

PET Studies of Phonetic Processing of Speech: Review, Replication, and Reanalysis

Robert J. Zatorre, Ernst Meyer, Albert Gjedde, and Alan C. Evans

Neuropsychology/Cognitive Neuroscience Unit and McConnell Brain Imaging Centre, Montreal Neurological Institute, McGill University, Montreal, Quebec, Canada H3A 2B4

Positron emission tomography was used to investigate cerebral blood flow (CBF) changes associated with the processing of speech. In a first experiment, normal right-handed volunteers were scanned under two conditions that required phonetic processing (discrimination of final consonants and phoneme monitoring), and one baseline condition of passive listening. Analysis was carried out by paired-image subtraction, with MRI overlay for anatomical localization. Comparison of each phonetic condition with the baseline condition revealed increased CBF in the left frontal lobe, close to the border between Broca's area and the motor cortex, and in a left parietal region. A second experiment showed that this area was not activated by a semantic judgment task. Reanalysis of data from an earlier study, in which various baseline conditions were used, confirmed that this region of left frontal cortex is consistently involved in phonetic tasks. The findings support a model whereby articulatory processes involving a portion of Broca's area are important when phonetic segments must be extracted and manipulated, whereas left posterior temporal cortex is involved in perceptual analysis of speech.

The phonological component of auditory linguistic processing has been the subject of several recent studies using PET functional brain imaging techniques (for reviews, see Démonet et al., 1993; Liotti et al., 1994). These studies have yielded partially consistent, but also partially contradictory evidence with respect to the cerebral regions that may be involved in phonological processes.

One of the principal controversies centers around the role of the left frontal cortex, in or near portions of Broca's area, in phonetic analysis. Several authors (Démonet et al., 1992, 1994; Zatorre et al., 1992; Paulesu et al., 1993; Fiez et al., 1995) have reported increases in cerebral blood flow (CBF) in this vicinity in tasks requiring phonetic judgments. One interpretation of these findings supports a role for articulatory recoding in phonological processes, based upon the putative articulatory contribution that is represented by activation of Broca's area (Zatorre et al., 1992). However, other investigators (e.g., Petersen et al., 1989; Rumsey et al., 1992; Sergent et al., 1992) have not observed Broca's area activation, but instead reported left posterior temporal or temporoparietal CBF increases in tasks involving rhyme judgments. These divergent results have led to a debate in the literature, and doubts have been expressed about the validity or generality of the conclusions (e.g., Sergent et al., 1992; Pinker, 1994; Poeppel, in press).

Several issues are raised by this debate, and it is the aim of this article to address them. First, there are empirical differences in the results of the various studies, which must be clarified and understood. There is also a clear need for replication and extension of the existing functional imaging database on auditory phonetic processes. Finally, there are some conceptual misunderstandings in the literature, which must be discussed.

Among these misunderstandings is the nature of the tasks that have been used to study auditory phonological coding. A distinction may be drawn between tasks that require judg-

ments of rhyme (as in the words "house" and "mouse," which rhyme by virtue of their similar syllabic structure), as contrasted with tasks that require manipulation of specific phonetic segments (e.g., the words "bag" and "pig," which both end with the same phonetic segment [g], but do not rhyme). It is precisely the latter type of tasks that have most consistently resulted in CBF increases in a portion of Broca's area. In the study by Zatorre et al. (1992), for example, pairs of monosyllabic words were presented, all of which had different vowels. By definition therefore none of the items rhymed. In the phonetic condition, subjects responded only if the words ended with the same phoneme. Their judgment thus required them to dissect the speech sound into its constituent elements, extract the relevant segment, and compare it to another segment. It was in the comparison of this phonetic discrimination condition to a passive listening baseline that activation in Broca's area was observed, together with a left parietal region.

In the study of Démonet et al. (1992), the task was more complex, because a sequence of phonemes had to be identified, but it also required phonetic units to be segmented and compared. This task also yielded activity within Broca's area when compared to a condition involving a sequence of pure-tone triplets. In a follow-up study, Démonet et al. (1994) attempted to dissociate the effect of phonetic ambiguity from the sequential processing requirements of their earlier task. These investigators reported the strongest Broca's area activity when both elements are present, but they also observed weaker CBF increases in this region even in tasks that did not have a sequential processing component, so long as phonetic ambiguity was present.

In contrast to these experiments, Petersen et al. (1989) presented pairs of visual words and asked subjects to determine if they rhymed or not; this was compared to passive viewing. Sergent et al. (1992) asked subjects to determine if a single visual letter sounded with "ee" or not, and this was compared to either a letter spatial task, or an object categorization task. Petersen et al. identified a left temporoparietal area as showing increased CBF. Sergent et al. also found activation in the left temporal lobe, somewhat more anteriorly than did Petersen et al. (1989) in one subtraction condition. Neither study found Broca's area involvement in these tasks; although Sergent et al. did observe activation of the left inferior frontal gyrus in one condition, they specifically denied the involvement of Broca's area.

Paulesu et al. (1993) also reported a left posterior temporal region activated in a rhyming task on visual letters. Unlike the other two studies examining rhyming, these authors did find a region near Broca's area involved in this task. It is also interesting to note that Rumsey et al. (1992), who used an auditory rhyme judgment task, found left temporoparietal CBF increases in their normal control subjects, consistent with the other findings, but they also found a small increase in the left posterior frontal area.

A superficial analysis of these apparently conflicting data

might conclude that there is little overlap across studies in the regions activated in phonetic processing tasks (Poepfel, in press). Closer scrutiny, however, reveals a potentially interesting pattern: activation of Broca's area in these studies seems to appear specifically when the judgment requires phonetic segmentation. Rhyme judgments do not necessarily require phonetic analysis, since no individual segments need be identified. These latter tasks consistently activated regions in the left superior temporal and/or parietal cortex, but Broca's area was found less consistently or not at all. It is possible that articulatory recoding (as indexed by the activation of Broca's area) would only be necessary if phonetic identification formed part of the task; this might still occur in rhyme judgments, but would not be obligatory.

The present study was conducted specifically in order to address the issue of the participation of Broca's area in phonetic processing. Experiment 1 consists of two activation tasks and a baseline condition of passive listening to speech. The first task was essentially a replication of the phonetic discrimination condition from Zatorre et al. (1992). The second task of experiment 1, phoneme monitoring, required subjects to depress a key whenever a specific target phoneme was heard. This task involves speech processes similar to those of phonetic discrimination, but since the target is given before scanning commences, and the same target is used for all trials, there is no need to perform a comparison between items in a pair, nor does the subject need to encode a separate target phoneme on each trial. There should therefore be a correspondingly reduced working memory load.

Another issue raised in interpreting the data from Zatorre et al. (1992) is that the stimulus list used contained half real words and half nonwords. It might be argued that the type of phonetic analysis required for familiar real words would operate via a different route than for nonwords (e.g., Liotti et al., 1994), and that articulatory recoding would only be necessary for one class of stimuli. To assess this possibility, the two new tasks in experiment 1 utilized only real words. Two other, relatively minor changes were introduced in the procedure for experiment 1. First, subjects maintained their eyes closed throughout scanning in order to determine whether CBF changes in the visual cortex observed previously could be attributed to extraneous visual stimulation. Second, subjects responded on every trial by pressing an appropriate key, whereas in the earlier study responses were made only to positive trials. This change means that no processes related to withholding or inhibiting a response would be present in any condition.

Experiment 2 presents data from a task that required semantic lexical categorization (word/nonword decision), using passive listening as a baseline. This task was included in order to provide a situation that would not require phonetic segmentation but would, nonetheless, involve higher-order cognitive processes. We predicted that subtraction of these two conditions would not produce activation near Broca's area, if that region is recruited specifically for phonetic analysis.

In addition to these new tasks, the present article also presents a reanalysis of the data from Zatorre et al. (1992), which, for clarity, shall be referred to here as experiment 3. The reanalysis was motivated by three factors. First, the statistical analysis method currently used in our laboratory (Worsley et al., 1992) establishes a different and more stringent criterion for accepting activation foci (see Materials and Methods for further details), which we believe to be more appropriate than the change-distribution method used before. Second, in the previous study we only reported CBF increases in task comparisons, whereas the importance of CBF decreases is now increasingly realized (Frith et al., 1991; Raichle et al., 1994;

Zatorre et al., 1994). Therefore, in the reanalysis we now present both types of CBF changes from the previous study.

The third and most important aspect of the reanalysis is that in the present article we present the results of two new comparisons derived from the previous data set. The two new subtractions compare the phonetic discrimination task (1) to another active task, involving pitch discrimination, and (2) to a more elementary control condition, involving stimulation with noise bursts acoustically matched to the syllables. These two subtractions allow us to test the generality of the Broca's area activation found in the 1992 study. In that study we had compared the phonetic discrimination task only to a passive listening condition as a baseline; it can be argued, however, that a comparison of two active tasks to one another is a better contrast, since both tasks would require stimulus comparison and decision components that are absent in the passive condition. To address this question, we therefore now present a direct comparison of the phonetic and pitch tasks.

The second new subtraction described in experiment 3 compares the phonetic condition to the simple noise condition. This subtraction addresses the possible criticism that the results of the original phonetic-passive speech comparison might be confounded because of automatic processes that might have been engaged in the "passive" condition, and which were not under experimental control. Since the noise condition contains no linguistic stimuli, but instead controls only for low-level acoustic input and motor response, this comparison should provide a further test of the hypothesis that the original pattern of activation is specifically related to phonetic judgments.

Materials and Methods

PET Scanning

PET scans were obtained using the Scanditronix PC-2048 system, which produces 15 brain image slices at an intrinsic resolution of $5.0 \times 5.0 \times 6.0$ mm (Evans et al., 1991a). Using the bolus $H_2^{15}O$ methodology (Raichle et al., 1983) without arterial blood sampling (Fox and Raichle, 1984), the relative distribution of CBF was measured in baseline and activated conditions. Individual high-resolution MRI studies (63 slices, 2 mm thick) were obtained from a Philips 1.5T Gyroscan and coregistered with the PET data (Evans et al., 1991b). An orthogonal coordinate frame was then established based on the anterior-posterior commissure line as identified in the MRI volume (Evans et al., 1992). These coordinates were used to apply a linear resampling of each matched pair of MRI and PET datasets into a standardized stereotaxic coordinate system (Talairach and Tournoux, 1988). PET images were reconstructed using a 20 mm Hanning filter to overcome residual anatomical variability, normalized for global CBF and averaged across subjects for each activation state. The mean state-dependent change image volume was then obtained, and converted to a t statistic volume by dividing each voxel by the mean standard deviation in normalized CBF for all intracerebral voxels (Worsley et al., 1992). Individual MR images were subjected to the same averaging procedure, such that composite images volumes sampled at approximately 1.5 mm in each dimension were obtained for both t statistic and MRI volumes. Anatomical and functional images were merged to allow direct localization on the MR images of regions with high t values.

The presence of significant focal changes in CBF was tested by a method based on 3-D Gaussian random field theory (Worsley et al., 1992). Values equal to or exceeding a criterion of $t = 3.5$ were deemed statistically significant ($p < 0.0004$, two-tailed, uncorrected).

Subjects

In experiment 1, 11 young healthy volunteers, 6 female, participated in the study after giving informed written consent. One subject did not complete the phonetic discrimination task due to technical difficulties. In experiments 2 and 3, one group of nine volunteers was tested, none of whom participated in experiment 1.

Subjects in all experiments were right-handed native speakers of

Table 1
Phonetic discrimination—passive words

Region	Brodmann area	Coordinates (mm)			t Value
		x	y	z	
Blood flow increases					
1. M Midbrain	—	-1	-21	-15	3.93
2. L Broca's area	44/45	-35	20	21	3.66
3. L Posterior cingulate gyrus	23	-20	-19	30	3.59
Blood flow decreases					
4. R Parietotemporal operculum	42/40	50	-23	18	4.73
5. L Superior frontal gyrus	8	-28	18	48	4.22
6. L Insula-temporal operculum	—	-44	-6	2	3.87
7. L Posterior superior temporal gyrus	42	-58	-31	8	3.84
8. L Fusiform gyrus	19	-20	-68	-9	3.74
9. L Transverse temporal gyrus	41	-39	-28	15	3.63
10. R Insula	—	35	8	15	3.50

English and reported normal hearing. All procedures used were approved by an institutional ethics review committee.

Stimuli

Experiment 1

Ten different pairs of monosyllabic real English words spoken by a female speaker (e.g., "fan-pin," "tell-big") were recorded, digitized, and stored on computer disk. Words within a pair always had a different vowel, and half of the pairs ended with the same consonant sound. The phoneme [b], which was used as the target in the monitoring task, appeared on four of the ten stimulus pairs, twice in the first word of the pair, twice in the second word. The syllables always differed in fundamental frequency within a pair, with half the pairs recorded with a rising intonation, and the other half with a falling intonation.

Experiments 2 and 3

These stimuli were identical to those of experiment 1, except that half of the syllables were nonwords (e.g., "tid" "gan"). The pairs of stimuli were equally divided such that half the trials contained one word and one nonword, while the other half contained either both words or both nonwords.

Two different tokens of each syllable were recorded to avoid possible use of any extraneous acoustic cues. The mean interstimulus interval was approximately 300 msec. Intertrial interval varied according to subjects' reaction times, but had a minimum of 1 sec and a maximum of 3 sec. Stimuli were delivered binaurally over insert earphones (Eartone type 3A).

Procedure

All stimulus conditions were begun several seconds before scanning, and continued for several seconds after the end of the scan. Stimuli were delivered at the rate of one pair of words every 3 sec. Instructions were given just before each task was started, and several practice trials were given prior to scanning. A different random order of stimuli was presented to each subject for each condition. Subjects kept their eyes closed throughout the scanning period during experiment 1; in experiments 2 and 3 eyes were open with dim room illumination.

Experiment 1

Passive Words. Subjects were instructed to listen to the pairs of words; after each trial they were to press one of two keys in an alternating fashion with the index and middle fingers of the right hand.

Phonetic Discrimination. In this condition subjects heard the same pairs of real words as presented for passive listening, and were instructed to press one or another key according to whether the words did or did not end with the same consonant sound.

Phonetic Monitoring. In this condition subjects were given the target phoneme [b] immediately prior to scanning, and were told to press one key if the target occurred in either word of the pair, or the other key if it did not occur. They then listened to the identical

Table 2
Phonetic monitoring—passive words

Region	Brodmann area	Coordinates (mm)			t Value
		x	y	z	
Blood flow increases					
1. L Supramarginal gyrus	40	-31	-50	38	4.42
2. L Cerebellum	—	-12	-73	-20	4.03
3. L Medial occipital lobe	18	-16	-73	9	4.00
4. R Superior occipital lobe	19	24	-81	21	3.88
5. M Occipital lobe	18	-1	-76	5	3.65
6. L Fusiform gyrus	19/37	-34	-57	-9	3.57
7. L Broca's area	44	-44	8	27	3.57
8. L Precentral gyrus	6/4	-39	-9	42	3.54
Blood flow decreases					
9. R Inferior frontal gyrus	45	48	25	2	5.35
10. L Inferior frontal gyrus	47	-25	18	-15	4.93
11. L Superior frontal gyrus	8	-15	32	57	4.77
12. L Inferior frontal gyrus	47/11	-17	37	-12	4.32
13. L Frontal pole	10/9	-9	60	30	4.20
14. L Middle frontal gyrus	8	-38	32	42	4.08
15. R Orbital frontal gyrus	11	9	22	-17	3.70
16. R Temporal pole	38/22	52	10	-8	3.70
17. L Medial frontal pole	10/9	-12	58	9	3.66
18. L Middle frontal gyrus	9	-36	44	31	3.66
19. L Superior frontal gyrus	6	-35	3	60	3.51

list of stimuli used in the other conditions, and responded by appropriate key presses.

The order of presentation of the two latter conditions was counterbalanced across subjects; the passive words condition was always given first.

Experiment 2

Passive Speech Syllables. Subjects were instructed to listen to the pairs of words/nonwords; after each trial they were instructed to alternate responding with a key press or with no response.

Semantic Categorization. This task required subjects to respond only if both items within the pair matched in terms of semantic category (i.e., both words or both nonwords). When the items did not match, subjects were instructed to withhold their response.

Experiment 3

For further details see Zatorre et al. (1992).

Noise. Pairs of filtered noise bursts, equated for intensity, duration, amplitude envelope, spectral content, and interstimulus interval with the speech syllables were presented. Subjects alternated key press with no response across trials.

Passive Speech Syllables. Same as for experiment 2.

Phonetic Discrimination. Subjects were instructed to respond only if the two stimuli ended with the same consonant sound.

Pitch Discrimination. Subjects responded when the pitch of the second syllable was higher than that of the first, and withheld their response otherwise.

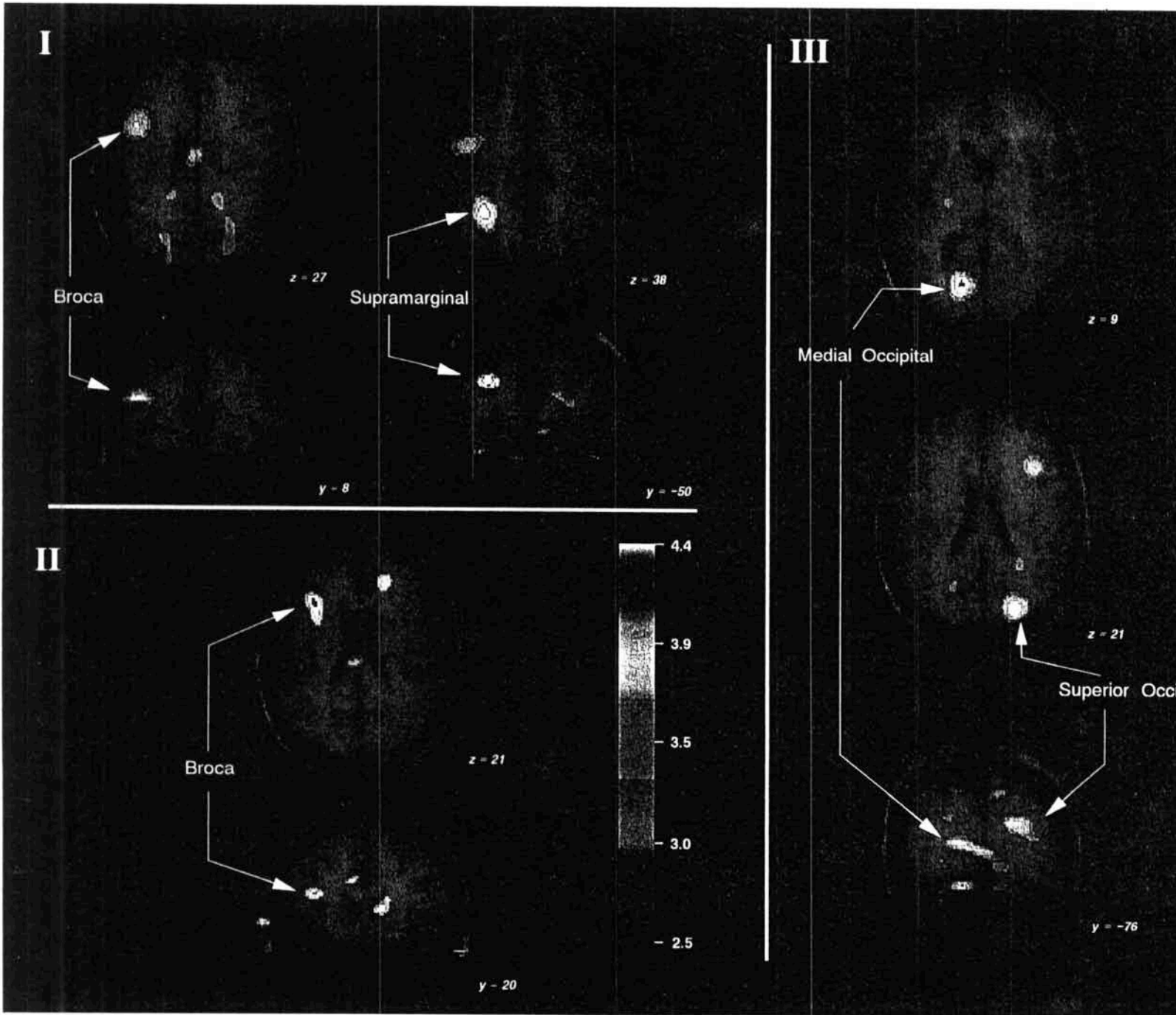
The order of presentation of the phonetic, pitch, and semantic tasks was counterbalanced across subjects.

Results

Experiment 1

Tables 1 and 2 present the stereotaxic coordinates of all significant CBF increases and decreases observed from the subtractions in experiment 1. Figure 1 shows some of the CBF increases associated with these tasks.

The most notable result from experiment 1 is that both phonetic discrimination and monitoring tasks demonstrated significant CBF increases in a portion of Broca's area, as predicted (Fig. 1, panels I and II). Additionally, a CBF increase in the left parietal lobe was also observed in one subtraction (panel I). The phonetic monitoring task (Table 2) additionally



activated a number of occipital cortical areas, as well as the left fusiform gyrus (see Fig. 1, panel III).

CBF decreases in the phonetic discrimination task (Table 1) were observed bilaterally in the temporal-insular region, in the left transverse temporal gyrus, and in the left superior frontal gyrus. CBF decreases in the phonetic monitoring task (Table 2) were found in various portions of the left frontal lobe, but in some right inferior frontal regions as well.

Experiment 2

The comparison of the semantic discrimination task to passive speech syllables yielded only three significant foci of CBF increase: in the anterior and posterior cingulate region, and in the right prefrontal cortex (Table 3). As predicted, no CBF change in the vicinity of Broca's area was noted.

CBF decreases were observed bilaterally in the insular region, in the vicinity of the right central sulcus, in the left superior frontal area, and in the transverse temporal gyrus on the right side.

Experiment 3

The reanalysis of the phonetic discrimination minus passive speech condition from Zatorre et al. (1992) revealed, of course, the same foci as previously published (Table 4); of these, the largest *t* value belongs to the Broca's area activity. Decreases in CBF were confined to the right hemisphere in this subtraction, and involved frontal and temporal cortices.

Table 5 shows that Broca's area also demonstrated a CBF increase when the pitch discrimination task is subtracted from the phonetic discrimination task. Although the *t* value in this case (3.28) is just below the criterion for significance according to a whole-brain significance test, the stereotaxic coordinates of this focus are quite close to those of the other Broca's area activations, rendering it likely to be a legitimate observation (as opposed to a chance false-positive). Decreases of CBF were found in the right superior temporal gyrus and in the left opercular region in this subtraction.

Table 6 shows the comparison of the phonetic discrimination task to the noise condition; once again, the largest CBF increase is found in Broca's area. In addition, in this condition there are significant foci bilaterally in the superior and middle temporal regions, in the left inferior frontal cortex, and in the right lateral cerebellum. CBF decreases in this comparison were observed predominantly in the right hemisphere, including insular and inferior frontal cortices, as well as in the left inferior frontal pole.

In order to permit more direct comparison of the precise position of CBF increases within or near Broca's area, Figure 2 shows the location of all the relevant foci identified in Tables 1-6 on sagittal and coronal projections of a left hemisphere. This figure also plots the foci described by Démonet et al. (1992, 1994) in two of their phonetic discrimination tasks. Note the close correspondence of the points from the various conditions, all of which cluster within a radius of 1.5

Table 3
Semantic discrimination—speech

Region	Brodmann area	Coordinates (mm)			<i>t</i> Value
		x	y	z	
Blood flow increases					
1. M Posterior cingulate gyrus	23	3	-28	22	4.28
2. M Anterior cingulate gyrus	24	3	3	24	4.07
3. R Middle frontal gyrus	9	29	5	35	3.91
Blood flow decreases					
4. R Insula	—	38	6	8	4.27
5. L Insula	—	-34	-21	21	4.06
6. R Pre/post central gyrus	4/3	56	-13	44	3.91
7. L Middle frontal gyrus	6	-35	5	53	3.80
8. R Transverse temporal gyrus	41	44	-21	13	3.70

cm of one another, in the superior and posterior portion of area 44 near the junction with area 6.

Discussion

To summarize the main results, the phoneme monitoring condition of experiment 1 (Fig. 1, panel I; Table 2) closely replicated our earlier data (Zatorre et al., 1992). In particular, we observed activation of a portion of Broca's area near the border with the motor cortex, as well as the left superior parietal region during phoneme monitoring. In the phoneme discrimination condition of experiment 1 (Fig. 1, panel II; Table 1) we also observed activation within area 44, albeit somewhat more inferiorly and medially located. Judging from the MRI, the anatomical location of this focus would appear to lie deep within a sulcus.

The reanalysis of our previous study (experiment 3) demonstrates the robustness of the principal findings. Most importantly, when we compared the two active judgment conditions—phonetic discrimination and pitch discrimination—to one another, we once again obtained CBF increases in Broca's area. Subtraction of the noise stimulation condition from the phonetic judgment condition also confirmed the same finding. In addition, this subtraction yielded asymmetrical temporal-lobe activation, with the left temporal CBF focus being situated more posteriorly than the right temporal region. Finally, no CBF increases anywhere in the left frontal cortex were observed in experiment 2, which involved a semantic lexical decision, and not a phonetic discrimination.

A comparison of the relative location of the activation sites in or near Broca's area elicited by the various conditions is shown in Figure 2. The foci were strictly lateralized to the left in all cases, and can be seen to lie within remarkably close proximity to one another, arguing against claims of minimal overlap across studies of phonological processing (Poepfel, in press). We now discuss each set of findings in more detail before turning to a more general discussion.

Figure 1. Averaged PET subtraction images are shown superimposed upon the averaged MRI scans for the 11 subjects tested in phonetic monitoring (panels I and III) and discrimination (panel II) tasks of experiment 1. Subtraction of the control from activated state in each case yielded the focal changes in CBF shown as a *t* statistic image. The range of *t* values for the PET data is coded by the color scale (see Tables 1 and 2 for precise *t* values of each focus). Stereotaxic coordinates, in millimeters, are derived from the human brain atlas of Talairach and Tournoux (1988), and refer to anterior-posterior position (*y*) relative to the anterior commissure (positive = anterior), and superior-inferior position (*z*) relative to the commissural line (positive = superior). Panel I shows two of the foci associated with phonetic monitoring minus passive words. The two merged PET/MRI sections to the left illustrate the focus near Broca's area (focus 7 in Table 2), in a horizontal section (above, *z* = 27) and the corresponding coronal section (below, *y* = 8). The two images to the right show the supramarginal region that was also activated in this subtraction (focus 1 in Table 2), in horizontal (*z* = 38) and coronal (*y* = -50) views. Panel II shows the focus in the vicinity of Broca's area for the phonetic discrimination minus passive words comparison (focus 2 in Table 1), in both horizontal (*z* = 21) and coronal (*y* = 20) sections. Panel III depicts some of the visual cortical areas that demonstrated CBF increases in phonetic monitoring minus passive words. The top two horizontal sections (*z* = 9 and 21) display the locations of foci in the medial and superior occipital regions, respectively. The corresponding location of these foci in a coronal section can be seen in the bottom image (*y* = -76).

Table 4
Phonetic discrimination—speech

Region	Brodmann area	Coordinates (mm)			t Value
		x	y	z	
Blood flow increases					
1. L Broca's area	44/6	-48	3	24	4.33
2. M Posterior cingulate gyrus	31	7	-31	21	3.69
3. R Occipital pole	17	15	-93	11	3.53
4. M Anterior cingulate gyrus	24	-1	13	27	3.01
5. L Superior parietal lobe	7/40	-29	-59	45	2.89
6. L Inferior temporal gyrus	20	-62	-35	-18	2.85
Blood flow decreases					
7. R Superior mid frontal gyrus	8/6	39	10	49	4.28
8. R Insula/frontal operculum	—	46	8	8	3.92
9. R Superior mid frontal gyrus	6	52	3	40	3.88
10. R Superior temporal gyrus	22	55	-2	2	3.80
11. R Transverse temporal gyrus	41	46	-19	12	3.72

These data are reanalyzed from Zatorre et al. (1992); *t* statistic values below 3.5 are presented for purposes of comparison with previous data.

Activation of Broca's Area

The consistent CBF increases in a portion of Broca's area allow us to address certain critiques. For example, Pinker (1994) has argued that a task such as ours "involves a whole slew of linguistic and cognitive processes other than phonology, such as parsing and remembering words, perhaps orthographic recoding, and the overhead of remembering the task and generating the appropriate button-press. So . . . the areas that light up after you subtract passive listening are not at all specific to phonology, and . . . show no overlap with the areas . . . in some other lab, which might string together some other arbitrary collection of procedures" (p 97). It now seems clear, however, that the activation pattern is not merely an artifact, or the result of an arbitrary set of procedures. The comparison between the two active judgment conditions (phonetic discrimination and pitch), in particular, allows us to control for many nonspecific task demands that are nearly identical in the two conditions, such as retaining each syllable in memory, effecting the comparison, making a judgment, organizing and executing the motor response, sustained attention, remembering the task instructions, and so forth. If the Broca's area activation were related to one of these aspects of the task, then it should have disappeared in the phonetic discrimination minus pitch subtraction.

Conversely, even though phoneme monitoring (experiment 1) involves rather different task demands from phonetic discrimination, both yielded similar locations of activation foci, notably in the vicinity of Broca's area and, less consistently, in the left parietal cortex. We interpret this to mean that these superficially different tasks make demands on the same underlying phonetic processing network.

The fact that experiment 2 (lexical judgment) did not yield CBF increases anywhere in the left frontal cortex is as important as the consistency of the findings in the various phonetic conditions. This result demonstrates an important dissociation, such that the region in question is evidently specifically related to phonetic processing, since it does not show up in the semantic judgment condition, which arguably is as complex in its cognitive demands as are the phonetic tasks.

The present data also allow us to address a different critique of these studies, in that the passive condition undoubtedly encompasses a large number of automatic processes that may be difficult to specify and/or control. Some authors (e.g., Sergent et al., 1992; Démonet et al., 1993) have therefore argued that the activation patterns observed in such comparisons are difficult to interpret, since the nature of the auto-

Table 5
Phonetic discrimination—pitch discrimination

Region	Brodmann area	Coordinates (mm)			t Value
		x	y	z	
Blood flow increases					
1. L Posterior cingulate gyrus	30/23	-16	-57	-6	3.91
2. R Fusiform gyrus	19	38	-69	-8	3.53
3. L Broca's area	44/6	-56	6	29	3.28
4. R Occipital pole	17/18	15	-99	-3	3.02
5. L Parietal lobe	39	-38	-69	21	2.93
Blood flow decreases					
6. R Superior temporal gyrus	22	59	1	0	3.68
7. L Frontal operculum	47	-42	18	-2	3.55

These data are reanalyzed from Zatorre et al. (1992); *t* statistics values below 3.5 are presented for purposes of comparison with previous data.

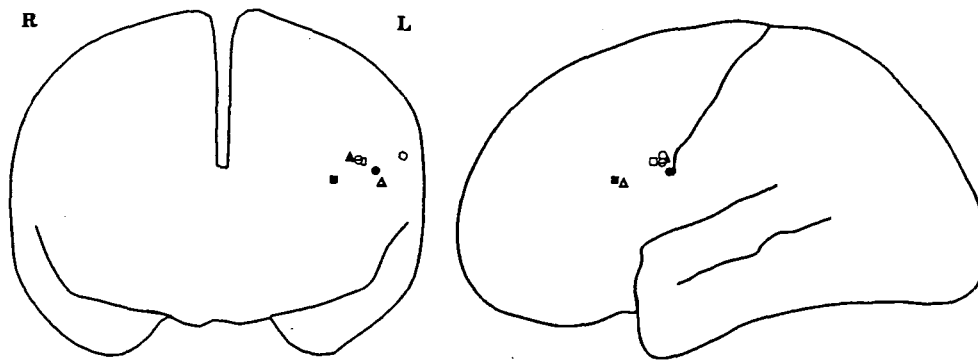
matic processes engaged in the so-called passive condition are unknown. However, in experiment 3, subtraction of the noise condition (in which no automatic speech processing could possibly be present, since there was no speech stimulation) from the phonetic condition also yielded CBF increases in Broca's area. Thus, even when we eliminate possible confounds arising from uncontrolled processes in passive listening, the findings stand.

The relatively consistent findings described in the present report confirm and extend our original results, and lend weight to our interpretation of the role of Broca's area in phonetic processing. The findings of Démonet et al. (1992, 1994), using very different tasks, but that specifically required phonetic processing, are also in agreement with this conclusion. The stereotaxic positions reported by these authors, using a different PET scanning device and a different method of data analysis, is quite close to that obtained in our studies (see Fig. 2). It is interesting that all of these foci consistently cluster in the most superior and posterior aspect of cytoarchitectonic area 44, near the border with area 6, rather than to the inferior aspect of the third frontal convolution, or to opercular areas more traditionally associated with Broca's area. Activation in the latter location has been reported with tasks requiring overt (Petrides et al., 1993) or covert (Wise et

Table 6
Phonetic discrimination—noise

Region	Brodmann area	Coordinates (mm)			t Value
		x	y	z	
Blood flow increases					
1. L Broca's area	44/6	-43	5	27	4.39
2. L Middle temporal gyrus	21	-58	-13	-3	4.30
3. L Inferior frontal gyrus	47	-56	20	-5	3.87
4. R Superior temporal g. (anterior)	38	56	33	-13	3.61
5. R Lateral cerebellum	—	47	-76	-21	3.61
6. R Superior temporal gyrus	22/21	59	-16	0	3.13
Blood flow decreases					
7. R Superior frontal gyrus	8	29	27	51	5.15
8. R Supramarginal gyrus	40	60	-37	36	4.06
9. R Insula/frontal operculum	—	42	6	8	3.98
10. R Insula/frontal operculum	—	35	-7	9	3.98
11. M. Thalamus	—	1	-21	11	3.80
12. R Superior frontal gyrus	6	39	5	54	3.76
13. R Superior frontal gyrus	8	29	44	39	3.67
14. L Frontal pole	10	-32	55	18	3.63
15. L Frontal pole	9	-11	61	27	3.50

These data are reanalyzed from Zatorre et al. (1992); *t* statistic values below 3.5 are presented for purposes of comparison with previous data.



- Phonetic – Speech
 - Phonetic – Pitch
 - ◻ Phonetic – Noise
 - Phonetic – Real Words
 - ◻ Phonetic Monitoring – Real Words
 - ▲ Phonemes – Tones
 - ▲ SeqAmb – Tones
- Zatorre et al., 1992
- Zatorre et al., (present study)
- Démonet et al. 1992
- Démonet et al. 1994

Figure 2. Summary diagram demonstrating the location of activation foci near Broca's area identified in Tables 1–6 on coronal (front view) and sagittal (lateral view) projections of a left hemisphere. For comparison purposes, the locations of foci described by Démonet et al. (1992, 1994) in phonetic discrimination tasks are also shown. The symbols represent the center (most significant voxel) of extended regions of CBF increase identified in each comparison. The brain outlines and major sulci were generated from an averaged MRI data set, transformed into stereotaxic space (Talairach and Tournoux, 1988).

al., 1991) vocal production. The highly consistent anatomical placement of the region shown in Figure 2 may possibly indicate the existence of a functional subregion within Broca's area related to phonetic operations.

It is important to note, however, that other findings of activity near Broca's area are not identical to those reported here. Fiez et al. (1995) have identified a left frontal opercular zone (Brodmann area 45) involved in various types of tasks that also require phonetic analysis (e.g., vowel discrimination, detection of CVC target syllables). These authors, too, favor the interpretation that this site is related to some form of articulatory recoding. However, the area identified (Talairach coordinates $-40, 16, 8$) likely represents a separate functional region from that obtained in the present study. Similarly, the region observed by Paulesu et al. (1993) in a visual rhyming task (located at coordinates $-46, 2, 16$) is more inferior and posterior than any observed in the present investigation. It will therefore be important for future research to specify more clearly the precise contribution of subregions within classically defined Broca's area to what may be broadly termed phonetic processing.

The conclusion that part of Broca's area participates in phonetic processing should in no way be taken to imply that other regions, particularly the left posterior temporal or temporoparietal region, do not play a role in the phonetic analysis of speech sounds. Experimental conditions in which subjects listen to speech syllables have consistently yielded (1) bilateral anterior superior temporal activation, and (2) asymmetric left posterior temporal CBF increases (Petersen et al., 1988, 1989; Wise et al., 1991; Zatorre et al., 1992). Functional MRI data have also corroborated this finding (Binder et al., 1994). Thus, when passive listening is used as the baseline state, any neural activation in these regions would be subtracted away. It seems clear that "passive" listening would include an important phonetic processing component that would be engaged automatically, but that is not observable in subtractions using passive listening as a baseline.

The degree to which automatic processes are engaged by the passive condition is shown most dramatically by the results of experiment 2. Although the task explicitly requires

semantic judgment, the only areas of activation are seen in the cingulate gyrus and one right frontal region. The most likely explanation for this pattern is that the passive condition, in fact, entails essentially full semantic processing, so that when it is used as a baseline such processes are subtracted out. What remains is most likely related to response organization or some other nonsemantic aspect of the judgment.

Activation of Parietal Cortex

The activation of the left parietal region (near Brodmann area 40), which was observed in our original data, was also replicated fairly closely in experiment 1 using the monitoring task, in which it was the strongest activation peak (Fig. 1, panel I). Curiously, however, parietal activation was not so consistently identified in the other comparisons. In the phonetic discrimination condition of experiment 1 there is a focus in the superior portion of the left hemisphere (focus 3 in Table 1), but its location is quite medial, and it is unlikely that this represents activity within a parietal-lobe sulcus. In the phonetic minus pitch comparison of experiment 3, the focal CBF increase closest to area 40 was located relatively inferiorly and posteriorly, near the parietotemporal junction (focus 5 in Table 4); in the phonetic discrimination minus noise comparison (Table 5) it was absent altogether.

These discrepancies notwithstanding, a left parietal role in phonetic judgments under at least some circumstance seems undeniable. Although its precise functional role is still unclear, Paulesu et al. (1992) have speculated that area 40 may be related to phonological storage. Such a conclusion, which is partly supported by lesion evidence (e.g., Shallice and Vallar, 1990), is not entirely inconsistent with the present findings, but the data are not completely converging either. Paulesu et al. did not observe activation of area 40 in their rhyming task, presumably as a consequence of the low load on phonological memory, whereas we did observe it in two of our phonetic tasks (discrimination in the 1992 study, and monitoring in the present experiment 1). This may be because both of our phonetic tasks include a significant memory component. However, the stereotaxic location of the focus reported by Paulesu et al. ($-44, -32, 24$) is relatively far removed from the sites

identified in our data. It is therefore not clear whether the same neural substrate may be involved.

Activation of Visual Cortices

In our earlier report (Zatorre et al., 1992), activation in the occipital cortex had been attributed to possible extraneous visual stimulation caused by eye movements. In experiment 1, however, subjects' eyes were closed, and yet once again activation of visual cortical regions was obtained in the phonetic monitoring condition (Table 2, foci 3-6; see panel III of Fig. 1), albeit not in the same location as the earlier data. No visual cortical regions were found in the phonetic discrimination task of experiment 1 (Table 1), however.

It now seems clear that putative visual areas can be active in the absence of direct visual input during auditory stimulation, as similar findings have also been reported by Démonet et al. (1994) with speech stimuli, by Zatorre et al. (1994) during perception of melodies, and by Perry et al. (1993) in a vocalization task. The possibility that eye movements may be responsible for visual cortical activity still remains, as some authors have reported striate and extrastriate CBF changes associated with eye movements in darkness (Petit et al., 1993; Paus et al., 1995). Nonetheless, another compelling interpretation of such data is that visual imagery processes are invoked by subjects in performing these tasks, and that the activation of regions in the occipital lobe reflects this. Such an interpretation is supported by PET data from Kosslyn et al. (1993), who tested subjects performing visual imagery tasks, and reported activation of various visual regions even with eyes closed. What remains to be explained is the precise functional description to attribute to these results, such that one might be able to predict which specific areas might be recruited for visual imagery processes and the circumstances under which this may occur.

CBF Decreases

Several recent PET studies using the subtraction technique have emphasized the importance of CBF decreases (e.g., Frith et al., 1991; Raichle et al., 1994). One way to conceptualize these changes is that they reflect relative neuronal activity that accompanies the reference task as compared to the "active" task. Another way to think of these changes is that they reflect deactivation of a particular region during the performance of a given task relative to another task. In any case, since the various reference tasks in the present study were quite different from one another (noise, passive speech, pitch judgments), it is not surprising that there is little agreement in the location of CBF decreases across the various subtractions.

However, the baseline conditions in experiments 1 and 2, and the phonetic discrimination minus speech syllables comparison of experiment 3 were quite similar, since all three involve passive listening to pairs of speech sounds. Inspection of the CBF decreases in these three comparisons reveals some correspondence in that in all cases there are changes in the perisylvian region (superior temporal, opercular, or insular cortices), most consistently on the right, but also bilaterally. This result is, in part, similar to findings of Frith et al. (1991) and Raichle et al. (1994), who reported bilateral CBF decreases in the sylvian-insular cortices during the performance of word generation tasks as compared to hearing and repeating words.

One interpretation of these CBF decreases is that some information processing that takes place in the temporosylvian region during passive listening does not occur during active phonetic or semantic judgments, thereby leading to a relative CBF decrease. The fact that decreases often occur in the right hemisphere (including the right primary auditory region in

two instances) suggests that certain nonlinguistic aspects of speech processing (such as pitch or voice quality) may be involved. This possibility makes sense if one assumes that this aspect of the signal is automatically processed under the relatively unconstrained passive listening situation, but that it is not relevant in the phonetic tasks, and is therefore deemphasized during their performance. This conjecture is rendered feasible by a considerable body of data implicating the right superior temporal gyrus specifically in aspects of pitch processing (Milner, 1962; Sidtis and Volpe, 1988; Zatorre, 1988; Zatorre and Samson, 1991; Zatorre et al., 1994). A complementary pattern of CBF decreases in the left primary auditory cortex was observed by Zatorre et al. (1994) in comparisons of pitch judgment tasks with passive listening to tone sequences.

One puzzling result that is not in agreement with this idea is that in the phonetic discrimination task of experiment 1 a CBF decrease was seen near the left primary auditory region (foci 7 and 9 in Table 1), in addition to decreases in the right temporal and insular areas. Thus, it appears that CBF decreases can occur in or near the auditory cortices in either one or both hemispheres in subtractions involving phonetic judgments compared to passive listening. The specific conditions under which such changes may occur evidently remain to be completely specified.

Final Comments

Putting the results of the present investigation together with other findings, it is possible to develop a preliminary model to account for the data. It is reasonable to assume that neural processes in the superior temporal gyri are initially responsible for perceptual analysis of the complex incoming speech stream. Neurophysiological studies of auditory cortices reveal the presence of neuronal populations sensitive to acoustic features that are present in speech sounds, such as frequency modulation (e.g., Whitfield and Evans, 1965), or onset times (e.g., Steinschneider et al., 1982). It is therefore likely that the CBF activation in the left and right anterior superior temporal area observed during "passive" speech (Petersen et al., 1988; Wise et al., 1991; Zatorre et al., 1992; Binder et al., 1994) reflects the operation of such neural systems.

The posterior region of the left superior temporal plane, roughly coextensive with classically defined Wernicke's area, likely plays a special role in speech processing, since this region is not activated by simple tones or noise stimuli (Lauter et al., 1985; Zatorre et al., 1992), or by auditory tonal discrimination tasks (Démonet et al., 1992, 1994; Perry et al., 1993; Zatorre et al., 1994), but is consistently activated by speech stimuli (Petersen et al., 1988, 1989; Wise et al., 1991; Zatorre et al., 1992; Binder et al., 1994). Furthermore, Price et al. (1992) found that CBF increases linearly with rate of word presentation in most of the right and left superior temporal region, but is constant in the left posterior temporal area. This finding suggests that perceptual analysis takes place bilaterally in the superior temporal gyri, since such analysis would be dependent on the amount of acoustic input per unit time, whereas the left posterior temporal region presumably performs a more abstract level of analysis. The processing carried out within this left posterior temporal area is not fully understood, but probably involves the analysis of speech sounds leading to comprehension, and may operate at the syllabic or whole-word level.

This aspect of speech processing appears to be distinct, however, from processes that engage the network that includes the portion of Broca's area and left parietal regions identified above. In the phonetic tasks in question, a relatively abstract pattern-extraction process must take place, since individual phonetic units belonging to the same category may

have very different acoustic manifestations. It is therefore apparently insufficient to rely on a whole-syllable representation to perform this type of task; rather, recourse must be made to a specialized mechanism that is able to compute the similarity between phonetic segments that are differently encoded acoustically by virtue of being embedded in syllables with different vowels. We would argue that this type of judgment calls into play the specialized articulatory recoding system whose neural manifestation is activity in a portion of Broca's area.

We would further argue that this network operates upon information processed at the level of the superior temporal gyri, since no additional activity in temporal-lobe structures was observed in comparisons involving phonetic discrimination or monitoring from experiments 1 or 3, nor in the semantic comparison of experiment 2. We therefore conclude that all necessary computations for perceptual analysis are carried out automatically by temporal-lobe mechanisms. Moreover, when we compare the phonetic judgment task to the noise condition in experiment 3 (which controls only for low-level auditory processing and motor response), we do observe asymmetric left posterior temporal activity, suggesting that whatever processes engage Broca's area in such a task require input from the temporal neocortex.

Some converging evidence for this model can be found from studies of aphasia. There are data indicating that aphasic patients with left anterior damage demonstrate specific phonological deficits, in addition to their well-known production and articulation disorders (e.g., Blumstein et al., 1977; Gainotti et al., 1982), although it is often difficult to specify the lesion site in this literature. There is also evidence that neurosurgical patients with excision in the left central area are impaired at identification of embedded phonemes (Taylor, 1979). These observations in patients with damage in or near the 44/6 junction are consistent with our proposal, because their difficulties in certain phonological tasks could be explained as a failure to access an articulatory representation that is required for identification of phonetic segments.

Cortical stimulation studies are also relevant: Ojemann and Mateer (1979) noted that disruption in phonetic tasks was often observed at sites that also led to disruption of orofacial movements. This association suggests that articulatory-motor processes and phonetic processes share an overlapping neural representation, a conclusion that accords well with our model. Note, however, that disruption was obtained not only from stimulation of Broca's area and surrounding cortex, but could also be elicited from perisylvian cortex more generally.

The present account of the cerebral mechanisms underlying speech processing is partly in agreement with the motor theory of speech perception (Liberman and Mattingly, 1985). However, whereas a strong form of this theory might posit that all speech perception is accomplished via articulatory recoding, the present results would suggest that such recoding is only necessary when segmental extraction and identification of phonetic units is entailed. Under "passive" listening conditions, Broca's area activation was not observed, and yet it is clear that the stimuli are processed and understood. Indeed, in experiment 2, which required explicit semantic judgment, there was little activation above and beyond the passive listening phase, suggesting that full semantic processing takes place during the passive condition. Therefore, our data would not support the view that all aspects of speech perception are necessarily mediated via articulatory recoding. Rather, the left posterior temporal region would seem to be more directly related to specialized speech decoding, as described above. In our view, the region of Broca's area at the border of the precentral gyrus would only be recruited when a more specific fine-grained phonetic analysis is required. An important

issue for future research will be to understand how and when such phonetic operations are important in the processing of speech in real-life situations.

Notes

We thank the technical staff of the McConnell Brain Imaging Unit and of the Medical Cyclotron Unit for their invaluable assistance, and P. Neelin and S. Milot for their technical expertise. Funding was provided in part by Grants MT 11541 and SP-30 from the Medical Research Council of Canada, by the McDonnell-Pew Cognitive Neuroscience Center, and by an award to R.J.Z. from the Fonds de la Recherche en Sante du Quebec.

Address correspondence to Robert J. Zatorre, Montreal Neurological Institute, 3801 University Street, Montreal, Quebec, Canada H3A 2B4.

References

- Binder JR, Rao SM, Hammeke TA, et al. (1994) Functional MRI of human auditory cortex. *Ann Neurol* 35:662-672.
- Blumstein SE, Baker H, Goodglass H (1977) Phonological factors in auditory comprehension in aphasia. *Neuropsychologia* 15:19-30.
- Démonet J-F, Chollet F, Ramsay S, Cardebat D, Nespoulous J-L, Wise R, Rascol A, Frackowiak R (1992) The anatomy of phonological and semantic processing in normal subjects. *Brain* 115:1753-1768.
- Démonet J-F, Wise R, Frackowiak RSJ (1993) Language functions explored in normal subjects by positron emission tomography: a critical review. *Hum Brain Mapping* 1:39-47.
- Démonet J-F, Price C, Wise R, Frackowiak RSJ (1994) A PET study of cognitive strategies in normal subjects during language tasks. *Brain* 117:671-682.
- Evans AC, Thompson CJ, Marrett S, Meyer E, Mazza M (1991a) Performance evaluation of the PC-2048: a new 15-slice encoded-crystal PET scanner for neurological studies. *IEEE Trans Med Imaging* 10:90-98.
- Evans AC, Marrett S, Torrescorzo J, Ku S, Collins L (1991b) MRI-PET correlation in three dimensions using a volume-of-interest (VOI) atlas. *J Cereb Blood Flow Metab* 11:A69-A78.
- Evans AC, Marrett S, Neelin P, Collins L, Worsley K, Dai W, Milot S, Meyer E, Bub D (1992) Anatomical mapping of functional activation in stereotaxic coordinate space. *Neuroimage* 1:43-53.
- Fiez JA, Tallal P, Raichle ME, Miezin FM, Katz WF, Petersen SE (1995) PET studies of auditory and phonological processing: effects of stimulus characteristics and task demands. *J Cognit Neurosci* 7:357-375.
- Fox PT, Raichle ME (1984) Stimulus rate dependence of regional cerebral blood flow in human striate cortex, demonstrated by positron emission tomography. *J Neurophysiol* 51:1109-1120.
- Frith CD, Friston K, Liddle PF, Frackowiak RSJ (1991) Willed action and the prefrontal cortex in man: a study with PET. *Proc R Soc Lond [Biol]* 244:241-246.
- Gainotti G, Miceli G, Silveri MC, Villa G (1982) Some anatomo-clinical aspects of phonemic and semantic comprehension disorders in aphasia. *Acta Neurol Scand* 66:652-665.
- Kosslyn SM, Alpert NM, Thompson WL, Maljkovic V, Weise SB, Chabris CF, Hamilton SE, Rauch SL, Buonanno FS (1993) Visual mental imagery activates topographically organized visual cortex: PET investigations. *J Cognit Neurosci* 5:263-287.
- Lauter JL, Herscovitch P, Formby C, Raichle ME (1985) Tonotopic organization in human auditory cortex revealed by positron emission tomography. *Hear Res* 20:199-205.
- Liberman AM, Mattingly IG (1985) The motor theory of speech perception revised. *Cognition* 21:1-36.
- Liotti M, Gay CT, Fox PT (1994) Functional imaging and language: evidence from positron emission tomography. *J Clin Neurophysiol* 11:175-190.
- Milner B (1962) Laterality effects in audition. In: *Interhemispheric relations and cerebral dominance* (Mountcastle VB, ed), pp 177-195. Baltimore: Johns Hopkins.
- Ojemann GA, Mateer C (1979) Human language cortex: localization of memory, syntax and sequential motor-phoneme identification systems. *Science* 205:1401-1403.
- Paulesu E, Frith CD, Frackowiak RSJ (1993) The neural correlates of the verbal component of short-term memory. *Nature* 362:342-345.
- Paus T, Marrett S, Evans AC, Worsley K (1995) Neurophysiology of

- saccadic suppression in the human brain. Fourth IBRO World Congress Neurosci, in press.
- Perry DW, Petrides M, Alivisatos B, Zatorre RJ, Evans AC, Meyer E (1993) Functional activation of human frontal cortex during tonal working memory tasks. *Soc Neurosci Abstr* 19:843.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1988) Positron emission tomographic studies of the cortical anatomy of single word processing. *Nature* 331:585-589.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1989) Positron Emission Tomography studies of the processing of single words. *J Cognit Neurosci* 1:153-170.
- Petit L, Orssaud C, Tzourio N, Salamon G, Mazoyer B, Berthoz A (1993) PET study of voluntary saccadic eye movements in humans: basal ganglia-thalamocortical system and cingulate cortex involvement. *J Neurophysiol* 69:1009-1017.
- Petrides M, Alivisatos B, Meyer M, Evans AC (1993) Functional activation of the human frontal cortex during the performance of verbal working memory tasks. *Proc Natl Acad Sci USA* 90:878-882.
- Pinker S (1994) On language. *J Cognit Neurosci* 6:92-97.
- Poeppel D (in press) A critical review of PET studies of phonological processing. *Brain Lang*, in press.
- Price C, Wise R, Ramsay S, Friston K, Howard D, Patterson K, Frackowiak RSJ (1992) Regional response differences within the human auditory cortex when listening to words. *Neurosci Lett* 146:179-182.
- Raichle ME, Martin WRW, Herscovitch P, Mintun MA, Markham J (1983) Brain blood flow measured with intravenous H_2O^{15} . II. Implementation and validation. *J Nucl Med* 24:790-798.
- Raichle ME, Fiez JA, Videen TO, MacLeod AK, Pardo JV, Fox PT, Petersen SE (1994) Practice-related changes in human brain functional anatomy during nonmotor learning. *Cereb Cortex* 4:8-26.
- Rumsey JM, Andreason P, Zametkin AJ, Aquino T, King C, Hamburger SD, Pikus A, Rapoport JL, Cohen RM (1992) Failure to activate the left temporoparietal cortex in dyslexia. *Arch Neurol* 49:527-534.
- Sergent J, Zuck E, Levesque M, MacDonald B (1992) Positron emission tomography study of letter and object processing: empirical findings and methodological considerations. *Cereb Cortex* 2:68-80.
- Shallice T, Vallar G (1990) The impairment of auditory-verbal short-term storage. In: *Neuropsychological impairments of short-term memory* (Vallar G, Shallice T, eds), pp 11-53. Cambridge: Cambridge UP.
- Sidtis JJ, Volpe BT (1988) Selective loss of complex-pitch or speech discrimination after unilateral lesion. *Brain Lang*, 34:235-245.
- Steinschneider M, Arezzo J, Vaughan HG (1982) Speech evoked activity in the auditory radiations and cortex of the awake monkey. *Brain Res* 252:353-365.
- Talairach J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. New York: Thieme.
- Taylor LB (1979) Psychological assessment of neurosurgical patients. In: *Functional neurosurgery* (Rasmussen T, Marino R, eds), pp 165-180. New York: Raven.
- Whitfield IC, Evans EF (1965) Responses of auditory cortical neurones to stimuli of changing frequency. *J Neurophysiol* 28:655-672.
- Wise RJ, Chollet F, Hadar U, Friston K, Hoffner E, Frackowiak R (1991) Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain* 114:1803-1817.
- Worsley KJ, Evans AC, 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.
- Zatorre RJ (1988) Pitch perception of complex tones and human temporal-lobe function. *J Acoust Soc Am* 84:566-572.
- Zatorre RJ, Samson S (1991) Role of the right temporal neocortex in retention of pitch in auditory short-term memory. *Brain* 114:2403-2417.
- Zatorre RJ, Evans AC, Meyer E, Gjedde A (1992) Lateralization of phonetic and pitch processing in speech perception. *Science* 256:846-849.
- Zatorre RJ, Evans AC, Meyer E (1994) Neural mechanisms underlying melodic perception and memory for pitch. *J Neurosci* 14:1908-1919.