Reading, hearing, and the planum temporale

Bradley R. Buchsbaum,* Rosanna K. Olsen, Paul F. Koch, Philip Kohn
J. Shane Kippenhan, and Karen Faith Berman

Department of Health and Human Services, Unit on Integrative Neuroimaging, Clinical Brain Disorders Branch, National Institute of Mental Health, National Institutes of Health, Bethesda, MD, USA

Many neuroimaging studies of single-word reading have been carried out over the last 15 years, and a consensus as to the brain regions relevant to this task has emerged. Surprisingly, the planum temporale (PT) does not appear among the catalog of consistently active regions in these investigations. Recently, however, several studies have offered evidence suggesting that the left posteromedial PT plays a role in both speech production and speech perception. It is not clear, then, why so many neuroimaging studies of single-word reading—a task requiring speech production—have tended not to find evidence of PT involvement. In the present work, we employed a high-powered rapid event-related fMRI paradigm involving both single pseudoword reading and single pseudoword listening to assess activity related to reading and speech perception in the PT as a function of the degree of spatial smoothing applied to the functional images. We show that the speech area of the PT [Sylvian–parietal–temporal (Spt)] is best identified when only a moderate (5 mm) amount of spatial smoothing is applied to the data before statistical analysis. Moreover, increasing the smoothing window to 10 mm obliterates activation in the PT, suggesting that failure to find PT activation in past studies may relate to this factor.
© 2004 Elsevier Inc. All rights reserved.

Keywords: Planum temporale; fMRI; Sylvian–parietal–temporal

Introduction

The planum temporale (PT) is emerging as a site of critical importance in several strands of neuroscientific research in the domain of language and auditory processing. The well-known observation of a leftward asymmetry in the size of the PT and its central location within the classically language-crucial Wernicke's area has made the PT a "prime suspect" when it comes to seeking the neural basis of abnormal linguistic behavior such as that seen in dyslexia (poor reading) and schizophrenia (e.g., auditory hallucinations and thought disorder) that cannot be easily explained by low level sensory dysfunction (Josse and Tzourio-Mazoyer, 2004; Josse et al., 2003; Shapleske et al., 1999).

In the cognitive neuroscience community, the PT is increasingly viewed as a relay station between the auditory-sensory cortex of the superior temporal lobe and other, mainly motor-oriented, cortical areas. For instance, Griffiths and Warren (2002) see the PT as a "computational hub" that "transform[s] incoming auditory patterns into information about acoustic objects and position that could be used in other cortical areas." In a similar vein, Hickok and Poeppel (2004) have posited that the posterior PT acts as an auditory-motor interface that transforms sound-based representations of speech in auditory cortex to their articulatory counterparts in frontal cortex. Both of these ideas place the PT within an auditory "dorsal stream" that has recently been proposed (Hickok and Poeppel, 2000; Rauschecker and Tian, 2000) in analogy to the well-known dorsal stream of the visual system (Ungerleider and Mishkin, 1982), and for which an anatomical basis has been established in the monkey (Romanski et al., 1999). While dorsal stream processing in vision has traditionally been aligned with spatial "where" functions, there is a growing literature that demonstrates the existence of visuomotor integration systems in the visual dorsal stream (Andersen, 1997; Milner and Goodale, 1995; Rizzolatti et al., 1996). Thus, many argue that the perceptual analysis of visual stimuli is not limited to a passive reconstruction of the external world, but rather involves a mode of analysis that has been termed "perception for action" (Fuster, 1997; Milner and Goodale, 1995)—a process that moves from the determination of an object's identity and spatial location ("what" and "where") to an assessment of that object's potentialities and prospective uses ("how"), especially those that would necessitate quick action on the part of the observer.

In the exercise of natural language, it is easy to see a similar perception-action cycle at work: conversation proceeds from speaker to hearer and back again, with each new message depending largely on that which preceded it. At the developmental level, it is clear that for a child to acquire language, he must learn

---

* Corresponding author. Department of Health and Human Services, Unit on Integrative Neuroimaging, Clinical Brain Disorders Branch, National Institute of Mental Health, National Institutes of Health, IRP, 9000 Rockville Pike, Building 10, Room 4C-101, Bethesda, MD 20892-1365. Fax: +1 301 496 7437.
E-mail address: brad.buchsbaum@nih.gov (B.R. Buchsbaum).
Available online on ScienceDirect (www.sciencedirect.com).

to connect the sounds of speech with the motor programs required to produce those same sounds. There are several reasons to believe that the neural system that implements this "connection" or "interface" between the centers for speech perception and speech production lies in posterior cortex in the vicinity of Wernicke's area. Most obviously, the symptoms associated with aphasias of the temporoparietal area (e.g., Wernicke and conduction aphasias) cut across any hypothetical boundary between receptive and productive language function. In conduction aphasia, which is most often caused by lesions around the posterior end of the Sylvian fissure, speech comprehension appears to be only mildly impaired, while production—whether via repetition, spontaneous speech, object naming, or reading—is marked by the presence of nonsemantic, or literal, speech errors (Benson et al., 1973; Damasio and Damasio, 1980). Wernicke's aphasia (Selnes et al., 1985), which is associated with more extensive temporal lobe lesions than conduction aphasia, is characterized by a broader and more severe language disturbance: one that affects phonemic, semantic, and grammatical aspects of both speech production and comprehension. Because of the more limited and production-weighted impairment seen in conduction aphasia, it has been proposed that this syndrome might emerge as a result of selective damage to an auditory-motor interface that lies somewhere near the junction of the temporal and parietal lobes (Hickok and Poeppel, 2004). Such a hypothesis makes a simple prediction that can be evaluated with the use of functional brain imaging, namely that, compared with a resting condition, this area should activate both during passive speech perception and during silent speech production. This prediction follows from the idea that a sensory-motor interface system carries out transformations from one representational class (e.g., sounds) to another (e.g., articulatory gestures) and that this work requires that such a system be engaged with regions upstream that process the relevant sensory input and with regions downstream that process the relevant output. Although the argument outlined above points to a posterior temporal lobe site as being the most likely candidate for such an auditory-motor interface, other authors have found evidence that similar computations (although not specifically in the context of language) may be carried out in ventral premotor cortex (Schubotz and von Cramon, 2004) or in the inferior frontal gyrus (Iacoboni et al., 1999). The neuroimaging literature reviewed below offers some evidence that a region in the posteromedial PT also demonstrates this bidirectional engagement in auditory and motor (articulatory) processing.

Several recent neuroimaging studies have found activation in the superior temporal region during speech production (Herholz et al., 1996; Hickok et al., 2000; Price et al., 1996). Wise et al. (2001) showed that two systems within classic Wernicke's area activate during silent speech, one located in the posterior superior temporal sulcus (STS) and the other located in posterior PT. In their study, this latter activation was not found during passive auditory perception. However, two studies (Buchsbaum et al., 2001; Hickok et al., 2003) have shown that the posterior PT, referred to in Hickok et al. (2003) as area Spt (Sylvian–parietal–temporal), activates both during the perception and silent rehearsal of speech and musical sequences. "Spt" is not a purely anatomical identifier, however, but rather a term that is used to describe a functional–anatomical relationship, similar to the coinage FFA for "fusiform face area" (Kanwisher et al., 1997). It is also a term that deliberately evokes the cytoarchitectonically defined region of auditory cortex, Tpt, which also typically resides in the posterior portion of the PT and sometimes extends superiorly into the planum parietale, or laterally

on to the superior temporal gyrus (Galaburda et al., 1978). In addition, Tpt shares cytoarchitectonic similarities with Brodmann area 44 (Broca area), with its prominent pyramidal cells in layer IIIc and broad lamina IV (Galaburda, 1982), further suggesting a link with its functionally defined cognate, Spt.

Activation in the PT/STG has also been found during the delay period of verbal memory tasks (Postle et al., 1999; Sakai and Passingham, 2003)—although far more studies of verbal working memory have not found evidence for superior temporal lobe participation in so-called "phonological storage" (e.g., Paulesu et al., 1993; Fiez et al., 1996; Awh et al., 1996; Jonides et al., 1998). The role of the PT during speech perception is currently in dispute. For instance, Binder et al. (2000) found that the PT responded equally to tones and speech during passive listening. Jancke et al. (2002), however, contrasted consonant–vowel syllables with tones and did find increased activation in the PT bilaterally. Other studies that have used more sophisticated control stimuli have generally concluded that the critical region for phonetic perception is in the superior temporal sulcus (STS) or middle temporal gyrus (MTG) (Belin et al., 2000; Scott et al., 2000; Vouloumanos et al., 2001), but not the PT.

Studies of single-word reading have for the most part failed to show activation in the PT. Indeed, a major review of neuroimaging studies of reading does not include the PT among the areas that are consistently found active (Fiez and Petersen, 1998). A more recent review (Turkeltaub et al., 2002) that used a probabilistic meta-analytic technique to generate "activation likelihood maps" in studies of single-word reading also failed to implicate the PT. Lack of power at the within-study level would, of course, preclude detection of PT activity in this kind of metaanalysis because it depends on coordinates of "peak" activity supplied in published tables. However, a high-powered ($n = 20$) fMRI study (Mechelli et al., 2003) of silent reading of words and pseudowords also failed to reveal a significant main effect of reading in the PT. In addition, numerous studies have shown that the superior temporal gyrus deactivates during verbal fluency tasks, although baseline conditions in such experiments have tended to require some form of speech, whether internal or overt (Frith et al., 1991, 1995; Warburton et al., 1996). On the other hand, studies involving rapid repetition of a single word or set of syllables have tended to find increased activation relative to rest in and around the superior temporal gyrus bilaterally (Paus et al., 1996; Price et al., 1996; Shergill et al., 2002; Wildgruber et al., 1999).

In short, then, there appear to be conflicting data about the role of the posterior superior temporal lobe, including the PT, in tasks that require some form of silent speech. Because there is some evidence that this area, or areas nearby, may very well deactivate during speech production, standard methods of assessing group activation by performing statistical inference on smoothed and stereotaxically normalized images are problematic. Smoothing could have the effect of blurring together—and therefore canceling out—the individual effects of two regions exhibiting this juxtaposition of positive and negative functional activity. For instance, one might imagine that a small and very focal region of activity in the PT, surrounded by a larger and more diffuse area of nonsignificantly deactivated voxels, could be drowned out by the application of a relatively large (e.g., 10–15 mm) smoothing kernel. A second difficulty with assessing PT activation in multisubject statistical maps has to do with the large intersubject variability in the shape and configuration of its posteriormost portion, which diverges into ascending and descending rami. In

some people, the part of the PT lying on the supratemporal plane (HPT, in Witelson and Kigar, 1992) diverges sharply superiorly, following the ascending ramus of the Sylvian fissure into the parietal lobe. In other cases, the PT essentially runs parallel to the temporal gyri before terminating in short ascending and posterior rami (see Westbury et al., 1999, for a thorough discussion of four canonical PT patterns). Because of this posterior variation in the anatomy of the PT, good intersubject registration in this area is difficult to achieve, and therefore, true functional activation in the posterior parts of the PT may be hard to detect in multisubject analyses.

The primary goal of the present study was to determine whether the posterior portion of the PT is active during both speech perception and silent single-word reading. To minimize nonspecific semantic factors (e.g., word imageability), task stimuli consisted of one-syllable pseudowords. We hypothesized that the following three factors might influence detection of reading-related activation in the posterior portion of the PT: (1) amount of spatial smoothing applied to functional volumes, (2) intersubject variability in the anatomical location of reading-related activation in the PT, and (3) the presence of deactivations in cortical regions surrounding the PT. In our statistical analyses, we take up each of these issues in an effort to more fully understand the factors that may have contributed to the relative infrequency with which the PT has been implicated in functions relating to speech production in the neuroimaging literature.

Methods

Subjects

Seventeen subjects (6 women, 11 men; 20–42 years old, mean age = 29.6) participated in the study after giving informed written consent. The experimental procedures were approved by the National Institute of Mental Health Institutional Review Board. No subjects had any history of psychiatric or neurological diseases. All subjects, as assessed by the Edinburgh Handedness Inventory, were determined to be strongly right-handed.

Task

A set of 89 one-syllable pronounceable pseudowords was recorded by a male speaker using Sound Edit on a Power Macintosh 7500 (HEAR events). The same set of pseudowords was visually presented for silent single-word reading (READ events). A rapid event-related design with READ and HEAR events randomly intermingled was used for stimulus presentation where the interstimulus interval (ISI) was geometrically distributed and with the additional constraint that the minimum allowed within-condition ISI was 1 s. For each event type (READ and HEAR), the average ISI was approximately 5.5 s and ranged from 1 to 25 s. The procedure for determining the event arrival times for each condition was as follows: a sequence of 1000 geometrically distributed numbers was generated using the *rgeom* function of the R Statistical Computing Language (www.R-project.org) with probability parameter = 0.17. From this vector, the first *n* values were chosen such that the sum of these ISIs was close to, but did not exceed 345 s (each scanning run was 360 s so the last event could occur no later than 15 s before the end of the run). This sequence of ISIs was then

cumulatively summed to generate the event arrival times for the READ condition. The same set of ISIs was then randomly permuted and cumulatively summed to generate the event arrival times for the HEAR condition. Thus, every run had the same number of events in each condition (ranging from 57 to 73) and the same average ISI. In addition, although all ISIs between events of the same type were guaranteed to be 1 s or greater, this was not true for between-condition ISIs which had no such restriction. Thus, READ and HEAR events could occur simultaneously (ISI = 0). Subjects were instructed to silently read all words appearing on the screen. They were specifically enjoined to pronounce (without moving lips) the words rather than just to "view" them. For the auditorally delivered words, subjects were simply asked to passively listen. Subjects were told that occasionally they would see and hear a word simultaneously and that, in this circumstance, they should still read the visually presented word silently. In effect, then, the entire task consisted of reading words silently while incidentally listening to words through headphones.

MRI data acquisition

Functional and structural images were acquired with a 3.0-T GE Signa scanner (Milwaukee, WI) using a GE birdcage head coil. Each subject performed at least six scanning runs, each of which lasted approximately 6 min. Functional images were collected with a gradient echo echoplanar imaging sequence (TR = 2 s; TE = 25 ms; FOV = 24 cm; flip angle = 90; 64 × 64 matrix). Image volumes were acquired in 24 axial slices (thickness, 5 mm; in-plane resolution, 3.75 × 3.75 mm). In addition, high-resolution MP-RAGE structural images were acquired in 124 axial slices (thickness, 1.2 mm; in-plane resolution, 0.975 × 0.975 mm). The experimental paradigm was programmed using Presentation software Version 5.5 (Neurobehavioral Systems) and ran on a Dell laptop set up in the control room. Visual stimuli were rear-projected onto a translucent screen placed outside the bore of the magnet and viewed via a mirror system attached to the head coil. Auditory stimuli were delivered via air conductance tubes connected to a pair of magnet-safe headphones (Avotec model SS-3100) placed around the subject's ears.

Data analysis

Image preprocessing and statistical analysis were carried out using FEAT (fMRI Expert Analysis Tool) Version 5.00, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The images of every scanning run were concatenated to form, for each subject, a set of six four-dimensional (ANALYZE 7.5) data files. After correction for sampling offsets in EPI slice acquisition, all runs were motion-corrected with the middle volume (the 90th image) serving as the registration reference. High-pass temporal (60-s cutoff) filtering was then applied to each of the four-dimensional data files. Each subject's high-resolution MRI was aligned with FLIRT (FMRIB's Linear Image Registration Tool) to the standard MNI (Minnesota Neurological Institute) template, and a 12-point affine transformation was derived and saved. All functional runs were then aligned with FLIRT to the high-resolution MRI, and again these rigid-body transformations were saved to disk.

Because one of the goals of the study was to examine whether spatial smoothing might affect signal detection power in the region

of the PT, the functional data sets were further processed in one of three ways: (1) not smoothed spatially (NO-SMOOTH), (2) smoothed with a 5-mm Gaussian kernel (5-SMOOTH), or (3) smoothed with a 10-mm Gaussian kernel (10-SMOOTH). The same statistical procedure described below was then applied to each of these data sets.

Statistical analysis was carried out in three stages (within run, across runs/within subject, and across subjects) using FLAME (FMRIB's Local Analysis of Mixed Effects). This strategy allows for the modeling of random effects at both the "run" (sometimes called "session") and subject levels. Furthermore, variances occurring at lower levels of the analysis are carried up to higher levels so that inferences made at the "group" level take into account the variances (interrun and intersubject) occurring in the nested levels.

Time series were modeled using multiple regression in which each task event type (READ, HEAR) was represented by a separate regressor that was formed by convolving a gamma function (alpha = 6, beta = 3) with the binary sequence (0 = off, 1 = on) representing for each second of scanning the presence or absence of the event. A third term, formed by the multiplication of the first two terms, was included to model possible nonlinear interactions of the independent variables. Each of these regressors was tested for a nonzero slope, and Z-transformed statistical images were generated and thresholded in two separate ways: (1) using clusters determined by $Z > 2.33$ ($P = 0.01$ uncorrected) and a (corrected) cluster significance threshold of $P = 0.01$, and (2) using an uncorrected threshold of $Z > 2.58$ ($P = 0.005$)—a cutoff targeted for the specific assessment of left posterior PT activation and equivalent to a straight Bonferroni correction (corrected $P = 0.05$) for 10 voxels. An activation map was also created to visualize regions active during both READ and HEAR conditions. These maps show those areas for which Z scores exceeded 2.58 ($P = 0.005$) in both conditions and thus represent the voxelwise intersection of the READ and HEAR activation maps. Finally,

individual data from each of the 17 subjects were examined specifically for PT activation, using an uncorrected threshold of $Z > 3.09$ ($P = 0.001$).

Results

In the introduction, we noted that many previous neuroimaging studies of single-word reading failed to find activation in the posterior PT. On the other hand, listening to auditory stimuli of any kind is well known to activate this area robustly. Thus, much of our statistical presentation is focused on the READ condition, while the HEAR activation allowed us to pinpoint the brain regions that responded during both task conditions. Also, we had two separate but related aims in the presentation of our statistical analyses. The first was to evaluate the a priori hypothesis that the left posterior PT activates during both speech perception and silent reading. Because this hypothesis was confirmed, we took up the question of why previous studies may have failed to show PT activation in single-word reading.

Does the PT activate during single-word reading?

To answer this question, we examined the READ group activation maps, thresholded at $Z > 2.58$ for all three levels of smoothing. We found a small area of activation in the vicinity of the left PT in both the NO-SMOOTH and FIVE-SMOOTH maps, while no suprathreshold voxels remained in the 10-SMOOTH condition. An axial slice cutting through this region of activity is shown at the three levels of smoothing, thresholded and unthresholded, in the bottom left panel of Fig. 1. The corresponding unthresholded z map images in the top panel (and the column of unthresholded sagittal images on the right) show that, as the smoothing kernel is increased, the area of enhanced activity in the
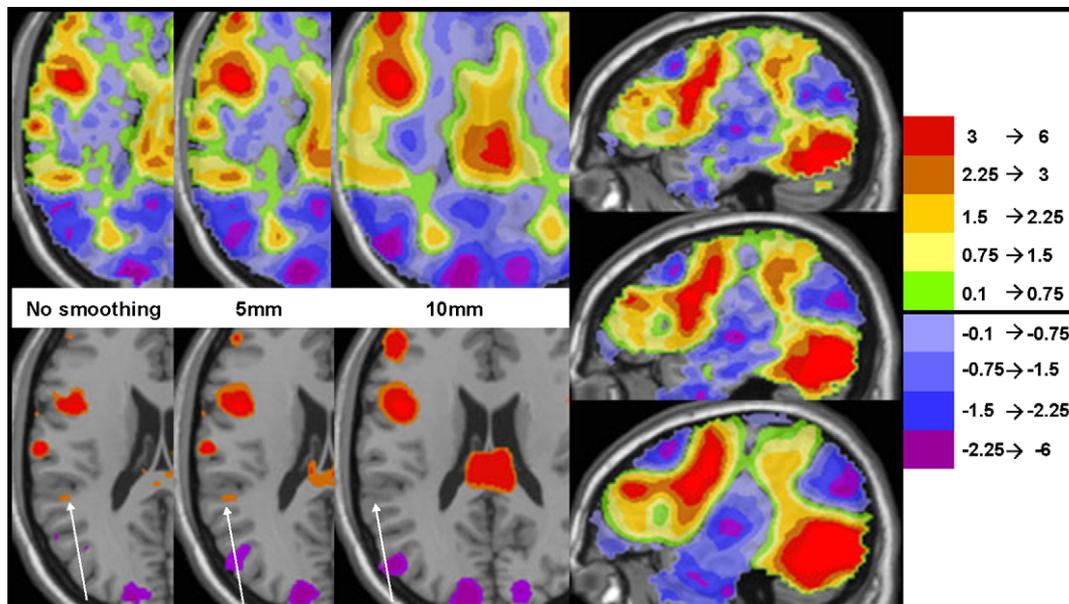

Fig. 1. Group READ activation in the planum temporale shown for all levels of smoothing. (Top left) Axial images showing unthresholded READ z maps for all levels of smoothing (from left to right: none, 5 mm, 10 mm). Talairach level: $Z = 21$. (Bottom left) Same axial slice as above, thresholded at $Z > 2.58$ and $Z < -2.58$. Arrows in left two slices point to enhanced activation in PT. Talairach level: $Z = 21$. (Right) Row of three sagittal slices showing unthresholded READ Z maps for all levels of smoothing (from top to bottom: none, 5 mm, 10 mm). Talairach level: $x = -50$.

region tends to blend into a large, diffuse cluster centered in the parietal lobe. However, at the $Z > 2.58$ threshold, the PT activation appears as an autonomous cluster in the NO-SMOOTH (11 voxels, maximum $Z = 2.925$, Talairach coordinates: $-50, -44, 20$) and 5-SMOOTH maps (23 voxels, maximum $Z = 2.97$, Talairach coordinates $= -50, -44, 19$). The location of this activation is located within the bounds of Westbury et al.'s (1999) probabilistic atlas of the PT (5–25% range). A box plot showing the distribution of z scores in the set of connected suprathreshold voxels in the PT for the 5-SMOOTH analysis appears in Fig. 2. As one might expect, as the smoothing kernel is increased, the variance of the Z scores in this small region decreases. It is also clear from this plot that the activation levels in the 10-SMOOTH voxels are markedly lower than in either the NO-SMOOTH or 5-SMOOTH voxels.

In a follow-up analysis, we took reported Talairach coordinates from three studies that have demonstrated posterior PT activation during inner speech (Hickok et al., 2003; Sakai and Passingham, 2003; Wise et al., 2001, see Introduction) and averaged them to form the centroid ($-48, -40, 20$) of a cubic region of interest (ROI) 6 mm on a side. The location is close, but not identical, to the maximum for the READ condition reported above. Voxel values from the READ and HEAR map were then extracted and averaged within the ROI for each subject, and one-tailed t tests were performed for both sets of values. Both tests were significant (READ, $t = 3.0318$, $df = 16$, $P = 0.004$; HEAR, $t = 4.3119$, $df = 16$, $P = 0.0003$), providing support for the validity of the semiexploratory analysis described in the previous paragraph.

Planum temporale activation after clusterwise significance thresholding

Because the most common method for deriving statistical thresholds in neuroimaging data involves some form of clusterwise correction, we examined activation maps for the READ condition after application of a clusterwise significance threshold ($Z > 2.33$, cluster significance threshold $P = 0.01$ (Worsley et al., 1992)). As it was evident from the single-subject analyses that activations in the posterior PT were very focal (though highly significant, see next section), it seemed likely that the region of PT activity in the group maps would be unlikely to survive clusterwise thresholding.

The set of voxels in the PT did, however, survive this more conventional thresholding scheme (again, only in the NO-SMOOTH and 5-SMOOTH maps). We noted earlier that this cluster appeared in the uncorrected READ maps ($Z > 2.58$) as a small cluster of voxels spatially unconnected to larger regions of activation located inferiorly in the superior temporal sulcus and superiorly in the parietal lobe. However, lowering the height threshold to $Z > 2.33$ for clusterwise significance assessment effectively transformed what was at the uncorrected threshold of $Z > 2.58$ a separate island of activity in the PT, to a peninsular extension of a much larger region (123 voxels) of activation in the posterior parietal lobe. Thus, while the set of PT voxels detected in the uncorrected analysis also survived cluster level thresholding, the bulk of the active region to which these voxels belong was located in a region anatomically removed from the PT. Had this bridge not been formed between the smaller PT cluster and the larger parietal cluster, the former region would not have survived the stringent clusterwise threshold. We are then left with the following question: is the apparent PT activation really just part of the parietal activation that has spread inferiorly due to the anatomical "blurring" that occurs in multisubject analyses? If this were the case, we would expect the largest perimeter of activation to occur in the 10-SMOOTH analysis—the only map in which the PT *failed* to reach statistical significance. Moreover, as can be seen in Fig. 5, while the PT voxels also activated during the HEAR condition, the parietal region did not. This argues that the posterior parietal and PT activations, though spatially contiguous at the cluster level threshold, have functional profiles that distinguish
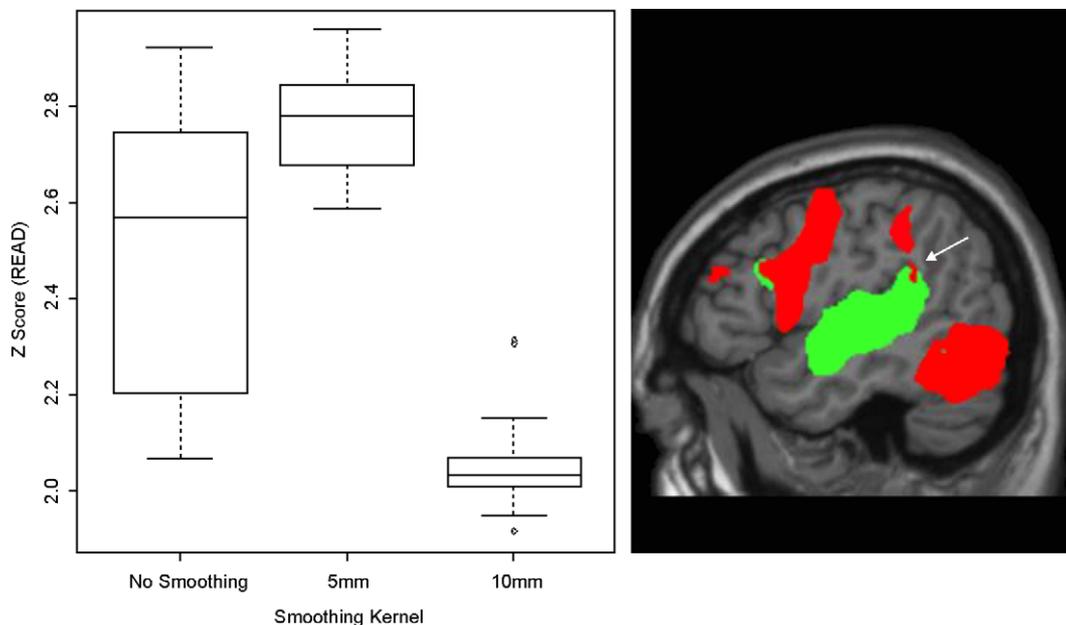

Fig. 2. Distribution of Z scores in planum temporale across smoothing levels. (Left) Box plot showing READ z scores across smoothing levels in cluster of 23 voxels that reached significance ($Z > 2.58$; $P = 0.005$, uncorrected) in 5-SMOOTH map. (Right) Sagittal image with arrow pointing to active area from which the values in the box plot were extracted. Green colors represent areas active ($Z > 2.58$, uncorrected) in HEAR condition. Red shows area active ($Z > 2.58$, uncorrected) during READ condition.

them. Because brain activations are commonly reported in tabular form, where each cluster is represented by its coordinate of peak intensity (e.g., maximum Z score), it is likely that with a conventional approach to significance assessment, the small region of activity in the PT would not have been remarked upon.

Planum temporale READ activation in single-subject analyses

Each of the 17 single-subject analyses for the READ condition were assessed for PT activation using an uncorrected threshold of Z > 3.09 (P = 0.001) or a Bonferroni-corrected threshold of 0.05 for 50 voxels. We used a more conservative threshold than in the semiexploratory group analysis because we could not rely on a priori Talairach coordinates to guide the search for active voxels (coordinates derived from group maps might well fall outside the bounds of the PT in a single subject's normalized brain). Thus, we used a threshold of Z > 3.09 (P = 0.001) coupled with the requirement that the voxel falls within the anatomical boundary of the PT according to the definition of Westbury et al., 1999. Using these criteria and examining analyses derived from the 5-SMOOTH data sets, we found left PT activation in the READ condition in 9 of 17 subjects for whom representative sagittal slices are shown in Fig. 3 (see also Table 1). We can see that, in each case, activation occurs in a fairly posterior portion of the PT and, except for one case (case 8 of Fig. 3), has a maximum Z value located at least 1 cm medial to the lateral surface of the brain. Where descending and ascending rami clearly diverge (cases 6 and 8 of Fig. 3), activation is seen in the descending ramus. In no case were two separate, unconnected clusters of voxels found in the region of the left PT; that is, activation loci shown in Fig. 3 are a part of one and only one cluster of activation found in the PT for that subject. The mean Talairach coordinate for the maximum Z

Table 1
Talairach coordinates and maximum Z values of active left PT clusters in single subject READ activation maps

Subject	Talairach coordinate	Max Z score
1	−50 −42 22	4.927
2	−50 −45 23	3.943
3	−55 −36 20	4.082
4	−53 −36 11	4.381
5	−57 −34 20	5.162
6	−63 −34 11	7.081
7	−51 −44 22	9.58
8	−63 −32 15	3.597
9	−53 −40 20	3.807

All coordinates have been transformed from MNI space using Matthew Brett's equations available at (http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml).

value of the nine activation foci was: $x = -55$, $y = -38.1$, $z = 18.2$, which corresponds quite well to the maximum READ activation in the 0-SMOOTH and 5-SMOOTH group analyses (see Table 1) and to the coordinates used for the ROI analysis. Significant activations were found in the right PT for only one subject (that subject not showing a corresponding left PT activation), although four subjects showed activation in a very lateral site in the right STG. No subject, therefore, showed bilateral activation in the PT for the READ condition. As expected, all subjects showed auditory activation in the PT bilaterally.

Are there regions of deactivation near the planum temporale?

The group activation maps for the READ condition show a strip of activation proceeding mediolaterally along the posterior part of
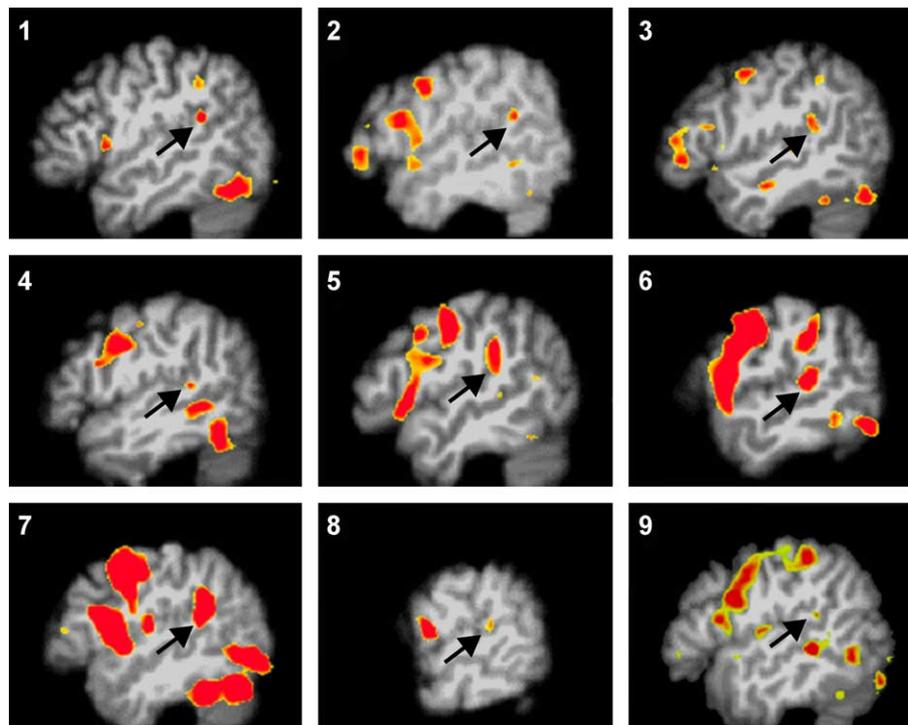

Fig. 3. Sagittal slices showing activation in posterior PT for READ condition. Images are thresholded at Z > 3.09 (P = 0.001) and overlaid on the subjects' corresponding Talairach normalized MP-RAGE.
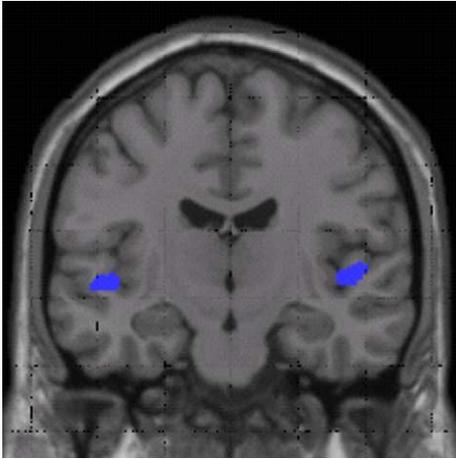
Fig. 4. Bilateral READ deactivation ($Z < -2.58$) in supratemporal plane anterior to Heschl gyrus. Coronal slice cutting through auditory cortex just anterior to primary auditory cortex, $y = -13$.

the PT that is surrounded by areas of subthreshold negative activity. The unthresholded sagittal images of Fig. 1 show that the PT activation is hemmed in by deactivations in insular cortex anteriorly and the angular gyrus posteriorly. Suprathreshold deactivations ($Z < -2.58$, $P = 0.005$) are also visible in regions in and around primary auditory cortex, bilaterally (left: 50, −18, 0; right: 46, −12, 0), just anterior to Heschl gyrus (see Fig. 4). These

deactivations do not reach threshold when a correction for multiple comparisons is made using a clusterwise correction threshold of $P < 0.01$ and a height threshold of $Z > 2.33$ ($P < 0.01$). Nevertheless, because such deactivations have been reported in the past and because of the bilateral pattern, it is likely that these deactivations are not due to chance alone.

The "hemming in" of the active portion of the PT in the READ condition can be better seen in individual subject data. Shown in Fig. 5 is an axial slice cutting through the PT of a single subject, where we can see in the overlaid unthresholded (top panel) READ activation images how regions of deactivation in the adjacent gyri surround the thin strip of positive activation in the PT gray matter.

Areas active during both reading and hearing

Several areas demonstrated activity during both READ and HEAR task conditions. An image (see Fig. 6) was created that for every voxel contains the value of the minimum of the two z scores from the READ and HEAR contrast maps, which was then thresholded at $Z > 2.58$ ($P = 0.005$), yielding a conjunction image (according to the definition of Nichols et al. in preparation) that tests against the null hypothesis that either of the two contrasts is nonsignificant. A list of areas that survived this thresholding procedure is supplied in Table 2. Of the several distinct areas of joint activation (see Table 2), two did not show a bilateral pattern. Both the posterior PT and a highly active cluster in sensory–motor
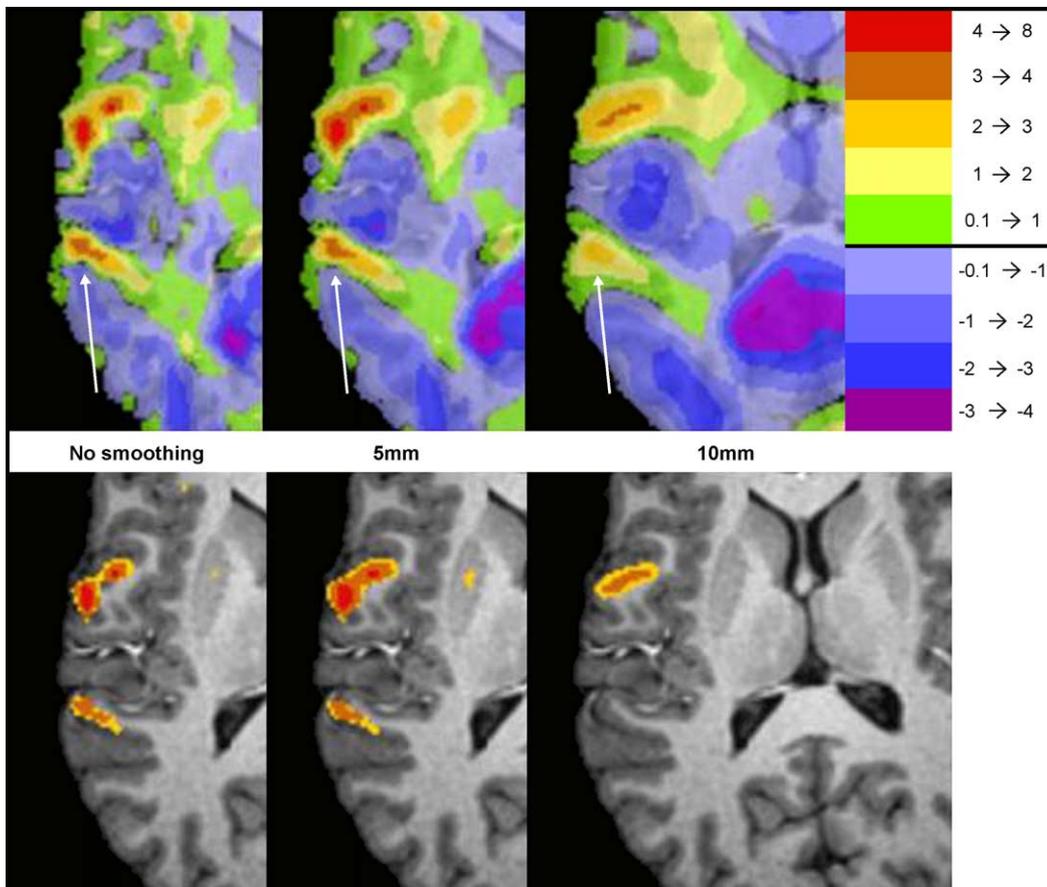

Fig. 5. Single-subject READ activation shown for all levels of smoothing. (Top) Row of three axial images showing unthresholded READ z maps for all levels of smoothing (from left to right: none, 5 mm, 10 mm). Arrows point to activated region in PT. (Bottom) Same axial slices as above, thresholded at $Z > 2.58$.
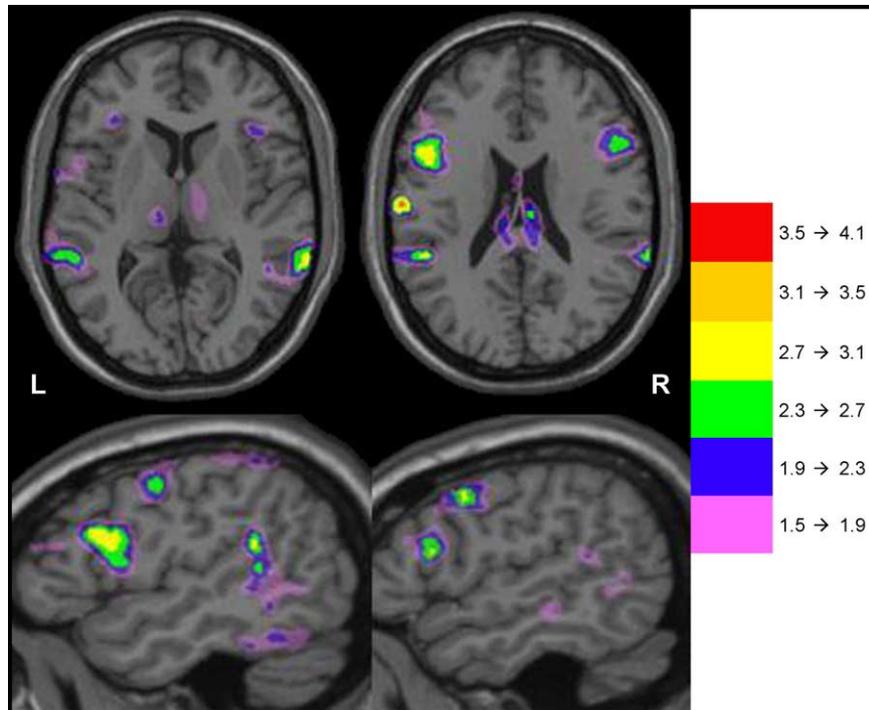
Fig. 6. Areas active during both READ and HEAR conditions. (Top) Axial slices at $z = 6$ and $z = 19$; Left is left, right is right. (Bottom) Sagittal slices at $x = -50$ and $x = 55$. Note that posteromedial PT activation only appears on the left (the right-sided activation in the upper right axial slice is in the posterolateral STG/STS, not the PT), while STS activation is bilateral.

cortex of the parietal operculum showed joint activation ($Z > 2.58$ READ and $Z > 2.58$ HEAR) only on the left.

Discussion

The results of this study provide evidence that the posterior PT activates during both silent reading and speech perception. The locus of activation is very close to that in previous work that found sustained responses (during both encoding and rehearsal) in tasks of auditory working memory that involved both speech and musical stimuli (Buchsbaum et al., 2001; Hickok et al., 2003). Here, we demonstrate that activation in this region during inner speech is not

contingent upon the presentation of a preceding to-be-remembered auditory stimulus. This supports the idea that Spt can be involved in ordinary speech production. Indeed, the fact that a lesion to the left temporoparietal region can cause deficits in speech production while leaving speech perception relatively intact—as in the case of conduction aphasia—is consistent with this view.

Most previous neuroimaging studies of silent reading have not found activation in the PT (although there are exceptions; see Nakada et al., 2001). It was our hypothesis that the general failure to find PT activation in the past might relate to the degree of spatial smoothing applied to the data during preprocessing. We have shown that activation in the PT decreased to a subthreshold level as we moved from a 5- to a 10-mm filter. Furthermore, examination

Table 2
A list of areas that exceeded $z > 2.58$ in both READ and HEAR activation maps

Hemisphere	Area	Number of voxels	Talairach	Z score[a]
L	Inferior frontal gyrus (BA 44/6)	189	−46 12 12	3.4
R	Inferior frontal gyrus (BA 46)	126	65 −42 13	3.35
L	Postcentral gyrus (BA 43)	65	−61 −11 17	4.09
L	Inferior frontal gyrus (BA 47)	56	−34 35 −2	3.32
R	Inferior frontal gyrus (BA 44)	36	50 20 14	2.94
L	Precentral gyrus (BA 6)	25	−55 −2 41	2.85
L	Planum temporale (BA 22)	18	−50 −38 20	2.96
R	Middle frontal gyrus (BA 9)	17	53 8 36	2.77
L	Superior temporal gyrus(BA 22)	13	−60 −40 13	2.96
R	Caudate nucleus	12	6 −16 22	2.96
L	Superior/middle temporal gyrus (BA 22/21)	11	−53 −40 9	2.93
L	Middle temporal gyrus (BA 22)	11	−55 −39 4	2.8
R	Inferior parietal lobule (BA 40/7)	3	38 −56 53	2.69
R	Middle temporal gyrus (BA 21/37)	2	65 −47 −1	2.66
L	Precentral gyrus (BA 6)	1	−65 2 33	2.7

[a] Z score is the minimum of the two (READ, HEAR) z values at the listed coordinate.

of the unthresholded group activation image for the READ condition reveals that the PT activation forms a small strip between two large swathes of cortex in the angular gyrus posteriorly and the insula/parietal operculum anteriorly that exhibit (mostly non-significant) deactivation during silent reading. Significant deactivation (at a $P = 0.005$, uncorrected threshold) was observed in temporal cortex bilaterally but was located in a region slightly anterior to primary auditory cortex and probably too distant to influence positive signal detection in Spt. Nevertheless, since Spt is located in the farthest corner of auditory cortex, as a kind of apical end (see Fig. 2, right panel), it is least insulated from effects that may leak in from other functional regions. Thus, for the posterior PT, in a task requiring silent single-word reading, the optimal smoothing kernel appears to be on the order of 5 mm. This is not to be taken as a methodological pronouncement on the question "how much to smooth" but rather as an empirical demonstration of how in a particular context the size of a smoothing kernel can effect the interpretation of activation maps (see Fransson et al., 2002; White et al., 2001 for more general discussions of the practical consequences of spatial smoothing in fMRI).

As our examination of single-subject activation maps demonstrates, however, area Spt does not activate uniformly across the sample of normal subjects. Thus, one might question the legitimacy of drawing inferences with regard to brain mechanism that are based on the activation patterns revealed in multisubject analyses. For instance, to make the statement that, say, primary visual cortex "activates" when subjects view a flashing checkerboard seems to imply that this physiological response is common to everyone (excluding certain subpopulations as, for instance, the blind). Indeed, in the case of the flashing checkerboard paradigm, failure to find activation in V1 for a particular subject would be cause for concern or reason to suspect an error in the analysis. In fact, that primary visual cortex should activate during visual stimulation is practically tautological: a functional term "visual" is embedded in the anatomical label. In more complicated cognitive paradigms, however, perfect intersubject functional–anatomical correspondence in activation patterns is not always achieved. Thus, as in the present case where only 50% of the subjects showed activation in Spt for the READ condition, the inference made at the group level (e.g., area X "activates") clearly cannot be applied to each and every member of the population. Thus, in the attempt to address the question "what does area X do?" we must be careful not to base our conclusions solely on the results from group activation maps. In the present case, the best we can say, empirically, is that most (9 of 17) people activate area Spt during reading—and, given a sample of 17 subjects, this preponderance was enough to produce a statistically significant result at the group level, although only when using thresholds targeted for an assessment of a very small proportion of the whole brain. Thus, interindividual variation in the presence or absence of activation in a region must be accounted for when developing and refining neurocognitive models of information processing, which almost always presuppose an underlying uniformity to the workings of the mind-brain.

One theoretical implication of our results concerns the anatomical localization of the phonological store component of Baddeley's (1986) model of working memory. Because auditory items have, by definition, obligatory access to the phonological store, Becker et al. (1999) argued that the neural realization of this cognitive component must activate during passive auditory stimulation. As those authors point out, however, the region most often implicated as the "neural correlate" of the phonological store

is located in the parietal lobe (BA 40), sometimes in a ventral location (Paulesu et al., 1993) but more often in superior/posterior parietal cortex (e.g., see Awh et al., 1996). In the present study, we have shown that this latter region, because it does not respond to passive auditory stimulation (although it does activate during silent reading), cannot be the neural locus of the phonological store. In addition, we have further refined the anatomical location of what probably corresponds to the more ventral locus found in the early positron emission tomography study of verbal working memory by Paulesu et al. (1993) and referred to in that study as the supramarginal gyrus. Examination of single-subject activation maps shows clearly that, aside from bilateral STS, the only posterior area active during both perception and production of speech lies in the gray matter of the posterior bank of the Sylvian fissure (area Spt), not in the supramarginal gyrus.

To conclude, we have demonstrated in a group of 17 normal subjects that a region in the posteromedial portion of the PT, area Spt, activates both while subjects silently read and also while they hear one-syllable pseudowords. Several other regions show this pattern, three frontal areas (inferior frontal gyrus, frontal operculum, and premotor cortex—all bilaterally), one left parietal area (sensorimotor cortex, BA 43), and posterior STS bilaterally. This pattern of overlap between activation derived from passive auditory speech perception and silent articulation is very similar to that found in Buchsbaum et al. (2001) and Hickok et al. (2003); specifically, each of these studies showed joint activation in the inferior frontal gyrus, premotor areas 4/6 and the posterior temporal lobe sites, Spt and STS, respectively. Wilson et al. (2004) have also shown perception/production overlap in both dorsal and ventral sites in premotor cortex.

Deactivations were seen bilaterally in a medial location just anterior to Heschl gyrus. Although deactivations in fMRI are still not well understood, there is evidence from neurosurgical mapping studies that many superior temporal lobe neurons are inhibited during the naming of objects (Ojemann, 2003). Intracellular recordings from auditory interneurons of the cricket have revealed a class of cells that are inhibited as the cricket chirps, and it is thought that these inhibitory signals arise as corollary discharges in the motor cortex (Poulet and Hedwig, 2003). It is tempting to speculate that such an explanation may account for the deactivations seen here, although it is a topic that requires thorough scrutiny, especially with techniques offering finer grained temporal resolution than fMRI. Our investigation of the effect of spatial smoothing and our analysis of single-subject data provide at least a hint as to why previous neuroimaging studies of reading (as reviewed in Fiez and Petersen, 1998; Turkeltaub et al., 2002) have not found evidence for PT involvement in silent reading. The picture is complex, but a number of factors may have prevented previous studies from detecting posterior PT activation during reading. Anatomical variability in the shape of the PT, lack of across-subject homogeneity in the functional network activated during reading, degree of spatial smoothing applied to data, requirement in most neuroimaging studies to impose stringent significance criteria to overcome the multiple comparison problem, and finally, the generally deactivated neighborhood wherein the speech portion of the PT resides may all have contributed to the consensus view that the PT is not involved in single-word reading. A further difficulty is that there is not a perfect way to apply an anatomical label to an activation that emerges from a statistical analysis performed on a group of brains that have been warped to a standard space. Probabilistic atlases such as that of Westbury et al.

(1999) can offer a principled means of attaching anatomical label to a activation coordinate that is derived from a multisubject analysis performed in a standard space.

These explanations, of course, do not address fundamental differences in the cognitive paradigms used in studies of single-word reading, among which include whether real or pseudowords were used, whether subjects were instructed to "view" or silently pronounce the items, and whether the baseline used for subtraction may have processing components that overlap with those involved in reading. This study offers further evidence that traditional posterior temporal "receptive" systems also play a role in speech production, and as has been known since the early language mapping studies of Ingvar (see 1983 review), systems in the prefrontal cortex are proactively involved in activities such as passive listening (or the observation of limb movements) that do not require an explicit action to be performed (Buccino et al., 2004; Rizzolatti and Arbib, 1998). However, whether these frontal motor systems, located primarily in premotor cortex and the inferior frontal gyrus, are actually necessary for speech perception is a question that remains controversial, although the lesion evidence argues strongly against it (Hickok and Poeppel, 2004).

Because of the limited temporal resolution of fMRI, it is not possible to determine in what direction information flows within the speech network. Are the superior temporal activations observed during silent reading the result of feedback (corollary discharge) from frontal regions (Paus et al., 1996)? Or do the first stages of speech begin in temporal cortex (Levelt et al., 1998) as phonemic representations that are only later mapped onto articulatory codes by way of the "mirror system" of the inferior frontal lobe (Buccino et al., 2004)? Future research must strive to integrate data from different methodologies, including transcranial magnetic stimulation, electroencephalography, magnetoencephalography, and fMRI to reconcile and elaborate both the chronometric and anatomical characteristics of the speech system.

References

Andersen, R.A., 1997. Multimodal integration for the representation of space in the posterior parietal cortex. Philos. Trans. R. Soc. Lond. B Biol. Sci. 352, 1421–1428.

Awh, E., Jonides, J., Smith, E.E., Schumacher, E.H., Koeppe, R.A., Katz, S., 1996. Dissociation of storage and rehearsal in working memory: PET evidence. Psychol. Sci. 7, 25–31.

Baddeley, A.D., 1986. Working Memory, vol. xi. Oxford Oxfordshire, New York, pp. 289.

Becker, J.T., MacAndrew, D.K., Fiez, J.A., 1999. A comment on the functional localization of the phonological storage subsystem of working memory. Brain Cogn. 41, 27–38.

Belin, P., Zatorre, R.J., Lafaille, P., Ahad, P., Pike, B., 2000. Voice-selective areas in human auditory cortex. Nature 403, 309–312.

Benson, D.F., Sheremata, W.A., Bouchard, R., Segarra, J.M., Price, D., Geschwind, N., 1973. Conduction aphasia. A clinicopathological study. Arch. Neurol. 28, 339–346.

Binder, J.R., Frost, J.A., Hammeke, T.A., Bellgowan, P.S., Springer, J.A., Kaufman, J.N., Possing, E.T., 2000. Human temporal lobe activation by speech and nonspeech sounds. Cereb. Cortex 10, 512–528.

Buccino, G., Binkofski, F., Riggio, L., 2004. The mirror neuron system and action recognition. Brain Lang. 89, 370–376.

Buchsbaum, B., Hickok, G., Humphries, C., 2001. Role of left superior temporal gyrus in phonological processing for speech perception and production. Cogn. Sci. 25, 663–678.

Damasio, H., Damasio, A.R., 1980. The anatomical basis of conduction aphasia. Brain 103, 337–350.

Fiez, J.A., Petersen, S.E., 1998. Neuroimaging studies of word reading. Proc. Natl. Acad. Sci. U. S. A. 95, 914–921.

Fiez, J.A., Raife, E.A., Balota, D.A., Schwarz, J.P., Raichle, M.E., Petersen, S.E., 1996. A positron emission tomography study of the short-term maintenance of verbal information. J. Neurosci. 16, 808–822.

Fransson, P., Merboldt, K.D., Petersson, K.M., Ingvar, M., Frahm, J., 2002. On the effects of spatial filtering—A comparative fMRI study of episodic memory encoding at high and low resolution. NeuroImage 16, 977–984.

Frith, C.D., Friston, K.J., Liddle, P.F., Frackowiak, R.S., 1991. A PET study of word finding. Neuropsychologia 29, 1137–1148.

Frith, C.D., Friston, K.J., Herold, S., Silbersweig, D., Fletcher, P., Cahill, C., Dolan, R.J., Frackowiak, R.S., Liddle, P.F., 1995. Regional brain activity in chronic schizophrenic patients during the performance of a verbal fluency task. Br. J. Psychiatry 167, 343–349.

Fuster, J.M., 1997. Network memory. Trends Neurosci. 20, 451–459.

Galaburda, A.M., 1982. Histology, architectonics, and asymmetry of language areas. In: Arbib, M.A., Caplan, D., Marshall, J.C. (Eds.), Neural Models of Language Processess. Academic Press, San Diego, pp. 435–445.

Galaburda, A.M., Sanides, F., Geschwind, N., 1978. Human brain. Cytoarchitectonic left–right asymmetries in the temporal speech region. Arch. Neurol. 35, 812–817.

Griffiths, T.D., Warren, J.D., 2002. The planum temporale as a computational hub. Trends Neurosci. 25, 348–353.

Herholz, K., Thiel, A., Wienhard, K., Pietrzyk, U., von Stockhausen, H.M., Karbe, H., Kessler, J., Bruckbauer, T., Halber, M., Heiss, W.D., 1996. Individual functional anatomy of verb generation. NeuroImage 3, 185–194.

Hickok, G., Poeppel, I.D., 2000. Towards a functional neuroanatomy of speech perception. J. Cogn. Neurosci., 45.

Hickok, G., Poeppel, D., 2004. Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. Cognition 92, 67–99.

Hickok, G., Erhard, P., Kassubek, J., Helms-Tillery, A.K., Naeve-Velguth, S., Strupp, J.P., Strick, P.L., Ugurbil, K., 2000. A functional magnetic resonance imaging study of the role of left posterior superior temporal gyrus in speech production: implications for the explanation of conduction aphasia. Neurosci. Lett. 287, 156–160.

Hickok, G., Buchsbaum, B., Humphries, C., Muftuler, T., 2003. Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area Spt. J. Cogn. Neurosci. 15, 673–682.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. Science 286, 2526–2528.

Jancke, L., Wustenberg, T., Scheich, H., Heinze, H.J., 2002. Phonetic perception and the temporal cortex. NeuroImage 15, 733–746.

Jonides, J., Schumacher, E.H., Smith, E.E., Koeppe, R.A., Awh, E., Reuter-Lorenz, P.A., Marshuetz, C., Willis, C.R., 1998. The role of parietal cortex in verbal working memory. J. Neurosci. 18, 5026–5034.

Josse, G., Tzourio-Mazoyer, N., 2004. Hemispheric specialization for language. Brain Res. Brain Res. Rev. 44, 1–12.

Josse, G., Mazoyer, B., Crivello, F., Tzourio-Mazoyer, N., 2003. Left planum temporale: an anatomical marker of left hemispheric specialization for language comprehension. Brain Res. Cogn. Brain Res. 18, 1–14.

Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. 17, 4302–4311.

Levelt, W.J.M., Praamstra, P., Meyer, A.S., Helenius, P.I., Salmelin, R., 1998. An MEG study of picture naming. J. Cogn. Neurosci. 10, 553–567.

Mechelli, A., Gorno-Tempini, M.L., Price, C.J., 2003. Neuroimaging studies of word and pseudoword reading: consistencies, inconsistencies, and limitations. J. Cogn. Neurosci. 15, 260–271.

Milner, A.D., Goodale, M.A., 1995. The Visual Brain in Action. Oxford University Press, Oxford.

Nakada, T., Fujii, Y., Yoneoka, Y., Kwee, I.L., 2001. Planum temporale: where spoken and written language meet. Eur. Neurol. 46, 121–125.

Ojemann, G.A., 2003. The neurobiology of language and verbal memory: observations from awake neurosurgery. Int. J. Psychophysiol. 48, 141–146.

Paulesu, E., Frith, C.D., Frackowiak, R.S., 1993. The neural correlates of the verbal component of working memory. Nature 362, 342–345.

Paus, T., Perry, D.W., Zatorre, R.J., Worsley, K.J., Evans, A.C., 1996. Modulation of cerebral blood flow in the human auditory cortex during speech: role of motor-to-sensory discharges. Eur. J. Neurosci. 8, 2236–2246.

Postle, B.R., Berger, J.S., D'Esposito, M., 1999. Functional neuroanatomical double dissociation of mnemonic and executive control processes contributing to working memory performance. Proc. Natl. Acad. Sci. U. S. A. 96, 12959–12964.

Poulet, J.F., Hedwig, B., 2003. Corollary discharge inhibition of ascending auditory neurons in the stridulating cricket. J. Neurosci. 23, 4717–4725.

Price, C.J., Wise, R.J., Warburton, E.A., Moore, C.J., Howard, D., Patterson, K., Frackowiak, R.S., Friston, K.J., 1996. Hearing and saying. The functional neuro-anatomy of auditory word processing. Brain 119 (Pt. 3), 919–931.

Rauschecker, J.P., Tian, B., 2000. Mechanisms and streams for processing of "what" and "where" in auditory cortex. Proc. Natl. Acad. Sci. U. S. A. 97, 11800–11806.

Rizzolatti, G., Arbib, M.A., 1998. Language within our grasp. Trends Neurosci. 21, 188–194.

Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. Brain Res. Cogn. Brain Res. 3, 131–141.

Romanski, L.M., Tian, B., Fritz, J., Mishkin, M., Goldman-Rakic, P.S., Rauschecker, J.P., 1999. Dual streams of auditory afferents target multiple domains in the primate prefrontal cortex. Nat. Neurosci. 2, 1131–1136.

Sakai, K., Passingham, R.E., 2003. Prefrontal interactions reflect future task operations. Nat. Neurosci. 6, 75–81.

Schubotz, R.I., von Cramon, D.Y., 2004. Sequences of abstract non-biological stimuli share ventral premotor cortex with action observation and imagery. J. Neurosci. 24, 5467–5474.

Scott, S.K., Blank, C.C., Rosen, S., Wise, R.J., 2000. Identification of a pathway for intelligible speech in the left temporal lobe. Brain 123 (Pt. 12), 2400–2406.

Selnes, O.A., Knopman, D.S., Niccum, N., Rubens, A.B., 1985. The critical role of Wernicke's area in sentence repetition. Ann. Neurol. 17, 549–557.

Shapleske, J., Rossell, S.L., Woodruff, P.W., David, A.S., 1999. The planum temporale: a systematic, quantitative review of its structural, functional and clinical significance. Brain Res. Brain Res. Rev. 29, 26–49.

Shergill, S.S., Brammer, M.J., Fukuda, R., Bullmore, E., Amaro Jr., E., Murray, R.M., McGuire, P.K., 2002. Modulation of activity in temporal cortex during generation of inner speech. Hum. Brain Mapp. 16, 219–227.

Turkeltaub, P.E., Eden, G.F., Jones, K.M., Zeffiro, T.A., 2002. Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. NeuroImage 16, 765–780.

Ungerleider, L.G., Mishkin, M., 1982. Two cortical visual systems. In: Ingle, D.J., Goodale, M.A., Mansfield, R.J.W. (Eds.), Analysis of Visual Behavior. MIT Press, Cambridge, pp. 549–586.

Vouloumanos, A., Kiehl, K.A., Werker, J.F., Liddle, P.F., 2001. Detection of sounds in the auditory stream: event-related fMRI evidence for differential activation to speech and nonspeech. J. Cogn. Neurosci. 13, 994–1005.

Warburton, E., Wise, R.J., Price, C.J., Weiller, C., Hadar, U., Ramsay, S., Frackowiak, R.S., 1996. Noun and verb retrieval by normal subjects. Studies with PET. Brain 119 (Pt. 1), 159–179.

Westbury, C.F., Zatorre, R.J., Evans, A.C., 1999. Quantifying variability in the planum temporale: a probability map. Cereb. Cortex 9, 392–405.

White, T., O'Leary, D., Magnotta, V., Arndt, S., Flaum, M., Andreasen, N.C., 2001. Anatomic and functional variability: the effects of filter size in group fMRI data analysis. NeuroImage 13, 577–588.

Wildgruber, D., Kischka, U., Ackermann, H., Klose, U., Grodd, W., 1999. Dynamic pattern of brain activation during sequencing of word strings evaluated by fMRI. Brain Res. Cogn. Brain Res. 7, 285–294.

Wilson, S.M., Saygin, A.P., Sereno, M.I., Iacoboni, M., 2004. Listening to speech activates motor areas involved in speech production. Nat. Neurosci. 7, 701–702.

Wise, R.J., Scott, S.K., Blank, S.C., Mummery, C.J., Murphy, K., Warburton, E.A., 2001. Separate neural subsystems within 'Wernicke's area'. Brain 124, 83–95.

Witelson, S.F., Kigar, D.L., 1992. Sylvian fissure morphology and asymmetry in men and women: bilateral differences in relation to handedness in men. J. Comp. Neurol. 323, 326–340.

Worsley, K.J., Evans, A.C., Marrett, S., Neelin, P., 1992. A three-dimensional statistical analysis for CBF activation studies in human brain. J. Cereb. Blood Flow Metab. 12, 900–918.