Lesion studies in monkeys have provided evidence that lateral prefrontal cortex is necessary for working memory, the cognitive processes involved in the temporary maintenance and manipulation of information. Monkey electrophysiological studies, however, have also observed prefrontal neuronal activity associated with cognitive processes that are nonmnemonic. We tested the hypothesis that the same regions of human prefrontal cortex that demonstrate activity during working memory tasks would also demonstrate activity during tasks without working memory demands. During echoplanar fMRI imaging, subjects performed a three-condition experiment (working memory task, nonworking memory task, rest). In the working memory task, subjects observed serially presented stimuli and determined if each stimulus was the same as that presented two stimuli back. The nonworking memory task in Experiment 1 required subjects to identify a single predetermined stimulus; in Experiment 2, subjects were required to make a button press to every stimulus. In all subjects in both experiments, the working memory task exhibited greater prefrontal cortical activity compared to either nonworking memory task. In these same prefrontal regions, greater activation was also observed during both nonworking memory tasks compared to rest. We conclude that human lateral prefrontal cortex supports processes in addition to working memory. Thus, reverse inference of the form "if prefrontal cortex is active, working memory is engaged" is not supported.

Key Words: functional MRI; working memory; prefrontal cortex; attention.

INTRODUCTION

Single-unit recordings in monkeys have revealed neurons in lateral prefrontal cortex (PFC) that increase their firing during a delay between the presentation of information and its later use in behavior (Fuster and Alexander, 1971; Funahashi et al., 1989). These studies have been taken as evidence that lateral PFC represents a neural correlate of working memory, the cognitive processes governing the temporary maintenance and manipulation of information (Goldman-Rakic, 1987). The necessity of this region for working memory has been demonstrated in monkey studies that have shown that lesions of the lateral PFC impair performance on delayed-response tasks (Gross, 1963; Bauer and Fuster, 1976; Funahashi et al., 1993). Similar impairments have been demonstrated in humans following PFC damage (Pierrot-Deseilligny et al., 1991; Verin et al., 1993; Ptito et al., 1995). Finally, functional neuroimaging studies of normal humans have been interpreted as demonstrating involvement of the PFC during working memory tasks (Jonides et al., 1993; Cohen et al., 1994; D'Esposito et al., 1995a).

Single unit recording studies in monkeys during delayed response tasks have also observed PFC neurons that are active during periods in addition to the delay period (i.e., after the cue has been presented and prior to the required motor response). For example, Funahashi et al. (1989) have identified PFC neurons that respond during any combination of cue, delay, and response periods. Although delay-specific neurons were the most common (28%), other types were identified frequently (e.g., 24% of neurons responded only to the motor response). Thus, the primary purpose of this study was to investigate the role of human lateral PFC in processes other than working memory. Such processes may include stimulus encoding, sustained attention to stimuli, preparation for a motor response, and the motor response itself.

Most human functional imaging studies of working memory using cognitive subtraction methodology have not emphasized the role of PFC in nonmnemonic cognitive processes and sometimes suggest that PFC is specific for working memory. Moreover, the interpretation of some functional imaging studies of other cognitive domains (i.e., language, visuoperception) has relied upon post hoc interpretations of observed PFC activation by their task as being due to the engagement of working memory processes (Cuenod et al., 1995; Cohen et al., 1996). Such an interpretation tacitly assumes that PFC is specific for working memory. The
demonstration that the same PFC region activated during tasks that engage working memory is also recruited during nonmemory processes, would dispute this assumption. In light of the results of electrophysiological studies cited above, we predicted that this pattern of PFC activation would be observed.

Functional neuroimaging studies of working memory are typically conducted by comparing the signal during a task proposed to engage working memory to a “control” task that does not engage this construct. As there is general agreement that, by definition, these control tasks do not require working memory, the control task compared to a resting baseline would be a logical candidate for testing our hypothesis that PFC regions that demonstrate activation associated with working memory also display activation in association with non-working memory processes. This hypothesis was tested for both verbal and spatial domains.

**METHODS**

**Subjects**

We studied eight right handed subjects (five women, three men, ages 20–29 years) who were recruited from the undergraduate and medical campuses of the University of Pennsylvania. Subjects were excluded if they had any medical, neurological, or psychiatric illness or if they were taking any prescription medications. Six subjects performed Experiment 1 and two additional subjects performed Experiment 2.

**Experimental Paradigms**

In each subject, two experiments were performed, each consisting of three conditions: a working memory task, a nonworking memory task, and rest. The working memory tasks in both experiments utilized a two-back design (Kirchner, 1958; Gevins and Cutillo, 1993) which has previously been demonstrated to evoke PFC activation (e.g., Cohen et al., 1994; D'Esposito et al., 1998a). Both verbal and spatial versions of the tasks were administered to each subject. Since verbal and spatial working memory have been proposed to be distinct systems (Baddeley, 1986; Goldman-Rakic, 1987), and a previous imaging study using verbal and spatial n-back tasks found hemispheric differences in frontal activation (Smith et al., 1996), both tasks were included in this study to increase the yield of activated PFC regions that could be used for hypothesis testing.

**Experiment 1**

In the verbal condition (Fig. 1), stimuli were all the letters of the alphabet, presented in upper case. During

![FIG. 1. The stimuli used in the verbal and spatial working memory tasks and nonworking memory tasks are shown. Correct stimuli are shaded.](image-url)
the working memory task, subjects were instructed to determine whether each presented letter was the same as that presented two stimuli previously. In the corresponding nonworking memory task, subjects were instructed to identify an occurrence of the letter “X.”

In the spatial condition (Fig. 1), a square was presented in one of 12 different locations around an imaginary circle centered on a fixation cross. During the working memory task, subjects were instructed to determine whether each square being presented was in the same position as the square presented two stimuli previously. In the corresponding nonworking memory task, subjects were instructed to identify the occurrence of a stimulus in the 12 o’clock position. In both the verbal and spatial tasks, subjects were instructed to respond only to correct targets by pushing a keypad with their right thumb.

Experiment 2

In this experiment, the verbal and spatial working memory tasks from Experiment 1 were used. However, a different nonworking memory task was used. During this task, subjects were instructed to indicate with a button press every time a stimulus appeared. The rationale for including this additional nonworking memory task was to counter the following possible criticism. That is, in the nonworking memory condition in Experiment 1, a representation of the predetermined stimulus (“x”) must be maintained throughout the task and may engage working memory. In the nonworking memory task in this experiment, no trial-specific information must be maintained across the task. In the working memory task, subjects were instructed to respond to correct targets with their right thumb and incorrect targets with their left thumb, whereas in the nonworking memory task, subjects responded to all targets with both thumbs.

All subjects were scanned during three runs of both the verbal and spatial conditions. Each experimental run consisted of a 40-s block of the working memory task, a 40-s block of the nonworking memory task, and a 40-s block of the rest condition, repeated three times (yielding a total run duration of 6 min). Three subjects in Experiment 1 and the 2 subjects in Experiment 2 performed a version in which the tasks were presented in a fixed order (working memory task, nonworking memory task, rest). The other three subjects in Experiment 1 performed a version of the task during which the three conditions were presented in pseudorandom order. This allowed us to rule out the possibility that any results were due to an order effect. In each nonrest task, the ratio of targets to distractors was approximately 1/7 and stimuli were presented one per second. The visual stimuli were generated by a Macintosh Powerbook computer and back-projected via a LCD panel and an overhead projector onto a screen that subjects viewed through a mirror mounted at the top of the MRI head coil. In all tasks, stimuli were white and presented on a black background.

MRI Technique

Imaging was carried out on a 1.5 T SIGNA scanner (G.E. Medical Systems) equipped with a fast gradient system for echo-planar imaging. A standard radio frequency (RF) head coil was used with foam padding to comfortably restrict head motion. High-resolution sagittal and axial T1-weighted images were obtained in every subject. In each activation run, 180 gradient echo, echoplanar images sensitive to BOLD contrast (Kwong et al., 1992; Ogawa et al., 1992), were obtained in the axial plane at each of 16 contiguous, 5-mm slices (TR = 2000ms, TE = 50ms) at a resolution of 64 × 64 pixels in a 24-cm field of view (in-plane resolution was 3.75 × 3.75 mm). Twenty seconds of “dummy” gradient and RF pulses preceded the actual data acquisition to approach tissue state steady state magnetization.

Data Analysis

Off-line data processing was performed on a SUN Sparc workstation using software written in Interactive Data Language (Research Systems, Boulder, CO). A slice-wise motion compensation method was used to remove spatially coherent signal changes by applying a partial correlation method to each slice in time. The details of this approach have been described elsewhere, as well as our observation that this technique reduces voxel variance to a greater degree than rigid-body realignment alone (Zarahn et al., 1997a).

Analyses were performed using statistical parametric mapping (SPM (Friston, 1994/1995)). Each subject's raw data were smoothed spatially by convolution with a three-dimensional, three-voxel (11.25 mm) FWHM Gaussian kernel. Voxel-wise analysis was performed using a general linear model for serially autocorrelated observations (Worsley and Friston, 1995). Included within the model was an empirical estimate of intrinsic temporal autocorrelation (Aguirre et al., 1997; Zarahn et al., 1997a), global signal change covariates, and sine and cosine regressors for frequencies below that of the task. These components have been demonstrated empirically to hold the map-wise false positive rate at or below tabular values (Aguirre et al., 1997). Data were smoothed temporally with an empirically derived estimate of the hemodynamic response (Zarahn et al., 1997a).

In each subject, the results from the first of three runs were used to generate regions of interest (ROI) within PFC to be tested on the data from the second and third runs. This design allowed us to narrow our hypothesis testing on restricted regions within the PFC on a second independent dataset. Each statistical map
from the first experimental run (for the working memory vs nonworking memory task comparison) was thresholded at the minimum t value that revealed a distinct cluster of voxels within prefrontal cortex (t value range 2.5–4.0). Note that the threshold applied to the data from the first run will have no impact upon type I error (i.e., the false positive rate) for this study, as the hypotheses were tested in these regions. In fact, low thresholds chosen for the first run induce a bias toward type II error when tested in subsequent runs.

Next, using the time series from the second and third runs, t values were calculated for the working memory vs nonworking memory and the nonworking memory vs rest comparisons within each ROI. Since the time series were spatially averaged, each ROI was collapsed to a single voxel and a threshold of $t = 1.65$ ($\alpha = 0.05$) was used as the significance threshold in each region (for a one-tailed comparison). Local maxima within each of these regions of interest were identified and their Talairach coordinates noted. For display purposes, these thresholded maps, and the T1 anatomical images were transformed to standard Talairach space by a 12-parameter affine transformation (Friston et al., 1995), with nonlinear deformations (Ashburner and Friston, 1996).

RESULTS

Behavioral Performance

Across all subjects and experimental runs, the mean accuracy ($\pm$ standard deviation) of performance for the working memory task for the verbal condition was $90 \pm 9\% \ (d' = 3.63)$ and for the spatial condition was $95 \pm 9\% \ (d' = 5.13)$. The mean reaction times for the verbal condition was $603 \text{ ms} \ (\pm 134)$ and for the spatial condition was $579 \text{ ms} \ (\pm 138)$. In Experiment 1, the mean accuracy of performance on the nonworking memory task was $99 \pm 5\% \ (d' = 5.08)$ and $100 \pm 0\% \ (d' = 6.18)$ for the verbal and spatial conditions, respectively. The mean reaction times for the nonworking memory task were $531 \text{ ms} \ (\pm 63)$ and $469 \text{ ms} \ (\pm 70)$ for the verbal and spatial conditions, respectively. In Experiment 2, the mean reaction times for the nonworking memory task were $323 \text{ ms} \ (\pm 99)$ and $342 \text{ ms} \ (\pm 46)$ for the verbal and spatial conditions, respectively.

Experiment 1

Verbal Working Memory

In the first run (i.e., ROI generation run) of the working memory task, unilateral right PFC activation was identified in three subjects, unilateral left PFC activation in one subject and bilateral PFC activation in two subjects. These PFC ROIs are displayed in Fig. 2 and the local maxima for each of these regions are presented in Table 1. In four subjects activation was observed within middle frontal gyrus (Brodmann's areas 9 or 46) and in two subjects activation was within inferior frontal gyrus (areas 44/45).

Using the PFC ROI identified in the first experimental run, the concatenated data from the remaining two runs were used to test the hypothesis. In each ROI, statistical tests between the working memory vs nonworking memory task and the nonworking memory task vs rest were performed. As expected all six subjects replicated significant activation in the working memory vs nonworking memory task comparison within the ROIs (Fig. 3). The nonworking memory task vs rest comparison also demonstrated significant PFC activity in all six subjects.

Spatial Working Memory

In the first run (i.e., ROI generation run) of the working memory task, unilateral right PFC activation was identified in three subjects, unilateral left PFC activation in two subjects, and bilateral PFC activation in one subject. These PFC regions are displayed in Fig. 2 and the local maxima are presented in Table 1. In five subjects activation was observed within middle frontal gyrus (areas 8, 9, 46) and in one subject activation was within inferior frontal gyrus (areas 44/45).

Using the PFC ROIs identified in first experimental run, the concatenated data from the remaining two runs were used to test the hypothesis. Again, as expected all six subjects replicated significant PFC activity in the working memory vs nonworking memory task comparison within the ROIs (Fig. 3). The nonworking memory task vs rest comparison also demonstrated significant PFC activity in all six subjects.

Experiment 2

In the first run of both the verbal and the spatial conditions (i.e., ROI generation run), bilateral PFC activation, within middle frontal gyrus (areas 9/46) was identified in both subjects (RK and DB) (Fig. 2; Table 1). Using these PFC ROIs to probe the remaining data, during both the verbal and the spatial conditions, both subjects exhibited significant PFC activity in the working memory vs nonworking memory task comparison, as well as in the nonworking memory task vs rest comparison (Fig. 3).

DISCUSSION

In this study, voxels within PFC were identified in all subjects where significantly greater activity was present during the working memory task, whether spatial or nonspatial, as compared to the corresponding nonworking memory task. This finding is consistent with many other functional neuroimaging studies of work-
FIG. 2. SPM $t$ of the working memory task vs non-working memory task comparisons, for each subject, for both the verbal and spatial conditions in the hypothesis generating run. The regions presented in this figure were used to probe the data from the remaining experimental runs. Coordinates for the local maxima of these regions of interest are presented in Table 1. Three axial slices ($z = +19, +22, +25$ mm) are presented for each subject. Subject's initials are presented on the left side of the figure.
ing memory that have used the n-back paradigm (Cohen et al., 1994; Awh et al., 1996; Schumacher et al., 1996; Smith et al., 1996; D’Esposito et al., 1998a) and thus further supports the view that lateral PFC supports maintenance and manipulation of information across short periods of time. However, an additional finding, which confirmed the principal hypothesis of this study, was that subjects also demonstrated significantly greater activity in lateral PFC during the nonworking memory task, as compared to a resting baseline. A critical feature of the design of this study was that also require instructions (Fuster, 1995) and are not impaired on nondelay tasks which also require instructions (Funahashi et al., 1993). Second, by cognitive subtraction logic, remembering the instructions is present in all tasks being compared and this would not differentially activate regions. In Experiment 2, a different nonworking memory task from Experiment 1 was used: this task also activated PFC, and plausibly should not qualify as requiring working memory processes even if the more inclusive definition of working memory is adopted. In this task, subjects were asked to make a button press to every stimulus that was presented. Thus, only a representation of the instructions had to be maintained, but no representation of any single target stimulus.

In summary, our results provide strong evidence that lateral PFC is active in humans during nonworking memory processes which is the same region that is active during working memory. As mentioned in the introduction, the nonworking memory condition could require numerable distinct processes such as stimulus encoding, sustained attention to stimuli, preparation for a motor response, or the motor response itself. This study could not distinguish among these possibilities. However, these results are consistent with models which posit that memory is a property of neural networks which also mediate perceptuo-motor processes (Fuster, 1995). Thus, the findings of this fMRI study were predicted based on monkey electrophysiological studies which have investigated extensively the response characteristics of single neurons in lateral PFC. For example, Fuster and colleagues (Rosenkilde et al., 1981; Fuster et al., 1982) have recorded during delayed matching-to-sample (DMS) and delayed response (DR) tasks during three major task components: (1) the presentation of information to be remembered, (2) the delay period, and (3) the presentation of a cue which prompts a response contingent upon the stored informa-

<table>
<thead>
<tr>
<th>Subject</th>
<th>Task</th>
<th>Hemisphere (Brodman’s area)</th>
<th>x</th>
<th>y</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA</td>
<td>Verbal</td>
<td>Left (9)</td>
<td>-30</td>
<td>32</td>
<td>30</td>
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<tr>
<td></td>
<td></td>
<td>Right (46)</td>
<td>38</td>
<td>44</td>
<td>18</td>
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<tr>
<td>CA</td>
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<td>Left (46)</td>
<td>-39</td>
<td>12</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Right (44/45)</td>
<td>38</td>
<td>47</td>
<td>0</td>
</tr>
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<td>KH</td>
<td>Verbal</td>
<td>Left (45/46)</td>
<td>37</td>
<td>26</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Right (46)</td>
<td>37</td>
<td>34</td>
<td>21</td>
</tr>
<tr>
<td>AM</td>
<td>Verbal</td>
<td>Left (9/46)</td>
<td>-30</td>
<td>36</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>-31</td>
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<td>40</td>
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<td>-39</td>
<td>9</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Right (46)</td>
<td>33</td>
<td>38</td>
<td>20</td>
</tr>
<tr>
<td>HT</td>
<td>Verbal</td>
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<td>-25</td>
<td>46</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Spatial (9)</td>
<td>35</td>
<td>50</td>
<td>20</td>
</tr>
<tr>
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<td>Verbal</td>
<td>Left (9/46)</td>
<td>-25</td>
<td>29</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Right (9)</td>
<td>39</td>
<td>46</td>
<td>37</td>
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<tr>
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<td>Left (46)</td>
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<td>32</td>
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<td></td>
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<td>33</td>
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<td>DB</td>
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<td>-35</td>
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<td>15</td>
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</table>
tion. In addition to finding cells that reacted during the delay period (i.e., memory cells), they described cells reacting to the presentation of the information to be remembered (i.e., red or green light in the DMS task; left or right white light in the DR task) and the stimuli that prompted a response. These cells were found throughout dorsal and ventral regions of lateral PFC.

Goldman-Rakic and colleagues (Funahashi et al., 1990, 1989) have further characterized the response properties of single neurons within lateral PFC during working memory tasks. In an oculomotor delayed response paradigm, eye movements were controlled for by only analyzing trials during which the monkey remained fixated. In these studies, neurons were identified that responded selectively to the all three components of the oculomotor delayed response task (i.e., cue, delay, and response) as well as any combination of these components. Recording was also performed during a visual probe task during which monkeys were trained to maintain fixation during the presentation of peripheral visual stimuli. Receptive fields found during presentation of visual stimuli in both the delayed response and the visual probe tasks were highly congruent.

There are also human studies in which lateral PFC activity has been observed during nonworking memory processes, although not concomitant with activation observed in a working memory task. For example, our nonworking memory task in Experiment 1 is similar to a set of tasks used with PET (Pardo et al., 1991) and fMRI (Lewin et al., 1996) aimed at investigating the

![Bar graphs of the t values of the working memory vs nonworking memory task comparisons, working memory vs rest comparison, and the nonworking memory vs rest task comparisons in the PFC regions of interest derived from the first experimental run (Fig. 2). The dotted line represents the significance threshold (t = 1.65). Data from both the verbal and spatial conditions are presented.](image)

**FIG. 3.** Bar graphs of the t values of the working memory vs nonworking memory task comparisons, working memory vs rest comparison, and the nonworking memory vs rest task comparisons in the PFC regions of interest derived from the first experimental run (Fig. 2). The dotted line represents the significance threshold (t = 1.65). Data from both the verbal and spatial conditions are presented.
neural basis of sustained attention. Subjects performing a somatosensory vigilance task (i.e., detection of a brief pause in a volley of suprathreshold touches) or a visual vigilance task (i.e., detection of near-threshold luminance changes of a stimulus) activated right lateral PFC (Brodman’s areas 8, 9, 44, 46). Other PET studies have shown PFC activation during tasks that required sustained attention to auditory stimuli (Cohen et al., 1988; Tzourio et al., 1997). McCarthy and colleagues have studied similar detection tasks, along with working memory tasks (McCarthy et al., 1994, 1996). Lateral PFC was activated in a spatial working memory task, as well as during two control tasks (i.e., detection of a dot in an object or detection of a red object) relative to a resting baseline. The strength of activation during these detection tasks was noted to be approximately one-half (and sometimes approaching) the magnitude observed in the working memory task.

Sustained attention tasks have also been studied in patients with focal cortical lesions. Frontal-lobe lesion patients, compared to patient with posterior cortical lesions, had a greater false positive rate and lower sensitivity during detection of an occasional novel stimulus from a string of letters or line stimuli (Salmaso and Denes, 1982). Right frontal-lobe lesion patients, compared to left frontal-lobe, left temporal-lobe or right-lobe temporal lesion patients, were impaired at counting the number of successive stimuli (2–11 binasural digits or pulses delivered to the right or left index finger) (Wilkins et al., 1987). Frontal-lobe lesion patients, compared to temporal-lobe lesion patients or control subjects, made more errors at detecting occurrences of target characters embedded in rows of characters (Richer et al., 1993). Finally, frontal-lobe lesion patients, compared to control subjects, showed longer reaction times and missed more targets on a task that was identical to our nonworking memory task in Experiment 1 (Rueckert and Grafman, 1996). Combined these studies suggest that lateral PFC is necessary for other cognitive processes besides working memory.

Although not the primary focus of this study, another finding was that the location of activation within lateral PFC was variable from subject to subject. This was evident even when comparing activation only between the verbal or the spatial conditions across subjects. This type of intersubject variability has been explored previously by our lab (D’Esposito et al., 1995b) as well as others (Cohen et al., 1994). Many possible interpretations exist for this phenomenon but few have been explored in the neuroimaging literature. Two such possibilities include differing behavioral strategies among subjects on a complex task, such as the n-back task, or differences in structure-function relationships between subjects. The majority of subjects had activation within middle frontal gyrus (Brodman’s areas 9 or 46), but some subjects had activation that extended more dorsal (area 8) or ventral as far as inferior frontal gyrus (areas 44/45). However, this type of structure-function variability did not impact on our ability to test our hypotheses because our study utilized a within subject design. In fact, the reliability of our method is demonstrated by our ability to locate a specific region of activation in one experimental run, and demonstrate that this same region also had activation in the same task on an independent set of subsequent experimental runs.

We conclude that the function of human lateral PFC is not specific for working memory. An important area for further research will be to define more narrowly the specific component processes that engage PFC. This goal could not be accomplished in the current study and is likely a major limitation of all functional neuroimaging studies that use block designs. Since the temporal resolution of fMRI is sufficient to allow discrimination of neural events on the order of seconds (Zarahn et al., 1997b), event-related fMRI experimental designs which exploit this resolution can be used to address these issues more directly (Zarahn et al., 1996; D’Esposito et al., 1998b).

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