Research Article

FUNCTIONAL MAGNETIC RESONANCE IMAGING OF SEMANTIC MEMORY PROCESSES IN THE FRONTAL LOBES

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Abstract—*Frontal-lobe activation during semantic memory performance was examined using functional magnetic resonance imaging (fMRI), a noninvasive technique for localizing neural activity associated with cognitive function. Left inferior prefrontal cortex was more activated for semantic than for perceptual encoding of words, and for initial than for repeated semantic encoding of words. Decreased activation for semantic encoding of repeated words reflects repetition priming, that is, implicit retrieval of memory gained in the initial semantic encoding of a word. The left inferior prefrontal region may subserve semantic working memory processes that participate in semantic encoding and that have decreased demands when such encoding can be facilitated by recent semantic experience. These results demonstrate that fMRI can visualize changes in an individual's brain function associated with the encoding and retrieval of new memories.*

Advances in magnetic resonance imaging (MRI) have produced a new method for identifying brain regions that mediate specific aspects of human thought, functional MRI (fMRI). Like positron emission tomography (PET), fMRI measures changes in microvasculature surrounding metabolically active brain tissue. Specifically, fMRI detects changes in the magnetic state of blood dependent on the degree of oxygenation (Ogawa, Lee, Nayak, & Glynn, 1990). Because MRI allows for the acquisition of both structural and functional images, it is well suited for localizing neural activation in an individual. So far, fMRI studies have identified regions that are involved in vision (Belliveau et al., 1991; Engel et al., 1994; Schneider, Noll, & Cohen, 1993), movement (Kim et al., 1993), language (McCarthy, Blamire, Rothman, Gruetter, & Shulman, 1993), and attention (J.D. Cohen et al., 1994), but this technique has just begun to be used to study fundamental memory processes.

The present study examined frontal-lobe activation associated with encoding and retrieving word meaning. It is well known that words are remembered better if encoded for meaning (semantic or deep encoding) than for appearance (perceptual or shallow encoding; Craik & Lockhart, 1972). In the present study, semantic encoding was required to judge whether words had abstract or concrete meanings. Perceptual, or nonsemantic, encoding was required to judge whether words appeared in upper- or lowercase letters. A PET study found greater activation, in a group average, in the left frontal lobe for semantic than for perceptual encoding of words (Kapur et al., 1994). We hypothesized, therefore, that fMRI would reveal greater activation in the left frontal lobe for semantic than for perceptual encoding of words in individuals.

Semantic encoding may occur more efficiently for repeated than for initial encoding of a word, a phenomenon known as repetition priming. Because no explicit reference is made to the initial presentation of the word, such repetition priming constitutes an example of implicit memory retrieval (Graf & Schacter, 1985). PET studies have found decreased occipital-lobe activation associated with perceptual (visual) repetition priming (i.e., less activation for repeated vs. initial processing; Buckner et al., 1995; Squire et al., 1992). We hypothesized that fMRI would reveal decreased left-frontal activation associated with semantic repetition priming. The decreased activation would reflect memory gained in the initial semantic analysis of words and thus provide one of the first visualizations in an individual human brain of a change associated with long-term memory. Finally, we hypothesized that the same left-frontal region would be implicated for semantic encoding and semantic repetition priming.

METHOD

A behavioral study was conducted to validate the presence of semantic encoding, via its effect on explicit memory for words, and implicit semantic retrieval, via repetition priming. The imaging study was performed with the same materials and tasks.

Participants

Participants came from the Stanford community. Sixteen volunteers (ages 18–30) participated in the behavioral study for $10 payments, and 4 right-handed male volunteers (ages 23–32) participated in the imaging study for $20 payments.

Materials

The stimuli were 480 words three to eight letters long. Half of the words were abstract and half concrete. The words were divided randomly into sets of 20 words. Each set contained 5 abstract words in uppercase (e.g., "TRUST"), 5 abstract words in lowercase (e.g., "love"), 5 concrete words in uppercase (e.g., "CHAIR"), and 5 concrete words in lowercase (e.g., "book"). Words in each set were placed into a pseudorandom order with the constraints that no more than 4 abstract or con-

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crete and no more than 4 uppercase or lowercase words appeared consecutively.

Tasks

Encoding and semantic repetition tasks were examined in both behavioral and imaging studies. In addition, a perceptual repetition task was examined behaviorally. On each trial of all tasks, a word appeared centrally on a computer monitor for 1 s, and there was a 1-s intertrial interval before the next word appeared. Subjects were instructed by a card as to which task to perform prior to each set of 20 words, and asked to respond quickly and accurately. Responses were made by pressing a squeeze ball (imaging study) or button (behavioral study). Two consecutive sets constituted a cycle. There were eight sets of words (four cycles) per task in the imaging study and four sets (two cycles) per task in the behavioral study.

In the encoding task, participants performed alternately semantic or perceptual encoding decisions upon sets of 20 words; each word used in this task appeared once. For semantic encoding, participants judged whether each word referred to something abstract or concrete; half the subjects were to respond to every abstract word and the other half to every concrete word. For perceptual encoding, participants judged whether each word appeared in upper- or lowercase; half the subjects were to respond to every word in uppercase letters and the other half to every word in lowercase letters. Word orders were constant across participants, and the order of alternating encoding tasks (i.e., semantic or perceptual encoding first) and response instructions (i.e., which category of words to respond to) were counterbalanced across participants.

In the semantic repetition task, participants performed in all cycles the semantic encoding task of judging whether each word was abstract or concrete. Every second set contained the same words shown in the previous set, but in a different, random order (none of the words appeared in the encoding task). The perceptual repetition task was identical, except that perceptual encoding decisions (uppercase/lowercase judgments) were made.

Imaging Procedure

Participants performed the encoding and semantic repetition tasks while activation was recorded in two 7-mm-thick sections (in-plane resolution of 2.4 × 2.4 mm) acquired separately in the coronal plane of Talairach and Tournoux (1988) at 32 mm and 39 mm rostral to the anterior commissure (Fig. 1). Scanning was performed during the encoding and semantic repetition tasks, in that order, first in the more posterior section and then in the more anterior section. Stimuli were generated from a computer and back-projected via a magnet-compatible projector onto a screen located above the subject's neck; visual images were viewed from a mirror mounted above the subject's head. Subjects were asked to squeeze a ball in response to either concrete or abstract words and either upper- or lowercase words.

Imaging was performed with a 1.5 T whole-body MRI scanner (General Electric Medical Systems Signa, Rev. 5.3). Two 5-in.-diameter local receive coils were used for signal amplification. Head movement was minimized by using a bite-bar formed with each subject's dental impression. A T2* sensitive gradient echo spiral sequence (Meyer, Hu, Nishimura, & Macovski, 1992) was used with parameters of TR = 75 ms, TE = 40 ms, flip angle = 23°, 20 interleaves per image, and an acquisition time of 1.5 s per image. For each of the four recordings, 224 images were acquired continuously over a 336-s session. T1-weighted, flow-compensated spin-warp anatomy images (TR = 500 ms, minimum TE) were acquired for sections that received functional scans.

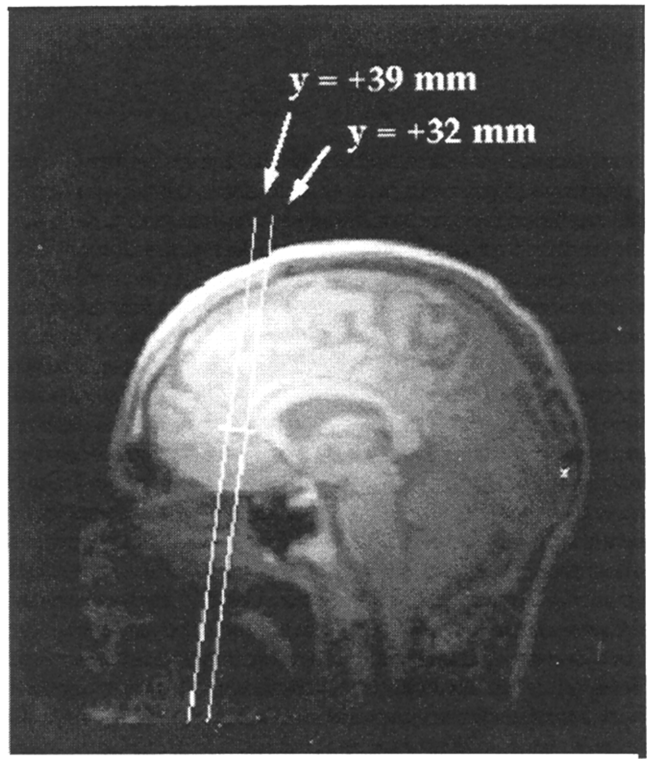


Fig. 1. Locations of coronal sections analyzed in this study, depicted on a sagittal localizer image. The sections were obtained at 32 mm and 39 mm rostral to the anterior commissure.

Behavioral Procedure

Subjects performed, in order, the encoding, semantic repetition, and perceptual repetition tasks. Subjects were then asked to recall as many of the words as they could from all sets following a 30-s delay period during which they counted backwards by 3s.

RESULTS

Behavioral Results

For the encoding task, participants made perceptual judgments (M = 405 ms, SD = 36) more quickly than semantic judgments (M = 637 ms, SD = 100), $t(15) = 10.68$, $p < .0001$.

Subjects recalled more words after semantic encoding than after perceptual encoding, $t(15) = 7.49$, $p < .0001$ (Fig. 2a).

For the semantic and perceptual repetition tasks, mean median reaction time was calculated for each set of words and analyzed in a repeated measures analysis of variance (ANOVA) with factors of task (semantic vs. perceptual), cycle (first vs. second), and presentation (initial vs. repeated; Fig. 2b). Subjects responded more quickly in the perceptual than in the semantic condition, $F(1, 15) = 130.1$, $p < .001$, and more quickly for repeated than initial presentation of words, $F(1, 15) = 8.90$, $p < .01$. There was a Task × Presentation interaction, $F(1, 15) = 12.0$, $p < .01$. There was no effect of cycle, and no other interaction was significant.

Repeated measures ANOVAs with factors of cycle (first vs. second) and presentation (initial vs. repeated) were performed separately for the semantic and perceptual repetition tasks. For the semantic repetition task, there was repetition priming: Subjects responded more quickly for repeated than for initial presentation, $F(1, 15) = 11.77$, $p < .01$, but they did not respond more quickly overall across blocks. For the perceptual repetition task, there was no repetition priming (no effect of presentation). Subjects responded quickly in this task from the outset, and may not have been able to show any further reduction in response latency.

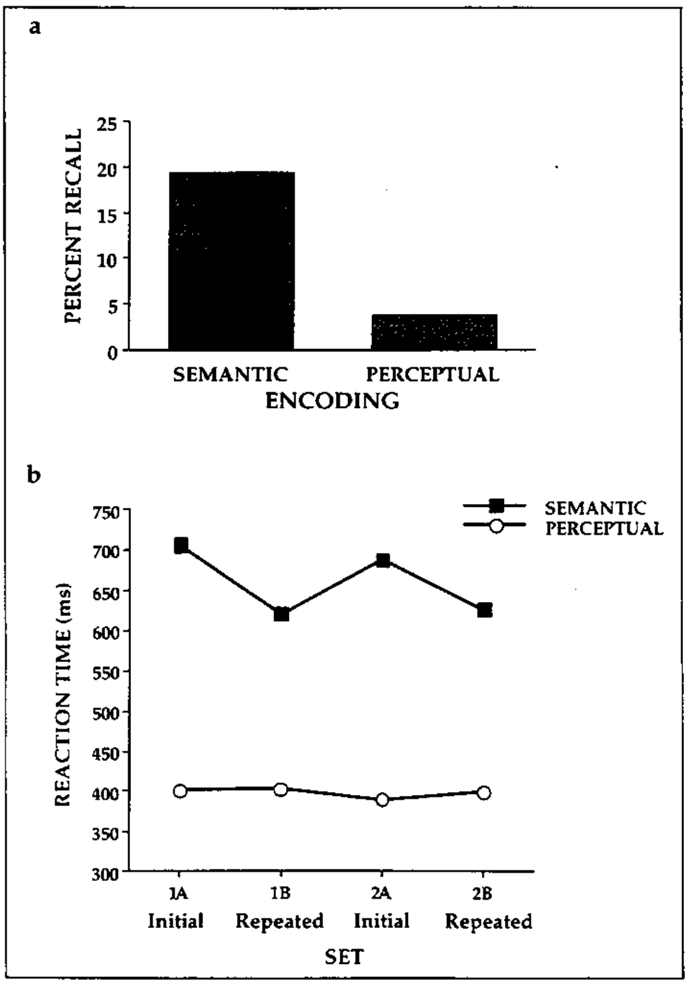


Fig. 2. Performance of subjects on tests of memory. (a) Mean percentages of words recalled after semantic encoding (deciding if a word was abstract or concrete) or perceptual encoding (deciding if a word appeared in upper- or lowercase). (b) Mean median reaction times for performing semantic decisions (closed squares) and perceptual decisions (open circles) for words upon initial (Sets 1A and 2A) and repeated (Sets 1B and 2B) presentations in the repetition task.

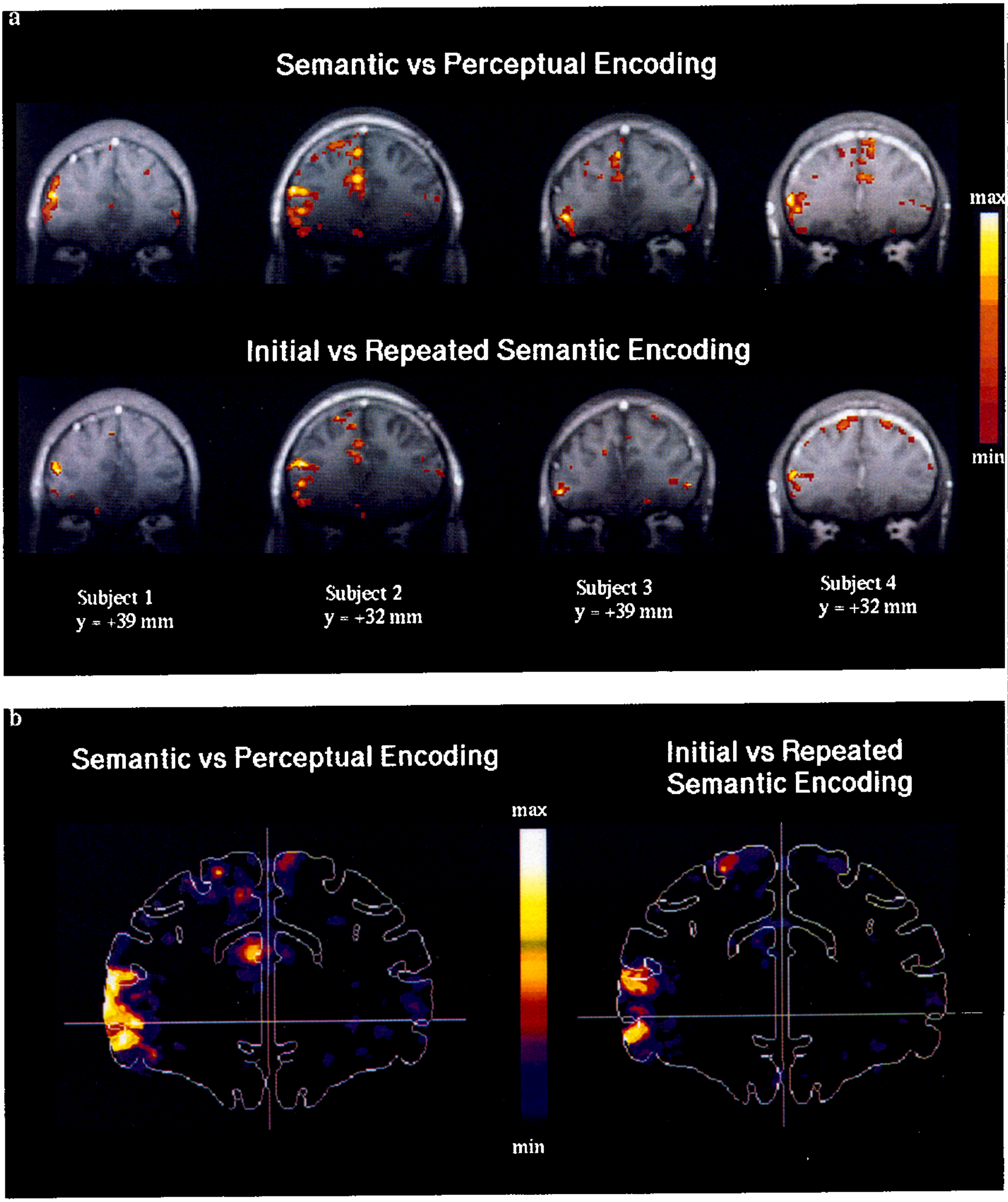
Imaging Results

Analysis of individual images and construction of composite images were performed as described in Demb et al. (1995) and Desmond et al. (1995). For the encoding task, activation was compared between semantic and perceptual encoding conditions. For the semantic repetition task, activation was compared between the first and second presentation of words for semantic judgments. Essentially, pixels for which activity over time correlated above a statistical threshold with the alternating behavioral conditions were identified and overlaid on the corresponding structural scans (Fig. 3a). All significant pixels from both sections from all participants were superimposed in a common space to yield composite images (Fig. 3b).

During the encoding task, each subject showed more activation in left inferior prefrontal cortex for semantic than for perceptual encoding of words (Fig. 3). Specifically, increased activation occurred in the left inferior frontal gyrus, in a region corresponding to Brodmann areas 45, 46, and 47. To a lesser extent, there was also more activation for semantic than for perceptual encoding in left cingulate cortex (area 32) and in a superior left-frontal region (area 8). During the semantic repetition task, each subject showed more activation for initial than for repeated semantic encoding of words in the same left inferior prefrontal region and, again to a lesser extent, the same superior frontal region (Fig. 3). There were no systematic changes in activation in corresponding right prefrontal cortex or any other region. Also, no region in these sections showed greater activation for perceptual than for semantic encoding, or for repeated than initial semantic encoding.

To measure similarity in activation patterns between encod-

Fig. 3. (opposite) Functional activation maps. The left side of each image corresponds to the left side of the brain. In (a), each vertical pair of images comes from one section (indicated at bottom) of a subject. All points shown passed the statistical threshold for significance. Functional maps are normalized and scaled with the lowest significant correlation magnitudes appearing in dark red and the highest in bright yellow and white. Greater activation is evident in subjects during semantic versus perceptual encoding (upper row) and during initial versus repeated semantic encoding (lower row). The composite images in (b) are averaged across all sections from all subjects and displayed on a coronal section ($y = +35$ mm) from the stereotaxic atlas of Talairach and Tournoux (1988). The color scale indicates the amount of overlap in individual functional maps, with white indicating maximum overlap. The image on the left shows increased activation during semantic versus perceptual encoding in left inferior prefrontal cortex and left cingulate cortex. The image on the right shows increased activation during initial versus repeated semantic encoding of words in left inferior prefrontal cortex.


a
Semantic vs Perceptual Encoding
Initial vs Repeated Semantic Encoding
max
min
Subject 1
y = +39 mm
Subject 2
y = +32 mm
Subject 3
y = +39 mm
Subject 4
y = +32 mm
b
Semantic vs Perceptual Encoding
Initial vs Repeated
Semantic Encoding
max
min

ing and semantic repetition tasks, correlations between functional activation maps were computed for each individual by gridding the maps with 1.1 cm × 1.1 cm boxes. Only pixels that overlapped brain tissue were considered; a total of approximately 70 boxes were analyzed per subject. For each box, the total number of significant pixels contained in the box for each of the two experimental tasks was obtained, and a Pearson product-moment correlation was computed on these pairs of numbers. On a subject-by-subject basis, there was a mean positive correlation of .70 (range: .58–.83) between which boxes of pixels were activated significantly in the two tasks.

DISCUSSION

Semantic Encoding

Subjects recalled six times more words after semantic than after perceptual encoding, and in each individual, the fMRI study found greater activation of left inferior prefrontal cortex for semantic than for perceptual encoding. The input (visual words), output (two-choice response), and stimuli (across participants) were constant between encoding conditions. Therefore, the observed activation reflected differences in semantic versus perceptual encoding. PET studies comparing tasks have found increased activation in the same region for other conditions that enhance semantic encoding; for example, activation of the inferior prefrontal cortex was found to be greater for making living/nonliving than for making letter judgments (Kapur et al., 1994), for generating than for reading words (Petersen, Fox, Posner, Mintun, & Raichle, 1988), and for studying words while performing an easy rather than a difficult concurrent task (Shallice et al., 1994).

Using the same encoding task used in the present study, we have further characterized the nature of this left-prefrontal activation. It represents semantic processing rather than task difficulty (Demb et al., 1995), and it is intimately linked to language processes, because it is lateralized to the language-dominant hemisphere as validated by Wada testing (Desmond et al., 1995).

Semantic Repetition Priming

Participants exhibited repetition priming by making semantic judgments more quickly for repeated words than for new words. The priming was word-specific (response times did not change significantly for new words across blocks) and task-specific (response times did not change significantly for repeated words in the perceptual encoding task). In each individual brain, the fMRI study found less activation in left prefrontal cortex for repeated than for initial semantic processing of words. The input (visual words), output (two-choice response), stimuli (same words presented twice), and semantic judgment were constant between conditions. Therefore, the decrease in left-frontal activation reflected the consequence of prior semantic encoding of each word. Using the same task, we have shown that the decrease in activation is specific to repeated semantic encoding, rather than to other aspects of processing repeated words (Demb et al., 1995). To our knowledge, this is one of the first visualizations of a change related to long-term memory in an individual's brain function (other recent reports include N.J. Cohen et al., 1994; Stern et al., 1994).

The frontal locus of reduced activation associated with semantic repetition priming concurs with a PET finding (Blaxton et al., in press), but differs from the occipital locus of reduced activation associated with visuo-perceptual repetition priming (Blaxton et al., in press; Buckner et al., 1995; Squire et al., 1992). The different loci of reduced activations are consistent with behavioral, neuropsychological, and neuroimaging dissociations between semantic (conceptual) and perceptual forms of repetition priming (Blaxton, 1989; Blaxton et al., in press; Fleischman et al., 1995; Gabrieli, Fleischman, Keane, Reminger, & Morrell, 1995; Keane, Gabrieli, Mapstone, Johnson, & Corkin, 1995). The left-frontal decrease differs also from right-frontal increases in activation associated with explicit retrieval (Buckner et al., 1995; Shallice et al., 1994; Squire et al., 1992; Tulving et al., 1994; but see Blaxton et al., in press), and thus provides further evidence for a brain-based distinction between explicit and implicit retrieval processes.

The present study found the same brain region increasing in activation during semantic encoding and decreasing in activation during semantic repetition priming. The quantitative fMRI co-localization of semantic encoding and semantic repetition priming activations on a brain-by-brain basis provides direct evidence that repetition priming in a given domain reflects experience-induced changes in the same neural network that subserves encoding or initial processing in that domain. This finding parallels a PET study that found reduced activation in the same left-prefrontal region as participants repeated generation of verbs corresponding to repeating nouns (Raichle et al., 1994). The present fMRI results complement and extend the PET study by showing that memory-based reductions in left-prefrontal activation can be seen after a single practice trial, and that the reduction does not depend on the nature of the output (a verbal response selection from many possible verbs or a two-choice manual response).

A Locus for Semantic Working Memory?

Goldman-Rakic (1987) proposed that prefrontal cortex mediates domain-specific working memory representations that guide action in the absence of external, perceptual cues. PET studies have visualized right-prefrontal activation associated with spatial working memory tasks (Jonides et al., 1993) and left-prefrontal activation, posterior to that in the present fMRI study, associated with phonological working memory tasks (Paulesu, Frith, & Frackowiak, 1993).

We postulate that left inferior prefrontal cortex mediates semantic working memory. In the present study, the action was the semantic decision about whether a word was abstract or concrete in meaning. A region in left inferior prefrontal cortex may access semantic information, stored in more posterior language cortex, that is needed to make the decision about whether a word is abstract or concrete. More semantic information is needed to decide whether a word is abstract or concrete than to decide if a word appears in upper- or lowercase. Consequently, more activation is seen for semantic than for perceptual encoding. Memory acquired in the initial semantic processing of a word enhances the efficiency with which semantic knowledge is accessed in the repeated semantic processing of a word. Consequently, less activation is seen for repeated than for initial semantic processing of a word. Thus, in this region, activation increases as demands on semantic working memory increase (semantic vs. perceptual encoding), and activation decreases as demands on semantic working memory decrease because of the acquisition and implicit retrieval of word-specific memories (repeated vs. initial semantic judgment). By this view, the process visualized in left inferior prefrontal cortex may be thought of as a search for meaning.

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