NEUROBIOLOGY OF LEARNING AND MEMORY **70,** 284–303 (1998)
ARTICLE NO. NL983854

On the Relations among Priming, Conscious Recollection, and Intentional Retrieval: Evidence from Neuroimaging Research

Daniel L. Schacter

Department of Psychology, Harvard University, Cambridge, Massachusetts 02138

and

Randy L. Buckner

Department of Psychology, Washington University, St. Louis, Missouri 63130; and MGH-NMR Imaging Center, Department of Radiology, Harvard Medical School, Cambridge, Massachusetts 02138

Neurobiological distinctions among forms of memory have been investigated mainly from the perspective of lesion studies in nonhuman animals and experiments with human neurological patients. We consider recent neuroimaging studies of healthy human volunteers using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) that provide new information concerning the neural correlates of particular forms of memory retrieval. More specifically, we consider evidence indicating that priming, a form of implicit retrieval, is associated with decreased activity in various cortical regions. We also consider evidence suggesting that two components of explicit retrieval—intentional or effortful search and successful conscious recollection—are preferentially associated with increased activity in prefrontal and medial temporal regions, respectively.

One of the most prominent themes in recent behavioral and cognitive neuroscience research is that memory is not a unitary or monolithic entity, but instead consists of various dissociable forms (cf., Cohen & Eichenbaum, 1993; Gabrieli, Fleischman, Keane, Reminger, & Morrell, 1995; Schacter & Tulving, 1994; Sherry & Schacter, 1987; Squire, 1994) and component processes (Roediger & McDermott, 1993). Much of this research has been pursued within the context of the distinction between explicit and implicit forms of memory (Graf & Schacter, 1985; Schacter, 1987a; cf. Squire, 1994, for the related distinction between declarative and nondeclarative forms of memory). Explicit memory refers to conscious recollection of previous experiences, as revealed by standard tests of recall and recognition that require intentional retrieval of previously acquired information. Implicit memory refers to nonconscious effects of past experiences on subsequent behavior and performance, such as

This work was supported by NIA AG08441, NIH DC03245, and grants from the Charles A. Dana Foundation and Human Frontiers Science Program. We thank Wilma Koutstaal and Larry Squire for comments and discussion, and thank Carolyn Brenner for assistance with preparation of the manuscript.

Address requests for reprints and correspondence to Daniel L. Schacter, Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138.

1074-7427/98 $25.00

priming or skill learning, that are revealed by tests that do not require conscious recollection of previous experiences. Numerous studies have shown that explicit and implicit forms of memory can be dissociated experimentally, both in individuals with normal memory functions and in patients with memory disorders attributable to various kinds of brain damage (for reviews, see Roediger & McDermott, 1993; Schacter, Chiu, & Ochsner, 1993).

As noted by Graf and Schacter (1985) and by Schacter (1987a), the explicit/implicit distinction attempts to capture important differences between the ways in which memory for previous experiences can be expressed: as conscious recollections or as automatic, nonconscious changes in performance or behavior. However, as pointed out by Schacter (1987a), and discussed at length in subsequent articles (e.g., Richardson-Klavehn & Bjork, 1988; Schacter, Bowers, & Booker, 1989; Richardson-Klavehn, Gardiner, & Java, 1994), explicit memory can also be subdivided into two different and potentially dissociable dimensions of retrieval. First, explicit memory can refer to an intentional or voluntary aspect of the retrieval process. Thus, when people intentionally or voluntarily try to recall a recent experience, this effortful search could be characterized as explicit retrieval. Viewed from this perspective, explicit memory is defined by the intentional, voluntary effort involved in thinking back to a past experience, whereas implicit memory is defined as unintentional retrieval. Second, explicit memory can refer to a phenomenological quality that characterizes the output of the retrieval process: a conscious recollective experience (Tulving, 1983) that entails subjective awareness that one is remembering information acquired in the past. From this perspective, explicit memory is defined by the presence of such phenomenological awareness of the past—conscious recollection—whereas implicit memory is characterized by the absence of any such recollective awareness.

In this article we consider the relations among conscious recollection, intentional retrieval, and nonconscious influences of past events from the perspective of recent research using two prominent functional neuroimaging techniques: positron emission tomography (PET), which measures changes in regional cerebral blood flow, and functional magnetic resonance imaging (fMRI), which measures changes in blood oxygenation level associated with changes in blood flow and volume. A growing number of studies have used PET and fMRI to provide information about brain regions implicated in various aspects of encoding and retrieval processes (for recent reviews, see Buckner & Koutstaal, 1998; Cabeza & Nyberg, 1997; Ungerleider, 1995; Fletcher, Frith, & Rugg, 1997). We suggest that evidence obtained from neuroimaging studies using PET or fMRI can provide useful converging evidence that may help to clarify the relations among conscious recollection, intentional retrieval, and nonconscious influences that have so far been considered mainly from a cognitive perspective. We begin by reviewing recent studies that have provided relevant evidence concerning nonconscious priming effects, and then consider studies that have examined components of explicit retrieval. We conclude by applying findings and ideas arising from these studies to studies in which interactions between implicit and explicit retrieval processes are of central concern.

PRIMING AND NEUROIMAGING

Priming refers to changes in the ability to identify, complete, or make decisions about a stimulus as a function of a prior encounter with the stimulus

(Tulving & Schacter, 1990). Thus, for example, after studying a list of common words (e.g., FLOWER), and given instructions to complete a three-letter stem (FLO____) with the first word that comes to mind, subjects are biased to complete the stem with words from the study list (i.e., FLOWER), compared with other possible completions (e.g., FLOOD, FLOAT). Priming effects on word completion and similar tasks are thought to reflect the operation of non-conscious, implicit retrieval processes because they occur even when subjects exhibit little or no explicit memory for previously studied words, and they can be dissociated from explicit remembering by a variety of experimental and subject variables (for reviews, see Roediger & McDermott, 1993; Schacter et al., 1993). Perhaps the most convincing evidence that priming need not involve explicit memory is provided by studies showing that amnesic patients, who exhibit severely impaired explicit memory as a result of damage to medial temporal and diencephalic brain regions (Squire, 1992), often exhibit entirely normal priming effects (cf., Gabrieli et al., 1995; Graf, Squire, & Mandler, 1984; Hamann, Squire, & Schacter, 1995; Schacter, Church, & Treadwell, 1994; Warrington & Weiskrantz, 1974). Indeed, recent evidence indicates that certain forms of priming can be fully preserved even in an amnesic patient whose explicit memory deficit is so severe that she or he is unable to attain above-chance scores on forced-choice tests of explicit recognition memory (Hamann & Squire, 1997).

Several recent functional neuroimaging studies have explored priming on a variety of implicit retrieval tasks. In an early set of studies by Squire and colleagues (Buckner, Petersen, Ojemann, Miezin, Squire, & Raichle, 1995; Squire, Ojemann, Miezin, Petersen, Videen, & Raichle, 1992) and follow-up studies by Schacter, Alpert, Savage, Rauch, and Albert (1996a) and Backman, Almkvist, Andersson, Nordberg, Winblad, Reineck, and Langstrom (1997), word-stem completion was explored for evidence of priming-related activation changes. Subjects studied words prior to PET scans and were then asked to complete the word stems to form the first words that came to mind. As noted earlier, prior exposure to a list of words yields a bias to produce the study words; primed words are also produced more quickly than novel words. At the functional-anatomical level, each of these studies showed that posterior perceptual processing areas, which were activated during completion of novel stems, showed reduced activation when word stems were primed. Such an effect may reflect a neural correlate of perceptual priming: after exposure to a stimulus, subsequent processing is faster and requires less neural activity. Blaxton, Bookheimer, Zeffiro, Figlozzi, Gaillard, and Theodore (1996) have shown a similar finding during word-fragment completion, thus generalizing the finding to a distinct, but related, word generation task. Object naming (Martin, Haxby, La Londe, Wiggs, & Ungerleider, 1995) and object categorization (Buckner and Koutstaal, 1998) also show priming-related visual cortex reductions, thereby further extending the domain of this phenomenon. Not all priming phenomena are necessarily accompanied by blood flow reductions (e.g., Schacter, Reiman, Uecker, Polster, Yun, & Cooper, 1995), but the appearance of the phenomenon across tasks and conditions is impressive.

The foregoing findings are generally consistent with the idea that priming can be attributable, at least in part, to facilitation of perceptual processes. However, the selective locus of the priming effects is surprising in view of the finding that more extensive patterns of brain activation are observed during stem completion of novel, nonprimed words. Specifically, robust left prefrontal activation is observed during word-stem completion (as well as during many other verbal production tasks). Yet, in these early studies of word-stem completion, few if any changes within prefrontal areas were reported in association with priming [Schacter et al., 1996a, did report a left prefrontal (Brodmann area 47) blood flow increase in association with priming].

Raichle, Fiez, Videen, MacLeod, Pardo, Fox, and Peterson (1994) and Gabrieli and colleagues (Demb, Desmond, Wagner, Vaidya, Glover, & Gabrieli, 1995; Gabrieli, Desmond, Demb, Wagner, Stone, Vaidya, & Glover, 1996) demonstrated that, under appropriate conditions, robust and consistent reductions could be detected in higher-order prefrontal brain regions when words were repeated across verbal processing tasks requiring semantic elaboration (Demb et al., 1995; Gabrieli et al., 1996). Raichle et al. (1994) had subjects generate verbs that were meaningfully related to presented nouns (e.g., given "dog", subjects might generate "walk"). Unpracticed performance of this task activated many areas, including portions of left prefrontal cortex. After many repetitions with the same set of nouns, however, task performance no longer activated left prefrontal cortex, suggesting again that repeated item exposure can lead to reduced neural activity in specific brain areas. Demb et al. (1995) noted a similar phenomenon. Subjects were presented words and asked to classify them as abstract or concrete. Left prefrontal regions showed reduced activation during performance with repeated items compared with novel items, even after a single item exposure. Wagner, Desmond, Demb, Glover, and Gabrieli (1997b) recently noted a similar prefrontal reduction for semantic classification of object pictures. Taken together with the earlier word-stem completion findings, these data suggest that blood flow reductions can be observed across multiple regions, depending on the exact task and context.

An important question left open by these studies concerns which task parameters drive anatomical and functional specificity of the observed activation reductions. As noted, the initial studies of word-stem completion demonstrated activation reductions in posterior areas associated with perceptual processing, whereas verb generation and word categorization showed additional reductions in left prefrontal brain areas. These tasks are all similar in many respects: subjects receive cues and are asked to generate words or make decisions about the words, but the manifestations of priming differed across the several studies. We believe the explanation does not lie solely in the tasks on which repetition effects are revealed, but rather in how the target items were initially exposed during study (Buckner & Koutstaal, 1998). In all of the prior studies of word-stem completion, subjects engaged in an orienting task during study, not a word-stem completion task. Thus, the same items were repeated (at least partially) from the study list to the word-stem test, but the task itself changed. In the studies of Raichle et al. (1994) and Demb et al. (1995) that showed prefrontal reductions, however, the identical task was performed across item repetitions. This observation leads naturally to two predictions: (1) prefrontal reductions should be diminished—or possibly eliminated—when items are initially presented under different task conditions than at test, even for the same tasks that have shown robust prefrontal reduction when repeated exactly (e.g., Demb et al., 1995); and (2) tasks such as word-stem completion, which typically show priming effects in across-task conditions, should show priming-related prefrontal reductions when the exact task is repeated. In a series of fMRI studies, we have recently provided evidence that supports both of these predictions.

Buckner, Koutstaal, Schacter, Petersen, Raichle, and Rosen (1997) demonstrated that both word-stem completion and verb generation show left prefrontal reductions when the exact same cues and the same task are repeated. Subjects performed word-stem completion with a repeating set of stem cues during certain fMRI task blocks, and with novel word-stem cues during other blocks. Contrasting the novel with the repeated blocks, fMRI data showed reduced activation for repeated word stems in left dorsal and inferior prefrontal regions. A parallel design was used for verb generation and similar results were obtained. Thus, contrary to the idea that word-stem completion is a purely perceptually driven task that manifests priming solely as a result of perceptual overlap of items across repetitions, the overall patterns of functional neuroimaging data indicate a more complex picture. Word-stem completion, like verb generation or word categorization, is neither an entirely perceptually driven task nor an entirely conceptually driven task. Rather, item and task overlap determines which kinds of processes will be biased and, therefore, manifest priming-related modulations. Such an idea is consistent with the transfer-appropriate processing framework (Roediger, Weldon, & Challis, 1989) and is also consistent with the idea that specialized domain-specific subsystems can be biased via priming (Tulving & Schacter, 1990).

Studies by Demb et al. (1995) and Wagner, Buckner, Koutstaal, Schacter, Gabrieli, and Rosen (1997a) have directly tested the notion that task processes modulate prefrontal activation reductions in a functionally specific manner. In each of these studies, items were repeated across two tasks: one involving a perceptual decision and the other involving the conceptual (abstract/concrete) decision described earlier. Demb et al. (1995) showed that when items were repeated across the perceptual decision task, no activation reductions were observed in left prefrontal cortex. However, this result only partially establishes functional specialization, because the perceptual decision task likely did not activate left prefrontal cortex initially; accordingly, it is difficult to interpret a lack of activation reduction. Wagner et al. (1997a) extended this earlier study by examining an across-task paradigm where words were presented initially during the perceptual decision task and were tested again on the abstract/concrete decision task. This manipulation revealed that (1) left dorsal prefrontal cortex was activated by the abstract/concrete decision task and (2) the activation was not reduced as a consequence of prior exposure to the items in the perceptual decision task. By contrast, a second condition that involved repetition of the exact items and task demands with the abstract/concrete decision task replicated the reductions initially noted by Demb et al. (1995).

Taken collectively, the findings across all of the foregoing studies demonstrate convincingly at least one neural correlate of implicit memory: repetition of items during a task can lead to decreases in the amount of activation present in specific brain areas. Moreover, as described above, the reductions appear to be selective, depending on item and task overlap across repetitions. However, our discussion so far has not addressed whether the reductions are partly or entirely attributable to explicit memory—either intentional or unintentional recollection of previously presented items. We elaborate on this issue later, but for now note that "explicit contamination" is an unlikely explanation for two reasons.

First, in one of the experiments by Schacter et al. (1996a), priming-related reductions in posterior visual cortex were observed after words were studied during a perceptual orienting task that produced low levels of explicit recall.

Second, although these data do not address whether conceptual priming effects associated with reductions in prefrontal regions are attributable to explicit contamination, recent fMRI data concerning priming in amnesic subjects suggest that they are not. Gabrieli et al. (1996) and later Buckner and Koutstaal (1998) reported data showing left prefrontal activation reductions in patients with organic amnesia, who show little recall or recognition of previously studied words. Amnesic patients are extremely unlikely to spontaneously adopt explicit retrieval strategies or benefit from unintentional explicit awareness of earlier study episodes. Thus, the presence of prefrontal activation reductions in amnesics suggests that some, if not all, of the effect is attributable to implicit retrieval processes. Explicit retrieval processes, as discussed in the next section, appear to have a separate set of functional-anatomical correlates.

COMPONENTS OF EXPLICIT RETRIEVAL: SUCCESSFUL CONSCIOUS RECOLLECTION VERSUS INTENTIONAL RETRIEVAL EFFORT

Neuroimaging studies of explicit retrieval have for the most part proceeded separately from studies of priming, although several studies discussed later in the paper have examined the two together. Such studies have revealed evidence for the activation of numerous brain regions during explicit retrieval in a variety of different tasks and conditions, with preferential engagement of specific brain regions in many of these tasks (for reviews, see Buckner & Petersen, 1996; Cabeza & Nyberg, 1997; Fletcher et al., 1997). We focus on two brain regions, anterior prefrontal and medial temporal, because these regions have been the primary focus of concern in studies that have addressed the relations between conscious recollection and intentional retrieval and that are central to this article.

One of the more surprising findings from neuroimaging studies of explicit retrieval is that various regions of prefrontal cortex have been consistently activated during both recall and recognition tasks (Buckner & Petersen, 1996; Nyberg, Cabeza, & Tulving, 1996; Fletcher et al., 1997), including an anterior frontopolar region [centered at or near Brodmann area (BA) 10] that shows particularly marked right-sided activation, a dorsolateral region (in the vicinity of BAs 9 and 46) and sometimes a more posterior frontal/opercular region (in the vicinity of BA 47; for discussion, see Buckner, 1996). These regions, including the anterior frontopolar activations, have also shown activation in tasks that do not demand explicit retrieval (MacLeod, Buckner, Miezin, Petersen, & Raichle, in press). Their consistent activation during explicit retrieval tasks, however, brings them to the forefront of neuroimaging studies of recollective processes. Although it has been known for some time that prefrontal cortex plays some role in explicit retrieval (cf., Fuster, 1989; Schacter, 1987b; Squire, 1987; Wheeler, Stuss, & Tulving, 1995), it is also known that damage to prefrontal regions does not produce a severe amnesic syndrome of the kind typically seen after damage to the medial temporal lobes. In light of these observations, the persistent finding of prefrontal activations during explicit retrieval was unexpected. Conversely, many neuroimaging studies of explicit retrieval have failed to find evidence of hippocampal/medial temporal activation (e.g., Andreasen, O'Leary, Arndt, Cizadlo, Hurtig, Rezai, et al., 1995; Buckner et al., 1995; Buckner, Raichle, Miezin, & Petersen, 1996b; in press-a; in press-b; Petrides, Alivisatos, & Evans, 1995; Fletcher, Frith, Grasby, Shallice, Frackowiak, & Dolan, 1995; Tulving, Kapur, Markowitsch, Craik, Habib, & Houle, 1994b). In view of the aforementioned data concerning medial temporal damage and the amnesic syndrome, this observation is also surprising (for discussions of alternative hypotheses, see Buckner et al., 1995; Cabeza & Nyberg, 1997; Buckner & Tulving, 1995; Martin, Wiggs, & Weisberg, in press; Ungerleider, 1995).

Most relevant to the present purposes, a number of studies have examined prefrontal or medial temporal regions in the context of the distinction between successful conscious recollection, on the one hand, and intentional retrieval effort, on the other. From the perspective of neuroimaging, this distinction is a fundamental one: when a brain region shows increased activity during explicit retrieval, the increase could in principle be attributable either to the successful recollection of target material or to the effort made in attempting to retrieve the target material, independent of whether retrieval is successful. To separate out successful conscious recollection from intentional retrieval effort, two main experimental strategies have been used: (1) producing high and low levels of successful retrieval by manipulating study conditions, and (2) manipulating the number of previously studied items that appear during a particular test. We consider studies that have used each type of strategy.

Consider first an experiment by Schacter et al. (1996a) that used a stem-cued recall task, which was performed as a follow-up to Schacter and colleagues' stem completion priming experiment noted earlier. Squire and colleagues' (1992) study had shown both right anterior prefrontal and medial temporal (right parahippocampal gyrus) blood flow increases during stem-cued recall compared with a baseline condition in which subjects completed stems of nonstudied items with the first word that came to mind. However, this observation alone does not indicate whether the anterior prefrontal or medial temporal activations are specifically linked with intentional efforts to retrieve target items or successful conscious recollection of them. Moreover, two follow-up studies by Buckner et al. (1995) showed robust activation of the right anterior prefrontal regions, but failed to find evidence of medial temporal activation on the stem-cued recall test when either the sensory modality or typecase of target stimuli differed at study and test.

In the Schacter et al. (1996a) experiment, prior to PET scanning subjects studied a list composed of two different types of words. Words in the "high recall" condition appeared four times and subjects judged the number of meanings associated with each item, whereas words in the "low recall" condition appeared once and subjects judged the number of *t*-junctions (i.e., numbers of points where two lines meet) in the item. After seeing study lists in which both types of items were shown for 5 s each, stem-cued recall was tested during separate scans for high-recall words and low recall words. The logic underlying the experiment is that regions that are selectively activated during the high recall condition, when subjects correctly recall most of the study list words, are preferentially associated with successful conscious recollection, whereas regions that are activated during the low recall condition, when subjects recall few study list words, are preferentially associated with intentional efforts to search memory.

Subjects remembered many more words in the high recall condition than in the low recall condition. Analysis of PET data revealed blood flow increases in the hippocampal formation during the high recall condition compared with a baseline condition in which subjects completed nonstudied three-letter stems with the first word that came to mind (bilateral), or compared with the low recall condition (right hippocampus/parahippocampal gyrus). By contrast, there were no hippocampal increases in the low recall condition. These results confirm Squire and colleagues' (1992) previous findings of parahippocampal activation during stem-cued recall and also suggest that Schacter and colleagues' failure to observe hippocampal activation during priming is not simply attributable to some general difficulty with reliably activating the hippocampal formation.

Perhaps more importantly, the fact that Schacter et al. observed hippocampal activation during the high but not the low recall condition points toward a possibly important distinction regarding the nature of hippocampal activity during explicit retrieval. The hippocampal formation does not seem to be activated by the effort involved in intentional attempts to remember a past event. In the low recall condition, subjects tried to remember study list words, but successfully recalled relatively few of them. Instead, hippocampal activation may be related to the level or type of recollection in a particular situation—some aspect of the actual conscious recall of a past event, as opposed to the effort involved in attempting to remember the event. Consistent with these suggestions, the Schacter et al. (1996a) results are supported by other PET findings showing greater hippocampal activation in high than in low recognition memory conditions (Rugg, Fletcher, Frith, Frackowiak, & Dolan 1997; Schacter et al., 1995; cf. Nyberg, McIntosh, Houle, Nilsson, & Tulving, 1996).

Schacter et al. (1996a) also reported that, in contrast to the hippocampal activations in the high recall condition, certain areas within prefrontal cortex were robustly activated in the low recall condition. More specifically, anterior/dorsolateral prefrontal regions showed bilateral blood flow increases in the low recall minus baseline comparison and left-sided increases in the low recall minus high recall comparison. These data thus raise the possibility that blood flow increases in anterior prefrontal cortex during stem-cued recall reflect primarily the effort involved in attempting to remember past events, as opposed to the actual experience of recollection (for discussion of possible differences between left and right prefrontal activations, see Schacter et al., 1996a).

In a subsequent study using the same paradigm, Schacter, Savage, Alpert, Rauch, and Albert (1996b) found that elderly adults (mean age of approximately 70), just like college students in the Schacter et al. study (1996a), showed significant hippocampal blood flow increases in the high recall condition compared with the low recall condition. By contrast, older adults showed different patterns of prefrontal blood flow increases in the low recall condition, exhibiting more posterior, predominantly left-sided activations than did the younger subjects. These findings suggest that older adults may use different intentional retrieval strategies than younger adults in the low recall condition and also further support the distinction between hippocampal activations that are related to successful conscious recollection and prefrontal activations that are related to intentional retrieval effort.

Further relevant evidence from the same paradigm has been provided in a more recent PET study by Heckers, Rauch, Goff, Savage, Schacter, and Alpert (1997), who studied schizophrenic patients and age-matched control subjects (mean age of approximately 40 for both groups). The control subjects, just like college students and elderly adults in the two earlier studies, showed significant hippocampal blood flow increases in the high recall condition compared with the low recall condition. By contrast, schizophrenics exhibited no such increases. However, schizophrenics did exhibit robust anterior prefrontal increases in the low recall condition compared with baseline; control subjects also showed prefrontal increases in the low recall condition, but they were somewhat posterior to the prefrontal increases shown by the schizophrenics. These findings reinforce the functional distinction between hippocampal and prefrontal activations during the stem-cued recall test, and suggest that schizophrenic patients, in contrast to normal elderly adults in Schacter et al. (1996b), show specific abnormalities in activating hippocampal regions in conditions that promote high levels of successful conscious recollection.

Nyberg, Tulving, Habib, Nilsson, Kapur, Houle, Cabeza, and McIntosh (1995) examined similar distinctions between high and low performance conditions in an old/new recognition test, using a deep versus shallow encoding manipulation to create high and low recognition conditions; they also included a new condition in which most of the target words had not appeared previously on a study list. Cross-modal testing conditions were used, with the study list presented auditorily and the test list presented visually. Compared with a control condition in which subjects simply read words, each of the high recognition, low recognition, and new conditions were associated with increased blood flow in right dorsolateral prefrontal cortex. However, there were no differences in prefrontal activations across the high, low, and new recognition conditions, suggesting that the prefrontal blood flow increases that were observed compared with the reading control condition reflect intentional/effortful aspects of retrieval rather than successful recognition. There was no evidence of activation in the hippocampus during either the high or low recognition conditions [consistent with the cross-modal findings of Buckner et al. (1995)], although there was some evidence of parahippocampal gyrus activation in the low recognition condition.

A more recent study by Rugg et al. (1997) used a similar strategy to separate conscious recollection from intentional retrieval, but also included an incidental memory test that did not require intentional retrieval. Rugg et al. carried out a PET experiment that used a 2×2 design in which type of encoding (deep or shallow) and type of retrieval (intentional or unintentional) were fully crossed. Subjects studied word lists and either generated sentences for each word (deep encoding) or made judgments about the letters in each word (shallow encoding). Following each type of encoding task, they were given either an old/new recognition test (intentional retrieval) or an animate/inanimate decision task (unintentional retrieval). Deep encoding produced more accurate memory on the intentional retrieval task. Performance was at ceiling levels on the unintentional task, but the authors note that subjects reported spontaneously noticing that test words came from the study list more often after deep than shallow encoding—a rough index of unintentional conscious recollection.

Analyses of the PET data revealed two key findings. (1) There was greater right prefrontal activation during intentional retrieval than unintentional retrieval after both deep and shallow encoding; the locus of this common activation was slightly posterior to the region activated in their earlier study. (2) There was greater activation in left medial temporal lobe areas after deep encoding than after shallow encoding during both intentional and unintentional retrieval. Thus, these data suggest that hippocampal activity during retrieval is observed with high levels of conscious recollection, regardless of whether subjects voluntarily try to remember the study list items. By contrast, the right prefrontal activation was quite sensitive to the requirement to engage in intentional retrieval, regardless of whether subjects achieve high or low levels of conscious recollection.

Several studies have attempted to separate retrieval effort and success by manipulating the proportion of old items presented to subjects during a particular scan. The reasoning here is that presenting large numbers of old items during a particular scan will produce more successful retrievals than presenting only a few old items. In general, these studies have focused on issues concerning the characterization of right anterior prefrontal activations. In a PET study, Kapur, Craik, Jones, Brown, Houle, and Tulving (1995) compared blood flow during a "high target density" scan (34/40 old items) with a "low target density scan (6/40 old items). They found that compared with a baseline control in which subjects made semantic judgments about new words, right anterior prefrontal regions showed blood flow increases in both the high and low target density conditions. However, there were no differences in prefrontal activity between conditions, thereby suggesting that right anterior prefrontal activity is more closely associated with retrieval effort than retrieval success. By contrast, Rugg, Fletcher, Frith, Frackowiak, and Dolan (1996), also using PET, found evidence of greater right anterior prefrontal activity during both a high density scan (16/20 old items) and a low density scan (4/20) than during a "new recognition" scan in which subjects made judgments about new words only. These results imply some association between retrieval success and right prefrontal activation. Moreover, Rugg et al. observed trends for greater right anterior prefrontal activation in the high than in the low density scan, although only at a less stringent statistical criterion than was used for the other findings [see Rugg et al. (1996) for discussion of possible reasons for differences between their study and previous findings].

Several recent fMRI studies may help to resolve the seemingly conflicting results regarding the relation between anterior prefrontal activations and successful conscious recollection versus intentional retrieval effort. In an examination of old/new recognition memory, Wagner, Desmond, Glover, and Gabrieli (1997c) found that with standard test instructions, where subjects were not informed regarding the composition of studied versus nonstudied items in a particular condition, there was no evidence that right anterior prefrontal activations were greater when numerous old items were tested (high recognition condition) compared with when few or no old items were tested (low recognition condition). However, when subjects were given different instructions—they were informed about the old/new composition of a test and told to respond only to the "oddball" items within a scan (e.g., during a high recognition scan, they were told that test items were mostly old and that they should respond only to the few new items)—Wagner et al. (1997c) reported evidence of greater right anterior prefrontal activation during high than low recognition test conditions. These observations led Wagner et al. to conclude that anterior prefrontal activations during retrieval are not specifically tied to successful retrieval, but rather reflect the adoption of retrieval strategies that may vary across different testing contexts.

Two recent fMRI studies point toward a similar conclusion. In one study (Buckner, Koutstaal, Schacter, Wagner, & Rosen, in press-b), we manipulated levels of recognition memory by varying type of prior encoding, with one set scans including items that had been studied previously under deep encoding conditions and another set of scans including items that had been studied previously under shallow encoding conditions. Deep encoding yielded high levels of recognition success with low levels of effort, and shallow encoding yielded low levels of recognition success with high levels of effort. On the one hand, effort-related prefrontal modulation was detected in left dorsal prefrontal regions and bilateral frontal-opercular cortex [conceptually consistent with Schacter et al. (1996a)]. On the other hand, consistent with Rugg et al. (1996), we found evidence of greater right anterior prefrontal activation during the high recognition scans than during the low recognition scans, a possible signature of retrieval success.

In a companion study, Buckner, Koutstaal, Schacter, Dale, Rotte, and Rosen (in press-a) used newly developed procedures for obtaining and analyzing event-related fMRI data (Rosen, Buckner, & Dale, 1998) to explore further brain areas related to retrieval success. In standard PET and fMRI studies, items are segregated into test blocks that correspond to particular experimental conditions, and estimates of blood flow and volume are based on estimates of activity averaged across a test block. In event-related fMRI, items from different experimental conditions can be randomly intermixed, in a manner analogous to standard cognitive and behavioral studies; brain activity related to particular types of items can be selectively averaged, in a manner analogous to the electrophysiological analysis of event-related potential data (for discussion of event-related fMRI, see Buckner, Bandettini, O'Craven, Savoy, Petersen, Raichle, & Rosen, 1996a; Dale & Buckner, 1997; Rosen et al., 1998; Josephs, Turner, & Friston, in press; Zarahn, Aguirre, & D'Esposito, in press). The evidence linking right anterior prefrontal activation with retrieval success in the studies by Buckner et al. (in press-b) and Rugg et al. (1996) came from blocked trial procedures. Buckner et al. (in press-a) reasoned that if such effects are related to successful recognition, as opposed to more general contextual or strategic factors, then event-related fMRI analyses should show greater anterior prefrontal activation for successfully recognized items compared with correct rejections (i.e., new items that subjects correctly indicate had not appeared previously on the list). Moreover, if successful retrieval is a necessary condition for observing right anterior prefrontal activity, then no significant activations should be observed in this region for correctly rejected items. Contrary to these suggestions, Buckner et al. (in press-a) found significant right anterior prefrontal activation when subjects correctly rejected new words that had not been studied previously, and found no right anterior prefrontal differences between successfully recognized and correctly rejected words. Buckner et al. (in press-a) suggested that, consistent with the arguments of Wagner et al. (1997a), the apparent association between successful recognition and right anterior prefrontal activation by Buckner et al. (in press-b) and Rugg et al. (1996) may indicate the operation of context-sensitive retrieval strategies.

Some insight into the nature of these processes is provided by time-course analyses of brain activity in the Buckner et al. (in press-a) event-related fMRI study and in another event-related fMRI study of true and false recognition memory by Schacter, Buckner, Koutstaal, Dale, and Rosen (1997a). Both studies found evidence that right (and left) anterior prefrontal activations exhibit a late onset relative to virtually all other brain regions. One possible explanation of this effect is that anterior prefrontal regions are involved in effortful postretrieval monitoring activities (for discussion of alternative possibilities, see Buckner et al., 1997a; Schacter et al., 1997a).

In summary, although numerous issues remain to be resolved, PET and fMRI studies of hippocampal and prefrontal activation provide two suggestions. First, anterior prefrontal blood flow increases are associated with some aspect or aspects of intentional retrieval or monitoring processes. Second, when activation increases are detected within the hippocampal formation, they are associated with successful conscious recollection, as opposed to effort or intent to retrieve. In considering this latter suggestion, we must also be mindful of the fact that many retrieval studies have failed to modulate activation within the hippocampal formation. As we discuss in the next section, the data further suggest that the role of medial temporal lobe structures in retrieval is selective, and that medial temporal activation may reflect factors in addition to those specifically related to explicit retrieval.

INTERACTIONS BETWEEN FORMS OF RETRIEVAL: PRIMING OF STEM COMPLETION AND THE PROBLEM OF ''EXPLICIT CONTAMINATION''

As noted earlier, observations of spared priming in amnesia provide compelling evidence that priming involves nonconscious retrieval processes. However, in studies with healthy volunteers it is often difficult to rule out the possibility that subjects are using some form of explicit retrieval to perform a nominally implicit task (Jacoby, 1991; Schacter et al., 1989). At least two forms of such "contamination" from explicit retrieval processes are possible: (1) subjects catch on to the fact that their memory is being tested and intentionally retrieve study list words while performing the priming task; (2) subjects follow instructions and provide the first word that comes to mind (or follow analogous instructions on other priming tasks), but they unintentionally recollect that they had studied target items on the previous study list [for detailed discussion of various ways in which this could occur, see Schacter et al. (1989)]. Schacter (1987a) and Richardson-Klavehn and Bjork (1988) have noted that explicit memory often takes the form of unintentional or involuntary recollections of previous experiences in which there is no deliberate, effortful attempt to think back to the past; instead one is spontaneously "reminded" of a past event that is accompanied by conscious recollective experience. Involuntary remindings are a familiar part of memory function in everyday life, perhaps exemplified most notably in the writings of Marcel Proust, whose epic novel *In Search of Lost Time* provides numerous vivid examples of involuntary but fully conscious recollections of the past (see Schacter, 1996, Chap. 1).

A variety of experimental strategies and criteria have been proposed to try to rule out or estimate the contributions of explicit memory contamination that are produced by intentional retrieval on the one hand and unintentional or involuntary recollection on the other (cf. Bowers & Schacter, 1990; Richardson-Klavehn et al., 1994; Schacter et al., 1989; Jacoby, 1991). We now consider how some of the previously considered findings from neuroimaging studies may provide additional insights into this issue.

Consider the previously mentioned PET study of stem completion priming versus explicit recall by Squire et al. (1992). In this experiment, subjects initially studied a list of familiar words prior to PET scanning. They were then scanned during a stem completion task in which subjects provided the first word that came to mind in response to three-letter word stems that were presented visually. Two relevant scans were carried out during the stem completion task: for one scan, it was possible to complete stems with study list words (priming), and for the other, stems could be completed only with new words that had not been presented on the study list (baseline). In a separate scan, subjects were provided with three-letter stems of study list words, and were asked to think back to the study list (explicit cued recall).

As noted earlier, when estimates of blood flow during the priming scan and baseline scan were compared, priming was associated with decreased blood flow in the extrastriate occipital cortex. More importantly for the present purposes, Squire et al. also reported small but significant blood flow increases in the right hippocampal formation in the priming condition compared with the baseline condition. This finding was surprising in light of the previously mentioned evidence that amnesic patients characterized by medial temporal lobe damage often exhibit normal priming (Squire et al. also observed right parahippocampal gyrus blood flow increases in the cued recall vs. baseline comparison).

In light of previous results from amnesic patients indicating that normal priming can occur even when the hippocampal formation is damaged, it is possible that the observed activation of the hippocampal region reflects one of the two previously mentioned forms of "contamination": subjects may have intentionally retrieved words from the study list or, alternatively, they may have provided the first word that comes to mind and involuntarily recollected its prior occurrence. Consideration of Squire and colleagues' behavioral data indicates an unusually high level of priming that is consistent with some form of explicit memory contamination; the proportion of stems completed with study list targets in the priming condition (0.72) was nearly identical to the proportion of stems completed with study list targets in the explicit recall condition (0.76; the baseline completion rate for nonstudied items was 0.08). Consistent with this suggestion, Squire et al. used short study lists and brief study test delays; subjects saw all target words twice during the study phase and performed a "deep" encoding task (pleasantness rating) that promotes high levels of explicit memory. It is possible that some or all of these influences conspired to produce either voluntary or involuntary contamination of priming performance from explicit memory. Of the two possibilities, we believe involuntary contamination is the most likely explanation. Two sources of behavioral data point toward this conclusion. First, subjects were no more likely to recall words on the second half of the test lists than the first half as might be predicted if subjects began to intentionally recall items once aware of the embedded study words (Buckner, unpublished observations). Second, reaction times during production of novel words during the primed stem completion were indistinguishable from the novel words produced during the baseline blocks (Buckner et al., 1995). The implication is that subjects were not spending any extra time searching for items. By contrast, in stem-cued recall, where subjects were intentionally trying to retrieve items, a highly significant increase in reaction time is associated with novel word production, perhaps a direct behavioral reflection of the added processes related to voluntary explicit retrieval.

Alternatively, it is conceivable that the hippocampal region plays a more prominent role in priming than is generally acknowledged and that the parahippocampal activations observed by Squire et al. in connection with priming are an integral part of the priming effect (as opposed to an epiphenomenal "add-on" from explicit memory). Although this idea appears contradicted by data showing preserved priming in amnesic patients, Ostergaard and Jernigan (1993) have claimed that priming is frequently impaired in amnesic patients and that apparent preservation of priming in amnesia is attributable to various methodological artifacts. Hamann, Squire, and Schacter (1995) have provided evidence and arguments to the contrary, but the possibility that hippocampal activation during priming reflects something other than explicit memory contamination must be considered.

Consistent with this latter suggestion, Squire and colleagues' finding of parahippocampal activation during explicit stem-cued recall cannot be interpreted unequivocally as evidence that some form of explicit retrieval occurred during priming of stem completion performance. In subsequent experiments using a similar explicit cued recall procedure, Buckner et al. (1995) failed to observe hippocampal blood flow increases when either modality of study and test words differed (i.e., words were study in the auditory modality), or the typecase of study and tested words differed (i.e., visually tested words were studied in lowercase and tested in uppercase). In the latter condition, the proportion of study list words recalled (0.73) was virtually indistinguishable from the proportion of words recalled when items were studied and tested in the identical typecase (0.76). Yet significant hippocampal activation during explicit recall was observed only when words were studied and tested in the same typecase. We will return shortly to this finding, which is consistent with other (previously mentioned) failures to observe hippocampal activation during explicit retrieval.

In addition to the foregoing pattern of hippocampal blood flow increases, the experiments by Squire et al. (1992) and Buckner et al. (1995) yielded one other consistent finding that is critical to our discussion: explicit recall in all three experimental conditions (i.e., same typecase/modality, different typecase, different modality) was associated with significant activation in the right anterior prefrontal cortex, whereas no right prefrontal activations were observed in association with priming. The region of the right prefrontal cortex that showed blood flow increases during explicit recall has been characterized by similar increases in virtually all studies of explicit retrieval, often in conjunction with less robust increases in the left anterior prefrontal cortex (for reviews, see Buckner, 1996; Tulving et al., 1994a). Important for our purposes, in contrast to the prominent activation of the right anterior prefrontal cortex during stem-cued recall, neither Buckner et al. (1995) nor Squire et al. (1992) reported evidence of blood flow increases in this region during priming of stem completion.

In an attempt to elucidate the issues raised by the Squire et al. (1992) and Buckner et al. (1995) experiments, Schacter et al. (1996a) examined the possibility that the hippocampal activation that Squire et al. observed in their priming condition reflects "contamination" from explicit memory. To address the latter issue, Schacter et al. (1996a) attempted to eliminate explicit contamination by using a nonsemantic study task in which subjects count the number of *t*-junctions in each of the target words. Previous studies of stem completion priming have shown robust priming following the t-junction counting task, even though subjects have little explicit memory for the target items (Bowers & Schacter, 1990; Graf & Mandler, 1984). Therefore, if the priming-related hippocampal activation observed by Squire et al. reflects contamination from explicit memory, using the t-junction encoding task should eliminate both the explicit contamination and the associated hippocampal blood flow increases.

Analysis of behavioral data indicated that, compared with the Squire et al. experiment, explicit contamination had been severely reduced or eliminated: the absolute magnitude of the priming effect was comparable to priming in previous experiments in which explicit contamination could be ruled out (Bowers & Schacter, 1990; Graf & Mandler, 1984). Analysis of PET data showed no evidence of blood flow increases in the vicinity of the hippocampal formation associated with priming, but, as noted earlier, revealed priming-related blood flow decreases in extrastriate occipital cortex.

These findings are consistent with the idea that the priming-related hippocampal activations reported by Squire et al. (1992) reflect contamination from explicit memory, and are not an important or necessary component of stem completion priming. The fact that priming-related blood flow decreases in extrastriate occipital regions occurred in each of the Squire et al., Buckner et al., and Schacter et al. experiments, whether or not hippocampal activations were observed, is consistent with the idea that perceptual priming occurs independently of the hippocampal formation. In light of the failures by Buckner et al. and others to observe hippocampal activations during stem-cued recall, the absence of hippocampal activation during priming in the Schacter et al. experiment could simply reflect the fact that it is difficult to reliably observe evidence of hippocampal activation during retrieval (explicit or implicit). Moreover, even if the Schacter et al. data were tentatively accepted as support for the proposition that hippocampal activation during priming in the Squire et al. study is attributable to explicit memory contamination, they do not directly address the central issue of whether such contamination reflects intentional retrieval or involuntary recollection.

The findings discussed previously from Schacter and colleagues' (1996a) explicit retrieval experiment provide some insight into this issue: hippocampal activation was observed in association with successful conscious recollection, whereas anterior prefrontal activation was observed in association with intentional retrieval effort. Putting together the results of the Squire et al., Buckner et al., and Schacter et al. experiments, it is possible to offer a hypothesis concerning the nature of the explicit memory contamination in the initial Squire et al. experiment. To the extent that hippocampal activation indicates successful conscious recollection, whereas anterior prefrontal activation indicates some aspect of intentional effort to retrieve, the finding of hippocampal activation in the absence of anterior prefrontal activation during priming in the Squire et al. experiment suggests the operation of involuntary conscious recollection (as opposed to deliberate, intentional "thinking back" to the study). Although this interpretation must be treated cautiously because of its post hoc nature, it is buttressed further by Rugg and colleagues' (1997) finding of greater left hippocampal activity after deep encoding than after shallow encoding during both intentional and unintentional retrieval tasks, and greater right anterior prefrontal activity during intentional retrieval than unintentional retrieval after both deep and shallow encoding. Putting the Rugg et al. results together with those of Squire et al. (1992) and Schacter et al. (1996a), there is evidence to support the proposition that increases in hippocampal activity during explicit retrieval, unaccompanied by corresponding increases in anterior prefrontal activity, constitute a signature for involuntary conscious recollection.

Although these assertions fit well with the results of several studies (Gabrieli et al., 1997; Nyberg et al., 1996; Rugg et al., 1997; Schacter et al., 1995, 1996a, 1996b; Squire et al., 1992), they do not accommodate the previously discussed finding by Buckner et al. that hippocampal activation was not observed when subjects recalled study list words in response to test cues that appeared in a different typecase than studied words, even though the overall level of recall was not significantly different from a same typecase condition that did produce hippocampal activation (Squire et al., 1992). Data relevant to this observation have been reported recently by Schacter, Uecker, Reiman, Yun, Bandy, Chen, and Curran (1997b), who used a paradigm in which subjects study novel shapes and later make old/new recognition judgments about previously studied objects and new objects. Schacter et al. (1995) had previously found significantly greater hippocampal activation during recognition judgments about studied objects compared with new objects. To determine whether physical similarity between studied and tested objects influences hippocampal activations, Schacter et al. (1997b) compared blood flow increases during an old/new recognition test when the identical objects were studied and tested with conditions in which either the orientation or the size of the objects was changed. Schacter et al. (1997b) found significant hippocampal activation for identical objects and also found significantly greater hippocampal activation during recognition of identical objects than during recognition of objects whose orientation or size had been changed between study and test. Although recognition accuracy was higher for identical objects than for orientation-changed objects, there were no significant differences in recognition accuracy for identical objects and size-changed objects. Thus, as in Buckner and colleagues' (1995) experiment, significant hippocampal blood flow increases were not observed when the physical features of studied and tested objects differed at study and test.

The generality and nature of these physical similarity effects remains unclear. It is conceivable that they are produced by the same or similar processes that link successful conscious recollection and hippocampal activations. Even when the absolute levels of performance did not differ between identical and changed stimulus conditions, the manner in which subjects remembered identical items may have differed from the manner in which they remembered changed items. For example, subjects' recollections may have been less vivid or less confident in the changed stimulus conditions compared with the identical stimulus conditions (Schacter et al., 1997b). Alternatively, as suggested by Buckner et al. (1995), perceptual functions in the hippocampal regions, independent of memory retrieval processes, may be relevant to observed effects of physical similarity between study and test on hippocampal activations.

CONCLUSIONS

The evidence reviewed in this article can be thought of as the early returns from an emerging field of study: neuroimaging of human memory. Although not all relevant data can be easily explained, the idea that nonconscious priming, intentional retrieval, and successful conscious recollection are each associated with characteristic patterns of blood flow increases and decreases has received some empirical support. These findings from PET and fMRI both complement and extend previous studies using purely cognitive techniques. Further development of both cognitive and neuroimaging approaches should yield patterns of converging evidence that can illuminate both explicit and implicit forms of memory.

REFERENCES

Andreason, N. C., O'Leary, D. S., Arndt, S., Cizadlo, T., Hurtig, R., Rezai, K., Watkins, G. L., Boles Ponto, L. L., & Hichwa, R. D. (1995). Short-term and long-term verbal memory: A positron emission tomography study. *Proceedings of the National Academy of Sciences of the United States of America,* **92,** 5111–5115.

Backman, L., Almkvist, O., Andersson, J., Nordberg, A., Winblad, B., Reineck, R., & Langstrom, B. (1997). Brain activation in young and older adults during implicit and explicit retrieval. *Journal of Cognitive Neuroscience,* **9,** 378–391.

Blaxton, T. A., Bookheimer, S. Y., Zeffiro, T. A., Figlozzi, C. M., Gaillard, W. D., & Theodore, W. H. (1996). Functional mapping of human memory using PET: Comparisons of conceptual and perceptual tasks. *Canadian Journal of Experimental Psychology,* **50,** 42–56.

Bowers, J. S., & Schacter, D. L. (1990). Implicit memory and test awareness. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* **16,** 404–416.

Buckner, R. L. (1996). Beyond HERA: Contributions of specific prefrontal brain areas to long-term memory retrieval. *Psychonomic Bulletin & Review,* **3,** 149–158.

Buckner, R. L., Bandettini, P., O'Craven, K., Savoy, R., Petersen, S. E., Raichle, M. E., & Rosen, B. R. (1996a). Detection of cortical activation during averaged single trials of a cognitive task using functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences of the United States of America,* **93,** 14878–14883.

Buckner, R. L., & Koutstaal, W. (1998). Functional neuroimaging studies of encoding, priming, and explicit memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America,* **95,** 891–894.

Buckner, R. L., Koutstaal, W., Schacter, D. L., Dale, A. M., Rotte, M., & Rosen, B. (in press-a). Functional–anatomic study of episodic retrieval: Selective averaging of event-related fMRI trials to test the retrieval success hypothesis. *NeuroImage.*

Buckner, R. L., Koutstaal, W., Schacter, D. L., Petersen, S. E., Raichle, M. E., & Rosen, B. R. (1997). fMRI studies of item repetition during word generation. *In Proceedings Cognitive Neuroscience Society, 4th Annual Meeting,* (p. 67).

Buckner, R. L., Koutstaal, W., Schacter, D. L., Wagner, A. D., & Rosen, B. R. (in press-b). Functional–anatomic study of episodic retrieval using fMRI: Retrieval effort versus retrieval success. *NeuroImage.*

Buckner, R. L., & Petersen, S. E. (1996). What does neuroimaging tell us about the role of prefrontal cortex in memory retrieval? *Seminars in Neurology,* **8,** 47–55.

Buckner, R. L., Petersen, S. E., Ojemann, J. G., Miezin, F. M., Squire, L. R., & Raichle, M. E. (1995). Functional anatomical studies of explicit and implicit memory retrieval tasks. *Journal of Neuroscience,* **15,** 12–29.

Buckner, R. L., Raichle, M. E., Miezin, F. M., & Petersen, S. E. (1996b). Functional anatomic studies of memory retrieval for auditory words and visual pictures. *Journal of Neuroscience,* **16,** 6219–6235.

Buckner, R. L., & Tulving, E. (1995). Neuroimaging studies of memory: Theory and recent PET results. *In* F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 10, pp. 439–466). Amsterdam: Elsevier.

Cabeza, R., & Nyberg, L. (1997). Imaging cognition: An empirical review of PET studies with normal subjects. *Journal of Cognitive Neuroscience,* **9,** 1–26.

Cohen, N. J., & Eichenbaum, H. (1993). *Memory, amnesia, and the hippocampal system*. Cambridge, MA: MIT Press.

Dale, A. M., & Buckner, R. L. (1997). Selective averaging of rapidly presented individual trials using fMRI. *Human Brain Map.*

Demb, J. B., Desmond, J. E., Wagner, A. D., Vaidya, C. J., Glouer, G. H., & Gabrieli, J. D. E. (1995). Semantic encoding and retrieval in the left inferior prefrontal cortex: A functional MRI study of task difficulty and process specificity. *Journal of Neuroscience,* **15,** 5870–5878.

Fletcher, P. C., Frith, C. D., Grasby, P. M., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). Brain systems for encoding and retrieval of auditory verbal memory: An *in vivo* study in humans. *Brain,* **118,** 401–416.

Fletcher, P. C., Frith, C. D., & Rugg, M. D. (1997). The functional neuroanatomy of episodic memory. *Trends in Neuroscience,* **20,** 213–223.

Fuster, J. M. (1989). *The prefrontal cortex* (2nd ed.). New York: Raven Press.

Gabrieli, J. D. E., Brewer, J. B., Desmond, J. E., & Glover, G. H. (1997). Separate neural bases of two fundamental memory processes in the human medial temporal lobe. *Science,* **276,** 264–266.

Gabrieli, J. D. E., Desmond, J. E., Demb, J. B., Wagner, A. D., Stone, M. V., Vaidya, C. J., & Glover, G. H. (1996). Functional magnetic resonance imaging of semantic memory processes in the frontal lobes. *Psychological Sciences,* **7,** 278–283.

Gabrieli, J. D. E., Fleischman, D. A., Keane, M. M., Reminger, S. L., & Morrell, F. (1995). Double dissociation between memory systems underlying explicit and implicit memory in the human brain. *Psychological Science,* **6,** 76–82.

Graf, P., & Mandler, G. (1984). Activation makes words more accessible, but not necessarily more retrievable. *Journal of Verbal Learning and Verbal Behavior,* **23,** 553–568.

Graf, P., & Schacter, D. L. (1985). Implicit and explicit memory for new associations in normal subjects and amnesic patients. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* **11,** 501–518.

Graf, P., Squire, L. R., & Mandler, G. (1984). The information that amnesic patients do not forget. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* **10,** 164–178.

Hamann, S. B., & Squire, L. R. (1997). Intact perceptual memory in the absence of conscious memory. *Behavioral Neuroscience,* **111,** 850–854.

Hamann, S. B., Squire, L. R., & Schacter, D. L. (1995). Perceptual thresholds and priming in amnesia. *Neuropsychology,* **9,** 1–13.

Heckers, S., Rauch, S. L., Goff, D. L., Savage, C. R., Schacter, D. L., & Alpert, N. M. (1997). Impaired hippocampal but preserved prefrontal activation during episodic memory retrieval in schizophrenia. Submitted for publication.

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language,* **30,** 513–541.

Josephs, O., Turner, R., & Friston, K. (in press). Event-related fMRI. *Human Brain Map.*

Kapur, S., Craik, F. I. M., Jones, C., Brown, G. H., Houle, S., & Tulving, E. (1995). Functional roles of prefrontal cortex in retrieval of memories: A PET study. *NeuroReport,* **6,** 1880–1884.

MacLeod, A. K., Buckner, R. L., Miezin, F. M., Petersen, S. E., & Raichle, M. E. (in press). Right prefrontal cortex activation during semantic monitoring. *NeuroImage.*

Martin, A., Haxby, J. U., La Londe, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science,* **270,** 102–105.

Martin, A., Wiggs, C. L., & Weisberg, J. (in press). Modulation of human medial temporal lobe activity by form, meaning, and experience. *Hippocampus.*

Nyberg, L., Cabeza, R., & Tulving, E. (1996). PET studies of encoding and retrieval: The HERA model. *Psychonomic Bulletin and Review,* **3,** 135–148.

Nyberg, L., McIntosh, A. R., Houle, S., Nilsson, L.-G., & Tulving, E. (1996). Activation of medial temporal structures during episodic memory retrieval. *Nature,* **380,** 715–717.

Nyberg, L., Tulving, E., Habib, R., Nilsson, L.-G., Kapur, S., Houle, S., Cabeza, R., & McIntosh, A. R. (1995). Functional brain maps of retrieval mode and recovery of episodic information. *NeuroReport,* **6,** 249–252.

Ostergaard, A. L., & Jernigan, T. L. (1993). Are word priming and explicit memory mediated by different brain structures? In P. Graf & M. E. J. Masson (Eds.), *Implicit memory: New directions in cognitive, development, and neuropsychology* (pp. 327–349). Hillsdale, NJ: Erlbaum.

Petrides, M., Alivisatos, B., & Evans, A. (1995). Functional activation of the human ventrolateral frontal cortex during mnemonic retrieval of verbal information. *Proceedings of the National Academy of Sciences of the United States of America,* **92,** 5803–5807.

Raichle, M. E., Fiez, J. A., Videen, T. O., MacLeod, A. M., Pardo, J. V., Fox, P. T., & Petersen, S. E. (1994). Practice-related changes in human brain functional anatomy during nonmotor learning. *Cerebral Cortex,* **4,** 8–26.

Richardson-Klavehn, A., & Bjork, R. A. (1988). Measures of memory. *Annual Reviews of Psychology,* **36,** 475–543.

Richardson-Klavehn, A., Gardiner, J. M., & Java, R. I. (1994). Involuntary conscious memory and the method of opposition. *Memory,* **2,** 1–29.

Roediger, H. L., III, & McDermott, K. B. (1993). Implicit memory in normal human subjects. In H. Spinnler & F. Boller (Eds.), *Handbook of neuropsychology* (Vol. 8, pp. 63–131). Amsterdam: Elsevier.

Roediger, H. L., III, Weldon, M. S., & Challis, B. H. (1989). Explaining dissociations between implicit and explicit measures of retention: A processing account. In H. L. I. Roediger & F. I. M. Craik (Eds.), *Varieties of memory and consciousness: Essays in honor of Endel Tulving* (pp. 3–41). Hillsdale, NJ: Erlbaum.

Rosen, B. R., Buckner, R. L., & Dale, A. M. (1998). Event related fMRI: Past, present, and future. *Proceedings of the National Academy of Sciences of the United States of America,* **95,** 773–780.

Rugg, M. D., Fletcher, P. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Differential activation of the prefrontal cortex in successful and unsuccessful memory retrieval. *Brain,* **119,** 2073–2083.

Rugg, M. D., Fletcher, P. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1997). Brain regions supporting intentional and incidental memory: A PET study. *NeuroReport,* **8,** 1283–1287.

Schacter, D. L. (1987a). Implicit memory: History and current status. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* **13,** 501–518.

Schacter, D. L. (1987b). Memory, amnesia, and frontal lobe dysfunction. *Psychobiology,* **15,** 21–36.

Schacter, D. L. (1996). *Searching for memory: The brain, the mind, and the past.* New York: Basic Books.

Schacter, D. L., Alpert, N. M., Savage, C. R., Rauch, S. L., & Albert, M. S. (1996a). Conscious recollection and the human hippocampal formation: Evidence from positron emission tomography. *Proceedings of the National Academy of Sciences of the United States of America.* **93,** 321–325.

Schacter, D. L., Bowers, J., & Booker, J. (1989). Intention, awareness, and implicit memory: The retrieval intentionality criterion. In S. Lewandowsky, J. C. Dunn, & K. Kirsner (Eds.), *Implicit memory: Theoretical issues* (pp. 47–69). Hillsdale, NJ: Erlbaum.

Schacter, D. L., Buckner, R. L., Koutstaal, W., Dale, A. M., & Rosen, B. R. (1997a). Late onset of anterior prefrontal activity during true and false recognition: An event-related fMRI study. *NeuroImage,* **6,** 259–269.

Schacter, D. L., Chiu, C. Y. P., & Ochsner, K. N. (1993). Implicit memory: A selective review. *Annual Reviews of Neuroscience,* **16,** 159–182.

Schacter, D. L., Church, B., & Treadwell, J. (1994). Implicit memory in amnesic patients: Evidence for spared auditory priming. *Psychological Science,* **5,** 20–25.

Schacter, D. L., Reiman, E., Uecker, A., Polster, M. R., Yun, L. S., & Cooper, L. A. (1995). Brain regions associated with retrieval of structurally coherent visual information. *Nature,* **376,** 587–590.

Schacter, D. L., Savage, C. R., Alpert, N. M., Rauch, S. L., & Albert, M. S. (1996b). The role of hippocampus and frontal cortex in age-related memory changes: A PET study. *NeuroReport,* **7,** 1165–1169.

Schacter, D. L., & Tulving, E. (Eds.). (1994). *Memory systems 1994.* Cambridge, MA: MIT Press.

Schacter, D. L., Uecker, A., Reiman, E., Yun, L. S., Bandy, D., Chen, K., Cooper, L. A., & Curran, T. (1997b). Effects of size and orientation change on hippocampal activation during episodic recognition: A PET study. *NeuroReport,* **8,** 3993–3998.

Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. *Psychological Review,* **94,** 439–454.

Squire, L. R. (1987). *Memory and brain.* New York: Oxford Univ. Press.

Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review,* **99,** 195–231.

Squire, L. R. (1994). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. In D. L. Schacter & E. Tulving (Eds.), *Memory Systems 1994* (pp. 203–231). Cambridge, MA: MIT Press.

Squire, L. R., Ojemann, J. G., Miezin, F. M., Petersen, S. E., Videen, T. O., & Raichle, M. E. (1992). Activation of the hippocampus in normal humans: A functional anatomical study of memory. *Proceedings of the National Academy of Sciences of the United States of America,* **89,** 1837–1841.

Tulving, E. (1983). *Elements of episodic memory.* Oxford, England: Clarendon Press.

Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994a). Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proceedings of the National Academy of Sciences of the United States of America,* **91,** 2016–2020.

Tulving, E., Kapur, S., Markowitsch, H. J., Craik, F. I. M., Habib, R., & Houle, S. (1994b). Neuroanatomical correlates of retrieval in episodic memory: Auditory sentence recognition. *Proceedings of the National Academy of Sciences of the United States of America,* **91,** 2012–2015.

Tulving, E., & Schacter, D. L. (1990). Priming and human memory systems. *Science,* **247,** 301–306.

Ungerleider, L. G. (1995). Functional brain imaging studies of cortical mechanisms for memory. *Science,* **270,** 760–775.

Wagner, A. D., Buckner, R. L., Koutstaal, W., Schacter, D. L., Gabrieli, J. D. E., & Rosen, B. R. (1997a). An fMRI study of within- and across-task item repetition during semantic classification. *In Cognitive Neuroscience Society, 4th Annual Meeting* (p. 68).

Wagner, A. D., Desmond, J. E., Demb, J. B., Glover, G. H., & Gabrieli, J. D. E. (1997b). Semantic repetition priming for verbal and pictorial knowledge: A functional MRI study of left inferior prefrontal cortex. *Journal of Cognitive Neuroscience,* **9,** 714–726.

Wagner, A. D., Desmond, J. E., Glover, G. H., & Gabrieli, J. (1997c). Prefrontal cortex and recognition memory: fMRI evidence for context dependent retrieval processes. Submitted for publication.

Warrington, E. K., & Weiskrantz, L. (1974). The effect of prior learning on subsequent retention in amnesic patients. *Neuropsychologia,* **12,** 419–428.

Wheeler, M. A., Stuss, D. T., & Tulving, E. (1995). Frontal lobe damage produces episodic memory impairment. *Journal of International Neuropsychological Society,* **1,** 525–533.

Zarahn, E., Aguirre, G., & D'Esposito, M. (in press). A trial-based experimental design for fMRI. *NeuroImage.*