PET Activation of Posterior Temporal Regions during Auditory Word Presentation and Verb Generation

Previous studies using positron emission tomography (PET) report blood flow changes in superior and middle temple gyri associated with auditory and language tasks (Petersen et al., 1988, 1989; Wise et al., 1991; Demonet et al., 1992; Howard et al., 1992; Sergent et al., 1992; Zatorre et al., 1992; Petrides et al., 1993; Raichle et al., 1994; Fiez et al., 1995). An important issue is whether these changes reflect the activation of a single functional region or multiple regions with distinct functional contributions. In the present study, we examined this issue by focusing upon two tasks for which we have previously reported posterior temporal blood flow changes: listening to auditorily presented words (Petersen et al., 1988, 1989), and generation of a verb in response to a visually presented noun (Raichle et al., 1994); see also Wise et al. (1991). We began by further characterizing a left temporoparietal region of change previously associated with auditory word presentation. This previously reported response was replicated, and the results were extended by demonstrating presentation of pseudowords also produced activation. We next asked whether the activation associated with auditory word presentation could be distinguished from that associated with the generation of verbs in response to visually presented nouns. It was found that the activations associated with these two tasks could be both functionally and spatially dissociated. Thus, two posterior temporal areas associated with auditory word presentation and verb generation appear to represent distinct areas concerned with word processing. More generally, the results demonstrate an approach for assessing the independence of two activated areas.

Blood flow changes in the posterior portions of the superior and middle temple gyri have been found in a number of different studies using positron emission tomography (Petersen et al., 1988, 1989; Wise et al., 1991; Demonet et al., 1992; Howard et al., 1992; Raichle et al., 1994). While across these studies many of the tasks share similarities (e.g., auditory presentation of stimuli (Petersen et al., 1988, 1989; Wise et al., 1991; Demonet et al., 1992; Howard et al., 1992)), there are also significant differences between the tasks; for example, in some cases subjects merely listened to auditorily presented words (Petersen et al., 1988, 1989; Wise et al., 1991), while in other cases subjects performed semantic or phonological judgments upon presented words (Wise et al., 1991; Demonet et al., 1992).

At present, it is unclear whether the posterior temporal changes observed across different PET studies reflect the activation of a single functional region, or whether multiple regions with distinct functional contributions can be defined. In the present study, we examine this issue by focusing upon posterior temporal and temporoparietal blood-flow increases we have previously associated with the performance of two different language tasks. For one task, subjects listened to auditorily presented nouns while maintaining visual fixation on the small dot. In the control condition, subjects maintained fixation on a small dot. Bilateral activation was noted along the middle portions of the superior temporal gyrus, at or near primary and extraprimary auditory areas (Brodmann areas 41 and 42). In addition, a left-lateralized temporoparietal focus of Julie A. Fiez,^{1,3} Marcus E. Raichle,^{1,2,3,4} David A. Balota,⁵ Paula Tallal,⁶ and Steven E. Petersen^{1,2,3,4,5}

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activation was found more posteriorly, at or near the posterior portion of Brodmann area 22 (Wernicke's area).

In contrast to the primary and extraprimary regions, the left temporoparietal region identified by Petersen et al. (1988, 1989) did not appear to be activated by passive presentation of relatively simple auditory stimuli, such as tone pips, clicks, and noise bursts (Roland et al., 1981; Mazziota et al., 1982; Lauter et al., 1985; Zatorre et al., 1992). On the basis of this pattern of activation, Petersen et al. (1988, 1989) hypothesized that the temporoparietal region might be related to speech-specific acoustic processing. Functional dissociations between linguistic and nonlinguistic stimuli have previously been reported in the visual modality (Petersen et al., 1990; Howard et al., 1992). For instance, Petersen et al. (1990) reported that visually presented words and pseudowords (pronounceable letter strings such as "floop") activated a group of contiguous areas in left medial extrastriate cortex, but not visually presented strings of consonant letters and letter-like forms (false fonts). In this study, we were interested in determining whether the left temporoparietal area activated by auditory presentation of words might also be activated by auditory presentation of pseudowords, in a manner analogous to the medial extrastriate activation observed for visual presentation of words and pseudowords, and as suggested by previous work in the auditory modality (Wise et al., 1991).

The experimental paradigm had the additional benefit of allowing us to determine whether the left temporoparietal activation associated with auditory word presentation could be replicated across experiments. This was of particular concern because of results found in a related study designed to investigate neural aspects of speech and temporal perception (Fiez et al., 1995). In the Fiez et al. study, subjects were presented with synthetic words under both a passive and an active detection condition. Contrary to our expectations, under these conditions significant left temporoparietal activation near that found by Petersen et al. (1988, 1989) was not found. This failure raised questions about the reliability of the activation noted by Petersen et al. (1988, 1989), and the possible importance of the task and stimulus differences between the studies by Fiez et al. (1995) and Petersen et al. (1988, 1989).

The second issue addressed in this study was the relationship between the left posterior temporal activation associated with the *auditory* presentation of words, and that associated with another task: generation of verbs in response to *visually* presented nouns (Raichle et al., 1994). In the study by Raichle et al., subjects were instructed to think of and say aloud appropriate verbs for visually presented nouns (what the nouns might be used for, or what they might do). As a control condition, subjects read aloud visually presented nouns. Greater activation in a posterior temporal region was observed when subjects read aloud visually presented nouns (Raichle et al., 1994). Along with left frontal, right cerebellar, and anterior cingulate regions, the left temporal region became significantly less active following practice on the verb generation task (Raichle et al., 1994); the magnitude of the left temporal activation also appeared to be affected by the rate of stimulus presentation, with significantly greater activation observed when the stimuli were presented at a rate of 1 every 1.5 sec (Raichle et al., 1994) than when they were presented at a rate of 1 per second (Petersen et al., 1988, 1989).

In the second section of the present report, our goal was to determine whether the regions of activation associated with the two tasks are both functionally and spatially distinct. This issue was of interest because although the two tasks differ significantly in their processing demands, some have hypothesized that they should share common functional regions of activation. For instance, Wise et al. (1991) theorized that both verb generation and listening to auditorily presented words involve, in part, a similar form of semantic analysis that accounts for the same posterior temporal activation found during both tasks. More generally, it has also been hypothesized that language processing involves a distributed set of regions that are automatically activated by presentation of linguistic material; thus, a common set of areas are expected to be activated during a wide range of language tasks (Demonet et al., 1993).

Replication and Extension of Auditory Word Presentation

Materials and Methods

The first issue we addressed was the response properties of the left temporoparietal area activated by auditory presentation of words (Petersen et al., 1988, 1989). In particular, we were interested in determining whether this left temporoparietal area might also be activated by auditory presentation of pseudowords. The experimental paradigm had the additional benefit of allowing us to establish the reliability of responses in the left temporoparietal area across experiments.

Subjects

Subjects were normal volunteers recruited from the undergraduate and medical campuses of Washington University. All were strongly right handed as judged by the Edinburgh handedness inventory (Raczkowski et al., 1974). Subjects were paid \$75 for their participation and gave informed consent in accordance with guidelines set by the Human Studies and the Radioactive Drug Research Committees of Washington University. Data were collected from three subjects: two males (age 21 and 26 years), and one female, 24 years old.

Stimuli

Word stimuli consisted of familiar nouns, verbs, and adjectives. They ranged in visual frequency from 1 to 1360 occurrences per 1 million words, with a mean of 122 ± 12 SE occurrences per million words (Kucera and Francis, 1967). The words were divided into three lists of 55 items. For each list of words a corresponding list of pseudowords was created by substituting one or more phonemes in each word to create a pseudoword (e.g., the matched pseudoword for the word "yard" was "dard"). Stimuli were recorded onto audio tape and presented at the rate of one item per second. The spoken duration of 548 \pm 6 msec SE. The spoken duration of the pseudowords ranged from 327 to 801 msec, with a mean duration of 566 \pm 6 msec SE.

The tape-recorded stimuli were replayed using an audio tape deck (Lux Corporation, Luxman model K-111). Audio signals from the tape deck and computer sound channel were amplified (Pioneer Electronic Corporation, model SX-1700), and played binaurally through receivers (Knowles insert receiver, model 1912) specially designed to snap into fitted plastic earmolds placed in each subject's ears (Lauter et al., 1985). The system was designed to mimic the filter characteristics of the human pinna and outer ear (Lauter et al., 1985).

Paradigm

Nine scans were conducted in each subject. Scans 2, 5, and 8 were control scans in which subjects were instructed to maintain fixation on a 5 mm dot displayed on a monitor suspended approximately 15 cm in front of them. For the active scans (scans 1, 3, 4, 6, 7, and 9),

subjects again maintained fixation on the displayed dot, but also were instructed to listen to the presented words or pseudowords. Each of the six lists was presented during a separate active scan, alternating between word and pseudoword lists. The order of list presentation (e.g., word and matched pseudoword lists A, B, and C) was varied across subjects.

Image Acquisition

Each subject laid on the scanner couch and a venous catheter was placed in the right arm. Subjects' heads were immobilized within a closely fitted, thermally molded, plastic facial mask individually made for each subject. Head alignment and planes of section were recorded with a lateral skull x-ray (Fox et al., 1985). For each scan, ¹⁵O-labeled carbon dioxide (C¹⁵O₂) was bubbled through saline to form ¹⁵O-labeled water (Welch and Kilbourn, 1985), which was administered as an intravenous bolus of 8–10 ml of saline containing 1 mCi/kg of body weight. Data were acquired using the PETT VI system employed in the low-resolution mode, which simultaneously acquires seven parallel slices with a center-to-center distance of 14.4 mm (Ter-Pogossian et al., 1982; Yamamoto et al., 1982). Images were reconstructed using filtered backprojection to a resolution of 17 mm full width at half-maximum.

Since blood-flow and radiation counts are nearly linearly related over normal physiological ranges, images of radioactive counts rather than blood flow were utilized. This eliminated the risk and discomfort of arterial catherization (Herscovitch et al., 1983; Fox and Mintun, 1989). In order to negate the effects of global fluctuations in blood flow and variations in the amount of isotope injected, the number of counts in each image was normalized to 1000 (Fox et al., 1987); magnitude data will therefore be given in terms of normalized counts.

Image Transformations

To place subjects into a standard anatomical format that allows comparisons to be made across subjects, each image was also transformed into the space of the Talairach stereotactic atlas (Fox et al., 1985, 1988; Talairach and Tournoux, 1988). Foci of change will be reported by listing three coordinates (x,y,z): the x-coordinate is the distance in mm to the left (-) or right (+) of midline, the y-coordinate is the distance in mm anterior (+) or posterior (-) to the anterior commissure, and the z-coordinate is the distance in mm above (+) or below (-) a horizontal plane which cuts through the anterior-posterior commissures.

The basis of all data analysis was a comparison of neuronal activity under two conditions. To isolate areas of activity change between task conditions, images generated during performance of one task were subtracted, on a pixel-by-pixel basis, from images generated during performance of another task. *Individual difference images* were created by subtracting the images acquired during two different scans (an "active task scan" and a "control scan") performed in a single subject. *Average difference images* were created by adding individual difference images together, and then dividing the resulting images by the number of contributing individual images; this yields an image of the mean regional changes across subjects and/or task conditions (Fox et al., 1988).

Data Analysis

Analysis of Temporoparietal Regional Magnitudes. A region of interest approach was used to assess whether the temporoparietal activation associated with auditory word presentation (Petersen et al., 1988, 1989) could be replicated across subjects, and whether the finding could be extended to auditory presentation of pseudowords. A temporoparietal region of interest was first identified using a passive auditory word minus fixation image created from a separate group of eight subjects (Petersen et al., 1988, 1989). The location of the peak temporoparietal response in this previous study was reported in terms of the Talairach 1967 atlas (Talairach et al., 1967), at x = -54, y = -30, z = 14. To define this response in terms of the Talairach and Tournoux (1988) atlas, data from the study by Petersen et al. (1988, 1989) were cast into the space of the Talairach 1988 atlas (as described in the Materials and Methods). Next, the location of the peak temporoparietal activation in this image was used to define a spherical region with a 7 mm radius centered at x = -53, y = -49, z = 18. The 7 mm radius was chosen because this value corresponds to the resolution of the algorithm used to automatically

identify all regions of change in individual and average difference images (Mintun et al., 1989).

Next, the region of interest was placed in each of the nine passive auditory word minus fixation and the nine auditory pseudoword minus fixation individual difference images from the present study (three repetitions of each stimulus condition in three subjects). The regional magnitude in each individual difference image was determined by calculating the average magnitude of all pixels located inside of the region of interest.

The 18 individual regional magnitudes were first analyzed using a two-factor ANOVA to determine whether significant differences between subjects or task repetitions existed. No significant effects of task repetition [F(2,9) = 0.60, p = 0.68] or subject [F(2,9) = 2.44, p = 0.14] were found. To determine whether the regional temporoparietal activation was significantly greater than zero, as hypothesized on the basis of previous results (Petersen et al., 1988, 1989), the regional magnitudes from the nine auditory word minus fixation difference images were then analyzed using a one-sample *t* test. In order to determine whether the temporoparietal activation extended to pseudowords, the same analysis was performed using the nine passive auditory pseudoword minus fixation individual difference images. A paired *t* test was used to compare the magnitude of regional activation in the words and pseudowords conditions.

Analysis of Temporoparietal Activation Locations. One limitation to a regional analysis is that a significant change might be found even though the region is encompassing only a portion of some large response centered fairly distantly. To compare the locations of temporoparietal activation between our earlier work (Petersen et al., 1988, 1989) and the current study, auditory stimulation minus fixation images from the present study were averaged across subjects and repetitions of the task conditions, yielding an N = 9 average difference image each for stimulus type (three subjects × three repetitions each of words and pseudowords). In *each* average difference image, the location and peak magnitude of the response focus nearest to the region of interest center defined from our previous work (x = -53, y = -49, and z = 18) was identified.

Identification of Other Regions of Activation. Though this study was motivated by a priori regions of interest from our previous work, we also examined the auditory word minus fixation and pseudoword minus fixation average difference images for other regions of activation using a change-distribution analysis (Fox et al., 1988; Fox and Mintun, 1989; Mintun et al., 1989). For both the auditory word minus fixation and the pseudoword minus fixation average difference images, all regions of change, both positive and negative, were first identified (Mintun et al., 1989). The distribution of foci magnitudes from each image was then compared to a standard noise distribution in order to determine whether the distribution was positively and/or negatively leptokurtotic, that is, whether there were significant positive or negative outliers in the distribution. If there were significant outliers, post hoc t values and corresponding p values were computed for each focus (Fox et al., 1988; Fox and Mintun, 1989). Because of limitations of this and other thresholding techniques (Hunton et al., 1994), the results from the outlier analysis should be considered to be an exploratory, or hypothesis-generating, examination of the data.

Results

In total, the results described below provide a clear replication of activation associated with word presentation relative to Petersen et al. (1988, 1989), and extend the findings to pseudowords.

Magnitude Analysis

There were significant changes of activity at the temporoparietal region of interest for both words and pseudowords (see Fig. 1). The mean magnitude of activation (in counts) across the individual difference images was 38 ± 13 SE for auditory presentation of words, and 34 ± 11 SE for pseudowords. Both values are significantly more positive than zero [t(8) = 3.17, p = 0.01, and t(8) = 2.87, p = 0.007, respectively]. This regional activation did not significantly differ between words and pseudowords [t(8) = 0.22, p = 0.83].

Location Analysis

Results from the location analysis provide strong evidence the change measured within the temporoparietal region reflects the activity of a region that is distinct from more anterior primary and extraprimary auditory areas. For both the passive auditory words minus fixation and pseudowords minus fixation average difference images, temporoparietal increases in activity were found very near the temporoparietal response to passive auditory words we previously reported (Petersen et al., 1988, 1989) at x = -53, y = -49, z = 18. For words, the center of the increase was located within 7 mm, at x = -51, y = -55, z = 18, with a peak magnitude of 49 counts. For pseudowords, the center of the increase was also within 7 mm, at x = -51, y = -55, z = 20, with a peak magnitude of 46 counts.

Identification of Other Regions of Activation

Using an outlier analysis to identify significant regions of change, significant leptokurtosis was found only for the positive distribution of foci magnitudes in both the auditory word minus fixation and the auditory pseudoword minus fixation average difference images. A post hoc analysis was used to identify all positive foci of change with Z scores corresponding to a p < 0.01. In the auditory word minus fixation image this identified one focus located at or near Brodmann area 41 on the right (x = 55, y = -15, z = 8) and two foci on the left (x = -51, y = -21, z = 14, and x = -59, y = -29, z = 16). In the auditory pseudoword minus fixation similar results were found, with two foci found at or near Brodmann areas 41 and 42 on the right (x = 53, y = -15, z = 10, and x = 53, -29, 20) and one on the left (x = -53, -21, 12). These results are consistent with the primary and secondary auditory responses we have previously associated with auditory word presentation (Petersen et al., 1988, 1989). Neither of the temporoparietal peaks identified in the location analysis reached significance using the outlier analysis; this failure is not unexpected, given recent evidence that the outlier analysis and other thresholding techniques are fairly conservative approaches which may fail to detect many reliable regions of change (Hunton et al., 1994).

Differences between Verb Generation and Auditory Tasks

Materials and Methods

The second issue we addressed was the relationship between the left temporoparietal area (Petersen et al., 1988, 1989) and the more ventrally situated posterior temporal area, which became active during the generation of verbs to visually presented nouns (Raichle et al., 1994). The activation of these two areas was examined both functionally and spatially in order to determine whether, within a confined area of left posterior temporal cortex, distinct areas concerned with processing words can be identified with PET functional imaging studies. Both analyses were based upon first defining regions of posterior temporal activation associated with each task condition. Next, the relationship between task condition (passive listening or verb generation) and the magnitude and location of activation relative to the two regions of interest was examined in independent groups of subjects.

Region of Interest Generation

We first defined posterior temporal regions of interest associated with both the passive listening and the verb generation task conditions. This was accomplished using data from one group of subjects who performed the passive listening task, and data from another group of subjects who performed the verb generation task.

To generate a region of interest using data from subjects listening to auditory words, an N = 9 average difference image was first created from the word presentation minus fixation images from the present study (three subjects × three repetitions). In this average image, the largest response that localized to left temporal cortex [with the exception of primary and extraprimary auditory cortex, as



Figure 1. (top) Sagittal sections showing activation of a temporoparietal region across two studies. The *left section* shows activation when auditory words were compared to a fixation point control condition in an earlier study (Petersen et al., 1988, 1989). This activation was used to define a region of interest applied to data from the present study. The *middle section* shows the replication of the activation associated with presentation of words, as previously described by Petersen et al. (1888, 1989). The *right section* shows the signification activation when pseudowords were presented. The PET data were taken from sagittal sections 55 mm to the left of midline, and superimposed upon a lateral brain outline. It should be noted that in all three sections activation can be seen in primary and extraprimary auditory areas, which are anterior to the temporoparietal region of interest in the present study.

Figure 2. (bottom) A lateral view of the brain showing the activation in two temporal regions. A temporoparietal region, defined using an auditory words-fixation average difference image from a separate group of subjects, is shown by the *blue circle*. A midtemporal region, defined using a verb generation-read nouns average difference image from a separate group of subjects, is shown by the *pink circle*. When the regions were applied to an independent group of subjects, greater activation was found in the temporoparietal region in the auditory words minus fixation condition than in the verb generation minus read condition, while the converse pattern of activation was found in the midtemporal region. The PET data were taken from a sagittal section 53 mm to the left of midline, and superimposed upon a lateral brain outline. In addition to the midtemporal activation in the verb generation minus read condition, significant frontal activation can also be found, as previously reported by Petersen et al. (1988, 1989) and Raichle et al. (1994).

determined by reference to the Talairach and Tournoux (1988) atlas[, was then identified. The center of the identified response was located at x = -51, y = -55, z = 18, and this coordinate defined the center of a temporoparietal region of interest.

To generate a region of interest using data from subjects performing the verb generation task, data were used from three subjects who performed the task as described by Raichle et al. (1994). These subjects failed to complete the entire scan sequence or they moved excessively between some scans; since our previous analyses necessitated the use of data from all scans in the sequence, these subjects were excluded from our prior analyses. However, all of these subjects did successfully complete the first verb generation and read scans without excessive movement, and, hence, they were appropriate for the present analysis. Using data from these three subjects, an N = 3verb generation minus read image was created, and then the largest response that localized to left temporal cortex was identified in this image. The center of the identified response was located at x = -55, y = -41, z = 2, and this coordinate defined the center of a middle temporal region.

Data Analysis

The locations and magnitudes of activations associated with the temporoparietal and middle temporal regions were next examined using data from an independent group of subjects. Two different analyses were used to determine whether the locations and magnitudes of activations in this independent group of subjects were significantly affected by the task condition (passive listening or verb generation) subjects performed.

Data Set for Magnitude and Location Analyses. The data set for the analyses consisted of data from 21 subjects not included in the region-of-interest generation step described above; hence, there is an independence between the subjects used to generate the temporoparietal and middle temporal regions of interest and the subjects in which the spatial and functional independence of the two regions is assessed.

Nine of the subjects participated in the study reported by Petersen et al. (1988, 1989). The subjects listened to words presented auditorily at a rate of 1 word per second; as a control condition, subjects maintained fixation. A passive auditory minus fixation individual difference image was created for each of these nine subjects.

The 12 verb generation subjects participated in the study reported by Raichle et al. (1994). The subjects were visually presented with nouns at a rate of one every 1.5 sec. They were instructed to think of and say aloud an appropriate verb (what the noun might be used for, or what it might do; e.g., "dog-bark," "bed-sleep") for each noun. As a control condition, subjects read aloud presented nouns. The data for the subjects came from their first performance of the verb generation task in this study, since Raichle et al. (1994) described changes in the functional activation associated with repeated performance of the verb generation task. A verb generation minus read individual difference image was created for each of these 12 subjects.

Regional Magnitudes across the Two Tasks. For both the temporoparietal and middle temporal regions, regional magnitudes were computed for each of the 9 passive auditory minus fixate and 12 verb generation minus read individual difference images. An analysis of variance (ANOVA) was then performed upon the regional magnitude across subjects and the two defined regions. The purpose of this analysis was to determine whether there was a significant effect of task condition (auditory words or verb generation, a factor that was measured across subjects) and/or an effect of location (posterior temporal vs middle temporal, a factor measured within subjects) upon the regional activation produced by each task.

Location of Activations across the Two Tasks. The second analysis was based upon the spatial location of the posterior temporal peak activation changes in individual difference images. To begin, a search center was defined midway between the two centers of two regions of interest identified in the first analysis. Thus, the search center for the second analysis was located at x = -53, y = -48, z = 10, midway between x = -51, y = -55, z = 18 (temporoparietal region) and at x = -55, y = -41, z = 2 (middle temporal region). All foci of change within 20 mm of the search center with a magnitude greater than 85 counts were then identified in each of the 21 individual difference images comprising the auditory word minus fixation and the verb generation minus read data set.

The search criteria were based upon a similar analysis performed in both task minus control and control minus control images (Hunton et al., 1994). While the use of a 20 mm radius for the location analysis may at first seem at odds with the use of the 7 mm radius used to define spherical regions of interest, the size difference reflects very different purposes. For the location analysis, the intent was to set a distance criterion large enough to encompass the variability in response locations expected across individual subjects (due to anatomical differences, limitations of registration algorithms, etc.). For a spherical region of interest analysis, the intent was to define a volume that was large enough to allow for some variation in the average location of a response across subjects, but which was not so large as to extend beyond the contours of a region of activation. The magnitude criterion was set high enough to minimize the identification of noise responses, but low enough to identify a sample sufficiently large for subsequent analysis (Hunton et al., 1994).

The x, y, and z coordinates of the foci identified using the search criteria were treated as dependent variables, and the task condition (auditory word minus fixation compared to verb generation minus read) was treated as an independent variable. A multivariate analysis of variance (MANOVA) was used to determine whether there was a significant effect of task condition on the location of temporal activation across subjects.

Results

Magnitude of Activation across Regions and Tasks

There was no significant effect of task upon the magnitude of activation found across the two regions [F(1,19) = 1.24, p = 0.28]. For the auditory word condition, the mean activation across the two regions was 36 ± 8 SE counts, while for the verb generation condition the mean activation across the two regions was 26 ± 6 SE counts. Nor was there a significant effect of region upon the magnitude of activation [F(1,19) = 1.52, p = 0.23]. For the temporoparietal region, the mean activation across the task conditions was 23 ± 7 SE counts, while for the middle temporal region the mean activation across the two task conditions was 38 ± 7 SE counts.

Most importantly, there was a significant interaction between the regions and task conditions [F(1,19) = 4.65, p = 0.04], as shown graphically in Figures 2 and 3. For the temporoparietal region (x = -51, y = -55, z = 18) greater activation was produced for the passive auditory word condi-



Figure 3. Graph showing magnitude of activation in the left temporoparietal and midtemporal regions in the auditory word and verb generation conditions. A significant area-by-condition interaction is found, indicating that these regions subserve different information processing operations.

tion (41 \pm 11 SE counts) than for the verb generation condition (9 \pm 7 SE counts).

The opposite pattern of activation was observed for the middle temporal region (x = -55, y = -41, z = 2), where greater activation was observed for the verb generation condition (43 counts \pm 8 SE) than auditory word condition (32 counts \pm 13 SE). While lower than the activation found in the verb generation task, the magnitude of change for the auditory word condition was still fairly high. We feel this apparent activation of the middle temporal region in the auditory word condition reflects the fact that our region of interest encompassed activation associated with primary and extraprimary auditory regions in the superior temporal gyrus, rather than evidence for activation of both the middle temporal and temporoparietal regions in the auditory word minus fixation condition. Further support for this interpretation comes from the results of the location analysis described below, and from visual inspection of Figure 2.

Location of Activation across Tasks

All foci meeting the search criteria from each of the 9 auditory word minus fixation and 12 verb generation minus read individual difference images are shown in Figure 4. The relationship between the response location (in terms of an x, y, and z coordinate) and the task condition was highly significant [F(3,20) = 15.58, p = 0.001]. Most of the variance between the two tasks occurred along the z-axis [F(1, 22) = 23.5, p 0.0001]; the mean z-coordinate for foci from auditory word minus fixation individual images was 14 mm, versus 2 mm for foci from verb generation minus read individual images. Differences along the x-axis and y-axis failed to reach significance (p = 0.75 and p = 0.10, respectively).

Discussion

The present results demonstrate that temporoparietal activation is reliably produced when subjects passively listen to auditorily presented, naturally voiced words, relative to performing a visual fixation control task. Both in terms of response location and magnitude of the activation, the original observation of temporoparietal activation by Petersen et al. (1988, 1989) was replicated despite changes in the presented items, speaker voice (male (Petersen et al., 1988, 1989) versus female in the present study), and subject anatomy. The obser-



auditory words-fixation focus verb generation-read nouns focus

Figure 4. A plot showing the distribution of location of foci from auditory word — fixation and verb generation — read noun individual difference images. A significant MANOVA difference was found between the locations plotted for the two groups, mainly in the z-coordinate.

vation that presentation of pseudowords also produces significant activation, with the peak of the response located very near the center of the response produced during presentation of words, extends the original results. Additionally, it was found that the activation associated with the word presentation condition could be dissociated both functionally and spatially from the activation associated with a verb generation minus read nouns condition. In the discussion below, we will explore these results in the context of several other PET studies involving auditory stimulus presentation, and in light of evidence from behavioral studies of normal and patient populations.

Other PET Studies of Auditory Lexical Processing

There have been a number of other PET studies in which auditory stimuli have been used in one or more task conditions performed by the same group of subjects (e.g., Frith et al., 1991; Wise et al., 1991; Demonet et al., 1992; Howard et al., 1992; Sergent et al., 1992; Zatorre et al., 1992; Grasby et al., 1993; Petrides et al., 1993). Interestingly, when auditory nonlinguistic stimuli have been compared to a nonauditory control task, posterior temporal activation near that found in the present study was not reported, although more anterior primary and extraprimary regions of activation were found (Roland et al., 1981; Mazziota et al., 1982; Lauter et al., 1985; Sergent et al., 1992; Zatorre et al., 1992).

The failure to find temporoparietal activation with the presentation of nonlinguistic auditory stimuli raises the possibility that the activation might be related to speech-specific acoustic processing, as previously hypothesized by Petersen et al. (1988, 1989). With respect to this hypothesis, data from several studies are particularly relevant. In these studies, activation associated with presentation of an auditory linguistic stimulus was compared to a nonauditory stimulus condition, as in the present study, or to an auditory nonlinguistic stimulus condition (Wise et al., 1991; Demonet et al., 1992; Howard et al., 1992; Zatorre et al., 1992). The results from these studies are discussed below, and summarized in Table 1.

Wise et al. (1991) have reported similar results for four different tasks involving auditory presentation of words and pseudowords. For one task, subjects passively listened to auditorily presented pseudowords. For two other tasks, subjects made decisions about whether word pairs were appropriately matched. In a fourth condition, subjects silently generated verbs in response to auditorily presented nouns. Relative to a rest control ("empty your mind"), significant left posterior temporal activation was observed for all four task conditions. Unlike bilateral primary and extraprimary auditory areas (which were also active), the left posterior temporal activation was found to be uncorrelated with the rate of stimulus presentation. Based upon its independence from presentation rate, and the fact that the region was the only one commonly activated by their word comprehension and retrieval tasks (verb generation, noun/noun and noun/verb comparisons), the authors suggested that this posterior temporal activation was related to word comprehension and semantic processing. Alternatively, the activation observed by Wise et al. (1991) may reflect the fact that stimuli were presented auditorily. This would be consistent with the results from the present study and our previous findings that posterior superior temporal/temporoparietal activation is associated with passive auditory, but not passive visual presentation of words and pseudowords (Petersen et al., 1988, 1989; Petersen et al., 1990).

Further evidence that posterior temporal activation may be specifically related to the auditory presentation of words comes from reports by Howard et al. (1992) and Demonet et al. (1992). In the study by Howard et al. (1992), left posterior temporal activation was identified when subjects repeated aloud auditorily presented words, versus a condition in which they said the word "crime" in response to auditorily reverserecorded words. In the study by Demonet et al. (1992), subjects performed three different tasks with auditorily presented stimuli. In a tones task, subjects were asked to detect pure tone triplets with a rising pitch. In a phonemes task, subjects detected pseudowords that contained a particular sequence of phonemes. In a words task, subjects detected word pairs containing a noun representing a small animal and the adjective representing a "positive" feature (e.g., "kind"). Two posterior temporal responses were identified in the words versus tones comparison, while in the phonemes versus tones comparison similarly located foci of activation were not found. These results suggest the activation may be specific to the words task, though it should be noted that significant poste-

Table 1 Left posterior superior and middle temporal activation across auditory word tasks							
Study	Comparison	Xcrd	Ycrd	Zcrd	Brodmann ar	Brodmann area VD <i>ª</i>	
Petersen et al. (1988, 1989)	Passive auditory words versus fixation	-53	-49	18	22	0	
Present study	Passive auditory words versus fixation	-51	- 55	18	22	6	
	Passive auditory pseudowords versus fixation	-51	- 55	20	22	7	
Wise et al. (1991)	Auditory word tasks versus reest (eyes closed)	46	- 38	8	22	16	
Howard et al. (1993)	Repeat auditory words versus hear & say "crime"	-48	- 38	-4	21/22	25	
Demonet et al. (1993)	Word semantic versus tone pitch judgement	48	-36	-8	21/20	29	
	Word semantic versus tone pitch judgement	-50	-38	-12	20/21	32	

* Vector distance (in mm) of locus from Petersen et al. (1988, 1989) temporoparietal locus.

rior temporal differences were not found when the word and phoneme tasks were directly compared.

Lack of Left Temporoparietal Activation across PET Studies

In the studies by Howard et al. (1992) and Demonet et al. (1992), posterior temporal activation was associated with auditory presentation of speech stimuli relative to complex nonspeech stimuli (tone triplets and reverse recorded words). These comparisons provide evidence that the posterior temporal activation may be speech specific. However, studies by Zatorre et al. (1992) and Fiez et al. (1995) provide evidence that significant temporoparietal activation is not always found when a task involves auditory presentation of linguistic stimuli. In the study by Zatorre et al. (1992), auditory presentation of pairs of speech syllables (e.g., fat-tid) was compared to auditory presentation of filtered noise bursts; the nearest focus found in this comparison was located at or near Brodmann area 42, nearly 2 cm anterior to the temporoparietal focus reported by Petersen et al. (1988, 1989). Similarly, as part of a study by Fiez et al. (1995), subjects passively listened to a set of six computer synthesized words (tack, pack, cap, cat, pat, tap). Relative to a fixation point control task, significant temporoparietal activation was not found, nor was it found for several other conditions involving presentation of naturally voiced words (for review, see Fiez et al., 1995)

The failure to find significant temporoparietal activation in the studies by Zatorre et al. (1992) and Fiez et al. (1995) demonstrates that auditory presentation of words does not produce significant temporoparietal activation under all conditions. Factors that may influence the activation of the region are the task and stimulus presentation conditions. For both the studies by Zatorre et al. (1992) and Fiez et al. (1995), in which relatively passive presentation of words did not activate the temporoparietal region, the word stimuli were phonologically similar (e.g., tack, pat, pack, etc.), required discrimination of brief rapidly changing temporal cues, and were repeated during a scan. Conversely, in studies in which words did activate the temporoparietal region, the words were not phonologically confusable (i.e., telephone, airplane, hammer), did not require discriminations based solely on brief temporal cues, and no words were repeated across a scan. Interestingly, even when the stimuli employed by Zatorre et al. (1992) and Fiez et al. (1995) were presented under conditions requiring acoustic-phonetic analysis, significant left temporoparietal activation was not found. However, in both cases significant left frontal activation was observed. These results suggest that the analysis of speech inputs may involve many different brain regions, each specialized for a different type of "phonological" process. As discussed more extensively by Fiez et al. (1995), the left frontal region may be particularly important for the analysis of rapidly changing speech and nonspeech stimuli, at a sublexical level. The possible contributions made by the left temporoparietal region to speech processing will be discussed below.

Relation to Behavioral Results

Taken as a whole, we believe that the results from both the present and previous studies implicate the posterior temporoparietal region in a form of auditory processing that appears specific to speech-like stimuli, though further experiments will be necessary to confirm this hypothesis. There are at least two possible ways in which this area may play a role in speech processing: activity en route to lexical processing and/or a form of short-term acoustic storage.

First, consider the possibility that this area is involved in processes en route to auditory lexical processing. At first, this possibility would seem unlikely because this area appears to be equally active for both words and pseudowords in the present study. However, this might be expected based on a number of current models of auditory lexical processing. For example, according to the Marslen-Wilson and Welsh cohort model (1978), as words are auditorily presented they activate cohorts or neighborhoods of similarly sounding words. Upon hearing the /b/ at the beginning of the word boy, all b words are activated. After recognizing the following vowel only the words with those two phonemes remain in the candidate set (e.g., bow, boat, bone), while other possible candidates are eliminated. In this way, as the auditory stimulus unfolds across time, any additional phonological information reduces the possible candidate set until only one candidate remains. According to this model, the primary difference between the analysis of the stimulus input for words and pseudowords is that for word stimuli the cohort is narrowed until there only remains a single candidate, while for pseudoword stimuli the total cohort is reduced to zero at some point as the stimulus unfolds. Hence, there is considerable similarity in the stimulus processing of words and pseudowords in this model, and one should find similar areas of brain activation across these two classes of stimuli, as the present results indicated. It is important to note that such predictions are not unique to the cohort model. Similar influences of neighborhood activation for words and pseudowords are also predicted by McClelland and Elman's (1986) TRACE model and Luce's (1986) Neighborhood Activation model.

Although the activation in the posterior temporal region may reflect a type of phonological analysis involved en route to lexical access, there is an alternative possibility that we believe more faithfully captures aspects of the available evidence. Specifically, consider the possibility that this area is related to a specific type of short-term storage for speechbased information. While several different types of speechbased short-term storage appear to exist (e.g., see Baddeley, 1986; Turner et al., 1987), the properties of one type have been extensively explored through behavioral studies in normals. These investigations have been based largely on paradigms in which subjects are asked to recall, in order of presentation, a set of auditorily presented stimuli (typically unrelated words or digits). Under such conditions, recall is significantly better for the most recently presented items, that is, the recency effect. Presumably, this extra source of acoustic/phonological information can be used to supplement recall for the most recently presented items. Furthermore, presentation of a redundant speech sound (e.g., the word "go") at the end of the list presumably reduces the availability of this extra speech-based information, and, hence, significantly reduces the recency effect (e.g., Crowder and Morton, 1969). In contrast, presentation of a nonspeech sound (such as a tone) produced very little decrement in the recency effect. This reduction in the recency effect by a redundant speech stimulus, compared to a redundant nonspeech sound, is referred to as the suffix effect.

The recency effect appears to be largely modality specific. Similar results are not found when stimuli are presented visually (Conrad and Hull, 1968; Crowder and Morton, 1969; Penny, 1975), though evidence for some nonauditory recency effects have been found using mouthed and lip-read stimuli (e.g., Nairne and Crowder, 1982; Greene and Samuel, 1986). Turner et al. (1987) present compelling data that suggests these nonauditory effects are mediated by different processes than those associated with auditory stimulus presentation.

There are a number of observations that support the notion that the posterior temporal region may be related to the type of speech-based storage center discussed above, though certainly other regions may be involved in other types of short-term verbal storage. The present PET study indicates

that there appears to be relatively little difference between words and pseudowords in the level of activation in this area. This is also consistent with the observation that suffix effects occur for both words and speech-like pseudowords, like "snoke" (e.g., Crowder and Morton, 1969; Balota and Duchek, 1991). In addition, the data from Wise (1991) indicates that presentation rate does not appear to modulate the activation in this area. This finding is also compatible with results from Watkins and Todres (1980) and Balota et al. (1992a), who have demonstrated suffix effects that can last over a considerable temporal interval (20 sec) between the last list item and the suffix. These results suggest that this type of auditory storage system can hold information in a useful format across extended durations. Finally, patients with damage to posterior superior temporal regions typically have a striking reduction in their verbal short term span (commonly defined as the number of digits or words correctly repeated immediately after presentation) when auditory stimulus presentation is compared to visual stimulus presentation; in addition, these patients, usually exhibit a much reduced auditory recency effect (Warrington and Shallice, 1969; Caramazza et al., 1981; Friedrich et al., 1984). This pattern of results has been interpreted as evidence for an acoustic storage deficit resulting from damage to posterior temporal regions (Warrington et al., 1971; Caramazza et al., 1981; Friedrich et al., 1984; Vallar and Papagno, 1986).

It is important to note that we clearly do not feel that the lexical processing account and the speech-based storage account of the activation in the left posterior temporal region are mutually exclusive. The lexical processing account emphasizes the on-line analysis of the stimulus input, while the speech-based storage account emphasizes the residual influences of such on-line analyses. Clearly, these are likely to be highly related processes. At present, we are primarily posing these alternatives as two candidate processes that involve the posterior temporal region; for alternative interpretations of superior temporal activations, see Frith et al. (1991) and Wise et al. (1991). Further experiments, using appropriate nonverbal control conditions, will be necessary both to confirm the speech-specific role of the left posterior temporal region and to characterize more fully the processes in which it is involved.

Dissociations between Language Tasks

The second issue addressed in this study was the relationship between the temporal activation associated with passive auditory word presentation, and that associated with generation of a verb in response to a visually presented noun. The results provide evidence that the region activated during the verb generation task is both spatially and functionally distinct from the region activated during the passive presentation of words. Thus, though the two identified regions are located near to each other, the different pattern of their activation suggests that they are related to different types of processing, contrary to previous suggestions that posterior temporal activation in these two tasks may reflect activation associated with semantic processing and word comprehension (Wise et al., 1991).

The different patterns of temporal activation for the passive auditory and verb generation tasks are also consistent with the different patterns of language impairments associated with posterior temporal damage. For instance, left-lateralized damage to the angular, superior temporal, and middle temporal gyri is typically associated with impaired repetition and comprehension of both auditory and visual material, with relatively fluent but nonsensical language production (Wernicke's aphasia) (Benson, 1979; Damasio, 1981; Mendez and Geehan, 1988). A recent attempt to correlate semantic fluency deficits with lesion location (Hart and Gordon, 1990) suggests that a posterior temporal region inferior to the superior temporal gyrus is particularly important. Interestingly, the location of the region discussed by Hart et al. (1990) is similar to that found during the verb generation task. However, the failure to find posterior midtemporal activation when subjects said aloud verbs in response to auditorily presented nouns (Petersen et al., 1988, 1989), and during a task in which subjects were asked to think of and say aloud jobs (Frith et al., 1991), raises concerns about the general role of this area in semantic processing. For a more extensive discussion of these issues, see Raichle et al. (1994).

General Implications of the Present Findings

The present results also provide strong evidence against the hypothesis that language processing involves a distributed set of regions that are automatically activated by presentation of linguistic material under all circumstances (Demonet et al., 1993). According to this hypothesis, activation of a common set of areas, representing a relatively complete processing of words, is expected across a wide range of language tasks. The present demonstration of differences between language tasks is consistent with numerous examples of task-dependent activation differences that have been identified using subtraction and other comparison methodologies (e.g., see Petersen et al., 1989; Wise et al., 1991; Zatorre et al., 1992). In addition, data from behavioral studies in normals have demonstrated that while some language processing occurs automatically, the processing is also subject to significant strategic control (e.g., see Posner, 1978; Kahneman and Treisman, 1984; Neely, 1991; Balota et al., 1992b).

Our results also demonstrate a strategy for assessing the independence of two nearby activated areas. While it is essential to make qualitative comparisons between published findings from different laboratories, in many cases it has been noted that the results of such comparisons raise important questions. For instance, there is considerable variability in the locations of responses found across the studies of auditory processing reviewed above (see Table 1). This variability may reflect factors such as anatomical variability across subject groups, differences in control conditions (e.g., auditory vs nonauditory control condition), and differences in the algorithmic implementation of statistical and anatomical registration methods. Alternatively, the different responses may reflect activation of functionally distinct regions. The variability in the response locations listed in Table 1 is, in some cases, greater than the separation between the different temporal regions studied in the present report. As the number of published studies which utilize PET and other neuroimaging techniques continues to grow, quantitative analysis of the differences between activations will become increasingly valuable as a means of resolving such issues.

Summary

Temporoparietal activation produced by passive presentation of auditory words was replicated across two groups of subjects. The results were extended by demonstrating that significant activation was also found when auditory pseudowords were presented. Furthermore, the results from two different analyses, one based on the spatial location of peak changes and the other upon the magnitude of regional changes, suggest that the temporoparietal activation is distinct from a nearby region of activation associated with the generation of verbs in response to visually presented nouns. Though there are several possible interpretations of the available data, an attractive hypothesis is that the temporoparietal region is related to an auditory storage center whose properties have been explored in behavioral studies of normal and patient populations.

Notes

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