RAPID COMMUNICATION

Neuroimaging a Single Thought: Dorsolateral PFC Activity Associated with Refreshing Just-Activated Information

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Neuroimaging studies of human working memory (WM) show conflicting results regarding whether dorsolateral prefrontal cortex (PFC) contributes to maintaining information in consciousness or is recruited primarily when information must be manipulated. Using functional magnetic resonance imaging (fMRI), we looked at a minimal maintenance process—thinking back to a single, just-seen stimulus (*refreshing*). We found greater activity in left dorsolateral PFC (BA9) when participants refreshed a word compared to reading a word once or a second time. Furthermore, recognition memory was subsequently more accurate and faster for items that had been *refreshed,* demonstrating that a single thought that maintains activation can have consequences for long-term memory. Our fMRI results call into question any class of models of the functional organization of PFC and WM that associates simple and/or maintenance processes only with ventrolateral PFC or that associates dorsolateral PFC only with more complex processes such as manipulation. © 2002 Elsevier Science

INTRODUCTION

Cognitive processes that maintain and manipulate information online—"working memory" (WM) processes (Baddeley, 1992)—are critical for all higher-order cognition. Neuroimaging studies consistently find activation of prefrontal cortex (PFC) in WM tasks, but there is disagreement about the functional organization of PFC. Some evidence associates ventrolateral PFC (VLPFC) with maintenance of information and dorsolateral PFC (DLPFC) with manipulation of information (D'Esposito *et al.*, 1998; Haxby *et al.*, 2000; Smith and Jonides, 1999). However, other evidence suggests that VLPFC is involved in manipulating information (D'Esposito *et al.*, 1999) and that DLPFC is involved in maintaining information (Cohen *et al.*, 1997). One reason for the controversy may be that the

WM tasks typically used are complex, involving multiple processes (recycling information, updating information, evaluating whether a test probe meets task criteria, etc.). As maintenance tasks become increasingly complex, they are likely to involve manipulation (e.g., chunking, Miller, 1956); and as manipulation tasks become increasingly complex, they are likely to require increased maintenance. Thus, using complex tasks to instantiate such general categories as "maintenance" and "manipulation" may not be a specific enough level of analysis to map the functional organization of PFC.

Here our goal was to isolate one component of more complex WM tasks. We investigated neural activity underlying an elementary, but critical, maintenance process—thinking briefly of a just-active representation (*refreshing)* (Johnson, 1992). Using functional magnetic resonance imaging (fMRI), we found greater activity in left DLPFC (BA9) when participants refreshed a word they had just previously read than when they read a word for the first time or read the same word again (Experiments 1 and 2). We also provide evidence to rule out alternative explanations (Experiments 2 and 3). Our findings show clear DLPFC activity associated with *refreshing* a single representation (a minimal act of maintenance) and demonstrate the feasibility of using fMRI to isolate individual component processes of reflection (Johnson and Hirst, 1993; Johnson and Reeder, 1997).

EXPERIMENT 1

Materials and Methods

Subjects. The Institutional Review Board at Princeton University approved Experiments 1–3. In all cases, participants were healthy, right-handed young adult volunteers from Princeton University who gave written informed consent. Experiment 1 had 12 participants (9 males, 3 females, mean age 20.25 years).
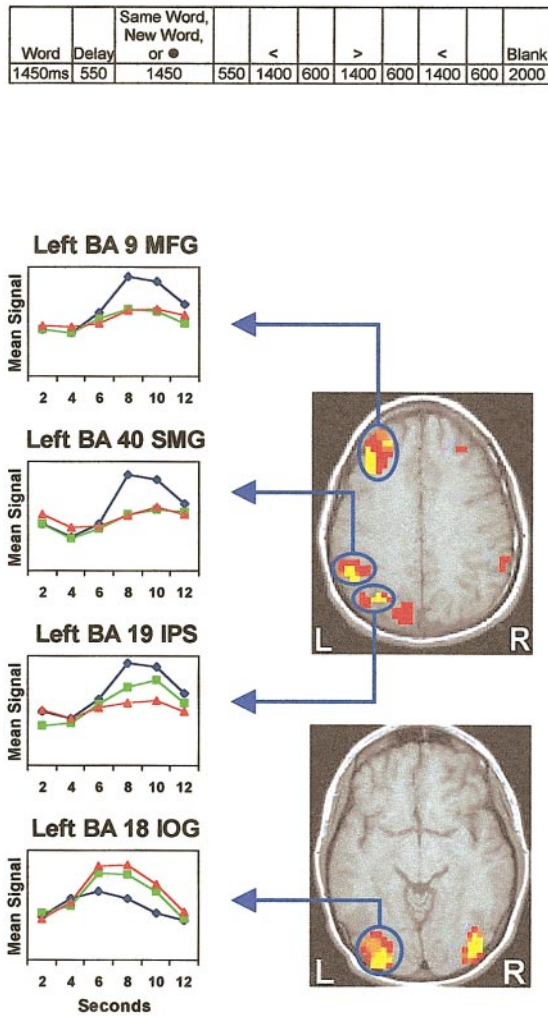
Word	Delay	Same Word, New Word, or ●	<	>	<	Blank
1450ms	550	1450	550	1400	600	1400	600	1400	600	2000

Left BA 9 MFG

Left BA 40 SMG

Left BA 19 IPS

Left BA 18 IOG

FIG. 1. Trial event sequence and timing for Experiment 1, together with regions of activation and their corresponding time courses. Regions shown were identified by the Condition by Time interaction; brighter colors represent areas within these regions that were identified in subsequent comparisons between conditions. For the time courses, the *x* axis represents time within a trial (seconds 2, 4, 6, 8, or 12, corresponding to volumes 1–6), the *y* axis represents mean signal intensity; blue diamonds, refresh; green squares, repeat; red triangles, read. The position of the peak reflects the lag in the hemodynamic response, typically 4–6 s.

Task design. During scanning, participants silently read individual words as they appeared on a screen. Some of the words were followed a half-second later by a repetition of the word (*repeat*), others were followed by a new word (*read*), and others were followed by a dot (●) that signaled participants to think of the word that had preceded the dot (*refresh*) (see Fig. 1). Stimuli consisted of 160 common one- to three-syllable words (e.g., *chime, proposal, toad*). Stimuli were projected onto a screen at the foot of the scanner, which participants viewed through a mirror. Each trial was 12 s long. Participants were told whenever they saw a word on the screen, to read it silently to themselves, and

when they saw a black dot, to think back to the just-previous word. They were told that when they saw an arrow, they should push a button with their left hand if the arrow pointed left and with their right hand if it pointed right. The arrows provided an 8-s task common to all conditions to allow the hemodynamic response associated with reading or refreshing words to return to baseline. This procedure is preferable to a "rest" period, which is likely to result in more variability among participants from uncontrolled mental activity.

Four runs of 30 trials each (10 per condition) were presented. In each run, Read, Repeat, and Refresh trials were pseudo-randomly intermixed, with a different order for each person. Across participants, each word occurred in each of the three conditions. About 10 min later, there was a surprise old/new recognition test consisting of 108 words from phase 1 (36 from each condition) and 108 new words intermixed in a pseudo-random order. Each test word was presented for 2 s with 1 s between words. Response and latency were recorded.

Imaging details. For all three experiments, a 1.5-T Signa scanner (GE Medical Systems) was used at Princeton Radiology Associates. T1-weighted anatomical images were acquired for each participant. For the functional scans, a gradient echo, spiral pulse sequence was used (Noll *et al.*, 1995), TR = 2000 ms, TE = 35 ms, flip angle = 65°, FOV 24. The 20 axial slices in each volume were aligned with the AC–PC line (resolution 3.75×3.75 mm in plane, 3.8 mm between planes). For all three experiments, each run began with 12 s of blank screen to allow tissue to reach steady-state magnetization, and each run was followed by a 2-min rest interval. The number of volumes for each person for each condition was 240 (Experiment 1), 252 (Experiment 2), and 240 (Experiment 3). After reconstruction, time series were shifted by sync interpolation to correct for the interleaved slice acquisition sequence. Data were motion-corrected using a 6-parameter automated algorithm (AIR; Woods *et al.,* 1992). A 12-parameter AIR algorithm was used to coregister participants' images to a common reference brain. For each experiment, data were mean-normalized across time and participants and spatially smoothed (3D, 8-mm FWHM gaussian kernel).

fMRI analyses. The data were analyzed using NIS software (Laboratory for Clinical Cognitive Neuroscience, University of Pittsburgh; and the Neuroscience of Cognitive Control Laboratory, Princeton University). In Experiment 1 we used an analysis of variance (ANOVA) with participant as a random factor. Run (1–4), Condition (Read, Repeat, Refresh), and Time within trial (volume 1–6) were fixed factors. Brain regions in the Condition by Time interaction were identified that had a minimum of six contiguous voxels, each significant at $P < 0.001$ (Forman *et al.,*

1995). To identify which of the conditions differed from each other, and the direction of the difference, the resulting regions were submitted to two-tailed planned contrasts (a minimum of six contiguous voxels, $P < 0.01$). These t maps were transformed to Talairach space, and areas of activation were localized using AFNI (Cox, 1996) and Talairach Daemon software (Lancaster *et al.,* 1998), as well as manually checked with the Talairach and Tournoux (1988) or Mai *et al.* (1997) atlases. A second ANOVA was conducted with the additional factor of accuracy (fast hits vs misses). Regions from the Condition by Time interaction with a minimum of six contiguous voxels at $P < 0.01$ were identified, and planned comparisons within each condition between fast hits and misses (minimum of six contiguous voxels at $P < 0.01$) were conducted. The coordinates reported in Table 1 represent local maxima in each region of activation that met these criteria.

Results and Discussion

Behavioral results. For the memory test, old words were intermixed with new words and participants were instructed to indicate whether or not they had encountered each word during phase 1. Linear trend analyses showed the expected advantage of refreshing (see Johnson *et al.,* 2002), both in the order of conditions for d' recognition memory scores ($F[1,11] = 4.47$, $P = 0.06$), Refresh (1.47) > Repeat (1.37) > Read (1.27), and response times on correct "old" items ($F[1,11] = 7.47$, $P < 0.025$), Refresh (850.11 ms) < Repeat (882.85 ms) < Read (905.84 ms).

fMRI results. Areas in which activity for the Refresh condition was greater than both the Read and the Repeat conditions included left DLPFC (middle frontal gyrus, BA9), left parietal cortex (supramarginal gyrus, BA40), and left intraparietal sulcus (IPS, BA19,7). These areas and their within-trial time courses are shown in Fig. 1 (coordinates for these and other areas of activation are shown in Table 1). For comparison, a time course is also shown for a visual region, inferior occipital gyrus (BA18), where activity in Refresh was less than Read and Repeat, as would be expected because the visual stimulus (a dot) was less complex in the Refresh condition.

To provide converging evidence for the impact of activation in DLPFC on subsequent long-term memory, we compared the Experiment 1 fMRI data for items that later were correctly and quickly (i.e., below the participant's mean correct response time) identified as "old" on the recognition test (fast hits) with that for items later incorrectly called "new" (misses) (see Wagner *et al.,* 1998). Within the area of left BA9 identified, there was greater activation in all conditions for items that would later be fast hits than for items that would later be misses. In addition, for Refresh, an area of left precuneus (BA19), and for Repeat, left inferior

parietal cortex (BA40) showed greater activation for fast hits than for misses (Table 1).

This experiment was designed to isolate a minimal maintenance process. However, because conditions were randomized in Experiment 1, participants had to switch tasks between trials. It is possible that task switching demands were greater for Refresh trials because refreshing was a less automatic task than reading words. Alternatively, the greater activation of BA9 in the refresh condition could reflect processing the dot cue or performing any mental operation in response to a symbolic cue. Experiments 2 and 3 were designed to rule out these alternative interpretations.

EXPERIMENT 2

Materials and Methods

In Experiment 2, to rule out the possible effect of task switching from intermixing the conditions, Refresh and Repeat trials were blocked by condition. Stimuli were words from the same pool used in Experiment 1. On each trial (see Fig. 2, Experiment 2) a column of three words was presented in the center of the screen for 1600 ms, followed by a 600-ms delay (blank screen). Participants (four males, four females, mean age 24.88 years) were told to silently read the three words. In the Refresh condition, at the offset of the delay, a dot appeared for 400 ms in one of the three locations previously occupied by a word, and participants were asked to think of the word that had been in that position. In the Repeat condition, one of the three words was re-presented in its same position for 400 ms, and participants simply read the word to themselves. Each 4-s trial ended with a 1400-ms blank screen. A scanning session included three runs, each with three 16-trial blocks of each condition (refresh and repeat in alternation). Each participant received a different order of blocks and, across participants, every word occurred in each condition.

fMRI analyses. Experiment 2 data were analyzed with a two-tailed t test comparing activation in the two conditions, Refresh vs Repeat. Regions were identified with a minimum of six contiguous voxels at $P < 0.01$.

Results and Discussion

As in Experiment 1, we found greater activation in Refresh than Repeat in left DLPFC (middle frontal gyrus, BA9), left parietal cortex (BA40), and left IPS (BA19,7). The left BA9 activation in Experiment 2, while smaller, overlapped the more posterior section of the region identified in Experiment 1. This finding suggests that the Refresh operation, not task switching, was the source of difference in activation in left BA9. The left parietal area was just anterior to the Experiment 1 left BA40 region, and the IPS region

TABLE 1

Regions of Activation for Experiments 1–3

Statistical contrast		Region	BA	x	y	z	t value
Experiment 1							
Refresh > Repeat and Read	L	GFM, GFS	9	−40	36	30	5.78*
Refresh > Repeat	R	GFM	8,9	31	36	44	3.79
Refresh > Repeat and Read	L	GSM	40	−50	−50	29	4.63*
Refresh > Repeat	R	GSM	40	61	−48	29	7.41
Refresh > Repeat and Read	L	GA, LPS (IPS)	19,7	−32	−70	35	3.79*
Repeat and Read > Refresh	L	GOI	18	−32	−95	−3	4.65*
Repeat > Refresh	R	GOI	18	32	−92	−6	5.51
Refresh condition							
Fast hits > Misses	L	GFM, GFS	9	−40	32	29	2.75
Fast hits > Misses	L	PCU	19	−17	−83	42	3.71
Misses > Fast hits	R	ACC	32	10	21	35	3.24
Repeat condition							
Fast hits > Misses	L	GFM, GFS	8/9	−35	24	46	2.65
Fast hits > Misses	L	GA, GSM (IPS)	40	−40	−47	40	3.05
Misses > Fast hits	B	ACC	32	±1	44	2	3.64*
Misses > Fast hits	R	GF	19	43	−72	−10	3.14
Read condition							
Fast hits > Misses	L	GFM, GFS	8/9	−29	36	41	2.81
Experiment 2							
Refresh > Repeat	L	GFM	9	−33	24	33	6.77
Refresh > Repeat	L	GSM	40	−46	−37	31	6.49
Refresh > Repeat	B	GSM	40	±37	−44	40	5.03*
Refresh > Repeat	B	GA, LPS (IPS)	19,7	±27	−66	36	3.78*
Refresh > Repeat	B	PCU	7,19	±12	−71	41	4.05*
Refresh > Repeat	L	GFI	44,45	−47	11	13	8.14
Refresh > Repeat	L	GFI	47	−33	19	−5	9.22
Refresh > Repeat	R	GFI	47	44	21	−5	7.46
Refresh > Repeat	R	GFS, GFD	10,11	4	58	−8	4.90
Refresh > Repeat	L	GTM	21	−58	−27	−1	8.59
Refresh > Repeat	R	GTM	21	67	−37	−5	9.04
Repeat > Refresh	R	GFM	9,8	27	32	35	4.97
Repeat > Refresh	R	ACC	33/24	3	19	18	4.64
Repeat > Refresh	L	PCU, PCC	31	−12	−48	34	4.15
Repeat > Refresh	R	CU	17	19	−95	2	6.54
Repeat > Refresh	R	GOI	18	36	−84	−1	7.31
Experiment 3							
Read > Dot > Up/Down	L	GFI	45/44	−50	19	5	3.15*,†
Up Down > Dot and Read	L	GSM	40	−40	−40	40	5.12*
Up Down > Read	L	PCU	7	−9	−70	37	5.66
Up Down > Read	B	GOI, GTI	19,37	±44	−69	−4	4.23*
Up Down > Dot	B	GF	19	±44	−69	−11	4.56*
Read > Dot	B	GOI, GF	18	±31	−90	−8	4.46*
Up Down > Dot	B	GOI	18	±37	−88	−7	4.92*

Note. BA, Brodmann area; B, bilateral; L, left; R, right; ACC, anterior cingulate; CU, cuneus; GA, angular gyrus; GFD, medial frontal gyrus; GF, fusiform gyrus; GFI, inferior frontal gyrus; GFM, middle frontal gyrus; GFS, superior frontal gyrus; GOI, inferior occipital gyrus; GOM, middle occipital gyrus; GSM, supramarginal gyrus; GTI, inferior temporal gyrus; GTM, middle temporal gyrus; IPS, intraparietal sulcus; LPS, superior parietal lobule; PCC, posterior cingulate; PCU, precuneus. Unless noted, $P < 0.01$. Asterisked t values represent the lower t value of two contrasts or bilateral areas. † $P < 0.05$.

overlapped the Experiment 1 region. The activation in IPS (Experiments 1 and 2) suggests that a cue to attend to an internal representation of a recent visual stimulus activates an area of parietal cortex similar to that activated by a cue to perceptually attend to a future visual stimulus in a cued location (Corbetta *et al.,* 2000). The larger number of bilateral (e.g., BA40, BA19,7) and new (e.g., BA44/45) brain areas recruited

during Refresh in Experiment 2 compared to Experiment 1 (see Table 1) may be related to the fact that one word was presented per trial in Experiment 1 whereas in Experiment 2, three items were presented per trial. Prior studies have found overall greater bilateral activity with increased task complexity (Nolde *et al.,* 1998; Raye *et al.,* 2000), and the activation in VLPFC, BA44/45, may reflect rehearsal associated
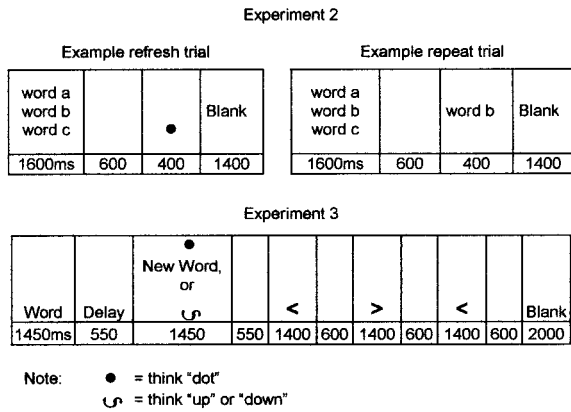
Experiment 2

Example refresh trial

word a word b word c		●	Blank
1600ms	600	400	1400

Example repeat trial

word a word b word c		word b	Blank
1600ms	600	400	1400

Experiment 3

Word	Delay	● New Word, or ↰		<		>		<		Blank
1450ms	550	1450	550	1400	600	1400	600	1400	600	2000

Note: ● = think "dot"
       ↰ = think "up" or "down"

FIG. 2. Trial event sequence and timing for Experiments 2 and 3.

with the increased number of items (Smith and Jonides, 1999).

EXPERIMENT 3

In Experiments 1 and 2, the Refresh condition was associated with seeing a dot and interpreting it as a cue to think of the preceding word. It could be argued that the activation associated with the Refresh condition was not specific to refreshing the previous stimulus, but was related to seeing a symbolic stimulus and carrying out the thought it cued. Experiment 3 tested this possibility and provided a second test of task switching.

Materials and Methods

Again participants (four males, three females, mean age 26.71 years) read words silently. The number of trials and within-trial event durations were identical to Experiment 1 (see Fig. 2, Experiment 3). On some trials a word was followed by a black dot which was a cue to think the word "dot," on some trials a word was followed by a novel abstract shape ("Up/Down" symbol) which was a cue to think "up" or "down," depending on its orientation, and on some trials a word was followed by a new word (Read condition). These conditions were intermixed as in Experiment 1. If the Refresh activation in Experiment 1 primarily reflected simply seeing a black dot, interpreting a cue and carrying out a thought, or task switching, we should see activation in Left BA9 in one or both of the "Dot" or "Up/Down" conditions compared to the Read condition.

fMRI analyses. The ANOVA factors were identical to Experiment 1, but the conditions were Read, Dot, and Up/Down. Regions in the Condition by Time interaction were identified that had a minimum of six contiguous voxels each significant at $P < 0.01$, followed by planned pairwise two-tailed contrasts (minimum of six contiguous voxels at $P < 0.01$).

Results and Discussion

Contrary to the alternative explanations noted above (e.g., task switching, interpreting and responding to a cue), in Experiment 3, there were no task-related differences in BA9 (Table 1). Only one area of PFC was identified by the Condition by Time interaction—left inferior frontal gyrus (BA44,45; $x = -50$, $y = 19$, $z = 5$); mean activations were ordered Read > Dot > Up/Down, $P < 0.05$. The results of Experiment 3 are consistent with the conclusion that the left middle frontal gyrus (BA9) activation found in Experiments 1 and 2 was not due to task switching, simply seeing a black dot, interpreting a symbolic cue, or just performing any intentional cognitive operation in response to a cue. In short, across the three experiments, increased left BA9 activity was found when participants thought back to (*refreshed*) the preceding word (Experiment 1), including when refresh trials were blocked (Experiment 2), but not for other thoughts (Experiment 3).

GENERAL DISCUSSION

If a representation that is activated by some external or internal stimulus is not the object of further reflective cognitive operations (Johnson, 1992; Johnson and Hirst, 1993), its activation declines quickly (Sperling, 1960). Our results support the idea that a simple maintenance process, *refreshing,* can be recruited to prolong (or increase) activation of representations, or resuscitate those with sufficient levels of activity; and this process is associated with activity in DLPFC (BA9). Furthermore, activation in this area is associated with better performance on a later recognition memory test.

Specifying the functional organization of PFC is currently one of the major goals of cognitive neuroscience (e.g., Goldman-Rakic, 1987; Duncan and Owen, 2000; Petrides, 2000). Our findings associate the reflective act of thinking of a single recently activated representation—a minimal, active, WM maintenance function—with DLPFC. This calls into question any model of PFC and WM that associates simple processes and/or maintenance processes only with VLPFC or that associates DLPFC only with complex processes such as manipulation. Furthermore, self-initiated maintenance processes comprise at least two reflective component processes (Johnson, 1992): *refreshing* produces a transient activation and, at least for verbal information, clearly involves DLPFC (the present studies); *rehearsing* bridges longer delays and, at least for verbal information, clearly involves VLPFC (e.g., Smith and Jonides, 1999).

Frequently used WM concepts such as manipulation, maintenance, selection, updating, and monitoring probably overlap in the component operations they include (Fletcher and Henson, 2001; Johnson *et al.,* 2002). In particular, *refreshing* a just-activated repre-

sentation is likely a component of many of these WM functions. We propose, for example, that in relatively simple "maintenance-only" WM tasks, refreshing sometimes may be initiated prior to or in conjunction with recruiting a subvocal rehearsal circuit (Smith and Jonides, 1999), particularly when multiple to-be-rehearsed stimuli are presented. In effect, refreshing may bridge the gap between perception and engaging a rehearsal circuit. More complex "maintenance-plus" or "manipulation" WM tasks such as ordering (e.g., alphabetizing) information in WM or the continuous *n*-back task may involve multiple refresh operations as participants rehearse, compare items, and update the rehearsal set. Thus, the DLPFC activity in, for example, ordering and 3-back tasks (Cohen *et al.,* 1997; Petrides *et al.,* 1993; Smith and Jonides, 1999) may in part result from refreshing information.

With respect to selection, investigators have attributed selection both to VLPFC (Fletcher *et al.,* 2000; Thompson-Schill *et al.,* 1997) and DLPFC (Rowe *et al.,* 2000). In a recent review, Fletcher and Henson (2001) suggest that whether VLPFC or DLPFC is involved may depend on whether selection is made from long-term memory (LTM) or WM, but they also note that an important source of the inconsistency between regions identified in neuroimaging studies may arise from the fact that cognitive processes are poorly defined (p. 874). Selection presumably foregrounds some representation(s) at the expense of others in the stream of consciousness (e.g., Broadbent, 1958). Selection could be accomplished by any one of a number of reflective (or perceptual) mechanisms that privilege the activation of some representations over others, for example, *refreshing* an item or *noting* a relationship between items (Johnson, 1992). In investigating the *refresh* process, our goal is to clearly define a component cognitive process and identify the brain regions associated with it.

Refreshing is associated with better long-term recognition memory indicating that it serves as one of many LTM encoding processes. Of course, there is much cognitive/behavioral evidence that encoding activities beyond a single refresh—rehearsal (Glenberg *et al.,* 1977), semantic judgments (Craik and Lockhart, 1972), organization (Bower, 1970; Mandler, 1967; Tulving, 1962), and comprehension (Bransford and Johnson, 1972)—improve episodic memory. These different encoding activities result in the activation of different amounts and combinations of information, with different consequences for LTM (e.g., a greater impact of rehearsal on recognition and of organization on recall). Complex encoding activities are presumably composed of combinations of component cognitive processes, including *refreshing* (e.g., Johnson and Hirst, 1993), and the brain regions activated during encoding should reflect the specific combinations of component processes recruited.

Because WM and encoding into long-term memory (and other cognitive functions such as problem solving) presumably draw on a common set of component processes (albeit in different mixtures), it is not surprising that the same brain regions tend to be reported in neuroimaging studies of WM and LTM encoding (see Cabeza and Nyberg, 2000; Duncan and Owen, 2000; Fletcher and Henson, 2001, for reviews). Finer distinctions within DLPFC and VLPFC, and in their interactions with other regions, may be possible as studies are more specifically directed at component processes that contribute to both WM and LTM.

Finally, although we have focused here on activity associated with *refreshing* in DLPFC, *refreshing* presumably is an interaction of DLPFC and other areas, for example, parietal cortex. In our studies, information about a word recently read may be temporarily represented in parietal cortex (e.g., Jonides *et al.,* 1998) and refreshing this representation may be initiated and/or sustained by activity of left DLPFC; or DLPFC might represent the refreshed information (Goldman-Rakic, 1995; Rao *et al.,* 1997)—these alternatives remain to be sorted out. Furthermore, exactly which other areas are involved in refreshing may depend on the type of information available. (We assume that the word information available to be refreshed in the present studies potentially includes visual, phonological, and some semantic features, e.g., Fowler *et al.,* 1981). Also, the area of DLPFC we have identified may participate in cognitive operations other than refreshing. It will take additional studies to characterize the refresh circuits associated with different types of information and to assess the specificity of component cognitive processes associated with the brain regions involved in these circuits.

ACKNOWLEDGMENTS

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