Function of the left planum temporale in auditory and linguistic processing


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Summary

Previous research suggests that the human left planum temporale (PT) plays an important role in language. To test this hypothesis, functional MRI (fMRI) data were collected from 12 normal right-handed subjects during passive and active listening to words and tone sequences. Several left hemisphere areas, including the superior temporal sulcus, middle temporal gyrus, angular gyrus and lateral frontal lobe showed stronger activation during the word conditions. This was not true of the PT, which responded equally to tones and words during passive listening and more strongly to tones during active listening. The PT is likely to be involved in early auditory processing, while specifically linguistic functions are mediated by multimodal association areas distributed elsewhere in the left hemisphere.

Keywords: language; planum temporale; brain mapping; auditory cortex

Abbreviations: EPI = echo-planar imaging; fMRI = functional MRI; PP = planum parietale; PT = planum temporale; SPL = sound pressure level; STG = superior temporal gyrus; STP = superior temporal plane; STPa = anterior superior temporal plane; STS = superior temporal sulcus; STSa = anterior superior temporal sulcus; STSp = posterior superior temporal sulcus

Introduction

The human PT is a roughly triangular region of the superior temporal plane located posterior to the primary auditory field (von Economo and Horn, 1930). It is, on average, larger in the left hemisphere, suggesting that it may play a specialized role in language and language lateralization (Geschwind and Levitsky, 1968; Wada et al., 1975; Steinmetz et al., 1991). Ischaemic lesions near to, or including, the left PT are associated with deficits of auditory discrimination and/or speech comprehension (Auerbach et al., 1982; Tanaka et al., 1987; Praamstra et al., 1991; Caplan et al., 1995). Asymmetry of the PT is altered in dyslexia, a developmental language disorder characterized by reading difficulty and deficits in the awareness of phonological structure in language (Galaburda et al., 1985; Hynd et al., 1990; Larsen et al., 1990; Leonard et al., 1993). While these lines of evidence suggest a linguistic function for the cortex of the left PT, this hypothesis has not been tested using functional imaging techniques such as PET or fMRI.

Several PET and fMRI studies employed passive or active listening to speech, including such stimuli as familiar words, familiar-sounding nonwords, words in unfamiliar languages, and nonsense syllables. Activated regions were observed in the superior temporal gyri (STG) bilaterally, including cortex posterior, anterior and lateral to the primary auditory area (Petersen et al., 1988; Wise et al., 1991; Price et al., 1992; Mazoyer et al., 1993; Binder et al., 1994). It is not yet known, however, whether these activation responses represent processing at an auditory level or a linguistic level, or whether specific anatomical subdivisions of the STG are recruited during language tasks. One reason for this uncertainty is that the authors of most studies did not compare activation with speech sounds to activation with nonlinguistic auditory stimuli. Two exceptions are Démonet et al. (1992), who compared active tasks using tone sequences and speech sounds in their PET study, and Zatorre et al. (1992) who used PET to compare passive listening to noise bursts with passive listening to speech sounds. Both groups observed foci in the left STG that were more responsive to speech sounds, yet these were located anterior and ventral to the PT, closer to the superior temporal sulcus than to the dorsal temporal plane (stereotaxic x = −54 to −58, y = −12 to −22, z = 0–8; see the atlas of Talairach and Tournoux, 1988). Neither group related the functional data to anatomical landmarks or commented on the spatial relationship of functional areas to the PT.
We performed two experiments using fMRI in normal right-handed subjects to test the hypothesis that the left PT is associated with language processing. These experiments were based on the assumption that areas involved in language-level processing would respond more strongly to linguistic stimuli or task conditions than to nonlinguistic stimuli or task conditions. A corollary of this assumption is that areas responding equally to linguistic and nonlinguistic conditions are likely to be involved in either sensory (auditory) processing or nonspecific executive functions such as maintenance of attention.

In the first experiment, subjects were scanned during passive auditory stimulation with English words and tone sequences, with the order of these conditions randomized and interleaved, and the rate and intensity of stimuli matched across conditions. In the second experiment, the same subjects were scanned during alternation between a linguistic task requiring semantic decisions about words and a nonlinguistic task involving analysis of tone sequences. In both experiments, statistical maps were then formed by combining data across subjects in standard stereotaxic space. Stereotaxic averaging is a commonly employed, objective means of determining overlap in activation patterns across subjects, but does not preserve information about individual anatomical structure. In a complementary analysis designed to link activation data directly to the PT, high-resolution MR images were used to identify the left PT cortex in each subject, defined on the basis of sulcal features. Differences in the intensity of activation by words and tones in both the passive and active experiments were then measured for the PT cortex and several surrounding regions of interest.

Methods

Subjects

Subjects were six men and six women, ranging in age from 20 to 40 years, with no history of neurological or audiological illness. All subjects indicated right hand dominance on the Edinburgh inventory (Oldfield, 1971). After a full explanation of the nature and risks of the research, subjects gave written informed consent for all studies according to a protocol approved by the MCW Human Research Review Committee.

General methods

Imaging was performed on a 1.5 Tesla General Electric (Milwaukee, Wis., USA) Signa scanner using 3-axis local gradient and insertable transmit-receive radiofrequency coils designed for echo-planar imaging (EPI) (Wong et al., 1992). Gradient-echo EPI time-series images were acquired for functional studies using the following conditions: 40 ms echo time, 3–4 s repetition time, 24 cm field of view, and voxel dimensions 3.75 × 3.75 × 8 mm. Sequential images were collected concurrently at three contiguous sagittal locations in the lateral left hemisphere using spatially interleaved acquisitions. While slice placement varied by a few millimeters from subject to subject, brain tissue located between stereotaxic x coordinates –62 and –42 was imaged in all subjects. This volume includes most of the PT and lateral temporal lobe, excluding part of the lateral temporal surface near the middle portion of the superior temporal sulcus (Talairach and Tournoux, 1988). High-resolution anatomical images of the entire brain were obtained during the same session using either a fast-spin-echo sequence for contiguous 4 mm sagittal slices or a three-dimensional, spoiled-gradient-echo sequence for contiguous 1.2 mm sagittal slices.

During scanning the room lights were dimmed and the subjects’ eyes closed. Stimuli were 16 bit digitally sampled pure tones and male speech sounds presented binaurally using a computer playback system, a magnetically shielded transducer system and air conduction through paired plastic tubes (Binder et al., 1995). The conducting tubes were threaded through tightly occlusive ear inserts that attenuated the average sound pressure level of the continuous scanner noise by 20 dB. The sound pressure level (SPL) of the stimulus averaged 100 dB SPL and remained constant across all subjects and all stimuli. The average intensity of the continuous scanner noise was ~75 dB SPL after attenuation by the ear inserts.

Passive listening experiment

The EPI series in the passive listening experiment consisted of multiple epochs of rest, during which subjects heard only the background scanner noise, alternating with periods of activation, during which additional auditory stimuli were presented (Fig. 1). English words and random tone sequences were used as comparison conditions, with the order of these conditions randomized and interleaved, and the rate and intensity of stimuli matched across conditions. The series began with a brief baseline period to allow image intensity to reach equilibrium, followed by 16 cycles (eight for each condition) during which activation alternated with rest every 12 s.

Word stimuli were monosyllabic, medium frequency, concrete English nouns (e.g. bus, fork, stream). Nearly all of the acoustic energy of these sounds was below 10 kHz, with
the greatest concentration between 50 and 2500 Hz. Stimuli were edited to a duration of 666 ms, allowing presentation of 18 stimuli during each activation period, at a rate of 1.5 words per second.

Tone stimuli were pure sine wave tones ranging in frequency from 50 to 2400 Hz. The frequency changed randomly and by at least 10 Hz in a step-wise manner every 666 ms (1.5 frequency shifts per second), resulting in presentation of 18 different tones during each activation period.

Subjects were instructed to listen to the sounds being played through the ear tubes, and to press a button whenever one of the 12 s blocks of sounds began or ceased.

**Active listening experiment**

The EPI image series in the active listening experiment began with a brief baseline period, followed by eight cycles during which performance of a semantically based word decision task alternated with performance of a tone pattern analysis task every 24 s (Fig. 1). These tasks are based on those employed by Démonet et al. (1992), and have been described elsewhere (Binder and Rao, 1994; Binder et al., 1995).

In the word task, subjects heard English nouns designating animals and they responded with a button-press to those they considered both ‘found in the United States’ and ‘used by people’. This task requires processing of speech at auditory, phonetic and semantic levels, as well as attention, working memory and motor response functions. In the tone task, subjects heard short sequences of ‘high’ (750 Hz) and ‘low’ (500 Hz) tones and responded with a button-press to sequences containing two ‘high’ tones. This task requires processing at an auditory level, as well as attention, working memory, and motor response functions. Tasks were matched for average SPL, trial rate (one trial per 3 s) and target rate (three targets per eight trials). In previous studies using these tasks, fMRI-detected responses occurring in phase with performance of the word decision task were lateralized to the left hemisphere in right-handed control subjects, and lateralization of these ‘language responses’ was strongly correlated with language lateralization as determined by the intracarotid amobarbital procedure in epilepsy patients (Binder et al., 1995, 1996).

**Time-series analysis**

Images in each EPI time-series were registered to the fourth image in the series to minimize the effects of head movement, using an automated alignment program based on the method of Woods et al. (1992). A cross-correlation technique was used to measure correspondence between observed signal changes and the timing of activation conditions, as represented by an ideal response vector (Bandettini et al., 1993). An automated program chose the best correlation (r) for each voxel within a temporal phase window matched to the timing of stimulus presentations and assigned to each pixel in the image the value rs, where s is the SD of the voxel signal over time. The value rs is equivalent to the amplitude of the ideal vector after a least-squares fit to the voxel data.

The ideal response vector employed for cross-correlation in the passive experiment was a sinusoid matched in phase and period to the 12 s activation cycles. The passive word and tone conditions were analysed separately by segmenting the original data by condition before the correlation test. This analysis thus yielded a map of responses to words relative to a resting state (words) and a map of responses to tones relative to a resting state (tones). Voxel-wise subtraction of the tones map from the words map in each subject yielded a difference image (passive words-tones) in which positive values represent greater activation by words, negative values greater activation by tones.

Analysis of data from the active task experiment was similar to that employed in the passive experiment, except that the ideal vector was adjusted to reflect the longer (24 s) activation periods used. Because there were no intervening rest periods between word decision and tone pattern tasks, only difference images (active words-tones) were generated in the analysis. The value rs in this case represents the difference in activation produced by the two tasks, with positive values indicating greater activation by the word task, and negative values indicating greater activation by the tone task.

**Stereotaxic averaging**

Transformation of data into three-dimensional, proportional stereotaxic space (Talairach and Tournoux, 1988) was accomplished using the ‘MCW-AFNI’ software package (Cox, 1995). This process involves manual placement of fiducial points on the three-dimensional anatomical images marking the anterior and posterior commissures and brain edges, followed by affine transformation and resampling of all anatomical and functional data to fit standard brain dimensions. Unthresholded, stereotaxically transformed functional data sets from each subject were smoothed slightly with a Gaussian filter of root mean square radius 4 mm to compensate for normal variation in sulcal/gyral anatomy across subjects (Steinmetz et al., 1990a; Toga et al., 1993). Single sample t tests were then performed on each group of functional maps to determine whether the average voxel value (representing either rs or differences in rs) at each stereotaxic location differed (in either a positive or negative direction) from zero. The images in Figs 3 and 4 below were thresholded at r(11) = 3.11, two-tailed P < 0.01, and surviving voxel clusters with a volume < 100 μl were eliminated. Peak foci in the passive and active word-tone difference maps were identified by thresholding at r(11) = 5.92, two-tailed P < 0.0001. A list of the size and centre of mass locations of voxels that exceeded this higher threshold and formed clusters >100 μl is given in Table 1.
As a measure of the validity of this technique, these landmarks were also determined in the right hemisphere as the sum of the linear distances between anterior and posterior limits at the four sagittal locations. In agreement with previous research (Geschwind and Levitsky, 1968; Wada et al., 1975; Steinmetz et al., 1991), this area index was greater in the left hemisphere than the right in nine of the 12 subjects, and significantly greater on the left for the group as a whole (two-tailed \( t \) test). The PT region of interest at each sagittal location consisted of the cortical ribbon of the superior temporal plane lying between these two landmarks.

The STPa region of interest consisted of the STP cortical ribbon lying between the PT and the grey matter–white matter junction at the point where the anterior STP turns inferiorly to become the temporal pole. The STSa region of interest consisted of the cortical ribbon on both banks of the STS lying anterior to the PT and excluding cortex on the temporal pole. The STSp region of interest consisted of the cortical ribbon on both banks of the STS ventral to the PT and excluding STS cortex posterior to the PT. The inferior limit of the PP region of interest was the same as the posterior limit of the PT. The superior limit of the PP was defined as the grey matter–white matter junction at the point where the posterior ascending ramus of the sylvian fissure ends or turns anteriorly in the parietal lobe. To check the validity of the PP landmarks, a PP area index was calculated for each hemisphere in each subject. This area index was greater in the right hemisphere than in the left in nine out of the 12 subjects, and significantly greater on the right for the group as a whole (two-tailed \( t \) test, consistent with previous observations (Rubens et al., 1976; Steinmetz et al., 1990b; Leonard et al., 1993). The PP region of interest consisted of the cortical ribbon of the caudal sylvian bank lying between these two landmarks.

The word–tone difference maps from the passive and active experiments were analysed with reference to the regions of interest. The average intensity value (representing differences in the level of activation by words and tones) was determined for each experiment in each region of interest of each subject using the unsmoothed functional maps. Single sample \( t \) tests were conducted on each region of interest to test the hypothesis that this amplitude measure differed (either positively or negatively) from zero.

**Results**

All subjects learned the tasks easily and tolerated the scanning procedure well. Movement artifacts were modest, and no image series was unusable in the 12 (consecutive) subjects. Button responses were consistently obtained in the passive experiment at the beginning and end of stimulus periods, with only 0.4% failures. Performance on the active tone task was also uniformly good, with subjects attaining an average score of 97.8% correct (range 95.3–100%). Responses by each subject on the word decision task were compared with those given by a group of 50 normal right-handed controls on the same stimulus set. Items to which control subjects

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**Region of interest analysis**

All landmarks and regions of interest were identified, without reference to the functional data, on sagittal anatomical images located at four stereotaxically defined positions \((x = -43, -47, -51, \text{ and } -55)\) in the left hemisphere; these locations correspond to sections through the PT from the Talairach and Tournoux atlas (Talairach and Tournoux, 1988). The anterior and posterior limits of the left PT defined a PT region of interest. Other regions of interest were the superior temporal plane anterior to the PT (STPa), which included the primary auditory region and planum polare, the anterior superior temporal sulcus (STSa), the posterior STS (STSp), and the planum parietale (PP). Figure 2 illustrates an example of these five regions of interest traced on one sagittal slice from one subject.

The anterior limit of the PT was defined as the grey matter–white matter junction at the floor of the anterior–most transverse temporal sulcus (Steinmetz et al., 1990b; Witelson and Kigar, 1992; Leonard et al., 1993). The posterior limit of the PT was defined as the grey matter-white matter junction at the point where the sylvian fissure turns superiorly toward the parietal lobe as the posterior ascending ramus (Rubens et al., 1976). As a measure of the validity of this technique, these landmarks were also determined in the right hemisphere, and a PT area index was calculated for each hemisphere as the sum of the linear distances between anterior and posterior limits at the four sagittal locations. In agreement with previous research (Geschwind and Levitsky, 1968; Wada et al., 1975; Steinmetz et al., 1991), this area index was greater in the left hemisphere than the right in nine of the 12 subjects, and significantly greater on the left for the group as a whole (two-tailed \( t \) test). The PT region of interest at each sagittal location consisted of the cortical ribbon of the superior temporal plane lying between these two landmarks.

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Fig. 3 Group activation maps at stereotaxic x coordinate 51: passive tones and passive words. The colour scale represents statistical probabilities associated with differences between stimulated and unstimulated states. Grey areas represent differences below the statistical threshold. The stereotaxic grid and brain outline are adapted from the atlas of Talairach and Tournoux (1988). The horizontal line passes through the anterior and posterior commissures, defining the y-axis of the system. The left vertical line in each panel passes through the anterior commissure, defining the z-axis. The PT and superior temporal gyrus are diffusely activated under both conditions. Activation in the tones condition includes the posterior end of the sylvian fissure and portions of the inferior parietal lobe. Activation in the words condition extends further ventrally than in the tones condition.

responded with a probability >0.75 were categorized as targets, and items to which controls responded with a probability <0.25 were categorized as foils. Subjects’ percent correct scores in discriminating targets from foils averaged 90.2% (range 76-100%).

Passive stimulation with either tones or words resulted in widespread activation of the STG, including the PT (Fig. 3). Surprisingly, passive tone stimulation produced activation further posteriorly along the lower bank of the sylvian fissure than did the word stimuli. In contrast, activation from words spread further ventrally toward the STS compared with tones. As illustrated in the average subtraction maps of Fig. 4, neither the PT nor the remainder of the STP showed significant differences between activation to words and tones. Voxels which were significantly more activated by passive words than tones clustered near the STS, while voxels which were significantly more activated by tones than by words clustered in the PP and posterior parietal operculum (Fig. 4).

In the active task experiment, voxels significantly more activated by the word task than by the tone task were found in the STS and middle temporal gyrus, the posterior inferior temporal gyrus, the angular gyrus, and the lateral frontal lobe, while voxels responding more strongly to the tone task were observed in the posterior PT and inferior parietal lobe (Fig. 4). Table 1 gives stereotaxic centre of mass locations for activation peaks in both the passive and active word-tone comparisons. No peaks associated with words were located in the PT or PP in either the passive or the active experiment.

These observations were confirmed in the landmark-based region of interest analysis, which revealed stronger activation to passive words than to tones in the STS regions of interest, no significant difference between passive words and tones in

the PT and STPa, and stronger responses to tones in the PP (Fig. 5). For the active experiment, word task activation was more intense than tone task activation in the STS regions and in the STPa. In contrast, the PT and PP demonstrated
Table 1 Stereotaxic centre of mass coordinates and size of activation clusters in the left hemisphere

<table>
<thead>
<tr>
<th>Volume (µl)</th>
<th>Coordinate (mm)</th>
<th>Atlas structure at centre of mass</th>
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<tr>
<td></td>
<td>x(l–r)</td>
<td>y(p–a)</td>
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<tr>
<td>Words &gt; tones (linguistic clusters)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Passive</td>
<td>333</td>
<td>−56</td>
</tr>
<tr>
<td>Active</td>
<td>1698</td>
<td>−45</td>
</tr>
<tr>
<td></td>
<td>1241</td>
<td>−53</td>
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<td></td>
<td>697</td>
<td>−46</td>
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<td>272</td>
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<td>211</td>
<td>−45</td>
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<tr>
<td></td>
<td>206</td>
<td>−45</td>
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<tr>
<td>Tones &gt; words (non-linguistic clusters)</td>
<td></td>
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</tr>
<tr>
<td>Passive</td>
<td>248</td>
<td>−47</td>
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<tr>
<td>Active</td>
<td>198</td>
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The activation clusters represent relative peaks in the word–tone difference maps, defined as contiguous voxels with positive (words > tones) or negative (tones > words) t > 5.92 (P < 0.0001).

Fig. 5 Word–tone differences measured using the region of interest method (see Fig. 2). Positive values indicate stronger responses to words. The PT showed equal responses to words and tones in the passive comparison, and stronger responses to tones in the active tasks. The PP responded more to tones in both passive and active experiments, and the STS regions of interest responded preferentially to words. The STPa favoured words, but less than the STS regions. Asterisks indicate differences which were significantly different from zero (*P < 0.01, **P < 0.005).

Discussion

Activation of the PT by both words and tones confirms the important role played by this region in auditory processing, as suggested by previous anatomical and physiological research. For example, the cytoarchitectonic fields of the PT lie immediately adjacent to primary auditory koniocortex, with which they are intimately connected, and receive direct auditory projections from the medial geniculate body, the subcortical relay nucleus for the auditory afferent system (Mesulam and Pandya, 1973; Jones and Burton, 1976; Galaburda and Pandya, 1983). On the basis of this and other anatomical evidence, the PT is considered part of a unimodal auditory system that extends over the lateral surface of the STG (Galaburda and Sanides, 1980). Electrophysiological recordings in monkeys (Leinonen et al., 1980; Pfingst and O'Connor, 1981; Baylis et al., 1987; Hikosawa et al., 1988) and humans (Celesia, 1976; Creutzfeldt et al., 1989) also suggest that the STP and lateral STG have a unimodal auditory function.

In contrast, the STS of monkeys contains several areas that receive input from visual, auditory, and somatosensory sources, suggesting that the STS has a role in multimodal integration (Jones and Powell, 1970; Seltzer and Pandya, 1978; Desimone and Gross, 1979; Baylis et al., 1987; Hikosawa et al., 1988). In so far as language is a function that integrates sensory information across modalities, language zones might be expected to have multimodal or even amodal neurophysiological characteristics, and to be positioned where processing streams arising from multiple modalities converge (Geschwind, 1965; Mesulam, 1985; Damasio, 1989). The data presented here are in agreement with these expectations in that the STP, including the PT, was activated equally by nonlinguistic and linguistic auditory stimuli, while more ventral areas centred on the STS showed a preference for linguistic stimuli and for the linguistic task. The other areas activated preferentially by the word decision task, including angular gyrus, lateral frontal lobe, and middle temporal gyrus, are also considered multimodal or amodal association areas (Mesulam, 1985).

In support of this dorsal–ventral distinction between auditory and linguistic areas in the temporal lobe, previous PET and fMRI studies demonstrated peaks of activation associated with linguistic-level processing in regions of the left temporal lobe ventral to the PT: namely in the STS, the middle temporal gyrus or the inferior temporal gyrus (Frith et al., 1991; Démonet et al., 1992; Howard et al., 1992; Raichle et al., 1994; Binder et al., 1995). Thus, it is unlikely that a lack of language activation in the vicinity of
the PT found in the present study is due simply to insensitivity of blood flow mapping techniques to such activation. This conclusion is also supported by the present study, in which activation associated with linguistic stimuli or linguistic task performance occurred in multiple areas of the left temporal, frontal and parietal lobes, but not in the PT.

The posterior portion of the left PT was more strongly activated by nonlinguistic stimuli (tone sequences) than by words. This preference for nonlinguistic stimuli was even more pronounced in the PP and neighbouring parietal operculum (approximately Brodmann area 40), and when subjects performed active tasks involving tone sequence analysis in comparison to analysis of words. The PP and portions of the posterior parietal operculum are probably auditory regions in the human brain (Galaburda and Sanides, 1980), yet association of this area and the PT with processing of tone sequences was unexpected. These stimuli are in a sense musical, and it may be that the PT, PP and parietal operculum play some special role in music perception (Mazzotta et al., 1982; Sergent et al., 1992; Schlaug et al., 1995). More explicitly, this role could relate to the psychological phenomenon of pitch perception, which is a visualization of spectral frequency on a spatial continuum from low to high. The perceptually salient positional shifts of the tone stimuli in the pitch domain might therefore elicit processing by neural networks also involved in spatial representation, located in inferior parietal cortex.

How can the findings of this study be reconciled with the well-established left/right size asymmetry of the PT, which has suggested to many observers a direct role for the PT in language processing? Indeed, in spite of our fMRI findings demonstrating no particular role for the PT in language-level processing, we confirmed this size asymmetry in the same subject sample. We offer here a tentative explanation for this discrepancy, based on morphometric data from this and other studies.

Like several other groups, we distinguished between the temporal and parietal portions of the posterior lower sylvian bank, and labelled these planum temporale and planum parietale. In agreement with these other researchers, we found a left > right asymmetry of the PT and a right > left asymmetry of the PP, implying relative symmetry of the total area of the posterior lower sylvian bank (Rubens et al., 1976; Steinmetz et al., 1990b; Witeison and Kigar, 1992; Leonard et al., 1993). In our sample, for instance, the sum of the PT and PP area indices did not differ between the left and right hemispheres (P > 0.1). These findings suggest that it is the shape rather than the size of the posterior sylvian fissure that is asymmetric. As illustrated explicitly in Fig. 6, the point of upward deflection of the fissure into the parietal lobe occurs much more anteriorly in the right hemisphere (Rubens et al., 1976), and the right planum is tilted forward slightly compared with the left (Cunningham, 1892).

Rather than being caused by enlargement of the PT, as has usually been assumed, these shape asymmetries in the posterior sylvian fissure could be a product of the relative size of nearby structures, such as the frontal lobe, perirolandic region, and posterior parietal lobe (Fig. 7). A larger frontal and perirolandic mass on the left, associated with left language and sensorimotor dominance, might push the point of upward deflection of the sylvian fissure posteriorly and tilt the planum back. A larger posterior parietal lobe on the right might conversely push the point of deflection anteriorly and tilt the planum forward. Previous studies showed asymmetries in these regions that lend support to this hypothesis, including a longer pars triangularis on the left, a larger frontoparietal operculum on the left, a larger inferior parietal lobule on the right, and a relative posterior
displacement of the post-central sulcus on the left (Cunningham, 1892; Connolly, 1950; Rubens et al., 1976; Steinmetz et al., 1990a; Foundas et al., 1995; Habib et al., 1995). Because asymmetry in the relative size of these regions is linked to hemispheric specialization, asymmetry of the PT covaries with functional lateralization, is strongly associated with language lateralization, and may even be useful as a marker for determining language dominance noninvasively (Foundas et al., 1994). In contrast to this association, however, the fMRI findings presented here make it unlikely that size asymmetry of the PT produces language lateralization.

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