

Conscious recollection and the human hippocampal formation: Evidence from positron emission tomography

(memory/visual cortex/hippocampus/frontal lobes)

DANIEL L. SCHACTER*[†], NATHANIEL M. ALPERT[‡], CARY R. SAVAGE^{‡§}, SCOTT L. RAUCH^{‡§},
AND MARILYN S. ALBERT^{§¶}

*Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138; and Departments of [‡]Radiology, [§]Psychiatry, and [¶]Neurology, Massachusetts General Hospital and Harvard Medical School, Boston, MA 02114

Communicated by Larry R. Squire, University of California, San Diego, CA, September 11, 1995

ABSTRACT We used positron emission tomography (PET) to examine the role of the hippocampal formation in implicit and explicit memory. Human volunteers studied a list of familiar words, and then they either provided the first word that came to mind in response to three-letter cues (implicit memory) or tried to recall studied words in response to the same cues (explicit memory). There was no evidence of hippocampal activation in association with implicit memory. However, priming effects on the implicit memory test were associated with decreased activity in extrastriate visual cortex. On the explicit memory test, subjects recalled many target words in one condition and recalled few words in a second condition, despite trying to remember them. Comparisons between the two conditions showed that blood-flow increases in the hippocampal formation are specifically associated with the conscious recollection of studied words, whereas blood-flow increases in frontal regions are associated with efforts to retrieve target words. Our results help to clarify some puzzles concerning the role of the hippocampal formation in human memory.

Understanding the role of the hippocampal formation in learning and memory constitutes an enduring problem in cognitive neuroscience. Studies of brain-damaged amnesic patients implicate the hippocampal formation in explicit or conscious memory for past events. By contrast, the hippocampal formation is thought to be uninvolved in a nonconscious or implicit form of memory known as priming (1–4). Yet previous attempts to test these ideas directly by studying the normal human brain with positron emission tomography (PET) have yielded inconclusive results.

In an early PET study by Squire *et al.* (5), subjects studied a list of familiar words (e.g., GARNISH) and were then tested with three-letter word stems (e.g., GAR__). When subjects were instructed to provide a word from the study list on a cued recall test (explicit memory), there were significant blood flow increases in the vicinity of the right hippocampal formation compared with a baseline condition in which subjects responded to stems of nonstudied words. In a separate scan conducted in the same experimental session, subjects were instructed to complete stems of previously studied words with the first word that comes to mind (implicit memory), and a priming effect was observed: subjects preferentially completed the stems with words from the study list. Compared with the baseline condition, priming was associated with decreased blood flow in extrastriate occipital cortex and increased blood flow in the right hippocampus/parahippocampal gyrus. Because amnesic patients with hippocampal damage show intact priming effects (6–8), the former finding is consistent with the idea that such effects are mediated by brain systems outside the

hippocampal formation. But the latter finding is inconsistent with this idea.

However, performance in the priming condition may have been “contaminated” by some form of explicit memory (9): subjects may have intentionally or unintentionally remembered the primed words (5). If such contamination accounts for hippocampal activation in the priming condition, then it should be possible to abolish hippocampal activation by eliminating explicit retrieval. Yet several PET experiments have failed to find hippocampal activation even in association with explicit retrieval (10–13). Most critically, Buckner *et al.* (14) reported a follow-up of the Squire *et al.* experiment in which subjects were given three-letter word beginnings and attempted to remember words that had been studied previously either in the auditory modality or in a different typographic case. Buckner *et al.* observed no evidence of hippocampal activations in either condition (14). Because subjects were attempting to remember target items in both the different-modality and different-case conditions, the absence of blood flow changes in the hippocampal formation suggests that trying to retrieve a past event is not sufficient to activate the hippocampus. Hippocampal activation may be more closely related to some aspect of the actual recollection of an event. By contrast, Buckner *et al.* (14) found that areas in prefrontal cortex showed blood flow increases in both the different-case and different-modality conditions, thus raising the possibility that frontal activations, which have been observed frequently in PET studies of explicit retrieval (5, 10, 12–16), are related to the effort involved in trying to remember recently studied items (11).

To test these hypotheses, we performed a priming experiment in which we attempted to eliminate conscious recollection and an explicit memory experiment in which we attempted to separate out the effort to recall an event from the actual recollection of it.

METHODS

Experimental Procedure. In the priming experiment, subjects studied target words in a way that ensured that they would later have poor explicit memory for them (6). Specifically, subjects performed a shallow, nonsemantic study task that requires them to indicate the number of T-junctions in a word. After the subjects had studied 24 familiar words (20 target plus 4 nontested buffers), PET scans were carried out while subjects responded to three-letter word stems, with separate blocks of stems for studied words (priming) and nonstudied words (baseline). During each 1-min scan, subjects were instructed to respond with the first word that came to mind and to do their best to complete each stem. We refer to the nonscanned study task, the scanned priming condition, and the scanned baseline

condition as a "study-test unit." The volunteers were then given two additional study-test units, thus yielding a total of three scans for primed words and three scans for baseline words. Order of conditions and items assigned to conditions was counterbalanced across subjects.

For the explicit memory experiment, one condition was designed to yield high levels of explicit recall and the other was designed to yield low levels of explicit recall. We accomplished this by manipulating how subjects studied a series of target words. Forty-eight different words (40 targets plus 8 buffers) were shown for 5 sec each; no scanning was performed during this study phase. The High Recall condition consisted of 20 target words that were presented four times each, with presentations distributed randomly throughout the list; each time one of these words appeared, subjects made a semantic judgment (they counted the number of meanings associated with each word). We reasoned that on a later memory test, subjects would easily recollect many of these words. The Low Recall condition consisted of 20 words that were presented only once; subjects made a nonsemantic judgment about each word (the T-junction counting task used in our first experiment). We reasoned that on a later test, subjects would recall few of these words despite trying hard to do so.

Two separate 90-sec blocks of three-letter stems, separated by a 10-min rest or study period, were presented on a computer monitor. One block contained stems that could be completed with the High Recall words and the other contained stems that could be completed with the Low Recall words; subjects were instructed to try to remember a study-list word that fit each stem. If they could not recall a study-list target, they were told to guess. Subjects were allowed up to 5 sec to respond to each stem. Immediately after their response, the next stem appeared. After subjects completed the two test scans, two further study-test units were administered. Prior to the first study-test unit and after the third, subjects performed the baseline task used in the previous experiment, in which they completed stems of nonstudied words with the first word that came to mind. Order of conditions and items assigned to conditions was completely counterbalanced across subjects.

Subjects. Six healthy male and two healthy female volunteers (mean age = 19.6 yr) participated in the priming experiment; five healthy male and three healthy female volunteers (mean age = 20.5 yr) participated in the explicit memory experiment. All subjects were screened to rule out the presence of medical, psychiatric, or neurological disorders.

PET Scanning. A gantry held the computer monitor, tilted so that the screen was readily visible from within the PET camera. PET data were acquired while subjects inhaled oxygen-15-labeled carbon dioxide ($[^{15}\text{O}]\text{CO}_2$) for 1 min. Each scan proceeded as follows: (i) subjects were reminded of the instructions to lie still, breathe normally, and to perform either the stem completion or cued recall task; (ii) the PET camera was started at time zero, and continued acquiring data for 90 sec; (iii) the stem completion (or cued recall) task started at time zero, preceded by four buffer items, and continued until completion of the block of 24 trials (all subjects required >90 sec to finish the stem completion or cued recall tasks); (iv) the final 60 sec of PET camera data acquisition (i.e., time 30 to 90 sec) coincided with the 60-sec period of active tracer inhalation; (v) at the end of this period, PET data acquisition and radiolabeled gas flow were terminated; (vi) following a 10-min tracer-washout period, the next scan was performed, until the series of eight scans was completed.

The PET facilities and procedures were very similar to those previously described (e.g., refs. 17 and 18). A General Electric-Scanditronix (Uppsala) model PC4096 15-slice whole-body tomograph was used (19). An individually molded thermoplastic face mask (True Scan, Annapolis, MD) was used to minimize head motion. Transmission measurements were made by using an orbiting pin source.

All brain images were corrected for interscan movement, by realignment with respect to the first scan, prior to further image processing. An automated motion-correction algorithm was employed (after ref. 20). Motion-corrected PET brain images were then transformed to the standard Talairach coordinate system (21) as previously described (e.g., refs. 17 and 22). Blood flow images were normalized to 50 ml/min per 100 g and were rescaled and smoothed with a 20-mm Gaussian filter.

Once the transformations of the PET data were performed and the data were expressed in stereotaxic space, statistical parametric maps (SPMs) were created. Each SPM was inspected for regions of activation with Z scores ≥ 3.00 for unplanned comparisons ($P < 0.001$, uncorrected for multiple comparisons), and >2.58 ($P < 0.005$) for planned comparisons involving the hippocampal formation, prefrontal cortex, and extrastriate occipital cortex.

RESULTS

Analysis of behavioral data from the priming experiment revealed that a significantly larger percentage of stems was completed with study-list words in the priming condition than in the baseline condition [30% vs. 17%; $F(1, 7) = 41.81$, $P < 0.0001$]. The magnitude of priming is comparable to similar effects obtained in conditions where explicit memory has been effectively eliminated (23, 24), but it is much smaller than the priming effect reported in the PET study of Squire *et al.* (5), reflecting the explicit contamination that likely occurred in that experiment. Analysis of priming effects separately for each study-test unit revealed nearly identical levels of priming in the first, second, and third test blocks ($F < 1$), providing additional evidence that subjects did not engage in intentional retrieval strategies, which would have inflated priming in later test blocks.

To examine relevant changes in regional cerebral blood flow, data from the three study-test units were combined to yield a single baseline condition and a single priming condition. When we compared these two conditions, we found that priming was associated with significant blood flow decreases in bilateral extrastriate occipital cortex (Brodmann area 19; Table 1/Fig. 1). The decrease on the right was in approximately the same location as in the previous study, whereas the decrease on the left had a more superior focus. By contrast, there were no significant blood flow changes in the vicinity of the hippocampal formation (maximum Z score = 0.33 for available points z axis = -12 to $+4$). In addition to the predicted blood flow changes in the extrastriate regions, we also observed other significant ($Z > 3.0$) decreases and increases in association with priming that will be discussed in a separate report. Baseline minus priming [decreases]: right insular cortex (39, -26 , 0), right thalamus (7, -30 , 4), right putamen (16, 2, 8), right motor/premotor cortex (61, -8 , 28), and right parietal cortex (area 7; 30, -55 , 52). Priming minus baseline [increases]: left prefrontal cortex (area 47; -39 , 30, -8), left precuneus (area 7; -13 , -51 , 56). All findings are expressed in Talairach coordinates as x , y , z .

In the explicit memory experiment, behavioral data confirmed that subjects remembered many more words in the High Recall condition (79%) than in the Low Recall condition [35%; $F(1, 7) = 205.74$, $P < 0.0001$]. However, the percentage of words recalled did not differ significantly across the three test blocks ($F < 1$). To examine associated blood flow changes, we compared the High and Low Recall conditions directly to one another, collapsing across the three test blocks. The logic of the comparison holds that brain regions that are specifically associated with the conscious recollection of a word should show significant blood flow increases in the High Recall minus Low Recall comparison, whereas regions that are specifically associated with the effort involved in trying to retrieve a

Table 1. Primary regions of interest exhibiting significant change in blood flow associated with the priming and explicit memory conditions [all additional findings ($Z \geq 3.00$) listed in text]

Contrast	Region	Z score (max pixel value)*	Max pixel coordinates†
Priming contrasts			
Priming minus Baseline	Right area 19	-3.10	33, -74, 0
	Left area 19	-3.23	-33, -79, 24
Explicit memory contrasts			
Low Recall minus High Recall	Left prefrontal (area 10/46)	3.81	-31, 43, 8
	Left anterior cingulate	3.25	-7, 15, 32
	Right precuneus (area 19)	3.70	5, -72, 32
High Recall minus Low Recall	Right hippocampal	2.82	25, -34, 0
	High Recall minus Baseline		
High Recall minus Baseline	Left hippocampal	3.38	-19, -39, -4
	Right hippocampal	3.96	15, -37, 0
Low Recall minus Baseline	Right orbitofrontal (area 11)	3.25	5, 35, -12
	Right anterior cingulate	3.77	7, 34, 0
	Left prefrontal (area 10)	3.47	-35, 54, 8
	Right prefrontal (area 10)	3.12	30, 46, 8
	Right prefrontal (area 9)	4.04	12, 47, 28

*Values represent the maximum pixel value (Z score units) within the region of interest from the statistical parametric map.

†Coordinates in Talairach space (21), expressed as x, y, z ; $x > 0$ is right of the midsagittal plane, $y > 0$ is anterior to the anterior commissure, and $z > 0$ is superior to the anterior commissure–posterior commissure plane.

recently studied word should show significant blood flow increases in the Low Recall minus High Recall comparison. Consistent with our hypothesis that prefrontal regions are related to retrieval effort, the Low Recall minus High Recall comparison revealed a significant blood flow increase in the left dorsolateral prefrontal cortex (Brodmann areas 10 and 46; Table 1). Previous studies have implicated this region in generating words and semantic associations (25–28). It is likely that attempts to generate candidate word responses occurred more frequently in the Low Recall condition than in the High Recall condition. This comparison also revealed significant increases in the left anterior cingulate and the right precuneus, which have been implicated previously in attentional processes, such as target selection (29, 30), that should have been

more relevant to the Low Recall than the High Recall condition.

Consistent with our hypothesis that the hippocampus is involved in some aspect of conscious recollection, the High Recall minus Low Recall comparison yielded only a single significant increase, in the right hippocampal formation (Table 1). The locus of this activation is nearly identical to the locus of the activation reported in the same-case condition of the earlier stem-cued recall study (5, 14).

To examine further the consistency of our results, we compared the High Recall and Low Recall conditions, with the Baseline condition in which subjects completed stems of nonstudied words with the first word that came to mind (Table 1/ Fig. 1). The logic was similar to our reasoning in the previous

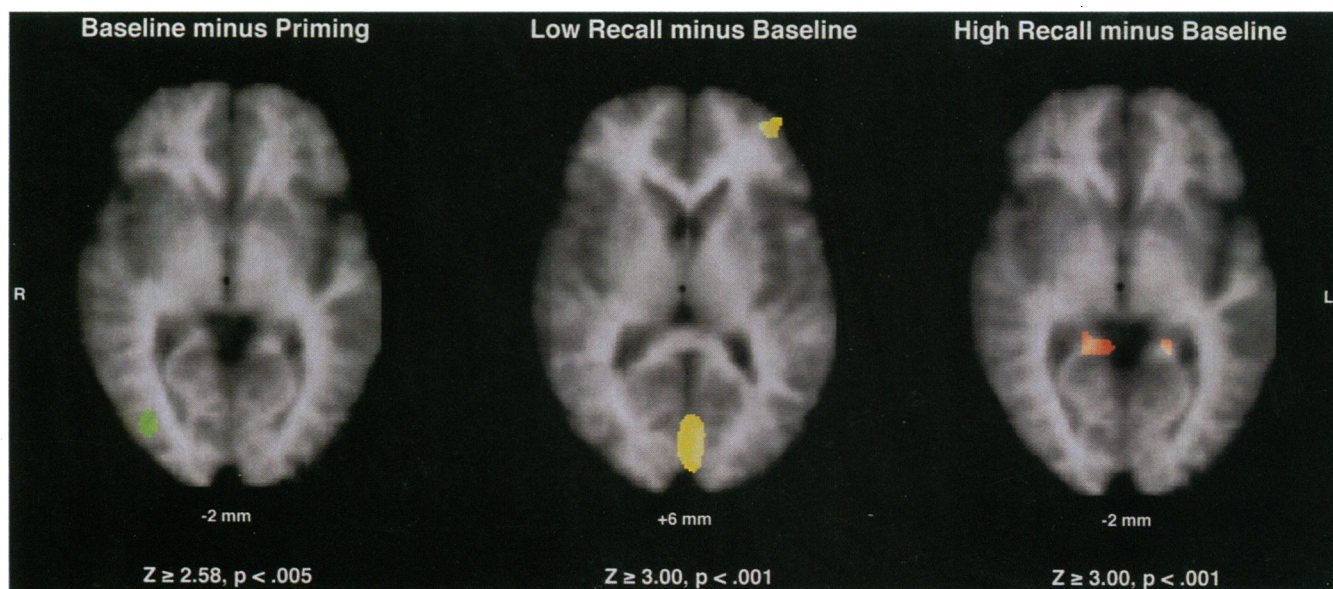


FIG. 1. PET statistical maps show territories of activation superimposed over averaged magnetic resonance images, transformed to Talairach space. Activations are thresholded to a Z score ≥ 2.58 for the Baseline minus Priming image and 3.00 for the Low Recall minus Baseline and High Recall minus Baseline images. Images are transverse sections, with z coordinates reflecting distance in millimeters from the anterior commissure–posterior commissure plane. The Baseline minus Priming image shows a region of significantly decreased blood flow (green) associated with priming in right visual association cortex (area 19). The Low Recall minus Baseline image shows regions of significantly increased blood flow (yellow) associated with high effort and low explicit recall (35% accuracy) in the left prefrontal cortex (area 10) and secondary visual cortex (area 18). The High Recall minus Baseline image shows regions of significantly increased blood flow (red) associated with high levels of explicit recall (79% accuracy) in bilateral hippocampal regions.

comparisons: brain regions associated with conscious recollection should show significant blood increases in the High Recall minus Baseline comparison, whereas regions associated with retrieval effort should show increases in the Low Recall minus Baseline comparison. In the High Recall minus Baseline comparison, there were extensive bilateral blood flow increases in the hippocampal formation, but no significant activations in the vicinity of the frontal lobes. The Low Recall minus Baseline comparison yielded extensive bilateral blood flow increases in the prefrontal cortex, especially in Brodmann area 10, but none in the vicinity of the hippocampal formation. Prefrontal cortex, particularly on the right side, has been activated in numerous previous PET studies of explicit retrieval (5, 10–14, 16), and the increases that we observed are close to previously reported ones. These results, together with the finding of significant left frontal activation in the Low Recall minus High Recall comparison, imply that the pervasive activation of frontal regions in previous memory studies reflects the effort involved in attempting to retrieve a past event. Both the High Recall and Low Recall minus Baseline comparisons yielded a number of other significant ($Z > 3.0$) blood flow increases that will be discussed in a separate report. High Recall minus Baseline: left cerebellum (–26, –68, –12), right cuneus (area 17; 3, –71, 8), bilateral supramarginal gyrus (area 40; –47, –28, 20; 47, –22, 20), and right visual association cortex (area 19; 26, –82, 24). Low Recall minus Baseline: left brain stem (–10, –13, –12), left cerebellum (–24, –50, –12), left secondary visual cortex (area 18, –3, –76, 4), right supramarginal gyrus (area 40; 41, –3, 16), left insular cortex (–34, –16, 16), and right cuneus (area 18; 7, –82, 24). All findings are expressed in Talairach coordinates as x, y, z .

DISCUSSION

Our major findings—that the hippocampal formation showed significant blood flow increases in the High Recall condition compared with the Low Recall and Baseline conditions, but no such increases during priming—provide new information about the role of the hippocampal formation in implicit and explicit memory. We first consider several puzzles that are clarified by our findings, and then we consider issues that remain to be clarified.

In view of our results, it now seems likely that previous findings of hippocampal activation during priming on the stem completion test were due to the influence of conscious recollection (5). Because frontal regions were not active during priming in the experiment of Squire *et al.*, this “contamination” from explicit memory probably reflects incidental or unintentional conscious recollection of words studied twice, under semantic encoding conditions, several minutes prior to the priming task. Our data support the idea that priming occurs independently of the hippocampal formation and depends instead on brain systems involved with the perceptual representation of words and objects (1–4).

Our data also help to clarify why the previous experiment by Buckner *et al.* (14) using the stem-cued recall test failed to detect significant blood flow increases in the vicinity of the hippocampus during explicit retrieval in both a different-case condition and a different modality condition. Our results suggest that hippocampal activation is more closely associated with the actual recollection of a past event than with the effort involved in attempting to remember the event. Simply instructing subjects to try to remember an event is probably not sufficient to produce significant blood flow increases in the hippocampal formation. These observations suggest that in the different-case and different-modality conditions of the experiments of Buckner *et al.*, the way in which subjects recollected studied items differed from the manner in which they recollected them in the same-case condition. Note that the absolute levels of recall in the different-case condition (73%) and

different-modality condition (62%) of Buckner *et al.* are closer to the levels of performance in our High Recall condition (79%) than in our Low Recall condition (35%). Although we must be cautious about between-experiment comparisons, these results suggest that the absolute level of recall may be less important in determining whether hippocampal activation is observed than the qualitative manner in which target events are remembered. Further research will be needed to specify exactly which features of recollection are most relevant to hippocampal activation.

This account is also consistent with the results of a study in which subjects studied and later tried to recognize structurally possible and structurally impossible novel visual objects (15). Right hippocampal activation was observed in association with explicit recognition of possible objects, but there was no corresponding activation in association with recognition of impossible objects. The possible objects were remembered more accurately than were the impossible objects. Our results thus suggest that differences in either the level or type of recollection associated with possible and impossible objects, respectively, account for the differential activation of the right hippocampal region during explicit recognition of the two types of objects.

Our hypotheses regarding conscious recollection and the hippocampus do not explain all relevant findings, however. We note first that factors other than conscious recollection, such as the novelty of a stimulus, can produce hippocampal activation (15, 31). The response of the hippocampal formation to a novel stimulus may be associated with its role in encoding and consolidation of new memories, whereas activations related to conscious recollection indicate a role for the hippocampus in memory retrieval.

However, in several studies that are quite similar to ours, where subjects presumably consciously recollected recently studied verbal materials, no hippocampal activations were observed (10–13). We make several observations. First, our study-test unit design used three separate replications for each subject of all critical comparisons to maximize power to detect hippocampal and other activations. Several of the experiments that failed to detect any evidence of hippocampal activation used only a single replication of critical comparisons (10–12), perhaps resulting in insufficient power to detect blood flow increases associated with hippocampal activity. Second, because the exact features of conscious recollection that are most relevant to hippocampal activation remain to be determined, it is possible that aspects of recollection that are most relevant to hippocampal activation played a more prominent role in our paradigm than in others. For instance, in one experiment that failed to observe hippocampal activation, some nonstudied items were presented with studied items during a single scan, possibly diluting the overall level of recollection (10). Other experiments used auditory presentation and test (12, 13, 16). Given the previously observed absence of hippocampal activation when modality and typographic case of stimuli differed at study and test (14), it is possible that reinstating visual information about a studied item, plus a high level of remembering, both contribute to blood flow increases in the hippocampal formation during explicit retrieval (see refs. 32 and 33 for data concerning visual information and recollective experience). Also, several experiments that failed to detect hippocampal activation used recognition tests (10, 11, 13, 16), whereas we used recall. Although the hippocampus was activated during recognition of novel visual objects in a study noted earlier (15), conscious recollection during recall and recognition may differ, such that it is more difficult to detect hippocampal blood flow increases in association with recognition than with recall. Additional studies will be needed to determine which of these factors, if any, are relevant to hippocampal activations in PET studies.

In contrast to inconsistent activation of the hippocampal formation in PET experiments, lesion studies with experimental animals and studies of human amnesic patients with hippocampal damage indicate a broader role for the hippocampus in explicit memory (for reviews, see refs. 3 and 34), which may reflect in part the hippocampal contribution to encoding and consolidation of memories alluded to earlier. By contrast, our results and the other PET evidence described in the preceding paragraph all bear on the role of the hippocampus in memory retrieval. The hippocampal formation may play a more limited role in retrieval than it does in encoding and consolidation. Alternatively, limitations on PET measurement techniques may account for some previous failures to detect hippocampal activity. While the exact role of the hippocampal formation in human memory retrieval remains to be specified, our study indicates that further exploration of specific aspects of conscious recollection is likely to be revealing.

Finally, our results also bear on the role of prefrontal cortex in explicit retrieval. Consistent with other recent PET data, they suggest that frontal regions play an important role in the retrieval effort associated with attempts to recall past events (11). The right anterior prefrontal cortex (area 10) in particular has been especially active during explicit retrieval (16). We observed activation of this area in the Low Recall minus Baseline comparison, but not in the Low Recall minus High Recall comparison, whereas left prefrontal cortex was active in both comparisons. One interpretation of this pattern is that right area 10 is especially relevant to shifting from semantic or lexical retrieval, which was required when subjects completed stems with the first word that came to mind in the baseline condition, to explicit or episodic retrieval, which was required when subjects tried to recall study list words. If so, it is curious that we did not see right frontal activity in the High Recall minus Baseline comparison, since the former involves episodic retrieval and the latter does not. This may be because words that have been studied four times in a semantic encoding condition, as in our High Recall condition, came to mind with little retrieval effort during the cued-recall test. An important problem for future research is to specify the conditions under which both right and left prefrontal regions play a greater or lesser role in efforts to retrieve recently experienced episodes.

We thank Kimberly Nelson for help with preparation of the manuscript and Brian Rafferty for experimental assistance. This research was supported by grants from the Charles A. Dana Foundation, Grant RO1 AG08441-06 from the National Institute on Aging, Grant T32 CA09362 from the National Cancer Institute, and Grants MH01215 and MH01230 from the National Institute of Mental Health.

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