

# THE ANATOMY OF PHONOLOGICAL AND SEMANTIC PROCESSING IN NORMAL SUBJECTS

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## SUMMARY

We assessed brain activation of nine normal right-handed volunteers in a positron emission tomography study designed to differentiate the functional anatomy of the two major components of auditory comprehension of language, namely phonological versus lexico-semantic processing. The activation paradigm included three tasks. In the reference task, subjects were asked to detect rising pitch within a series of pure tones. In the phonological task, they had to monitor the sequential phonemic organization of non-words. In the lexico-semantic task, they monitored concrete nouns according to semantic criteria. We found highly significant and different patterns of activation. Phonological processing was associated with activation in the left superior temporal gyrus (mainly Wernicke's area) and, to a lesser extent, in Broca's area and in the right superior temporal regions. Lexico-semantic processing was associated with activity in the left middle and inferior temporal gyri, the left inferior parietal region and the left superior prefrontal region, in addition to the superior temporal regions. A comparison of the pattern of activation obtained with the lexico-semantic task to that obtained with the phonological task was made in order to account for the contribution of lower stage components to semantic processing. No difference in activation was found in Broca's area and superior temporal areas which suggests that these areas are activated by the phonological component of both tasks, but activation was noted in the temporal, parietal and frontal multi-modal association areas. These constitute parts of a large network that represent the specific anatomic substrate of the lexico-semantic processing of language.

## INTRODUCTION

In the earliest theoretical papers on aphasia (Charcot, 1884), distinctions were made between a 'centre' for acoustic analysis, another for the 'auditory images of words' (Wernicke, 1874) and a third devoted to the meaning of words. Over the intervening century, substantial knowledge about the physiology of auditory perception in humans has been acquired (Seldon, 1985) but this is not matched by our knowledge of the neural structures which mediate phonological, lexical and semantic processing of heard words. Marked dissociations of these specific functions in aphasic patients have been reported only infrequently (Geschwind *et al.*, 1968; McCarthy and Warrington, 1984; Duhamel and Poncet, 1986; Hart and Gordon, 1990). Analyses of lesion sites in aphasic patients have suggested that, in right-handed subjects, phonological processing is mediated by

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neural structures close to the left sylvian fissure such as Wernicke's area (Selnes *et al.*, 1985), the insular cortex (Damasio and Damasio, 1983) or the supra-marginal gyrus (Benson *et al.*, 1973). By contrast, lexico-semantic processing seems to involve more widely distributed regions of association cortex in the left hemisphere (Geschwind *et al.*, 1968; Cappa *et al.*, 1981) such as the angular gyrus (Bouchard *et al.*, 1979), the posterior and inferior parts of the temporal lobe (Hart and Gordon, 1990; Rubens and Kertesz, 1983) or, even, the dorsolateral prefrontal areas (Alexander *et al.*, 1989a). We have studied cerebral activity with positron emission tomography (PET) during language activation tasks in normal humans in order to address directly whether there are separate areas dedicated to phonological and semantic processing of heard linguistic stimuli. Numerous studies using radiotracer imaging methods have been devoted to the cerebral correlates of language comprehension (Risberg *et al.*, 1975; Larsen *et al.*, 1977; Knopman *et al.*, 1982; Maximilian, 1982; Mazziotta *et al.*, 1982; Nishizawa *et al.*, 1982; Gur *et al.*, 1983; Démonet *et al.*, 1992; Howard *et al.*, 1992). Although some studies have partly confirmed well-established notions of language processing, others have produced unexpected (Knopman *et al.*, 1982) or even conflicting results (Petersen *et al.*, 1988; Wise *et al.*, 1991). The data from Wise *et al.* (1991) suggested that a considerable overlap may exist between the activated areas even when the tasks are theoretically different, for instance when they involve different types of language material (e.g. words versus non-words). The precise structure of the activation paradigm appears critical for the resolution of this issue. It might be that when tasks are used in which (i) no answer is required for subjects, (ii) too vague requirements are made (e.g. 'passive' listening) or (iii) the processing components are poorly specified (such as in a repetition task involving both phonological and lexico-semantic processes), across-task comparisons only demonstrate unspecific or mixed activations. Thus, in the present study, we chose to use monitoring tasks which keep subjects firmly engaged in particular language processes which are thought to be elicited by those tasks. These were two highly contrasted language tasks involving, on the one hand, sequential phonological monitoring of non-words and, on the other, multi-categorical semantic decisions on real words.

## METHODS

Changes in regional cerebral blood flow (rCBF) were calculated with PET by recording the distribution of integrated counts of cerebral radioactivity (Fox and Mintun, 1989) in nine, right-handed, healthy, French-speaking, male volunteers (aged  $35.7 \pm 6.1$  yrs) during the performance of three different cognitive tasks. Prior-written informed consent was obtained from each subject. The study was approved by the Hammersmith Hospital Ethics Committee and the radiation dose of 7.2 mSv per study was approved by the Administration of Radioactive Substances Advisory Committee of the Department of Health (UK).

### *Language stimuli*

The subjects performed each task twice and the order of the tasks in each subject was balanced (A-tones, B-phonemes, C-words; C, B, A) to avoid habituation and order effects. The across-task comparisons were performed by averaging between paired measurements. Task stimuli were recorded and digitized on a Macintosh II (Apple Computer Inc., Cupertino, CA, USA) using commercial software (SoundEdit 2.0.1, Farallon Computing Inc., USA) and the MacRecorder system. The stimuli were delivered binaurally at a rate of one per 3 s over 4 min. In each of the three tasks, 30% of the stimuli were targets, occurring in a pseudo-randomized order (with three targets per block of 10 stimuli). The first baseline task (tones)

consisted of monitoring for rising pitch within a series of triplets of pure tones. The second task (phonemes) consisted of monitoring for the phoneme /b/ in non-words which included the phoneme /d/ in a previous syllable. These non-words were consonant-vowel tri-syllabic (30% of stimuli), consonant-vowel tetra-syllabic (55% of stimuli) and the remaining 15% being tetra-syllabic non-words with a vowel as the first syllable. A phoneme was never repeated in the same non-word. The target-bearing non-words were all tetra-syllabic, the phonemes /d/ and /b/ being placed respectively in the second and the fourth syllables. Distractors were derived from targets by substituting all the vowels and either one of the target phonemes (75% of the distractors) or both (25% of the distractors). When only one target phoneme was substituted, it was replaced in 40% of cases by the corresponding unvoiced phoneme, thus generating distractor non-words bearing either /t/ /b/ or /d/ /p/ pairs. When present, the phoneme /d/ was placed in the second syllable in 96% of cases and in the first syllable in the remaining few cases. Neither target nor distractor non-words were repeated and filler phonemes were balanced among the French repertoire of vowels and consonants (except target consonants). In the third task (words), nouns of animals were monitored within a list of adjective-noun pairs according to two semantic criteria: animals of small size (smaller than a chicken or a cat) preceded by an adjective bearing a 'positive' feature (examples in Table 1).

### Procedure

All scans were performed in a quiet darkened room with the only background noise being that of the scanner. Subjects were asked to refrain from speaking and to press a button with the right index finger to indicate recognition of the appropriate targets. For each task and for each subject, hit rates were calculated.

### Reaction times

Reaction times were measured on a Macintosh II which also delivered the stimuli. The reference points were determined on the digitized sound files by inspection of sonograms and identification of the plosive points of the phoneme /b/ in the phonemes task and the onsets of target nouns in the words task. The reaction times measured during these two tasks were not directly comparable. However, we decided to characterize the two language tasks in terms of their time course using the following method. We assumed that each of these reaction times could be divided in two parts. The first part corresponded to the time required for the 'simple' detection of the target (such as the phoneme /b/ or nouns of animals). The second part corresponded to the time necessary to perform supplementary processing required to complete the task (such as the verification of the relevance of a detected item). We further assumed that the duration of the first part might be estimated by reaction times measured independently which could be subtracted from those recorded during the PET experiment itself. The residual times represented the semantic and the phonological processing times which were then compared.

Thus, a few days after the PET experiments, subjects were given two separate reaction time tasks. The

TABLE 1. DESCRIPTION OF THE TASKS

<i>Tasks</i>	<i>Stimuli</i>	<i>Processes involved</i>
Tone task (reference task) Monitoring for rising pitch on pure tones	Triplets of pure tones (each tone lasting 0.4 s) <i>Targets:</i> 500–500–1000 Hz; 3000–3000–4000 Hz <i>Distractors:</i> same frequency or lowest frequency in the third tone	Early acoustic processing
Phonemes task Monitoring of phoneme /b/ in non-words with a preceding phoneme /d/	Non-words with 3 or 4 consonant-vowel syllables (lasting 0.9–1 s) <i>Targets:</i> e.g. redozabu <i>Distractors:</i> only b (zotabive), or only d (godipuno), or neither	Acoustic analysis, analysis of sequence of phonemes
Words task Monitoring for nouns of small animals with 'positive' attribute in attribute-noun pairs	Adjective-noun pairs (lasting 1–1.2 s) <i>Targets:</i> 'positive' adjective+noun of small animal (smaller than a chicken), e.g. kind mouse <i>Distractors:</i> 'negative' adjective (e.g. horrible) or big animal (e.g. horse)	Acoustic analysis, phonological, semantic processes of words

reaction times obtained in a lexical decision task were used to estimate the duration of the detection period in the words task. The targets of the lexical decision task were matched to the targets of the words task in terms of lexical frequency, semantic category and syllabic structure. The distractors were concrete words with one phoneme altered. The reaction time for a given target in the lexical decision task was subtracted from the reaction time observed for the corresponding target in the words task to obtain a semantic processing time. For each subject, the mean and standard deviation of the semantic processing time was calculated. In the same way, we used an easier version of the phonemes task to subtract the corresponding reaction times from those obtained during the PET experiment and to estimate phonological processing times. This easier version consisted of detection of the same phoneme (*/b/*) in non-words with the same syllabic structure as the non-words used in the PET paradigm but without any requirement for monitoring preceding phonemes. Again, a mean and standard deviation of the phonological processing time was calculated for each subject. The semantic and the phonological processing times were then compared in our group of subjects.

#### *Positron emission tomography scanning*

Subjects were scanned on an ECAT 931-08/12 PET scanner (CTI Inc., Knoxville, USA) whose physical characteristics have been described (Spinks *et al.*, 1988). Subjects inhaled  $C^{15}O_2$  at a concentration of 6 MBq/ml and a flow rate of 500 ml/min through a standard oxygen face mask for a period of 2 min during scanning. The image resolution was  $7 \times 7 \times 8.5$  mm (x, y, z) at full width half maximum following correction for attenuation effects using measured transmission data and subsequent reconstruction with a Hanning filter (0.5 cut-off frequency). The reconstructed images were reformatted to contain  $128 \times 128$  volume elements (voxels) in 43 planes each of size  $2.05 \times 2.05 \times 2.25$  mm following bi-linear interpolation from the original 15 slices. Images were analysed using statistical parametric mapping (Friston and Frackowiak, 1991). Calculations and image matrix manipulations were performed in PRO MATLAB (Mathworks Inc., New York, USA) using SPM software (MRC Cyclotron Unit, London, UK) and ANALYZE (BRU, Mayo Clinic, Rochester, MN, USA) to display images on a SPARC I workstation (SUN Microsystems Europe Inc., Surrey, UK).

The intercommissural line was identified directly and automatically from the primary image volume using a least-squares minimization algorithm, and was then transformed into the standard three-dimensional coordinate space of Talairach and Tournoux (1988) (Friston *et al.*, 1989, 1991). In this space, one normalized scan voxel represents  $2 \times 2 \times 4$  mm in the stereotactic atlas. Stereotactic anatomical normalization allows voxel by voxel pooling of data and correlation of function with anatomy. In order to accommodate variations in functional anatomy between subjects, each image was smoothed with a Gaussian filter 10 pixels (20 mm) wide. This allows the constructive interference between scattered homologous functional foci from different individuals during averaging. Smoothing also suppresses high frequency noise in the scans and thus improves the signal to noise ratio. The scans representing activity during each task were then averaged voxel by voxel following normalization for differences in global flow (to a mean of 50 ml/dl/min) by analysis of covariance (ANCOVA) with global flow as the covariate. This procedure permits the calculation of an estimate of the adjusted error variance associated with the measurement of mean flow in each voxel. Task-specific brain activation was assessed by statistical comparisons with appropriate linear contrasts (weighting of the six condition means) using the *t* statistic (Friston *et al.*, 1990). This analysis was performed for all voxels in parallel, for each planned comparison. The resulting set of *t* values constitutes a statistical parametric map [SPM(*t*)]. The subset of voxels exceeding a threshold of  $P < 0.001$  in omnibus comparisons and remaining significant after correction for multiple non-independent comparisons ( $P < 0.05$ ) was displayed as a volume image rendered in three orthogonal projections. This threshold was chosen because empirical studies have shown it to protect from false positives using the chosen experimental design (Bailey *et al.*, 1991).

#### *Across-task comparisons*

The rationale of the planned comparisons between tasks was not based on a strict hierarchical method such as that described by Petersen *et al.* (1988). This hierarchical subtractive approach ('cognitive subtraction') implies that in a set of language tasks, a first task (e.g. the phonemes task) is entirely embedded in a second (e.g. the words task) which is supposed to tap 'higher-order' processes over and above processes involved in the first task. Instead, we postulated, *a priori*, that both tasks would involve the same or similar processes but that, in each task, an emphasis or differential loading would be placed on one or other process. Such graded differences between language tasks were explored in two ways: (i) assessment of patterns

of increases of activity for each task by comparison with the same baseline (tones) task; (ii) 'direct' comparison between the language tasks (activations in the words task compared with the phonemes task and the reverse) which would only display regions more specifically involved in one or other of the tasks. Finally, we also explored activations in the tones task by comparison with the language tasks considered as baseline tasks.

## RESULTS

### *Subjects' performances on the three tasks*

The phonemes task was significantly more difficult than the other two tasks as demonstrated by comparing the hit rates (Friedman test,  $P = 0.002$ ), false alarm rates (Friedman test,  $P = 0.02$ ) and  $d'$  values (Friedman test,  $P = 0.003$ ). In spite of this, the specificity of subjects' responses in the phonemes task remained acceptable since false alarm rates were low and the  $d'$  values were relatively high (Table 2).

TABLE 2. HIT RATES, FALSE ALARM RATES AND  $d'$  VALUES ON THE THREE TASKS IN EACH SUBJECT

Subjects	Tones task			Phonemes task			Words task		
	Hits (%)	False alarms (%)	$d'$	Hits (%)	False alarms (%)	$d'$	Hits (%)	False alarms (%)	$d'$
1	95	17	2.599	80	10	2.122	100	2	5.154
2	95	6	3.2	93	13	2.602	100	4	4.851
3	97	5	3.526	50	12	1.175	74	2	2.697
4	95	5	3.29	93	7	2.952	96	6	3.306
5	90	3	3.163	83	13	2.08	90	28	1.864
6	95	5	3.29	96	13	2.877	100	6	4.655
7	95	13	2.771	85	17	1.99	100	6	4.655
8	88	4	2.926	90	27	1.895	97	1	4.207
9	93	5	3.121	90	5	2.927	100	1	5.426
Mean	93.7	7.0	3.098	84.4***	13.0*	2.291**	95.2	6.2	4.091
±SD	±2.9	±4.7	±0.287	±13.9	±6.3	±0.597	±8.6	±8.4	±1.21

\*Friedman's test  $P = 0.02$ ; \*\*Friedman's test  $P = 0.003$ ; \*\*\*Friedman's test  $P = 0.002$ .

The phonological processing time was longer than the semantic processing time in each subject (Table 3). A two-factors ANOVA demonstrated highly significant differences between these two processing times ( $F = 58.655$ ,  $P = 0.0001$ ) and between subjects ( $F = 7.399$ ,  $P = 0.0001$ ) with a strong interaction between these factors ( $F = 3.739$ ,  $P = 0.0003$ ), suggesting that the difference between the two processing times is more marked in subjects with long phonological processing times.

### *Activations in the phonemes task compared with the tones task*

In this 'phonological' comparison, three regions were activated significantly (Fig. 1A). There were significant foci in the left temporal lobe which were located mainly in the superior temporal gyrus (Tables 4, 5). Activation was centred around the primary auditory cortex, without including it, and involved the anterior part of Wernicke's area, spreading also towards the anterior parts of the superior temporal gyrus. An activation was also found in the right temporal lobe, which was symmetrically located though far less extensive than on the left. Finally, areas 44 and 45 (Broca's area) were activated in the left hemisphere only.

TABLE 3. MEAN REACTION TIMES AND PROCESSING TIMES ON THE THREE TASKS IN EACH SUBJECT

Subjects	Phonemes task reaction times Mean $\pm$ SD (ms)	Words task reaction times Mean $\pm$ SD (ms)	Phonological processing times Mean $\pm$ SD (ms)	Semantic processing times Mean $\pm$ SD (ms)
1	1081 $\pm$ 482	917 $\pm$ 223	659 $\pm$ 466	242 $\pm$ 133
2	925 $\pm$ 228	818 $\pm$ 121	358 $\pm$ 133	63 $\pm$ 116
3	819 $\pm$ 119	1230 $\pm$ 358	366 $\pm$ 339	359 $\pm$ 312
4	1228 $\pm$ 352	934 $\pm$ 289	266 $\pm$ 329	185 $\pm$ 311
5	1225 $\pm$ 385	1098 $\pm$ 281	790 $\pm$ 385	179 $\pm$ 501
6	730 $\pm$ 244	811 $\pm$ 181	405 $\pm$ 270	119 $\pm$ 196
7	718 $\pm$ 297	834 $\pm$ 236	282 $\pm$ 283	10 $\pm$ 179
8	659 $\pm$ 282	760 $\pm$ 155	238 $\pm$ 274	56 $\pm$ 171
9	546 $\pm$ 237	710 $\pm$ 134	168 $\pm$ 126	111 $\pm$ 147
Mean $\pm$ SD	841 $\pm$ 376	880 $\pm$ 269	395 $\pm$ 361*	144 $\pm$ 258

\* $P = 0.0001$ , ANOVA comparing phonological processing times to semantic processing times.

TABLE 4. COORDINATES OF VOXELS OF MAXIMUM SIGNIFICANCE (Z-SCORE) IN THE THREE PLANNED COMPARISONS WITH SIGNIFICANT ACTIVATIONS

Areas	Phonemes-tones	Words-tones	Words-phonemes
	Z-value (coordin. x, y, z)*	Z-value (coordin. x, y, z)*	Z-value (coordin. x, y, z)*
Left superior temporal gyrus (T1)	Z = 5.675 (-56 -12 4) Z = 6.25 (-54 -14 0)	Z = 4.653 (-54 -22 4) Z = 6.076 (-54 -20 0)	n.s.
Left middle temporal gyrus (T2)	Z = 5.96 (-54 -14 -4) Z = 4.71 (-54 -12 -8)	Z = 6.49 (-54 -18 -4) Z = 5.86 (-48 -36 -8) Z = 5.38 (-50 -38 -12)	n.s.
Left inferior temporal gyrus (T3) and fusiform gyrus	Z = 3.84 (-52 -58 -12) n.s.	Z = 4.92 (-52 -56 -12) Z = 4.93 (-40 -40 -16)	n.s. Z = 3.99 (-40 -38 -16)
Right middle temporal gyrus (T2)	Z = 4.266 (48 -2 -12)	Z = 4.107 (52 -24 -12)	n.s.
Broca's area (Brodmann's areas 44, 45)	Z = 4.644 (-50 18 20)	n.s.	n.s.
Left supramarginal and angular gyrus (Brodmann's areas 40, 39)	n.s.	Z = 4.362 (-44 -56 36) Z = 4.127 (-46 -54 32) Z = 3.769 (-48 -52 28)	Z = 3.77 (-46 -56 36) Z = 3.89 (-48 -56 32) Z = 3.94 (-48 -56 28)
Left prefrontal (Brodmann's areas 8, 9)	n.s.	Z = 4.311 (-16 28 44) Z = 4.374 (-16 30 40) Z = 3.967 (-14 30 36)	Z = 3.537 (-20 30 44) Z = 3.878 (-20 30 40) Z = 3.732 (-18 32 36)
Left precuneus and Post-cingulate gyri (Brodmann's areas 31, 23)	n.s.	n.s.	Z = 4.18 (-2 -60 24) Z = 3.908 (-2 -60 20)

\*Negative values correspond to voxels to the left (x) or below (z) the intercommissural line, or behind the intersection of the intercommissural and vertical anterior commissural lines (y).

### Activations in the words task compared with the tones task

This 'semantic' comparison revealed a different pattern of activation (Fig. 1B; Tables 4, 5). The activation of the left temporal lobe was more widespread than in the

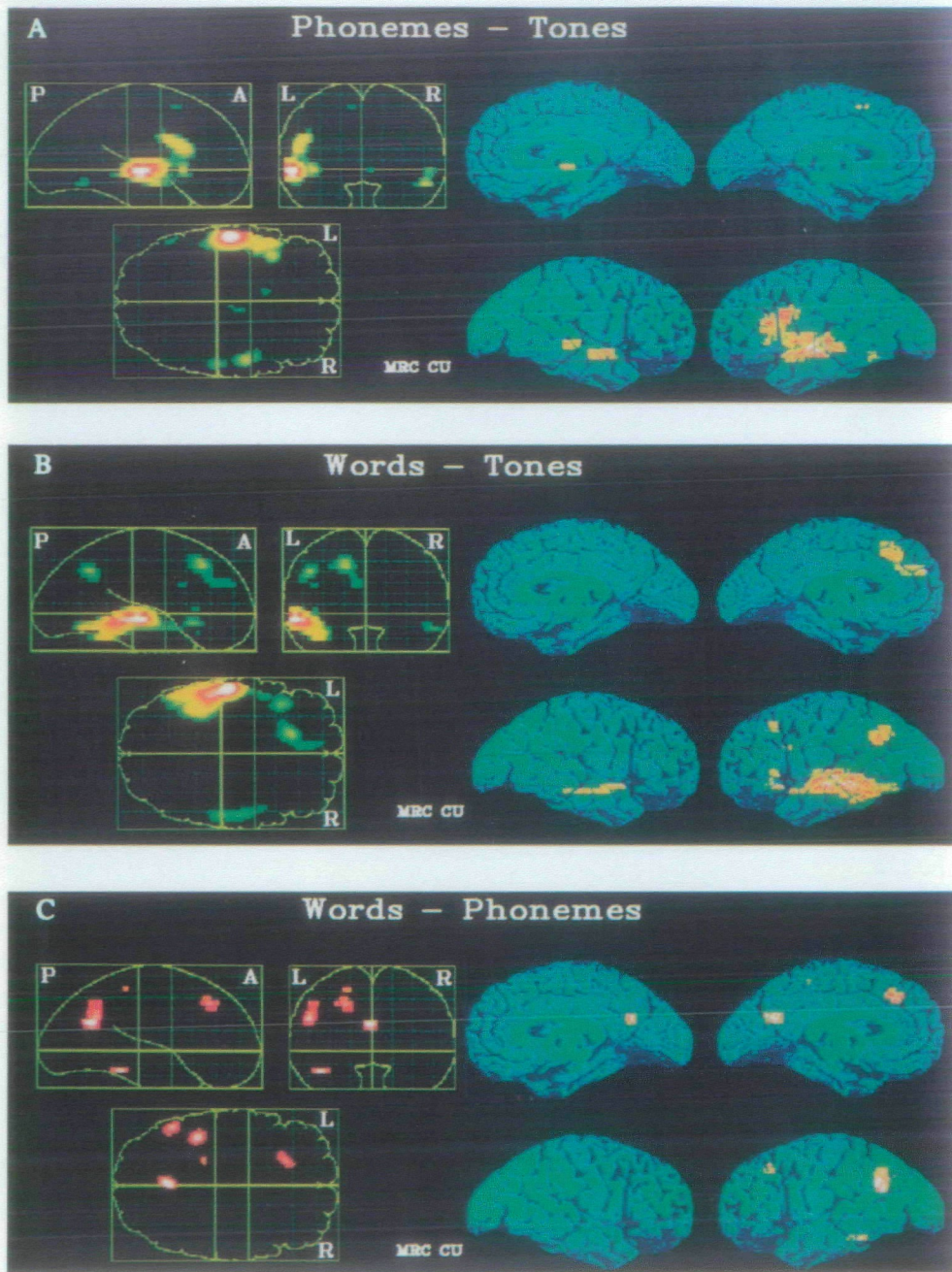


FIG. 1. Statistical parametric maps showing areas of significant changes in activity (i.e. voxels exceeding a threshold of  $P < 0.05$  with correction for multiple non-independent comparisons) in the three comparisons: phonemes-tones (A); words-tones (B); words-phonemes (C). Significant voxels are displayed as projections in the three orthogonal planes on the left of each figure. The grid is that of the atlas of Talairach and Tournoux (1988). The data are also rendered onto lateral and medial surface views of the brain on the right of each figure.

TABLE 5. MEAN VALUES OF CALCULATED REGIONAL CEREBRAL BLOOD FLOW IN THE MOST SIGNIFICANT VOXEL IN THE THREE TASKS

<i>Main significant voxel in the area (coordin. x, y, z)*</i>	<i>Tones task Mean rCBF** (ml/dl/min)</i>	<i>Phonemes task Mean rCBF** (ml/dl/min)</i>	<i>Words task Mean rCBF** (ml/dl/min)</i>
Left superior temporal gyrus (-54 -14 0)	49.4	52.0	51.8
Left middle temporal gyrus (-54 -14 -4)	50.0	51.4	51.8
Fusiform gyrus (-40 -40 -16)	57.5	58.0	59.5
Right middle temporal gyrus (48 -2 -12)	50.1	51.6	51.4
Broca's area (-50 18 20)	36.5	37.6	37.2
Left supramarginal and angular gyrus (-44 -56 36)	45.9	46.1	47.2
Left prefrontal (-16 30 40)	57.0	57.2	58.4
Left precuneus and posterior cingular (-2 -60 24)	69.1	68.0	69.3

\*Convention as in Table 4. \*\*Flows are normalized task-specific averages and represent the mean of a spherical region of diameter 10 voxels (20 mm), centred on the coordinate of the most significant voxel.

'phonological' comparison. The superior, middle and inferior temporal gyri were all activated, along with the middle part of the left fusiform gyrus. Though very small areas in the inferior pre-motor and prefrontal cortex (area 47) were activated, the main part of Broca's area was not significantly stimulated. Activations were found in the posterior part of the left supramarginal gyrus, spreading towards the boundary between the supramarginal and the angular gyri (areas 40 and 39) and in the superior part of the left prefrontal cortex (area 8). Symmetrical but less extensive activations were found in the right temporal lobe.

#### *Activations in the words task compared with the phonemes task*

The words-phonemes comparison (Fig. 1c; Tables 4, 5) confirmed the involvement of areas 40, 39 and 8 in semantic processing. Moreover, a small but significant activation was also found in the inferior part of the temporal lobe and in the left precuneus and posterior cingulate gyri (areas 31, 23).

#### *Activations in the phonemes task compared with the words task*

No significant increase was found in this comparison.

#### *Activations in the tones task compared with the language tasks*

Significant activations in the tones task by comparison with either the phonemes or the words task were located in the right inferior parietal and posterior superior temporal



regions. The coordinates of peak activities were as follows: tones-phonemes comparison: x, y, z: 50, -18, 24 ( $Z = 4.49$ ) and 48, -36, 16 ( $Z = 3.9$ ); tones-words comparison: x, y, z: 52, -26, 20 ( $Z = 5.08$ ) and 52, -32, 16 ( $Z = 4.95$ ).

## DISCUSSION

Our study demonstrates that different, though allied, areas of the brain are implicated in phonological and semantic processing of auditorily presented linguistic material. The main activation is located in the left temporal lobe. The role for the left temporal lobe in language perception was established by Wernicke's description of sensory aphasia. Dissociations of language processing abilities have been described in relation to auditory comprehension in aphasic patients. Duhamel and Poncet (1986) described a major impairment of phonological decoding in a patient demonstrating a relative preservation of semantics. Conversely, semantic processing has been found to be severely impaired in some patients with preserved phonological abilities (Geschwind *et al.*, 1968; Hart and Gordon, 1990). However, the confounding effects of the different size and site of brain lesions and language pathology frequently preclude precise localization of the neural structures relevant to the different cognitive components of language processing.

Recent advances in PET technology now offer a new approach to studying brain-language relationships in both normal and brain-damaged subjects using specifically designed activation paradigms (Nespoulous *et al.*, 1991) and functional mapping of cerebral activity changes. All our tasks were similar in terms of (i) monitoring, (ii) sequential structure of stimuli and (iii) rate of stimulus delivery. All the tasks were performed under controlled presentation conditions and designed to keep subjects fully engaged in the relevant cognitive task. The baseline task (tones) was designed to control for early acoustic processing of auditorily presented stimuli. Indeed, no activation was found in the primary auditory cortex in our task-baseline comparisons. The tones task will not have controlled for the processing of speech because this is composed of multiple frequencies with rapid frequency shifts and is therefore a much more complex sensory stimulus than are pure tones. The other two tasks (phonemes and words) both engaged early acoustic and phonological processing. As the stimuli in the phonemes task were non-words and subjects were asked to monitor the sequential phonemic organization, we assumed when designing the study, that there would be only little contribution from semantic processing. By contrast, in the words task, subjects needed to access lexical and semantic information stored in long-term memory and, possibly, mental images to make semantic judgements.

The neural structures associated with the phonological processes which were elicited by the phonemes task are demonstrated by the phoneme-tones comparison. These include the associative auditory cortex in the left superior temporal gyrus and the anterior part of Wernicke's area. Studies with dichotic listening (Dwyer *et al.*, 1982), with electrical cortical stimulation during neurosurgery (Ojemann, 1983) and of lesion sites in aphasic patients (Duhamel and Poncet, 1986), all support the notion that this is a region specialized for phonology.

Even though phonemic paraphasias in cases of Broca's aphasia (Nespoulous *et al.*, 1987) and disorders of phonetic discrimination after lesions (Blumstein *et al.*, 1977)

or electrical stimulations (Ojemann, 1983) have been reported, the activation we found in Broca's area in the phonemes-tones comparison was an unexpected result which have led us to speculate on the possible role of Broca's area in phonological processing. Classically, Broca's area is thought to be connected to Wernicke's area by the arcuate fasciculus (Geschwind *et al.*, 1968) and to be devoted to the pre-motor organization of articulation. It may also be involved in the initiation of speech (Alexander *et al.*, 1990), in the organization of articulatory sequences and in the covert formulation of language (inner speech) (Stuss and Benson, 1986). In a recent PET study, the silent generation of verbs appropriate to a heard target noun resulted in activation of the supplementary motor area and Broca's area (Wise *et al.*, 1991). The authors suggested that inner speech was a possible explanation of this result. The present experiment caused only a very small activation of the left supplementary motor area (Fig. 1A) and, hence, inner speech seems a less convincing explanation of activation in Broca's area in the phonemes task. It may be that this activation is associated with a 'phonemic' component of inner speech which is itself a complex phenomenon. According to subjects' performances, the phonemes task was more difficult than the other two tasks and was likely to be more demanding in attentional terms. However, activation of Broca's area could hardly be viewed as a consequence of the involvement of a general attentional factor for two reasons. First, Petersen *et al.* (1989) and Pardo *et al.* (1990), using different activation paradigms, identified the anterior cingulate region as a locus related to a general attentional factor which these authors called 'selection for action'. There was no significant activation in the phonemes task in this region, probably because such a general factor was also present, to some extent, in the other tasks. Secondly, activation of Broca's area, although seemingly smaller than in the present study, has also been found recently by Zatorre *et al.* (1992) in a rhyming task using pairs of heard syllables. This task was easier than our phonemes task according to the reported mean hit rate. Moreover, an activation of Broca's area in another rhyming task has been very recently found by others (E. Paulesu, C. D. Frith and R. S. J. Frackowiak, personal communication). We suggest that, during the phonemes task, subjects resorted to a strategy of sequencing and rehearsing phoneme strings and that the activation of Broca's area might reflect such a strategy. This strategy would be time-consuming and could account for the relatively long processing times measured in the phonemes task compared with those in the words task. Such a tentative interpretation would be compatible with various theoretical frameworks. In terms of speech perception, the activation of Broca's area in a phoneme monitoring task is consistent with the 'motor theory' of speech perception proposed by Liberman (Liberman and Mattingly, 1985). From an ontogenetic point of view, motor rehearsal of a heard sequence of phonemes might also be viewed as the reappearance in adults of a strategy to which young children resort during the period of language acquisition (Khul and Meltzoff, 1982). Finally, our phonemes task clearly must have involved working memory (Baddeley, 1986) so that activation of Broca's area could be related to the covert functioning of some aspects of Baddeley's 'articulatory loop' during the task and this interpretation is congruent with results recently obtained by E. Paulesu, C. D. Frith and R. S. J. Frackowiak (personal communication).

Activation of the right auditory association cortex observed in both phoneme-tones and words-tones comparisons may reflect a role for this area in the analysis of complex sounds, as suggested by Zatorre (1988). Indeed, the stimuli used in both active tasks

were much more complex than the pure tones of the reference task. Although clinical evidence as well as our findings indicate that the major part of language processing is predominantly left-sided, it may be that the right superior temporal areas, which are anatomically connected to the homologous areas on the left (Seldon, 1985) are co-activated when cognitive processes become more complex. These accessory auditory areas may play a role in the recovery from the consequences of left temporal lesions (Duhamel and Poncet, 1986).

Lexico-semantic processing, as demonstrated by the words-tones comparison, activated the inferior part of the left temporal lobe, a posterior part of the left supramarginal gyrus and a superior part of the left prefrontal cortex over and above the region in the left superior temporal gyrus seen in both phonemes-tones and word-tones comparisons. The words-phonemes comparison confirmed that such inferior temporal, inferior parietal and superior frontal regions constitute integral components of the neural system specifically associated with the comprehension of spoken words. Thus, in accordance with Damasio's (1989) and Mesulam's (1990) theoretical views, language comprehension which involves access to long-term memory, activates large-scale networks in which the flow of neural signals is fast, as demonstrated by short processing times. Crucial areas in such networks are likely to appear as foci of activation, such as the temporal, parietal and prefrontal regions we found activated by the words task. Although the present study cannot directly connect aspects of complex lexico-semantic processing to specific parts of these large networks, tentative interpretations can be drawn about the functional significance of each of these activation foci.

Patient studies show that lesions of the inferior part of the temporal lobe are associated with disorders of semantics, for example the syndrome of transcortical sensory aphasia (Rubens and Kertesz, 1983; Alexander *et al.*, 1989b). In addition, there are studies which suggest an involvement of this region in visual imagery (Goldenberg *et al.*, 1987; Farah *et al.*, 1989), a process which is likely to have contributed in some part to comprehension in our words task. The inferior temporal area activated in the words-phonemes comparison, though significant, appears very small. There are a number of possible explanations, some of which have been addressed previously (Wise *et al.*, 1991). There may be considerable anatomical overlap of the left posterior temporal neural networks involved in phonological, lexical and semantic processing. It may also be that hearing non-words results in some, possibly automatic, activation of the semantic system, as suggested by the cascade theory of McClelland and Rumelhart (1981). Such factors could result in small insignificant increases of rCBF in the left inferior temporal region in the phonemes task which were nevertheless sufficient to partially mask a bigger response in the same region during the words task. Indeed, we observed a small significant activation in the inferior temporal region in the phonemes-tones comparison. Semantic processing of words may involve many possible associations among a variety of semantic features and is likely to implicate a more widely distributed network than the earlier stages of word comprehension such as phonological processing. In terms of PET activation studies, this could mean relatively small increases in rCBF over relatively large areas of brain. Some of these areas of increase may not be detected above noise. Areas close to regions more intensively activated by an earlier, more anatomically confined processing stage may be masked because of the limited spatial resolution and the smoothing of data during analysis.

Anomic or amnesic aphasia has been attributed to lesions at the left temporo-parieto-occipital junction (Bouchard *et al.*, 1979), including the region of the supramarginal and angular gyri which we found to be activated in normal subjects. Recently, isolated semantic disorders have been reported in three patients in whom an overlap of the topography of the three lesions was found in a posterior region of the middle temporal gyrus and in a part of the angular and supramarginal gyri (Hart and Gordon, 1990). Very recently, a similar conclusion has been reached concerning the role of the left region of the middle temporal gyrus in semantic judgement tasks from electrical cortical stimulation studies (B. Gordon and J. Hart, personal communication, 1991). Categorical judgements on heard noun-noun and verb-noun pairs and the generation of verbs, all tasks that engage the semantic system, did not show activation of the left supramarginal gyrus (Wise *et al.*, 1991). However, a later study on a larger group of subjects has shown involvement of the left inferior parietal lobule in the verb generation task (R. J. Wise *et al.*, unpublished observations). Other authors (Petersen *et al.*, 1989; Zatorre *et al.*, 1992) also reported activations in the temporo-parietal junction which seem either more inferior or more superior in location than the locus we found in the boundary between area 40 and area 39. Since these data were obtained for rhyming tasks on real words, it follows that both phonological and lexical-semantic processing were implicated. Thus, the previous results remain hard to interpret because of the effects of mixed activations. By contrast, it seems clear that the activation focus we found at the supramarginal/angular junction in both the words-tones and the words-phonemes comparisons, is related to lexico-semantic processes and not to phonological ones.

The relationship between lexico-semantic processes and the left superior prefrontal region which we found to be activated by the words task is unclear. Lesions in this region do not induce aphasia but rather disorders of discourse, with inappropriate content and lack of social propriety (Alexander *et al.*, 1989a). However, according to Pandya and Yeterian (1985), such prefrontal areas are strongly and reciprocally connected to various inferior parietal and inferior temporal areas which are themselves interconnected.

Although the words-tones comparison showed a small activation in the inferior part of the prefrontal cortex (area 47) which is consistent with the finding of Petersen *et al.* (1988), the words-phonemes comparison failed to confirm that activation was specifically related to lexico-semantic processing. It is noteworthy that according to Petersen *et al.* (1989) such an activation of area 47 was more marked in the verb generation task than in a task of monitoring of nouns for a semantic category. Hence, it might be that this inferior prefrontal area is more related to language encoding processes than to semantic processes.

There remains the question as to why an activation was observed in the precuneus and posterior cingulate region in the words-phonemes comparison only. Cingulate cortex is classically viewed as a region associated with motivation and attention. Posterior cingulate cortex is included in a functional network related to directed attention for visual input (Mesulam, 1990) and it is also known to have 'extensive neocortical inputs from association cortices by which visual and other stimuli might activate cingulate neurons' (Vogt, 1985). A tentative interpretation of our findings is that, among the three tasks, the words task was most likely to involve the accessing of multi-modal representations, especially via mental imagery. Such an hypothesis would account for greater activation of the posterior cingulate in the words task than in the tones and phonemes task. Indeed,

among the three tasks, the phonemes task was associated with the lowest mean rCBF value in the posterior cingulate area (Table 5).

No significant activation was observed in the phonemes-words comparison. This suggests that the areas activated in the phonemes task were also all implicated in the words task. Thus, the phonological processing which automatically took place in the words task, induced a significant activation in auditory association temporal areas (as demonstrated by the words-tones comparison) and also activated Broca's area (*see* Table 5) to a level which was not significant in the words-tones comparison but which was sufficient to mask a significant contrast in the phonemes-words comparison.

Finally, we found right-sided temporo-parietal activations in the tones task compared with both language tasks. As, in the tones task, subjects had to make judgements on pitch of pure tones by comparison with the ones of preceding tones in heard triplets, a working memory component has been probably involved in this task. Thus, our finding is consistent with results from Zatorre and Samson (1991) who described performance on a short-term memory task for tonal pitch in epileptic patients who underwent temporal or frontal cortical excisions. Impairments in this task were found only in patients with right-sided excisions. In their recent PET activation study, Zatorre *et al.* (1992) described complementary data concerning a monitoring task for pitch in speech stimuli, giving rise to right-sided frontal activation.

This study directly demonstrates a differential activation of the brain for phonological and lexico-semantic processing of auditorily presented language material in normal humans. This is in good accord with dissociations observed in aphasic patients between these two basic types of language processing. The neural correlates of phonological processes are located primarily in the left associative auditory cortex and spread to Broca's area, whereas those corresponding to lexico-semantic processing, although demonstrating some overlap in the temporal lobe, are much more widespread and include multi-modal association cortical areas. Further studies are needed to investigate the precise relationships between these two large neural assemblies, the specific involvement of these multi-modal areas in the various cognitive components of word comprehension and the influence of strategies to which subjects resorted when executing the tasks.

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