sciences and Engineering Research Council of Canada. The authors wish to thank two anonymous reviewers for helpful comments on the manuscript.

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