Segregating Semantic from Phonological Processes during Reading

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Abstract

A number of previous functional neuroimaging studies have linked activation of the left inferior frontal gyrus with semantic processing, yet damage to the frontal lobes does not critically impair semantic knowledge. This study distinguishes between semantic knowledge and the strategic processes required to make verbal decisions. Using positron emission tomography (PET), we identify the neural correlates of semantic knowledge by contrasting semantic decision on visually presented words to phonological decision on the same words. Both tasks involve identical stimuli and a verbal decision on central lingual codes (semantics and phonology), but the explicit task demands directed attention either to meaning or to the segmentation of phonology. Relative to the phonological task, the semantic task was associated with activations in left extrasylvian temporal cortex with the highest activity in the left temporal pole and a posterior region of the left middle temporal cortex (BA 39) close to the angular gyrus. The reverse contrast showed increased activity in both supramarginal gyri, the left precentral sulcus, and the cuneus with a trend toward enhanced activation in the inferior frontal cortex. These results fit well with neuropsychological evidence, associating semantic knowledge with the extrasylvian left temporal cortex and the segmentation of phonology with the perisylvian cortex.

INTRODUCTION

Semantic memories are formed in many ways and may relate to the sensory properties of the referent, functional attributes, or associations with related objects and abstract concepts. Neuropsychological models suggest that this knowledge is distributed in a network of specialized cortical regions (Mesulam, 1990; Damasio, Grabowski, Tranel, Hichwa & Damasio, 1996), and functional neuroimaging studies have demonstrated that semantic tasks engage a system of widely distributed brain regions extending from the left superior occipital gyrus through the middle and inferior temporal cortices to the inferior frontal gyrus (Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). The specific roles of these interacting semantic regions remain to be elucidated because semantic tasks involve both semantic knowledge and the strategic operations required to make semantic judgements.

One debate concerns the role of the left prefrontal cortex. Lesions to the prefrontal cortex impair the ability to generate words that are semantically related to a target word, but they do not impair verbal comprehension. In functional imaging studies, activation of the left prefrontal cortex during generation of action words relative to word repetition was first demonstrated by Petersen, Fox, Posner, Mintum, and Raichle (1988, 1989) and has subsequently been shown when generation of category exemplars is contrasted to generation of rhyming words (Shaywitz, Pugh, et al., 1995). However, cued word generation is a complex task involving a number of processes other than semantic memory that are known to activate prefrontal structures (Frith, Friston, Liddle, & Frackowiak, 1991). Consequently, it is difficult to control the extent to which all these processes are involved in different generation tasks (Warburton et al., 1996) and therefore the contribution of semantic-specific processing is difficult to decipher.

Other studies have associated increased prefrontal activation with semantic processing when viewing real words is contrasted to viewing pseudowords (Petersen, Fox, Snyder, & Raichle, 1990; but see Price, Wise, & Frackowiak, 1996) and when the semantic decision is contrasted to orthographic decision (Kapur et al., 1994;
Demb et al., 1995; Gabrieli et al., 1996), visual decision (Vandenbergh et al., 1996) or passive word processing (Petersen et al. 1989). In contrast, no prefrontal activation has been reported when semantic decisions on words are contrasted with phonological decisions on nonwords (Demonet et al. 1992, 1994; Shaywitz, Shaywitz, et al., 1995, Pugh et al., 1996). These studies suggest that left prefrontal activation, seen when semantic decision is contrasted with visual decision or passive word processing, might be attributable to processes that are also shared by phonological decision. Left prefrontal activation could reflect strategic processes required for both semantic and phonological decisions (but not for visual or orthographic decisions); alternatively, there may simply be collateral phonological activation during semantic tasks.

Evidence for the involvement of phonological strategies during verbal decisions on visually presented words comes from a previous neuroimaging study (Price et al., 1994). It demonstrated that when subjects are instructed to decide if a letter combination represents a real word or not, increased activation (relative to visual decisions and reading aloud) is detected in brain regions associated with inner speech and subvocal articulation even though the task is not dependent on phonological codes. Evidence for collateral activation of phonology during semantic tasks comes from psychological experiments. For instance, Van Orden, Johnson, and Hale (1988) and Coltheart, Patterson, and Lea (1994) have demonstrated that when subjects are instructed to respond only to exemplars of a given category, they incorrectly accept words or nonwords that sound like category exemplars (e.g., *rows* as a flower; *sute* as an article of clothing).

The present neuroimaging study aims to identify the neural correlates of semantic knowledge by controlling for phonological and strategic processing in the baseline task. The semantic task was living/nonliving judgments on visually presented words, and the baseline task was syllable judgments on the same words. Implicit (unconscious) semantic and phonological processing will occur during both tasks; nevertheless, directed attention will selectively maximize the involvement of semantic processing during living/nonliving judgments and of phonological segmentation during syllable judgments. We were particularly interested in the response of the ventral anterior temporal cortex because previous neuroimaging studies of semantic processing, which have controlled for phonological processing (Demonet et al. 1992; Shaywitz, Shaywitz, et al. 1995; Pugh et al., 1996), did not investigate this area, while recent neuropsychological and neurophysiological studies have indicated it plays an important role in semantic processing (Hodges, Patterson, Oxbury, & Funnell 1992; Nobre & McCarthy, 1995; Vandenbergh et al. 1996).

**RESULTS**

**Reaction Time Data**

The mean reaction times (RT) for the semantic and phonological decisions were 768 and 860 msec, respectively. Although there was a strong trend for semantic decisions to be faster than phonological decisions, a repeated measures t test on the data revealed no significant difference of task. Examination of each individual's data showed that three subjects were faster with semantic decisions, and the other three were faster with phonological decisions. Errors were low (0 to 3%) for four of the subjects, but two made 15 and 16% errors in the phonological task (all false positive responses); one of these subjects was faster with semantic decisions, the other with phonological decisions.

**Activation Data**

The data were analyzed as a group of all six subjects and as a group with four subjects excluding the two subjects who made errors on the phonological task. Since the distribution of activations were the same in both analyses, only the grouped data from all six subjects are reported.

The living/nonliving judgments relative to syllable judgments activated the left temporal pole close to the amygdala in Brodmann's area (BA 28/38), the left posterior middle temporal gyrus (in BA 39 that spreads into the angular gyrus), and the head of the left caudate nucleus. In these areas activation exceeded the p < 0.001 threshold. When the threshold was reduced to p < 0.01, activation of the left middle temporal gyrus (BA 21), left inferior temporal gyrus (BA 20), left superior temporal sulcus (BA 21/22), and left medial superior frontal gyrus (BA 9) was identified.

The reverse contrast showed significant activations in both supramarginal gyri (BA 40), the right angular gyrus (BA 39), the left precentral gyrus (BA 6/44), and the left cuneus. When the threshold was reduced to p < 0.01, activation in the left superior temporal gyrus (BA 42) and the right medial frontal gyrus (BA 9) was identified.

The locations and peak Z scores of areas that exceeded the p < 0.001 threshold are given in Table 1, and activation above the p < 0.01 threshold are illustrated in Figure 1. Neither contrast revealed activation differences in the inferior frontal cortex. We considered the possibility that some regions of inferior frontal cortex were weakly activated during the semantic task but failed to reach the selected level of significance. If this were the case, we would not expect there to be a significant difference in regional cerebral blood flow (rCBF) responses in the temporal and frontal regions. To investigate this hypothesis, we analyzed the rCBF responses using a two-way ANOVA with condition (semantic or phonological) and region (frontal and temporal) as the
Table 1. The location coordinates and Z scores for the semantic-phonological and phonological-semantic contrasts. The location coordinates correspond to the stereotactic atlas of Talairach and Tournoux (1988) and are reported in the order x (− is left, + is right), y (− is posterior to the anterior commissure line, + is anterior to the anterior commissure line), z (− is inferior to the intercommissural line, + is superior to the AC-PC line).

<table>
<thead>
<tr>
<th>Location</th>
<th>Coordinates (x, y, z)</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Semantic-Phonological</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left anterior temporal lobe (BA 28/38)</td>
<td>−32, −4, −20</td>
<td>3.9</td>
</tr>
<tr>
<td>Left posterior temporal/angular gyrus (BA 39)</td>
<td>−50, −68, +16</td>
<td>3.4</td>
</tr>
<tr>
<td>Left caudate nucleus</td>
<td>−4, +6, +8</td>
<td>3.3</td>
</tr>
<tr>
<td>Phonological-Semantic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left supramarginal gyrus (BA 40)</td>
<td>−40, −46, +32</td>
<td>3.9</td>
</tr>
<tr>
<td>Right supramarginal gyrus (BA 40)</td>
<td>+34, −50, +36</td>
<td>3.5</td>
</tr>
<tr>
<td>Right angular gyrus (BA 39)</td>
<td>+40, −34, +40</td>
<td>3.3</td>
</tr>
<tr>
<td>Left precentral gyrus (BA 6)</td>
<td>+28, −62, +32</td>
<td>3.4</td>
</tr>
<tr>
<td>Left cuneus (BA 18)</td>
<td>−52, −2, +24</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>−14, −80, +20</td>
<td>3.5</td>
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</tbody>
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Factors. Data were selected from the voxels that had the highest Z scores in the frontal and temporal cortex during the semantic task. The most significantly active voxel in the inferior frontal cortex (Z = 1.6, p > 0.05) lay in BA 47 (coordinates according to Talairach and Tournoux, 1988: x = −30, y = 28, z = −8) and the most significantly active voxel in the temporal cortex (Z = 3.9, p < 0.001) lay in BA 28/38 (coordinates according to Talairach and Tournoux, 1988: x = −32, y = −4, z = −20). The main effects of condition and region were significant, and in addition there was a significant condition X region interaction (F = 3.9, df = 1, 140, p < 0.05), demonstrating that the temporal region was significantly more active than the frontal region during semantic decision.

Finally, we considered the possibility that left frontal activation was diminished by the repetition of the same words in the phonological and semantic tasks (Raichle et al. 1994), and we removed the conditions presenting previously seen items from the analysis. Although only half the data remained in the analysis, the semantic task was still associated with extrasylvian temporal activation with no inferior frontal activation. In contrast, there was a trend for increased inferior frontal activation in BA 44.

Figure 1. The regions activated (in white on gray models of the brain) when semantic decision on words is contrasted to syllable decision and when syllable decision is contrasted to semantic decision.
This study indicates that regions of the left extrasylvian temporal cortices are the most likely sites for semantic memories because there is enhanced activation during living-nonliving judgments even when phonological processing and strategic processes are controlled in the baseline task. The involvement of the left caudate nucleus is also demonstrated, although at present we have no explanation for the role of this structure.

The peak activations associated with semantic decisions were focused in the left temporal pole and a posterior region of the left middle temporal cortex just inferior to the angular gyrus. These findings are consistent with neuropsychological and neurophysiological data. In the neuropsychological literature, the importance of the left angular gyrus for comprehending written and spoken language has been well established for more than a century (Dejerine, 1892; Geshwind, 1965; Hart & Gordon, 1990). Lesions here result in dysgraphia with dysgraphia (Friedman & Albert, 1985; Hecaen & Kremin, 1976) and those patients with preserved spelling ability rely on spelling to sound correspondence rather than meaning (Roeltgen & Heilman, 1984; see also McCarthy & Warrington, 1990). More recently, the anterior temporal poles have been associated with semantic processing in patients with semantic dementia (Hodges, Patterson, Oxbury, & Funnell, 1992) and anosmia (Damasio et al., 1996). The patients with semantic dementia have profound loss of semantic knowledge resulting from atrophy (probably Pick’s disease) that commences in the anterior temporal poles and spreads back along the inferolateral temporal surface. Cortical and intracortical recording studies concur with neuropsychology associating semantic processing with the left anterior temporal pole (Nobre & McCarthy, 1995; McCarthy, Nobre, Bentin, & Spencer, 1995) and parietal regions (Connolly, Phillips, & Forbes, 1995).

In functional imaging studies, concurrent activation of the left anterior temporal pole and BA 39 has been reported during the semantic decision relative to the visual decision (Vandenberghhe et al., 1996), during sentence comprehension tasks (Mazoyer et al., 1993; Bottini et al., 1994), and when sentences construing real stories are contrasted to unlinked sentences (Fletcher et al., 1995). Activation of BA 39 (in the left posterior temporal cortex or the left angular gyrus) has been demonstrated, in the absence of anterior temporal activation, during word generation (Raichle et al., 1994; Shaywitz, Pugh, et al., 1995; Warburton et al., 1996) and during semantic decision on auditory words (Demonet et al., 1992; Demonet, Price, Wise, & Frackowiak, 1994) and seen words (Shaywitz, Shaywitz, et al., 1995). The only reading study that investigated the response of the temporo-parietal cortex during semantic tasks and found no activation is that by Kapur et al. (1994). This study used a high threshold of significance applying a X2 statistic on the statistical parametric mapping (SPM) t map to protect from false positives, a procedure that increases the likelihood of false negatives.

The most likely reason for the absence of ventral, anterior temporal activation in some of these imaging studies is that no a priori decision was taken to investigate this region. The PET studies used cameras with fields of view limited to 10 cm or less that could result in occlusion of ventral anterior temporal regions unless all the subjects were purposefully positioned to scan the ventral rather than dorsal surfaces. The functional magnetic resonance imaging (fMRI) studies used regions of interest that did not involve the temporal poles. In contrast, in the PET study reported by Damasio et al. (1996), regions of interest included the temporal poles, and activation was detected in association with naming objects and faces. Our findings concur with those of Damasio et al. and in addition demonstrate that left temporal pole activation is associated with mediating the meanings of words rather than with retrieval of phonology, which was removed by our control task.

The Syllable Decision Baseline Task

The syllable decision baseline task acted to control for the phonological and strategic processing involved in semantic decision, but in addition, syllable decisions require segmentation of phonology and short-term memory while the syllables are counted. Enhanced activation for syllable decisions was identified in both supramarginal gyri (BA 40), the right angular gyrus, the left precentral sulcus, and the left cuneus. Concurrent activation of the left supramarginal gyrus and the left precentral sulcus has previously been reported in association with phonological tasks by Demonet et al. (1994) and Paulesu, Frith, & Frackowiak (1993), who associate these regions with short-term memory processes. In particular, the supramarginal gyrus is linked to the phonological store, and the left precentral gyrus is linked to articulation. Activation of the left cuneus in concert with the left supramarginal gyrus has been reported by Price, Wise, et al. (1996) during visual presentation of words and pseudowords relative to consonant letter strings. During syllable decision, activation of the cuneus may reflect top-down modulation of visual processing if subjects attempted (unsuccessfully) to base their responses on the length of the word. The function of right parietal structures during syllable judgments is also a matter of conjecture but may relate to the counting aspect of the task. The purpose of this paper, however, was not to investigate the cognitive components of syllable judg-
ments. The syllable judgment acted as a control for the semantic decision, subtracting out phonological processing and the strategic processes required to make decisions on central lingual codes. Indeed, the trend toward longer reaction times and increased errors for the syllable decision indicate that this task increased processing demands relative to semantic decision. This is convenient for our interpretation of the semantic activations because any activation associated with the semantic task is therefore likely to reflect word meaning rather than the processes involved in verbal decisions.

**The Left Inferior Frontal Gyrus**

The importance of the left prefrontal cortex for seen, heard, and self-generated language is well established from lesion data. Damage to this region results in impoverished speech production and mild impairments in speech perception (Blumstein, 1995) but with no loss of semantic knowledge. In neuroimaging data, activation of many regions within the prefrontal cortex has been associated with a multitude of functions, but the specific functions of these areas are not yet clearly defined (see Buckner, Raichle, & Petersen, 1995).

Kapur et al. (1994), who found left prefrontal activation in BA 45, 46, and 47 during semantic decisions relative to orthographic decisions, accommodate the neuropsychological literature by suggesting that the left dorsolateral prefrontal cortex is a region specialized for manipulating semantic representations. We support this interpretation. In addition, we note that activation of the left prefrontal regions is also involved in phonological decisions (Sergent et al., 1992a; Shaywitz, Shaywitz, et al., 1995; Pugh et al., 1996) and that phonology is activated during semantic tasks (Van Orden et al., 1988; Coltheart et al., 1994; Price et al., 1994; Connolly et al., 1995).

The results of the present study do not permit us to assign functions to different regions of the prefrontal cortex because the absence of activation is a null effect. There may have been equal activation across tasks or weak activation in one task that failed to be detected. When the threshold of significance was reduced, prefrontal signals were detected in BA 44 ($Z = 2.4, p < 0.01$) during syllable decisions and in BA 47 ($Z = 1.6, p < 0.05$) for living/nonliving decisions. Further investigation of a wide variety of semantic tasks (relative to phonological tasks) is therefore required to establish whether there are regions specialized for semantic processing within the prefrontal cortex.

**Concluding Remarks**

This paper distinguishes between semantic knowledge and the strategic processes required to make verbal decisions on central lingual codes. We demonstrate that living/nonliving judgments, on visually presented words denoting objects, enhance activation in the left extrapyramidal temporal cortices even when phonological and strategic operations are removed in the baseline task. In addition, we suggest that the function of the left anterior and posterior extrapyramidal temporal regions may not be restricted to processing knowledge of objects because the same regions are activated when subjects read sentences construing a real story relative to unconnected sentences (Fletcher et al., 1995).

The distribution of the activations in the extrapyramidal temporal cortex accords well with lesion data (Alexander, Hiltbrunner, & Fischer, 1989; Damasio et al., 1996; Hodges et al., 1992), neurophysiological data (Connolly et al., 1995; Nobre & McCarthy, 1995) and some neuroimaging data (Damasio et al., 1996; Vandenberghe et al., 1996) but stands in contrast to neuroimaging studies that associate semantic knowledge with the left prefrontal cortex. We believe that no convincing evidence has so far been reported associating semantic knowledge with prefrontal activation when phonological processes and processes required to make verbal decisions are controlled. We conclude that the left extrapyramidal temporal cortices are the most likely sites of semantic knowledge.

**METHODS**

Six right-handed (Edinburgh handedness inventory) volunteers with English as their first language and no history of neurological disorders gave informed consent to participate in the study. There were two tasks. For the semantic decision task, the subjects were instructed to press a mouse button with their right index finger when a visually presented word referred to a living object, but not when it referred to a nonliving object. For the phonological task, the same finger press response was made when the word had two syllables but not when it had one or three syllables. There were an equal number of "present" responses for each task, and reaction times to each response were measured.

The stimuli were 150 words corresponding to familiar objects. Presentation was on an Apple computer at a rate of one word every 2500 msec with an exposure duration of 500 msec. The words were divided into six sets, matched for word frequency (Kucera & Francis, 1967), number of syllables, and word category (living or nonliving). Living objects were animals, vegetables, fruits, or body parts. Nonliving items were tools, kitchen utensils, buildings, and furniture.

Prior to scanning, each volunteer was familiarized with the tasks in a practice session using a set of words not used in the experimental conditions. There were 12 scans. The order of tasks alternated semantic and phonological judgments. Each of the six word sets was presented twice, once for a semantic decision and once for a phonological decision with the order of presentation counterbalanced such that for each subject half the...
words were seen initially for one task and the other half were seen initially for the other task.

The scans were obtained with a Siemens 953B (CTI, Knoxville, TN) dedicated PET head scanner (Spinks et al., 1992) using radio labeled water (H₂¹⁸O) as the tracer (Silbersweig et al., 1993). Images were reconstructed by filtered back projection (Hanning filter, cutoff frequency 0.5 Hz), giving a transaxial resolution of 8.5 mm full width at half maximum (FWHM). The reconstructed images contained 128 × 128 pixels, each 2.05 × 2.05 × 2.00 mm in size.

The data were analyzed with statistical parametric mapping (using SPM95 software from the Wellcome Department of Cognitive Neurology, London) using a blocked one-way ANCOVA with global activity as a (subject-specific) confounding covariate (Friston et al., 1995; Friston et al., 1996). Regionally specific differences were assessed using linear contrasts of effects due to task (semantic versus phonological) and the resulting set of voxel values for each contrast constitute a statistical parametric map of the t statistic SPM(t). Only activations that exceeded the p < 0.001 (Z score > 3.1) threshold are considered significant. However, since we were specifically looking for activation of the prefrontal regions, we also comment on those areas that exceeded a threshold of p < 0.01.

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