Hemispheric Specialization for Processing Auditory Nonspeech Stimuli

The left hemisphere specialization for speech perception might arise from asymmetries at more basic levels of auditory processing. In particular, it has been suggested that differences in "temporal" and "spectral" processing exist between the hemispheres. Here we used functional magnetic resonance imaging to test this hypothesis further. Fourteen healthy volunteers listened to sequences of alternating pure tones that varied in the temporal and spectral domains. Increased temporal variation was associated with activation in Heschl's gyrus (HG) bilaterally, whereas increased spectral variation activated the superior temporal gyrus (STG) bilaterally and right posterior superior temporal sulcus (STS). Responses to increased temporal variation were lateralized to the left hemisphere; this left lateralization was greater in posteromedial HG, which is presumed to correspond to the primary auditory cortex. Responses to increased spectral variation were lateralized to the right hemisphere specifically in the anterior STG and posterior STS. These findings are consistent with the notion that the hemispheres are differentially specialized for processing auditory stimuli even in the absence of linguistic information.

Keywords: asymmetry, fMRI, lateralization, spectral, temporal

Introduction

The possibility that the hemispheres are differentially specialized for processing information in the auditory domain has received a great deal of attention. One classical view posits that the left hemisphere is specialized for speech perception (Wernicke 1874). It is often also suggested that the right hemisphere is specialized for processing certain aspects of music (Bever and Chiarello 1974; Zatorre and others 1994; Ohnishi and others 2001; Tervaniemi and Hugdahl 2003). In the last 30 years, the debate over the nature of hemispheric specialization for auditory processing has grown, and the question as to its precise origin remains unresolved. It has been postulated that the left hemisphere specialization associated with speech perception, for example, arises as a result of the linguistic relevance and intelligibility of the input (Scott and others 2000; Shtyrov and others 2000; Narain and others 2003; Takegata and others 2004). An alternative hypothesis is that hemispheric specialization at higher levels of auditory cognition exists as a result of asymmetries in more basic auditory processing. Evidence for this hypothesis arose from an original study by Efron (1963), who showed that a group of aphasic patients had difficulty processing rapidly occurring auditory nonspeech stimuli. A number of investigations that followed proposed that rapid temporal processing might be crucial for speech comprehension (Tallal and Piercy 1973, 1974, 1975; Schwartz and Tallal 1980), although this particular viewpoint remains controversial.

The nature of hemispheric specialization for processing acoustic cues that may be relevant for speech processing is a central issue. A number of studies confirm a left hemisphere specialization for rapid temporal processing (Belin and others 1998; Liegeois-Chauvel and others 1999; Nicholls and others 1999; Zelchle and others 2004; Yamasaki and others 2005), whereas others have argued that the evidence is far from compelling (Scott and Wise 2004). One of the more convincing experimental demonstrations that the hemispheres exhibit functional asymmetry, even in the absence of linguistic information, comes from Zatorre and Belin (2001). Using positron emission tomography (PET) they showed that the primary auditory cortex (PAC) (Heschl's gyrus [HG]) responds to increasing temporal variation, whereas nonprimary areas (anterior superior temporal gyrus [STG] in particular) respond to increasing spectral variation. Moreover, they demonstrated that responses to temporal variation were left lateralized, whereas those to spectral variation were right lateralized. From these findings they argued that a trade-off exists between the hemispheres, the left with finer temporal resolution at the expense of spectral resolution and the right with finer spectral resolution at the expense of temporal resolution.

A similar hypothesis suggests that functional asymmetries in the auditory domain might be related simply to the time frames over which auditory information is processed in each of the hemispheres. Poeppel (2003), for example, claims that the left hemisphere extracts information from a short temporal integration window (~20–40 ms), whereas the right operates over a longer time frame (~150–250 ms; although the true windows may not be so specific). Recent experimental evidence adds weight to the notion that left–right differences occur as a result of differential feature extraction at early stages of auditory processing (Boemio and others 2005). It suggests that both hemispheres are sensitive to temporal structure and that this response becomes right lateralized as temporal structure increases, rather than as a result of increasing spectral complexity. Data from Patterson and others (2002) also support the hypothesis that the right hemisphere specialization for processing pitch information does not necessarily depend on spectral resolution. However, it is possible that temporal integration windows may be better thought of as relative rather than absolute and might depend on experience. For example, hemispheric specialization for processing particular acoustic cues has been suggested to vary with linguistic experience (Gandour and others 2000, 2003, 2004; Hsieh and others 2001).

Clearly, the precise nature of functional asymmetry and lateralization in auditory cortex is a complex issue that remains to be resolved. We therefore decided to test whether previous demonstrations of hemispheric specialization are replicable and

© The Author 2005. Published by Oxford University Press. All rights reserved.
For permissions, please e-mail: journals.permissions@oxfordjournals.org
to investigate lateralization effects in greater detail at the individual level. We used a set of stimuli similar to that of Zatorre and Belin (2001) in a functional magnetic resonance imaging (fMRI) experiment to investigate the proposed asymmetries in auditory nonspeech processing. Our specific aims were 1) to test the hypothesis that responses to increased temporal variation are left lateralized, whereas those to increased spectral variation are right lateralized, and 2) to examine the consistency of the proposed hemispheric asymmetries at the individual level as such data were not available in the original PET study. In the original study (Zatorre and Belin 2001), responses to increasing temporal variation were apparently restricted to the "core" or primary auditory areas. As PAC is thought to occupy only the posteromedial two-thirds of HG (Rademacher and others 1993; Penhune and others 1996; Hall and others 2002), we also used a specific region-of-interest (ROI) approach to test the hypothesis that activation in posteromedial HG is left lateralized in response to increased temporal variation, compared with increased spectral variation.

Materials and Methods

Subjects

Fourteen healthy volunteers (7 females, 7 males) with normal hearing (passed hearing screen at 20 dB) and minimal musical experience participated in the study, and all had English as their first language. Their ages ranged from 18 to 34 years (mean = 23.6 years), and all were right handed according to a handedness questionnaire adapted from the Edinburgh Handedness Inventory (Oldfield 1971). Participants gave written consent before taking part. Ethical approval was granted by the Central Oxford Research Ethics Committee.

Auditory Stimulation

Stimuli comprised pure tone patterns, identical to those used by Zatorre and Belin (2001) but segmented at 6-s intervals for the purposes of this experiment. They were taken from 3 conditions in which the frequency and duration of individual tones were varied (see Fig. 1 and Zatorre and Belin 2001 for further details). In the first condition ("standard" condition), stimuli consisted of alternating pure tones at 500 and 1000 Hz (i.e., separated by one octave). Stimuli were generated with a randomly determined duty cycle where the tone with the shortest duration and highest probability of occurrence was 667 ms. They were ramped on and off in counterphase using a 10-ms cosine function in order to avoid acoustic transients. The second condition ("temporal" condition) used stimuli with greater temporal rate of alternation. Stimuli again consisted of alternating pure tones at 500 and 1000 Hz, but in this condition the duration of the shortest possible tone, which had the highest probability of occurrence, was 21 ms (i.e., shorter mean duration). In the third condition ("spectral" condition) the rate of presentation of tones remained the same as in the standard (i.e., longer mean duration), but an increased number of frequencies were sampled in each stimulus. The octave range from 500 to 1000 Hz was divided into 32 logarithmically, and frequencies were selected at random from this distribution. The use of the term "spectral" to denote this third condition refers to the inclusion of an increased number of spectral components, over time, in each 6-s stimulus. It is not meant to imply, however, that the individual component tones of each spectral stimulus were harmonic-complex tones. Stimuli from this condition give a perception of dynamic pitch variation. Also of note is that the temporal and spectral conditions are equivalent to those at the maximal level of variation used by Zatorre and Belin (2001). It was not possible to include every level of variation employed by the previous authors owing to the time constraints imposed by sparse sampling fMRI. A baseline condition of silence was also included.

Procedure

Stimuli were presented binaurally at 72–77 dB sound pressure level using the sound system custom made by the Medical Research Council Institute of Hearing Research (Palmer and others 1998) with magnetic resonance–compatible electrostatic headphones (Sennheiser model HE 60) and modified industrial ear protectors (Bilsom model 2452). Headphone orientation was reversed for half of the subjects. Subjects were instructed to lie motionless and listen to the sounds, without performing any explicit task (they were familiarized with the stimuli prior to scanning but were not told to attend to any specific stimulus characteristics). Each subject participated in 2 functional imaging runs, which lasted 10 min and were counterbalanced across subjects. Within each run, 10 “trials” from each condition (standard, temporal, spectral, and silence) were pseudorandomly presented in an event-related manner.

A “sparse sampling” (Hall and others 1999) design was employed, with 1-s image acquisition occurring every 15 s, immediately after the end of each 6-s auditory stimulus. This ensured that the hemodynamic response was sampled at or near its peak, which occurs around 5–6 s after stimulus onset in auditory cortex depending on stimulus duration (Hickok and others 1997; Belin and others 1999; Glover 1999; HL Jamison, unpublished data). A period of 8-s silence followed each acquisition, to allow the hemodynamic response to return to baseline levels prior to presentation of the next stimulus (Belin and others 1999). This design ensured that all stimuli were presented in silence and not masked by the scanner noise. It also served to minimize any overlap between stimulus-related responses and those related to the noise generated by the scanner, which are known to interact in a complex and nonlinear fashion (Talavage and Edmister 2004).

Imaging

All scanning was performed on a Varian-Siemens 3-T scanner at the Centre for Functional Magnetic Resonance Imaging of the Brain. A Magnex head-dedicated gradient insert coil was used in conjunction with a birdcage head radiofrequency coil tuned to 127.4 MHz. Functional imaging consisted of 13 T<sub>2</sub><sup>*</sup>-weighted echo-planar image (EPI) slices (long repetition time [TR] = 15 s, short repetition time [tr] = 1 s, echo time [TE] = 30 ms) 3-mm thick with an in-plane resolution of 4 mm<sup>2</sup>. Slices were angled obliquely in parallel with the Sylvian fissure and centered on HG viewed on a parasagittal slice. In addition, for registration and anatomical localization purposes, a whole-brain T<sub>1</sub>-weighted scan with 1-mm<sup>3</sup> in-plane resolution and either 1.5- or 3-mm slice thickness (3D Turbo FLASH sequence, TR = 15 ms, TE = 69 ms) was acquired for each subject.

Data Processing

After removing the first image of each session to allow for T<sub>1</sub> magnetization equilibrium, functional images were realigned (Jenkinson

---

**Figure 1.** Schematic representation of an example stimulus from each of the 3 conditions, with frequency shown as a function of time. Stimuli in the standard condition (top) comprised alternating pure tones with fixed frequencies of 500 and 1000 Hz and randomized mean duration. In the temporal condition (bottom left), tones remained fixed at 500 and 1000 Hz but had a shorter mean duration, that is, greater rate of temporal alternation. In the spectral condition (bottom right), tones had a longer mean duration, as in the standard condition, but an increased number of frequencies were randomly sampled across each 6-s stimulus.
and others (2002) using the FSL software (http://www.fmrib.ox.ac.uk/fsl) in order to correct for small head movements. In 1 session for 1 subject artificial activation within the ventricles and around the edges of the brain occurred; as these phenomena are typical of excessive head movement, this session was removed from the analysis. Such artifacts were not present in any of the remaining data sets analyzed. Functional images were registered to the participant's structural scan and then to the MNI 152-average brain. Registration was checked to ensure accurate positioning of the raw EPI data relative to each subject’s anatomy. Finally, each image was smoothed with a 5-mm full-width half-maximum Gaussian filter. The FSL software was used to compute individual subject analyses, in which each of the 3 conditions were modeled separately, and mixed-effects group analyses were used to identify those areas that were significantly activated in each condition. Statistical images were thresholded at Z > 2.3 and P < 0.05 (cluster thresholding, corrected for multiple comparisons).

Analyses
The standard, temporal, and spectral conditions were directly contrasted to identify those areas of auditory cortex differentially responsive to increased variation in the temporal and spectral domains. ROI analyses were then conducted to compare activation levels between the hemispheres for those regions identified. In the first instance, ROIs were defined functionally, on the basis of activation clusters from the group analysis, to test the hypothesis that responses to greater temporal variation are left lateralized, whereas those to increased spectral variation are right lateralized.

To test responses in those areas described by Zatorre and Belin (2001) as demonstrating left and right lateralizations (i.e., HG and anterior STG, respectively), we also used a more regionally specific ROI approach. ROIs in HG were defined on the basis of individual anatomical information. In accordance with cytoarchitectonic data, the borders of HG were delineated anteriorly as the first transverse sulcus and posteriorly as Heschl’s sulcus (Penhune and others 1996; Rivier and Clarke 1997). In cases where more than one gyrus existed in the same hemisphere, only the region anterior to the second transverse sulcus was included (Rademacher and others 1993; Rivier and Clarke 1997). As PAC is thought to occupy only the postero medial two-thirds of HG (Rademacher and others 1993; Penhune and others 1996; Hall and others 2002), we divided HG into postero medial and anterolateral portions. Postero medial HG was defined as two-thirds of the medio lateral extent in the X plane and two-thirds of the posteroinferior extent in the Y plane. Anterolateral HG (which is not thought to contain PAC) was defined as encompassing one-third of the lateral extent of HG in the X plane and one-third of the anterior extent of the Y plane.

The mean percent BOLD signal change was then calculated for each mask in each subject. A paired t-test revealed that activation for the temporal > spectral contrast was significantly greater in the left hemisphere than the right (t[13] = 2.82, P < 0.014) (Fig. 3). Twelve of the 14 subjects individually demonstrated this left lateralization, and the group mean LI of -0.24 ± 0.08 was significantly different from zero (Z = 2.48, P = 0.013).

At the group level, the reverse contrast (spectral > temporal) revealed a significant activation cluster in the right posteriorSTS but not in the left (197 vs. 0 voxels; Fig. 2a and Table 1). This cluster mask was flipped about the x axis and used to examine lateralization at the individual level. Data extracted from this region in the left and right hemispheres showed that the number of activated voxels (Z > 2.3) was significantly greater in the right hemisphere cluster (t[13] = 2.20, P = 0.046). The mean percent BOLD signal change was also calculated for each mask in each subject, and a paired t-test revealed that activation was significantly greater in the right hemisphere than the left (t[13] = 5.63, P < 0.001) (Fig. 4). Twelve of the 14 subjects individually demonstrated this right lateralization, and the group mean LI of +0.71 ± 0.10 was significantly different from zero (Z = 3.10, P = 0.002). In the original PET study (Zatorre and Belin 2001), the same contrast revealed significant activation in the anterior STG bilaterally. To test for a similar response, we also examined our data using a relaxed statistical threshold. At an uncorrected voxel threshold of P < 0.01, we identified activation in both the right (Z = 3.39) and left anterior STG (Z = 3.03) (Table 1). We examined lateralization in this region for the spectral > temporal contrast using spherical ROIs with a radius of 5 mm, centered on the coordinates of these peaks (left x = -52, y = 10, z = -10; right x = 54, y = 12, z = -14). Although the mean percent BOLD signal change was on average greater in the right hemisphere, this difference did not reach significance. Differences in the number of active voxels (Z > 2.3) per ROI in each hemisphere were also not significant.
Contrasting the temporal with the standard condition (temporal > standard) revealed significant bilateral activation in a large region centered on HG and including surrounding regions of the STG (Fig. 2b). Both left and right clusters of activation included the posteromedial portion of HG, which is thought to be the location of PAC (Rademacher and others 1993; Penhune and others 1996; Hall and others 2002). At the group level, the spatial extent of the left hemisphere cluster was greater than that observed on the right (1512 vs. 1383 voxels; Table 2), and across individuals the number of activated voxels ($Z > 2.3$) per cluster mask was significantly greater on the left ($t_{13} = 2.65$, $P = 0.020$). A paired $t$-test revealed that mean percent BOLD signal change for the temporal > standard contrast was also significantly greater in the left hemisphere than the right ($t_{13} = 3.05$, $P = 0.010$) (Fig. 5a). Eleven of the 14 subjects individually demonstrated this left lateralization, and the group mean LI of $-0.19 \pm 0.06$ was significantly different from zero ($Z = 2.29$, $P = 0.022$).

In the previous study by Zatorre and Belin (2001), responses to increased temporal variation were apparently restricted to the core auditory areas. Using our high-resolution magnetic
imaging scans we decided to examine this finding in more detail and with respect to each individual subject’s anatomy. Activation was examined within posteromedial and anterolateral HG, which were defined as described in Materials and Methods for each subject separately. As ROIs were defined on an individual anatomical basis, they were not identical in size in each hemisphere. The number of significantly active voxels in each ROI was therefore calculated as a proportion of the total number of voxels in the ROI. In posteromedial HG, the proportion of activated voxels in the left was significantly greater than that in the right, at Z > 2.3 (t₁₄ = 3.56, P = 0.004). Also, 12 of 14 individuals had a relative left lateralization in mean percent BOLD signal change, with a group mean LI of −0.16 ± 0.07 that was significantly different from zero (Z = 2.36, P = 0.018) (Fig. 5b); a paired t-test comparing left and right mean signal changes narrowly missed significance (t₁₃ = 2.07, P = 0.059). In anterolateral HG, differences between the hemispheres in the proportion of activated voxels were not significant. The mean LI calculated on the basis of signal change in anterolateral HG was 0.00 ± 0.09, which was also not significant, and an equal number of subjects demonstrated left and right lateralization (Fig. 5c). These results indicate that the left lateralization observed for the temporal > standard contrast is more consistent in the posteromedial portion of HG, the putative location of PAC, and support the previous findings that increased temporal variation activates primarily core areas.

### Spectral > Standard Contrast

Contrasting the spectral with the standard condition (spectral > standard) revealed significant activation in lateral and anterior STG bilaterally, including the anterolateral but not the posteromedial portion of HG (Fig. 2c). In the right hemisphere, this cluster spread anteriorly along the STG to a greater extent than it did in the left (784 vs. 413 voxels; Table 2). As before, whole activation cluster masks were flipped about the x axis and added together to test the lateralization of responses related to this contrast. Across individuals, the number of activated voxels (Z > 2.3) was on average greater in the right hemisphere cluster, although this difference did not reach significance. A paired t-test also did not reveal a significant difference in mean percent BOLD signal change between the hemispheres for this contrast (Fig. 6a). The mean LI was +0.11 ± 0.10 and not significantly different from zero; 8 of 14 subjects individually demonstrated a right hemisphere lateralization.

In the previous study (Zatorre and Belin 2001), it was reported that responses to increasing spectral variation were right lateralized in anterior STG. We therefore decided to examine lateralization specifically in this region. For this analysis, spherical ROIs with a 5-mm radius were placed in anterior STG in both hemispheres to compute local means. These were centered on the coordinates of local maxima in this area from the group analysis for the spectral > standard contrast. As there was an absence of suprathreshold activity at the group level in the left anterior STG, the ROI from the right hemisphere was flipped about the x-axis to provide a comparison (center voxel coordinates: left x = −54, y = −14, z = 8; right x = 64, y = −12, z = 4; Table 2).

In anterior STG, there was a significant right lateralization in mean percent BOLD signal change for the spectral > standard contrast (t₁₄ = 2.76, P = 0.016). Eleven of 14 subjects demonstrated this pattern of activation, with a group mean LI of +0.46 ± 0.16 that was significantly different from zero (Z = 2.28, P = 0.023) (Fig. 6b). The average number of activated voxels (Z > 2.3) in this ROI was greater in the right hemisphere, although this difference did not reach significance. In lateral STG left-right differences were not significant (mean LI was −0.03 ± 0.14; 6 of the 14 subjects demonstrated a right lateralization) (Fig. 6c). These findings suggest that there was a significant and specific right lateralization at the subject level in the anterior STG for the spectral > standard contrast, which was not apparent from the initial ROI analysis based on large functional activation clusters.

### Table 1

<table>
<thead>
<tr>
<th>Region</th>
<th>Peak voxel coordinates</th>
<th>Voxels</th>
<th>Peak Z</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x</td>
<td>y</td>
<td>z</td>
</tr>
<tr>
<td>Temporal &gt; spectral</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left HG (+STG)</td>
<td>−56</td>
<td>−20</td>
<td>8</td>
</tr>
<tr>
<td>Right HG (+STG)</td>
<td>46</td>
<td>−2</td>
<td>12</td>
</tr>
<tr>
<td>Spectral &gt; temporal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right pSTS</td>
<td>46</td>
<td>−32</td>
<td>6</td>
</tr>
<tr>
<td>Left aSTG*</td>
<td>−52</td>
<td>10</td>
<td>−10</td>
</tr>
<tr>
<td>Right aSTG*</td>
<td>54</td>
<td>12</td>
<td>−14</td>
</tr>
</tbody>
</table>

Note: Areas identified in the group analysis by contrasting the temporal and spectral conditions directly. Peak voxel coordinates (in standard space) and Z scores are given, in addition to the number of voxels in a cluster at Z > 2.3. pSTS = posterior STS, aSTG = anterior STG. *Identified at uncorrected P threshold of <0.01.

Figure 3. Results of ROI analysis for the temporal > spectral contrast. (a) Mean percent BOLD signal change extracted from ROIs based on functionally defined activation clusters in the left and right HG. (b) LIs based on these ROIs. Rank-ordered individual data (black) and group mean (white) are shown (positive values indicate a relative right lateralization, whereas negative values indicate a left lateralization). *P = 0.05; error bars represent SEM.

Downloaded from http://cercor.oxfordjournals.org/ at Pennsylvania State University on February 28, 2014
The results of our fMRI study show that auditory stimuli with increased temporal variation activate HG bilaterally, whereas stimuli with increased spectral variation activate the STG bilaterally and a region of the right posterior STS. Relative activation in HG was left lateralized in response to increased rate of temporal alternation, whereas activity in posterior STS and anterior STG was right lateralized with increased number of spectral elements. Exploratory analyses also suggested that the left lateralization observed in response to increased temporal variation is greatest in the posteromedial portion of HG, which contains putative PAC.

**Differentiating Primary and Nonprimary Auditory Cortices**

The present data are consistent with research documenting the involvement of core auditory cortex in fine-grained temporal processing and the proposed hierarchical analysis of sound (Griffiths and others 1998; Gandour and others 2002; Boemio and others 2005). Recent imaging studies have shown that responses to pure tones are greatest in PAC, whereas areas outside this core region are more responsive to increasing temporal structure and complexity in the spectral domain.

**Discussion**

The results of our fMRI study show that auditory stimuli with increased temporal variation activate HG bilaterally, whereas stimuli with increased spectral variation activate the STG bilaterally and a region of the right posterior STS. Relative activation in HG was left lateralized in response to increased rate of temporal alternation, whereas activity in posterior STS and anterior STG was right lateralized with increased number of spectral elements. Exploratory analyses also suggested that the left lateralization observed in response to increased temporal variation is greatest in the posteromedial portion of HG, which contains putative PAC.
Distinctions between primary and nonprimary auditory cortices have also been made on the basis of sustained and transient temporal coding (Seifritz and others 2002) and phasic response patterns (Harms and others 2005). Areas found to be specifically activated by increased spectral variation in our study corresponded to nonprimary auditory cortex. Previously, Thivard and others (2000) demonstrated that lateral "belt" areas are more sensitive to stimuli containing spectral changes. Activity in nonprimary auditory cortex overlapping anterolateral HG has also been shown to correlate with pitch salience (Penagos and others 2004), and the observations of others support the notion that nonprimary regions are specialized for pitch processing and the spectral analysis of sounds (Patterson and others 2002; Warren and others 2003, 2005). Similarly, areas of the right STS, which was identified in this study by comparing spectral and temporal processing directly, have been highlighted as particularly responsive to aspects of vocal information such as prosody and intonation (Belin and others 2000, 2002; Lattner and others 2005).

**Functional Asymmetry in Auditory Cortex**

Our data show that when the temporal and spectral conditions were directly compared, resulting patterns of activation were asymmetric. Relative to the spectral condition, responses to the temporal condition were significantly greater in the left hemisphere (in HG), whereas suprathreshold activation in response to the converse contrast (i.e., spectral > temporal) occurred only in the right hemisphere (in STS). Given that more than one parameter varies between the 2 conditions, however, it is not possible to ascertain whether it is variation in the temporal or spectral domain, or both, that is responsible for these effects. Therefore, each condition was also separately compared with the standard condition to test more specifically whether responses to increased temporal variation or increased spectral variation were lateralized.

Increased temporal variation, relative to the standard condition, resulted in activation that was greater in spatial extent in the left hemisphere. ROI analyses based on functional activation clusters confirmed a significant left lateralization in signal change, which was relatively consistent across individuals. For the spectral > standard contrast, signal change extracted for each subject from functionally defined large cluster ROIs did not show a significant right lateralization. We speculate that this is due to the inclusion of anatomical regions with potentially different functional sensitivity within such relatively large ROIs, which may have obscured smaller, regionally specific effects; it has previously been shown that restricting analyses to specifically defined regions systematically improves laterality calculations (Rutten and others 2002). Indeed, our analysis using smaller ROIs centered on peak activation voxels in anterior STG confirms the pattern seen at the group level, that is, significantly greater activation in the right hemisphere compared with the left.

Using a specific ROI approach, we were also able to show that the left hemisphere lateralization observed in response to increased temporal variation was potentially greater in the posteromedial portion of HG, which has previously been shown to contain PAC (Rademacher and others 1993; Penhune and others 1996; Rivier and Clarke 1997). The anterolateral portion of HG did not show any consistent lateralization. The spherical ROI analysis showed significant right hemisphere lateralization in anterior STG specific to increased spectral variation. This asymmetry was relatively consistent across individuals and concordant with the finding of Zatorre and Belin (2001) that spectral changes recruit anterior regions of the STG bilaterally, with a greater response on the right. It must be noted, however, that although lateralization effects were significant in posteromedial HG and anterior STG, it was not the case that every subject consistently demonstrated lateralization in response to increased temporal or spectral variation.

Our findings are consistent with evidence that regions within the superior temporal cortex are independently specialized for
processing different dimensions of auditory stimuli, in the absence of linguistic information. They support the notion that the left hemisphere is specialized for temporal processing. Increased variation in the temporal domain produced activity in and around HG, which exhibited a consistent left lateralization. Evidence for the left hemisphere specialization for rapid temporal processing has been reported before (Mills and Rollman 1980; Belin and others 1998; Nicholls and others 1999; Zaalhe and others 2004; Yamaski and others 2005). Our finding that specific regions within the right hemisphere are more responsive to increased spectral variation is also consistent with patient data, for example, which demonstrate that lesions affecting the right temporal cortex impair specific spectral processing skills (Siddi and Volpe 1988; Robin and others 1990; Alcock and others 2000; Johnsrude and others 2000; Hyde and Peretz 2004; Murayama and others 2004). Right-left asymmetries are even noticeable in the peripheral auditory pathways of infants and neonates as early in processing as at the level of the cochlea (Khalfa and others 1998; Morlet and others 1999; Sinner and Cone-Wesson 2004).

There are a number of hypotheses that might account for these findings. The first of these is the spectral–temporal trade-off hypothesis of Zatorre and Belin (2001). The present data, particularly those concerning the direct contrasts between the temporal and spectral conditions, support the notion that the left hemisphere has finer temporal resolution at the expense of spectral resolution, whereas the right has finer spectral resolution at the expense of temporal resolution. The authors speculate that these differences might be related to structural asymmetries between the hemispheres. For example, it has been proposed that wider column spacing and greater axon myelination may facilitate rapid temporal processing in the left hemisphere (Penhune and others 1996; Anderson and others 1999; Buxhoeveden and Casanova 2000; see Hutslers and Galuske 2003, for a full review of structural asymmetries).

A similar explanation of these asymmetries, provided by the hypothesis of Poeppel and colleagues, is that they arise due to differences in the time frames over which auditory information is processed by the hemispheres. In this framework (Poeppel 2003; Boemio and others 2005), functional asymmetries in auditory processing are driven by differences in temporal structure between stimuli. Indeed, evidence exists to suggest that the right hemisphere lateralization, observed in this and other studies in response to dynamic pitch variation, need not depend on the spectral properties of the stimulus (Griffiths and others 1998; Patterson and others 2002). Furthermore, rather than having structural asymmetries as their substrate, Boemio and others (2005) propose that hemispheric differences in temporal processing, in areas such as the STS, might be based on differential input from the STG.

Another explanation for our findings is that there may have been differences in sequential integration between each of the conditions. In the temporal condition, for example, it might be the case that the sequence of rapidly alternating pure tones was perceived as 2 separate auditory streams, with tones being perceptually grouped according to attributes such as their pitch rather than their order in time. However, it is unlikely that auditory stream segregation accounts for our findings because the stimulus duration (6 s) was shorter and the frequency difference between tones (500 Hz) smaller than typically needed for this percept to occur (Bregman 1978; Rose and Moore 2000). Furthermore, stream segregation is most commonly observed when stimuli are patterned, for example, in ABA_ABA triplets (van Noorden 1975), and when listeners are specifically instructed to "listen out" for 2 separate streams (Rose and Moore 2000), and neither of these conditions apply to the present study.

Conclusions

Here we have extended observations showing that specific regions within the superior temporal cortex process acoustic cues asymmetrically even in the absence of linguistic information. Furthermore, we have tested this effect at the individual level, which will facilitate relating varying functional asymmetries to differences in structure. There are a number of possible explanations for this apparent hemispheric specialization; however, we believe that our data cannot be explained on the basis of differences in auditory stream segregation between the temporal and spectral conditions. When selecting subjects we controlled for linguistic and musical experience, both of which are known to affect functional asymmetry (Ohminshi and others 2001; Gandour and others 2003); we also believe, therefore, that differences in such experience are unlikely to account for the lateralization patterns observed here. In conclusion, our data do support the proposal that the left hemisphere is specialized for processing auditory stimuli containing rapid temporal changes and that the right hemisphere is specialized for processing changes in frequency information over a longer time window. These conclusions are in accord with both the spectral-temporal trade-off hypothesis (Zatorre and Belin 2001) and the notion of asymmetric temporal integration windows (Poeppel 2003; Boemio and others 2005).

Notes

We thank Robert Zatorre for the kind donation of auditory stimuli. This work was supported by the Wellcome Trust (HLJ and DVMB) and the Medical Research Council (KEW and FMM).

Address correspondence to Helen L. Jamison, Centre for Functional Magnetic Resonance Imaging of the Brain, John Radcliffe Hospital, Headington, Oxford OX3 9DU, UK. Email: jamison@fmrib.ox.ac.uk.

References


