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*Phil. Trans. R. Soc. Lond. B* 1998 **353**, 1861-1878
doi: 10.1098/rstb.1998.0338

THE ROYAL
SOCIETY

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Neuroimaging techniques that allow the assessment of memory performance in healthy human volunteers while simultaneously obtaining measurements of brain activity *in vivo* may offer new information on the neural correlates of particular forms of memory retrieval and their association with consciousness and intention. We consider evidence from studies with positron emission tomography and functional magnetic resonance imaging indicating that priming, a form of implicit retrieval, is associated with decreased activity in various cortical regions. We also consider evidence concerning the question of whether 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. Last, we consider recent efforts to probe the relation between the phenomenological character of remembering and neural activity. In this instance we broaden our scope to include studies employing event-related potentials and consider evidence concerning the neural correlates of qualitatively different forms of memory, including memory that is specifically associated with a sense of self, and the recollection of particular temporal or perceptual features that might contribute to a rich and vivid experience of the past.

**Keywords:** neuroimaging; episodic memory; memory retrieval; priming; frontal lobes; hippocampal formation

## 1. INTRODUCTION

Psychologists and neuropsychologists have long known of, and been fascinated by, apparent breaks or disruptions in the 'usual' relations between consciousness and memory. From within psychology, the familiar, but still intriguing, examples are many: fugue states and multiple or dissociated personalities, where parts of the self can be partly or completely amnesic for the experiences and undertakings of other aspects of the self (Kihlstrom & Schacter 1995; Schacter & Kihlstrom 1989), and the counterintuitive findings from hypnotic states (Kihlstrom 1997), in which information can be assimilated and subsequently used or acted on without any recognition of where that information was acquired ('source amnesia') (Evans & Thorn 1966; Schacter *et al.* 1984). However, it was from within neuropsychology—and specifically from studies of organic amnesia—that the strongest impetus to understand dissociations between conscious awareness and memory has derived. Demonstrations that amnesic patients could retain and express knowledge of a specific prior episode in the absence of any conscious or explicit recollection of that episode (see, for example, Cohen & Squire 1980; Graf *et al.* 1984; Jacoby & Witherspoon 1982; Schacter 1985; Milner *et al.* 1968; Moscovitch 1982; Warrington & Weiskrantz 1968, 1974) provided a new rationale for asking about similar dissociations in the memory of normal subjects and also a methodology for doing so. Based in large part on these studies with amnesic patients, studies of cognitively intact individuals also began to reveal striking demonstrations of 'remembering' without conscious awareness of a prior episode (see, for example, Graf *et al.* 1982; Eich 1984; Jacoby & Dallas 1981; Tulving *et al.* 1982).

Taken together, studies of normal and abnormal memory converged on a distinction between explicit and implicit forms of memory (Graf & Schacter 1985; Schacter 1987*a*) (compare with Squire (1994) for the related distinction between declarative and non-declarative 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 non-conscious effects of past experiences on subsequent behaviour and performance, such as priming or skill learning, that are revealed by tests that do not require the 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 (reviewed by Cohen & Eichenbaum (1993), Moscovitch *et al.* (1994), Roediger & McDermott (1993), Schacter & Buckner (1998*a*) and Schacter *et al.* (1993)).

As noted by Graf and Schacter (1985) and by Schacter (1987*a*), 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, non-conscious

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changes in performance or behaviour. However, as pointed out by Schacter (1987*a*) and discussed at length in subsequent articles (e.g. Richardson-Klavehn & Bjork 1988; Schacter *et al.* 1989; Richardson-Klavehn *et al.* 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. Secondly, 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.

Here we consider the relations between conscious recollection, intentional retrieval and non-conscious influences of past events from the perspective of recent research with the use of 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 (reviewed by Buckner & Koutstaal (1998), Cabeza & Nyberg (1997), Ungerleider (1995) and Fletcher *et al.* (1997)). We suggest that evidence obtained from neuroimaging studies with PET or fMRI can provide useful converging evidence that might help to clarify the relations between conscious recollection, intentional retrieval and non-conscious influences that have so far been considered mainly from a cognitive perspective. We begin by reviewing recent studies that have provided relevant evidence about non-conscious priming effects, and then consider studies that have examined components of explicit retrieval. Thereafter we apply findings and ideas arising from these studies to studies in which interactions between implicit and explicit retrieval processes are of central concern. In the final section we consider additional issues relating to the phenomenological experience of remembering—the nature of recollection, its connection to the self and to conscious awareness of particular qualitative features of past events—and how recent neuroimaging findings (including event-related potentials, which have proved particularly informative on these questions) also might inform us about this aspect of remembering that is most intimately connected with consciousness.

## 2. 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 (reviewed by Roediger & McDermott (1993) and 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 (compare Gabrieli *et al.* (1995), Graf *et al.* (1984), Hamann *et al.* (1995), Schacter *et al.* (1994) and 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 he is consistently unable to attain above-chance scores on either forced-choice or yes/no 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 *et al.* 1995; Squire *et al.* 1992) and follow-up studies by Schacter *et al.* (1996*a*) and Backman *et al.* (1997), word-stem completion was explored for evidence of priming-related activation changes. Subjects studied words before 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 the completion of novel stems, showed reduced activation when word-stems were primed. Such an effect might reflect a neural correlate of perceptual priming: after exposure to a stimulus, subsequent processing is faster and requires less neural activity. Blaxton *et al.* (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 *et al.* 1995) and object classification (Buckner *et al.* 1998*a*) 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 (see, for example, Schacter *et al.* (1995)), but the appearance of reductions across different task and stimulus conditions is striking.

The foregoing findings are generally consistent with the idea that priming might be attributable, at least in part, to the facilitation of perceptual processes and are also consistent with neuropsychological data showing

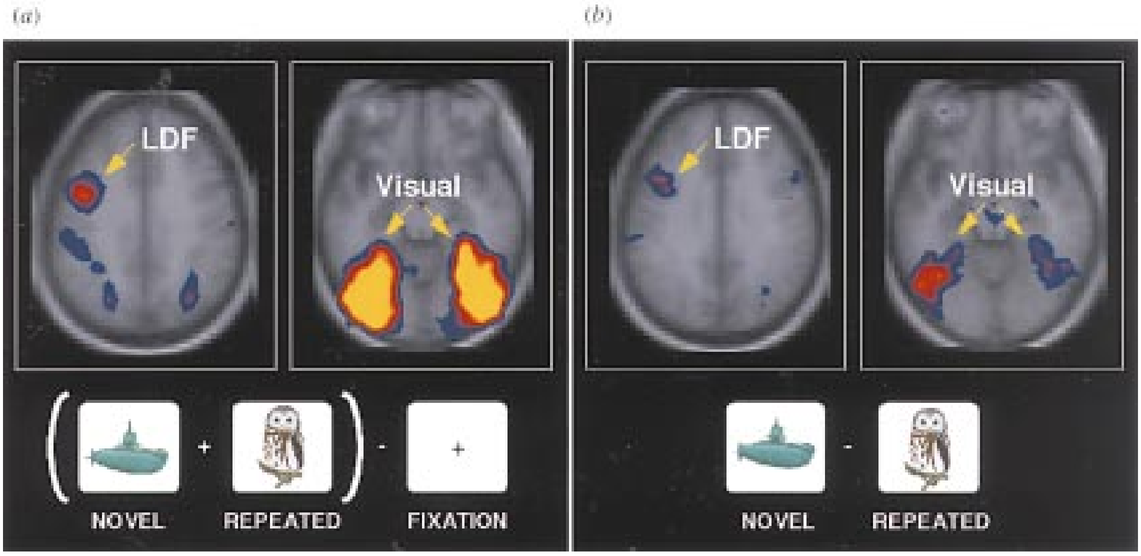

Figure 1. fMRI images of priming. The images in the upper row are fMRI data (coloured scale, with brighter colours indicating larger signal change) displayed on top of anatomical images. Images are from horizontal sections through the brain. The images below the fMRI data are a schematic representation of the comparison being imaged. (*a*) fMRI data show brain areas activated by an object classification task (for both novel and repeated items) compared with a low-level fixation control task, collapsing over both novel and repeated items, revealing the network of brain areas activated in common by both item types. These include the left dorsal frontal (LDF) cortex and visual areas. (*b*) When novel items are contrasted directly with repeated items, areas showing reduced activation in relation to priming are revealed.

impaired perceptual priming after lesions to posterior perceptual processing areas (Gabrieli *et al.* 1995; Keane *et al.* 1995). However, the selective locus of the priming effects (i.e. the restriction of the effects to perceptual processing regions) is surprising in view of the finding that more extensive patterns of brain activation are observed during stem completion of novel, non-primed words. Specifically, robust left prefrontal activation is consistently observed during word-stem completion (as well as during many other verbal production tasks and semantic retrieval tasks), yet in these early studies of word-stem completion, few if any changes within prefrontal areas were reported in association with priming (one exception was that of Schacter *et al.* (1996*a*), who did report a left prefrontal (BA 47) increase in blood flow in association with priming).

Raichle *et al.* (1994) and Gabrieli and colleagues (Demb *et al.* 1995; Gabrieli *et al.* 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) employed an associate word generation task in which participants were presented with nouns and were asked to generate verbs meaningfully related to the nouns (e.g. given the word 'dog', participants might generate 'walk' or 'bark'). Unpractised or 'naive' performance of this task activated many areas, including portions of the left prefrontal cortex. After many repetitions with the same set of nouns, however, task performance no longer activated the left prefrontal cortex, suggesting again that repeated exposure to items can lead to reduced neural activity in specific brain areas. Demb *et al.* (1995) noted a similar phenomenon with a word classification task in which participants were asked to decide whether presented words referred to entities that were abstract (e.g. hope) or concrete (e.g. cup). Left prefrontal regions showed reduced activation during performance with repeated items compared with novel items, even after a single exposure to an item. Using a semantic association task, Blaxton *et al.* (1996) similarly reported reduced activation of left inferior cortex (BA 47) as a function of prior performance: after a single study exposure to a word pair such as sky–eagle, subjects showed less activation when later asked to produce an associate to the cue sky than if sky was never previously presented and occurred only at test. Wagner *et al.* (1997*b*) and Buckner *et al.* (1998*a*) have recently noted similar prefrontal reductions for the semantic classification of object pictures. (See figure 1 for illustrative data from an object classification task.) 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 anatomic and functional specificity of the observed activation reductions. As noted, the initial studies of word-stem completion demonstrated reductions in activation 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 that 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 the study

(Buckner & Koutstaal 1998). In all of the prior studies of word-stem completion, participants were engaged in an orientating task during the study (for example, they were asked to rate how much they liked the presented words), not a word-stem completion task. Thus the same items were repeated (at least partly) 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: (i) 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 reductions when repeated exactly (see, for example, Demb *et al.* 1995); and (ii) tasks such as word-stem completion, which typically show perceptual processing priming effects in across-task conditions, should, in addition, 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 *et al.* (1997) demonstrated left prefrontal reductions as a function of prior stimulus exposure on a word-stem completion task under conditions where identical visual cues and the same task were repeated. Subjects performed word-stem completion with a repeating set of stem cues during certain fMRI task blocks: the same set of word-stems was presented five or six times, each time in a different order and in a separate task block; behavioural performance and neural activation during these blocks was then contrasted with novel task blocks during which new (never previously presented) word-stem cues were shown. 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 the verb-generation task described above and auditory word-stem completion (e.g. hear 'pur' and generate 'perfect' or 'purple' (Koutstaal *et al.* 1997)), 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 the perceptual overlap of items across repetitions, the overall pattern of findings suggests that 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 will therefore manifest priming-related modulations. Such an idea is consistent with a transfer-appropriate processing framework, which postulates that performance is facilitated relative to the degree to which the processes engaged at study and test overlap or 'recapitulate' one another (Blaxton 1989; Kolers 1973; Morris *et al.* 1977; Roediger *et al.* 1989) and is also consistent with the idea that specialized domain-specific subsystems can be biased via priming (Tulving & Schacter 1990; Schacter & Tulving 1994; Squire 1994).

Studies by Demb *et al.* (1995) and Wagner *et al.* (1997*a*) 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 or 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 the left prefrontal cortex. However, this result only partly establishes functional specialization, because the perceptual-decision task probably did not activate the left prefrontal cortex initially; accordingly, it is difficult to interpret a lack of activation reduction. Wagner *et al.* (1997*a*) 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- or concrete-decision task. This manipulation revealed that (i) the left dorsal prefrontal cortex was activated by the abstract- or concrete-decision task, and (ii) the activation was not reduced as a consequence of prior exposure to the items in the perceptual-decision task. In contrast, a second condition that involved repetition of the exact items and task demands with the abstract- or 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 seem to be selective, depending on item and task overlap across repetitions. However, three further points merit noting.

First, the evidence so far leaves open the question of whether precisely the same task must be repeated for reductions to be observed, or if certain elements of the task are more essential, and repetition of these elements alone would result in reduced neural activity. That is, the extent to which reductions might track with the degree of task component overlap remains largely unexplored. For example, in a behavioural study with the verb generation task, Seger *et al.* (1997) found that facilitation on this task was specific to the verbs that were generated rather than to the nouns, or to the noun–verb pairs. Priming, as shown by reduced response times, was essentially equivalent whether a previously generated verb was provided to the same noun as on prior trials, or to a novel noun. In this example there is some variation in the components of the task (e.g. the nature of the stimulus differed between initial exposure and the 'test' situation), but nonetheless a considerable portion of the task requirements remains constant. The extent to which the priming-related activation reductions observed in the left dorsal and inferior prefrontal regions might also be immune to these forms of (relatively limited) changes in the precise nature of the task remains to be explored.

Second, the reductions observed do not necessarily directly reflect the retrieval of semantic information but might reflect the facilitation of other processes, such as those involved in selecting and manipulating semantic representations (Price *et al.* 1997; Wagner *et al.* 1997*b*) and also concurrent phonological activation and decisions (Price *et al.* 1997). For example, Thompson-Schill *et al.* (1998) have suggested that activations in the left inferior frontal gyrus observed across multiple types of tasks are related to the requirement for the selection of information from competing alternatives in semantic memory, with greater activation observed under conditions demanding a high degree of selection than under conditions that require less selection. More generally, it has been proposed that certain regions within the left prefrontal cortex might 'act as a semantic executive system that accesses long-term semantic knowledge required to meet task demands and that computationally benefits from prior access to this knowledge' (Wagner *et al.* 1997*b*, p. 722) (also compare Demb *et al.* (1995) and Fiez (1997)). Interestingly, a recent case report with the use of both PET and intra-operative cortical stimulation provides evidence for a distinction between mere repetition and selection from memory; further, it suggested that retrieval and production of the response might dissociate (Klein *et al.* 1997). Whereas intra-operative stimulation of the left inferior frontal gyrus interfered with the patient's ability to provide synonyms of presented words, such stimulation did not interfere with the patient's ability to simply repeat those words. In a post-operative debriefing, the patient described the experience as 'thought-blocking' where, although he knew what word he wanted to say (possibly indicating successful retrieval) he was unable to say it (possibly demonstrating inability to perform the requisite translation into phonology or to perform other operations). Such observations are completely consistent with the kinds of interpretation given to the repetition reductions noted, which might reflect the diminished need for these areas in responding to overlearned stimuli (e.g. simple repetition) but their nevertheless critical contribution for generating responses in novel (unprimed) situations (Raichle *et al.* 1994).

Third, we also have not considered the possibility of whether priming-related reductions are partly or entirely attributable to explicit memory: either the intentional or unintentional recollection of previously presented items. We elaborate on this issue below, but for now note that 'explicit contamination' (i.e. an unintended contribution of explicit memory processes to performance) is an unlikely explanation on several counts.

(i) Similar findings have been obtained in normal subjects in a situation which, owing to the use of a perceptual orientating task, participants had generally low levels of explicit recall. In one of the experiments by Schacter *et al.* (1996*a*), priming-related reductions in the posterior visual cortex were observed during word-stem completion after words were studied during a T-junction counting task (participants were asked to count the number of places in which the letters of the words formed a T shape) and where levels of explicit recall were low.

(ii) In a behavioural task, employing a repeated task paradigm very similar to those employed in the fMRI studies, amnesic patients have demonstrated a pattern of response facilitation that was indistinguishable from that of normal controls (Seger *et al.* 1997) and similar to that observed in the fMRI studies using this paradigm (Buckner *et al.* 1997; Koutstaal *et al.* 1997).

(iii) 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 suggests that they are not. Gabrieli *et al.* (1996), and later Buckner & 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 will be discussed in the next section, seem to have a separate set of functional–anatomic correlates.

## 3. 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 below have examined the two together. Such studies have provided evidence for the activation of numerous brain regions during explicit retrieval in a variety of different tasks and conditions, with the preferential engagement of specific brain regions in many of these tasks (reviewed by Buckner & Petersen (1996), Cabeza & Nyberg (1997) and 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 relationship between conscious recollection and intentional retrieval that are central to this article.

One of the more surprising findings from neuroimaging studies of explicit retrieval is that various regions of the prefrontal cortex have been consistently activated during both recall and recognition tasks (Buckner & Petersen 1996; Cabeza *et al.* 1997; Nyberg *et al.* 1996*a*; Fletcher *et al.* 1997), including an anterior frontopolar region (centred at or near Brodmann area (BA) 10) that shows particularly marked right-sided activation, a dorsolateral region (in the vicinity of BA 9 and BA 46) and sometimes a more posterior frontal or 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 *et al.* 1998). 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 (compare Fuster (1989), Schacter (1987*b*), Squire (1987) and Wheeler *et al.* (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 view 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 or medial temporal activation (see, for example, Andreasen *et al.* 1995; Buckner *et al.* 1995, 1996*b*, 1998*b*,*c*; Petrides *et* *al.* 1995; Fletcher *et al.* 1995; Tulving *et al.* 1994*b*). 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 *et al.* (1997) and Ungerleider (1995)).

Most relevantly to the present purposes, a number of studies have examined prefrontal or medial temporal regions in the context of the distinction between, on the one hand, successful conscious recollection and, on the other, intentional retrieval effort. 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 the effort made in attempting to retrieve the target material, independently of whether retrieval is successful. To separate out the contributions of successful conscious recollection from those of intentional retrieval effort, two main experimental strategies have been used: (i) producing high and low levels of successful retrieval by manipulating study conditions, and (ii) 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.* (1996*a*) that used a stem-cued recall task, which was performed as a follow-up to the stem completion priming experiment of Schacter *et al.* noted above. The study by Squire *et al.* (1992) 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 non-studied 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.* (1996*a*) experiment, subjects studied a list composed of two different types of words before being PET scanned. 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 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 recall most of the study list words correctly, 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 non-studied three-letter stems with the first word that came to mind (bilateral), or compared with the low-recall condition (right hippocampus or parahippocampal gyrus). In contrast, there were no hippocampal increases in the low-recall condition. These results confirm the previous findings of Squire *et al.* (1992) of parahippocampal activation during stem-cued recall and also suggest that the failure of Schacter *et al.* (1996*a*) to observe hippocampal activation during priming was not simply attributable to some general difficulty with reliable activation of the hippocampal formation.

Perhaps more importantly, the fact that Schacter *et al.* (1996*a*) observed hippocampal activation during the high-recall but not the low-recall condition points towards 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 might 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 (compare also Schacter (1997)). Consistent with these suggestions, the Schacter *et al.* (1996*a*) results are supported by other PET findings showing greater hippocampal activation in high than in low-recognition memory conditions (Rugg *et al.* 1997; Schacter *et al.* 1995; compare Nyberg *et al.* 1996*b*).

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

In a subsequent study using the same paradigm, Schacter *et al.* (1996*c*) found that elderly adults (mean age approximately 70 years), like college students in the study by Schacter *et al.* (1996*a*), showed significant hippocampal blood flow increases in the high-recall condition compared with the low-recall condition. In 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 might 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 *et al.* (1998), who studied schizophrenic patients and age-matched control subjects (mean age approximately 40 years for both groups). The control subjects, like college students and elderly adults in the two earlier studies, showed significant (right) hippocampal blood flow increases in the high-recall condition compared with the low-recall condition. In contrast, schizophrenics exhibited no such increases. However, schizophrenics did exhibit robust anterior prefrontal increases in the low-recall condition compared to the baseline; control subjects also showed prefrontal increases in the low-recall condition, but these increases 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.* (1996*c*)—show specific abnormalities in activating hippocampal regions in conditions the promote high levels of successful conscious recollection.

Nyberg *et al.* (1995) examined similar distinctions between high- and low-performance conditions in an old- or 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 conditions (high recognition, low recognition and new) was associated with increased blood flow in the 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 or 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 (compare with McIntosh *et al.* 1997).

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.* performed a PET experiment that used a $2 \times 2$ 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). After each type of encoding task they were given either an old- or new-recognition test (intentional retrieval) or an animate- or inanimate-decision task in which subjects judged whether presented items were living or non-living (unintentional retrieval). Deep encoding produced more accurate memory on the intentional-retrieval task. Performance was at ceiling levels on the unintentional task, but Rugg *et al.* 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. First, 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. Second, 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. In contrast, the right prefrontal activation was quite sensitive to the requirement to engage in intentional retrieval, regardless of whether subjects achieved high or low levels of conscious recollection.

Several studies have attempted to separate retrieval effort and success by manipulating the proportion of 'old' or previously studied items presented to subjects during a particular scan. The reasoning here is that (all else being equal) 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 *et al.* (1995) compared blood flow during a high-target-density scan (34 out of 40 old items) with a low-target-density scan (6 out of 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, suggesting that right anterior prefrontal activity is more closely associated with retrieval effort than retrieval success. In contrast, Rugg *et al.* (1996), also using PET, found evidence of greater right anterior prefrontal activity during both a high-density scan (16 out of 20 old items) and a low-density scan (4 out of 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-density scan 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 a discussion of possible reasons for differences between their study and previous findings).

Several recent fMRI studies might 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- or new-recognition memory, Wagner *et al.* (1998) found that with standard test instructions, where subjects were not informed about the composition of studied versus non-studied 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) than 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.* (1998) 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 can vary across different testing contexts.

Two recent fMRI studies point towards a similar conclusion. In one study (Buckner *et al.* 1998*c*), we manipulated levels of recognition memory by varying the type of prior encoding, with one set of scans including items that had been studied previously under deep encoding conditions (abstract or concrete judgments) and another set of scans including items that had been studied previously under shallow encoding conditions (capital- or lowercase-letter judgment task). Deep encoding yielded high levels of recognition success with low levels of effort (as indicated by relatively brief response times), and shallow encoding yielded low levels of recognition success with high levels of effort (indicated by relatively long response times). 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.* (1996*a*)). 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 *et al.* (1998*b*) used newly developed procedures for obtaining and analysing event-related fMRI data (Rosen *et al.* 1998) to explore further the 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 behavioural 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 *et al.* (1996*a*), Dale & Buckner (1997), Rosen *et al.* (1998), Josephs *et al.* (1997) and Zarahn *et al.* (1997)). The evidence linking right anterior prefrontal activation with retrieval success in the studies by Buckner *et al.* (1998*c*) and Rugg *et al.* (1996) came from blocked trial procedures. Buckner *et al.* (1998*b*) 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 than for 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.* (1998*b*) 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.* (1998*b*) suggested that, consistent with the arguments of Wagner *et al.* (1997*a*), the apparent association between successful recognition and right anterior prefrontal activation described by Buckner *et al.* (1998*c*) and Rugg *et al.* (1996) might 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 event-related fMRI study by Buckner *et al.* (1998*b*), and in another event-related fMRI study of true and false recognition memory by Schacter *et al.* (1997*a*). Both studies found evidence that right (and left) anterior prefrontal activations exhibit a late onset relative to virtually all other brain regions. Although follow-up studies will be required for an interpretation of the relative contributions of neural and blood-flow related factors to this observed delay, one possible explanation of this effect is that anterior prefrontal regions are involved in effortful post-retrieval monitoring activities (for discussion of alternative possibilities, see Buckner *et al.* (1998*b*) and Schacter *et al.* (1997*a*); compare also the event-related potentials (ERP) findings discussed below, in the last section).

In summary, although numerous issues remain to be resolved, PET and fMRI studies of hippocampal and prefrontal activation provide two suggestions. First, increases in anterior prefrontal blood flow 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 most often 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 might reflect factors in addition to those specifically related to explicit or successful retrieval.

## 4. 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 non-conscious 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: (i) subjects come to realize that their memory is being tested and thereafter they change their strategy, intentionally retrieving study-list words while performing the (now 'nominal') priming task; (ii) subjects follow instructions and consistently provide the first word that comes to mind (or follow analogous instructions on other priming tasks), but they unintentionally recollect that they had studied some of the target items on the previous study list. For example, participants might unintentionally produce a studied word and then also notice that they had encountered the word at an earlier point in the session. Post-experimental debriefing of individuals has indicated that such spontaneous noticing of the relationship between a particular test item and earlier-presented materials can occur, and need not necessarily involve the alteration of participants' subsequent approach to the task (see, for example, Curran *et al.* (1996); compare Bowers & Schacter (1990)), although in some instances it might (for detailed discussion see Schacter *et al.* (1989)). Schacter (1987*a*) 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), chapter 1; also, for a recent effort to quantify and characterize the nature of such involuntary recollection in day-to-day life, see Berntsen (1996)).

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 (compare Bowers & Schacter (1990), Richardson-Klavehn *et al.* (1994), Schacter *et al.* (1989) and Jacoby (1991)). We now consider how some of the previously considered findings from neuroimaging studies might 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 before a PET scan. 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 presented visually. Two relevant scans were performed during the stem completion task: for one scan, it was possible to complete stems with study list words (the priming condition), and for the other, stems could be completed only with new words that had not been presented on the study list (the baseline condition). 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, completing the stems with previously studied words (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 versus baseline comparison).

In view 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 might have intentionally retrieved words from the study list or, alternatively, they might have provided the first word that came to mind and involuntarily recollected its prior occurrence. Consideration of the behavioural data of Squire *et al.* indicates an unusually high level of priming, which 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 non-studied items was 0.08). Consistent with this suggestion, the study conditions used by Squire *et al.* were conducive to high levels of explicit memory: they used short study lists and brief study-test delays; in addition, subjects saw all target words twice during the study phase and performed a 'deep' encoding task (pleasantness rating) known to promote 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 that involuntary contamination is the most likely explanation. Two sources of behavioural data point towards this conclusion. First, subjects were no more likely to recall words on the second half of the test lists than the first half, contrary to what might be expected if subjects began to intentionally recall items once they became aware of the embedded study words (R. L. Buckner, unpublished observations). Second, participants' response times during the production of novel words during the primed stem-completion blocks were indistinguishable from those for 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 as might be expected if, during the primed blocks, participants were engaging in an explicit search and provided new responses only after they had searched for but failed to retrieve a suitable study item. In contrast, in stem-cued recall—where subjects were intentionally trying to retrieve items—a highly significant increase in reaction time was associated with novel word production, perhaps a direct behavioural reflection of the added processes related to voluntary explicit retrieval.

Alternatively, it is conceivable that the hippocampal region has a more prominent role in priming than is generally acknowledged, and that the parahippocampal activations observed by Squire *et al.* (1992) 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 seems 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 artefacts. Hamann *et al.* (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, the finding by Squire *et al.* (1992) 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 with a similar explicit cued recall procedure, Buckner *et al.* (1995) failed to observe hippocampal blood flow increases when either the modality of the study and test words differed (i.e. words were studied auditorily but tested visually), or the typecase of study and test words differed (i.e. visually tested words were studied in lowercase and tested in capitals). 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 same typecase (0.76). However, significant hippocampal activation during explicit recall was observed only when words were studied and tested in the same typecase. We shall 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 or 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 increases in blood flow 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 (reviewed by Buckner (1996) and Tulving *et al.* (1994*a*)). Importantly for our purposes, in contrast with 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 experiments of Squire *et al.* (1992) and Buckner *et al.* (1995), Schacter *et al.* (1996*a*) 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.* (1996*a*) attempted to eliminate explicit contamination by using a non-semantic study task in which subjects count the number of T-junctions in each of the target words (i.e. the numbers of points where two lines meet). Previous studies of stem completion priming have shown robust priming after 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.* (1992) reflects contamination from explicit memory, then use of the T-junction encoding task should eliminate both the explicit contamination and the associated hippocampal blood flow increases.

Analysis of the behavioural data suggested that, compared with the experiment of Squire *et al.*, explicit contamination had been severely reduced or eliminated: the absolute magnitude of the priming effect was comparable with that of priming in previous experiments in which explicit contamination could be ruled out (Bowers & Schacter 1990; Graf & Mandler 1984). Analysis of the PET data showed no evidence of increases in blood flow 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 experiments of Squire *et al.*, Buckner *et al.* (1995) and Schacter *et al.* (1996*a*)—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 experiment of Schacter *et al.* could simply reflect the fact that it is difficult to reliably observe evidence of hippocampal activation during retrieval (either explicit or implicit). Moreover, even if the data of Schacter *et al.* were tentatively accepted as support for the proposition that hippocampal activation during priming in the study of Squire *et al.* 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 the explicit retrieval experiment of Schacter *et al.* (1996*a*) provide some insight into this issue: hippocampal formation activation was observed in association with successful conscious recollection, whereas anterior prefrontal activation was observed in association with intentional retrieval effort. If the results of the experiments of Squire *et al.*, Buckner *et al.* and Schacter *et al.* are put together, it is possible to offer an hypothesis concerning the nature of the explicit memory contamination in the initial experiment of Squire *et al.* 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 experiment of Squire *et al.*, suggests the operation of involuntary conscious recollection (as opposed to deliberate, intentional 'thinking back' to the study phase). Although this interpretation must be treated cautiously because of its *post hoc* nature, it is buttressed further by the finding (Rugg *et al.* 1997) 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 results of Rugg *et al.* together with those of Squire *et al.* (1992) and Schacter *et al.* (1996*a*), 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*b*; Rugg *et al.* 1997; Schacter *et al.* 1995, 1996*a*,*c*; 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 from 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 *et al.* (1997*b*), who used a paradigm in which subjects study novel shapes and later make old- or new-recognition judgments about previously studied objects and new objects. Schacter *et al.* (1995) had previously found significantly greater changes in blood flow in the region of the hippocampal formation during recognition judgments about studied objects compared with new objects. To determine whether physical similarity between studied and tested objects influences hippocampal formation activations, Schacter *et al.* (1997*b*) compared blood flow increases during an old- or 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 (but subjects were instructed to designate items as 'old' whenever they recognized an object from the study list, regardless of whether it was in the same orientation or size as at study). Schacter *et al.* (1997*b*) found significant hippocampal activation for identical objects, and also found significantly greater left 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 the experiment of Buckner *et al.* (1995), significant increases in hippocampal blood flow were not observed when the physical features of studied and tested objects differed at study and test. (One exception concerned the comparison of orientation-changed old objects against new objects, which also showed a modest right hippocampal increase; however, there were no significant increases in hippocampal blood flow in the comparisons of either the orientation-changed or size-changed items against a passive viewing condition, whereas for the identical items this comparison showed significant increases in bilateral hippocampal blood flow.)

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 participants remembered identical items might have differed from the manner in which they remembered changed items. For example, subjects' recollections might have been less vivid or less confident in the changed-stimulus conditions compared with the identical-stimulus conditions (Schacter *et al.* 1997*b*). This difference in phenomenological experience might not necessarily have reflected differences in subjects' efforts to retrieve information. Indeed, in contrast with the earlier experiment of Schacter *et al.* (1995), there was little evidence of frontal lobe blood flow increases in any of the main comparisons, and more focused comparisons of the activations observed for the various types of studied items (identical, orientation changed, size changed) showed a frontal activation increase only in the orientation-changed condition (probably associated with processes involved in rotating test objects to the study orientation). It is possible that participants' experiences of the identical objects might have involved something akin to involuntary explicit memory, with the greater perceptual match of the cues eliciting a relatively automatic output from the hippocampus (compare Moscovitch 1994), and comprising a form of cue-dependent rather than strategic or controlled accessing of memory. Alternatively, as suggested by Buckner *et al.* (1995), perceptual functions in the hippocampal regions—independent of memory retrieval processes—might be relevant to observed effects of physical similarity between study and test on hippocampal activations. It will prove interesting in future studies to further reconcile all of these results and those from the additional studies that have not noted hippocampal formation activation in relation to successful recollection (see, for example, Rugg *et al.* 1996; Buckner *et al.* 1998*b*,*c*). As noted, a wealth of the present data have suggested that, under certain conditions, hippocampal formation activity might be associated with successful recollection.

## 5. THE EXPERIENCE OF RECOLLECTION

The studies of explicit memory discussed so far have involved recognition or recall of experimentally presented materials. However, the association between consciousness and memory might seem especially relevant for more personally significant and complex events from one's past—events that are more closely interconnected with one's ongoing concerns, values, and sense of oneself as existing in and through time (Tulving 1985; Wheeler *et al.* 1997). Moreover, it might be of particular interest to examine the relation not only between processes of successful recollection in the sense employed up to this point—where 'recollection' refers to the correct recognition or recall of previously presented items—but also between different types of recollective experience. In particular, cognitive research has shown that correct recognition decisions might be based on different types of phenomenological experience (Gardiner & Java 1993; Mandler 1980; Tulving 1985) and different degrees and forms of accompanying qualitative information (Johnson *et al.* 1993; Johnson & Raye 1981), ranging from a comparatively general or vague sense of familarity, with few or no accompanying details concerning the context in which the item or stimulus was previously encountered, to a comparatively rich, highly detailed and vivid re-experiencing of the original episode—including recollection of spatial–temporal information, sensory-perceptual details, and also one's thoughts, judgments, expectations, and so on. Can neuroimaging results also inform us regarding these 'fuller' experiences of recollection?

Although few PET or fMRI studies have examined recollection of pre-experimental episodes, a study by Baron *et al.* (1994) using PET to assess cerebral blood flow and metabolism during a case of transient global amnesia provides relevant, and largely congruent, data. Transient global amnesia involves a condition of isolated and temporary anterograde amnesia of acute onset (probably associated with ischaemia), that clears within a short time (sometimes within minutes, but not lasting longer than 24 hours). Baron *et al.* performed a PET scan during the latter part of a transient global amnesia episode undergone by a 60-year-old woman, at which time she was still experiencing some anterograde and retrograde amnesia (for example, she could not remember all of the details concerning how it was that her arm was in a plaster cast; this had resulted from a fall 10 days earlier). The PET scan revealed a broad region of reduced activity in the right dorsal lateral prefrontal cortex and also a (less marked) reduction in the right thalamus, but no evidence for hippocampal decreases. These frontal and thalamic asymmetries in metabolism were no longer apparent in a later follow-up scan, after amelioration of the amnesic state.

Some evidence concerning the recollection of more personal pre-experimental materials can also be derived from a study by Andreasen *et al.* (1995*b*). During the non-specific 'rest' scans that are sometimes used as a low-level baseline control condition, normal subjects report that they engage in various types of thoughts, particularly about events of the past few days and anticipated or planned activities of that day or subsequent days. In a comparison of this (silent) resting state against a condition where participants verbally reported a specific episode from their past, Andreasen *et al.* (1995*b*) found greater right frontal activation in the rest condition than in a focused episodic-memory condition in which participants were instructed to recall and describe a single specific experience from their past. This difference was unexpected: the focused episodic-memory task was clearly the 'most classic retrieval task' and, on the basis of the PET and fMRI findings reviewed above, might have been expected to be associated with frontal increases. Andreasen *et al.* proposed that the elevated activation in the rest condition might be attributed to two factors. First, because participants were forewarned, before the scan, of the forthcoming episodic-retrieval task and were encouraged to select the episode that they planned to describe, the greater portion of the retrieval process might, in fact, have already occurred before the scan. Second, the amount of retrieval in the episodic task might have been small relative to that in the alleged resting condition (where presumably multiple different episodes might have been retrieved); indeed, Andreasen *et al.* proposed that the baseline condition might be construed as 'random episodic silent thinking' rather than 'REST' in its usual sense of implying an absence of activity. Although this proposal has some plausibility, and underscores an important methodological point regarding the possible implications of using extended periods of undirected activity as a baseline comparison (for discussion, see Shulman *et al.* (1997)), there is clearly a danger of circularity here: the true extent to which individuals were engaging in episodic retrieval during the rest scan is unknown, and such retrieval was probably interspersed to varying degrees with other forms of thought that were not specifically associated with memory *per se*. In addition, there were many differences between the focused-retrieval task and the resting baseline condition that could have contributed to the comparison; conclusively attributing the findings to episodic retrieval is therefore not possible.

More direct and controlled data on the phenomenology of recollection is provided by several recent studies with event-related potentials (ERPs). These studies attempted to differentiate between brain activation observed when, on the one hand, participants recollected contextual information, and when, on the other, they remembered the 'mere fact' of the intra-experimental occurrence of a stimulus, or did not correctly retrieve specific targeted contextual information. Several studies that have examined electrophysiological activity during recognition memory testing have reported more positive ERPs in response to words that are correctly judged as 'old' than for words that are correctly rejected as 'new'; this 'old or new' effect lasts for about 500 ms, onsets at about 300–400 ms after stimulus and, from about 600 ms on, tends to be left-lateralized, particularly at temporo-parietal sites (reviewed by Rugg (1994)). A number of studies have also examined ERPs, not simply as a function of old or new judgments, but with the aim of determining whether experiences of recollection that are accompanied by additional contextual information, or other specific details concerning the earlier occurrence of the item rather than simple 'familiarity' in the absence of such details (see, for example, Mandler 1980; Gardiner & Java 1993), might also be marked by differences in neural activity.

Using a method in which participants themselves provide introspective reports regarding whether their recollective experience involves 'remembering' (mnemonic experience accompanied by additional episodic details) versus 'knowing' (familiarity in the absence of such details), Smith (1993) compared old items given 'remember' responses with old items designated as simply 'known.' As in previous studies, items correctly judged to be old showed greater positivity than those correctly judged to be new; however, in addition, words that were given remember judgments also differed from those given know judgments such that the late positive component observed in the overall analysis was more positive for the remembered items than for the known items. This difference was not present at onset 400–550 ms after stimulus, but was significant at onset 550–700 ms after stimulus. No differences between items later given 'remember' versus 'known' responses were observed when the ERPs present during study were examined (all of the items were deeply encoded with an interesting or not interesting orientating task), suggesting that the divergence in these responses arose because of differences operative at the time of retrieval. These processes were not associated with any one particular topographical region, as relatively greater positivity for recollect (R) than know (K) responses was apparent at frontal, central and parietal sites. (For an additional study employing the R or K approach, but with true and false recognition, see Duzel *et al.* (1997)).

In subsequent work, Wilding *et al.* (1995) and Wilding & Rugg (1996), employed more objective criteria for determining the recollection of context. Wilding *et al.* (1995) presented study items in different modalities (auditory or visual) and then examined event-related potentials separately for items that were correctly identified as old and for which modality at study was correctly identified (hit–hit) versus items that were identified as old but with an incorrect source judgment (hit–miss). In two experiments, one with test words presented visually (experiment 1) and another with test words presented auditorily (experiment 2), they found that a late positive-going component was greater for 'hit–hit' than for 'hit–miss' items. In experiment 1, hit–miss responses did not differ from correct rejections (i.e. there was no old or new effect for these items); in experiment 2, hit–miss responses also showed an old or new effect, but this effect was comparatively restricted relative to that observed for the hit–hit responses: whereas both hit–hit and hit–miss ERPs were more positive than ERPs for correct rejections between 400 and 800 ms after stimulus, after 800 ms to about 1300 ms, the hit–hit ERPs continued to be more positive than those for correct rejections but the waveforms for hit–miss and correct-rejection responses no longer differed.

These findings clearly suggest that neural responses might differ not only as a function of yes or no recognition, but also as a function of the degree or extent of recollection. A further study by Wilding & Rugg (1996) pointed to a similar conclusion. Subjects gave old or new judgments followed by a source decision in which they judged whether words had been presented in a male or a female voice at study. As in previous studies, there was an old or new effect such that, from about 400 ms after stimulus, both hit–hit and hit–miss responses were accompanied by a more positive ERP at parietal sites (left > right); however, in the later phases of the trial, a hit–hit versus correct-rejection difference was also observed in right frontal sites, whereas the hit–miss versus correct-rejection difference in this later phase for frontal sites was much less apparent; further, whereas the effect distributed over left posterior cortex seemed to have disappeared within 1 s, the right frontal effect persisted across the entire recording epoch and still showed no signs of dissipating at well over 1 s. Nonetheless, in both experiments, it seemed that these two effects (the time-limited left posterior effect, and the more persisting right frontal effect) differed quantitatively rather than qualitatively: that is, both the time-course and scalp distribution of ERPs for the hit–hit and hit–miss responses were generally quite similar but were more pronounced for the hit–hit responses.

Several additional strategies have also been employed to examine the nature of recollection and its neural correlates. Wilding & Rugg (1997) recently used a memory exclusion paradigm (Jacoby 1991) in which participants listened to words read in a male or female voice and then were asked to designate as 'old' only items that were spoken in a specific voice (e.g. the male voice), thereby 'excluding' items that were presented in the other voice; items that were old but not in the target voice were to be designated as 'new', as also were the never-presented items. (Note that to obtain acceptable levels of accuracy on this 'exclusion' task, participants also performed a different encoding task for items associated with each voice.) ERP analyses again showed two separable components: a left-lateralized phasic temporo-parietal response was observed for both old items that were correctly designated as targets and old items that were incorrectly thus designated (although somewhat smaller in magnitude for the latter than the former); however, a right-lateralized frontal response was found only for the correctly designated target items.

ERPs accompanying judgments of source by healthy older adults and younger adults have also recently been compared. In a list-discrimination paradigm in which participants were asked to decide on which of two study lists the test words had been presented, Trott *et al.* (1997) found that whereas both older and younger adults showed a reliable (and similar) posterior old or new effect between approximately 500 and 800 ms, only younger adults showed a longer lasting old or new effect at prefrontal and frontal sites (both hit or hit and hit or miss judgments showed increased frontal positivity). These results were quite similar to results from an earlier report (Senkfor & Van Petten 1996) examining older and younger adults' memory for source (male or female voice). During the source judgment task, these researchers found an old or new effect but, in addition, found a large late positivity at prefrontal sites; this difference was found regardless of the accuracy of the source (voice) judgment and was lower in elderly adults than in younger adults.

Last, in yet another approach, Paller *et al.* (1995) compared ERPs during performance of an implicit task (lexical decision) under conditions where participants' prior exposure to the items was varied, with one condition likely to lead to later recollection (a mental-imaging task in which subjects were asked to image the referent of the word and then to decide whether it was smaller or larger than the video monitor) and the other less likely to yield recollection (subjects were asked to decide whether the word contained one or more syllables). Post-experimental measures confirmed that (as expected) the encoding manipulation led to differences in recognition accuracy but did not affect implicit task performance: lexical decision latencies for words in the 'image' and 'syllable' conditions were facilitated equally relative to a novel baseline condition. Nonetheless, the electrophysiological measures obtained during the implicit task showed an overall studied versus non-studied difference, such that studied words showed more positive ERPs than did non-studied words. Furthermore, this effect was larger for words from the image task than for words from the syllable task. These results suggest that there was a neural correlate of conscious recollection during a task that did not require such recollection and might have reflected the 'unintentional' or involuntary forms of recollection described previously for fMRI and PET studies.

Overall, these further findings show that recollection might not comprise an 'all or none' process but rather is a matter of degree: the left-lateralized temporo-parietal old or new effect was often greater for items accompanied by conscious judgments indicative of the recollection of contextual information (but was still observed for items unaccompanied by such recollection) and these more contextually rich judgments were also more likely to be accompanied by a right-lateralized frontal component of longer duration (which, although sometimes observed only for correct judgments, at other times was also observed for incorrect judgments, albeit at a reduced magnitude). From a functional–anatomic perspective, it is possible that the left-lateralized temporo-parietal effect reflects processes dependent on the medial temporal lobes, including the hippocampus and related structures. Reports that this effect might be eliminated or reduced in patients with lesions to these regions are consistent with this possibility (Smith & Halgren 1989; Johnson 1995). However, because scalp electrodes have been found to be insensitive to ERP activity generated in the hippocampus and adjacent structures (Rugg 1995), it has been suggested (Wilding & Rugg 1996) (compare also Tendolkar *et al.* (1997)) that the source of these effects might more probably be in cortical regions that receive input from the medial temporal system (see, for example, Teyler & DiScenna (1986)). In contrast, the right frontal component might be associated with strategic search for, or recovery of, information about context (Moscovitch 1994). Observations that this component is associated with contextual recollection are consistent with data showing disproportionately impaired source memory in patients with prefrontal lesions (Schacter *et al.* 1984, 1996*b*; Shimamura & Squire 1987; Janowsky *et al.* 1989). These observations are also consistent with other neuroimaging findings suggesting impaired or decreased strategic processing among older adults (see, for example, Schacter *et al.* (1996*c*)), and who, under certain conditions, have also been found to show particular deficits for source compared with item memory (Spencer & Raz 1994, 1995). However, as with findings investigating true and false memories with fMRI (Schacter *et al.* 1997*a*), frontal involvement does not seem to be uniquely or necessarily associated with correct recollection; it might be associated with effortful search for contextual information (compare also Allan & Rugg 1997) or the recollection and evaluation of details that are objectively 'incorrect' though not subjectively recognized as such (compare Duzel *et al.* (1997) and Johnson *et al.* (1997); for general reviews of the possibility of mistaken recollection and the constructive and inferential nature of memory see Johnson *et al.* (1993) and Schacter *et al.* (1998)).

## 6. CONCLUSIONS

Although it is still relatively early in the development of research on neuroimaging and memory to reach any definitive conclusions regarding how evidence from neuroimaging might elucidate the relations between consciousness and memory, the present review clearly suggests that these techniques can provide an important additional source of data beyond that obtained from lesion studies with animals or patients, or abnormal memory. In many respects the precise functional and anatomic roles of different brain regions in recollection and the conditions that modulate them remain undetermined. Nonetheless, the idea that non-conscious priming, intentional retrieval and successful conscious recollection are each associated with characteristic patterns of increases and decreases in blood flow has received some empirical support. There is also evidence that neural correlates of memory might differ, at least quantitatively, as a function of the degree and nature of recollection. Additional efforts to differentiate between not only the nature of an individual's intentions during memory retrieval (voluntary or involuntary) and the degree of success and effort attending retrieval, but also the nature of the recollective content experienced (e.g. recollection of contextual or source information), are likely to refine and extend the suggestions made here. Further development of both cognitive and neuroimaging approaches, and especially increasing comparative efforts that capitalize on the strengths of the different imaging methods (e.g. fMRI, PET and ERPs), should yield patterns of converging evidence that can illuminate both explicit and implicit expressions of memory, further informing us of the multiple of ways in which we might manifest the influence of past learning and experiences both with and without conscious recollection of that past.

This article is an expanded version of Schacter & Buckner (1998*b*). The work was supported by NIA AG08441, NIH DC03245 and grants from the Charles A. Dana Foundation and Human Frontiers Science Program. We thank Carolyn Brenner for assistance with preparation of the manuscript.

## REFERENCES

Allan, K. & Rugg, M. D. 1997 An event-related potential study of explicit memory on tests of cued recall and recognition. *Neuropsychologia* **35**, 387–397.

Andreasen, 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*a* Short-term and long-term verbal memory: a positron emission tomography study. *Proc. Natn. Acad. Sci. USA* **92**, 5111–5115.

Andreasen, N. C., O'Leary, D. S., Cizadlo, T., Arndt, S., Rezai, K., Watkins, G. L., Boles Ponto, L. L. & Hichwa, R. D. 1995*b* Remembering the past: two facets of episodic memory explored with positron emission tomography. *Am. J. Psychiat.* **152**, 1576–1585.

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. *J. Cogn. Neurosci.* **9**, 378–391.

Baron, J. C., Petit-Taboué, M. C., Le Doze, F., Desgranges, B., Ravenel, N. & Marchal, G. 1994 Right frontal cortex hypometabolism in transient global amnesia: a PET study. *Brain* **117**, 545–552.

Berntsen, D. 1996 Involuntary autobiographical memories. *Appl. Cogn. Psychol.* **10**, 435–454.

Blaxton, T. A. 1989 Investigating dissociations among memory measures: support for a transfer appropriate processing framework. *J. Exp. Psychol. Learn. Mem. Cogn.* **15**, 657–668.

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. *Can. J. Exp. Psychol.* **50**, 42–56.

Bowers, J. S. & Schacter, D. L. 1990 Implicit memory and test awareness. *J. Exp. Psychol. Learn. Mem. Cogn.* **16**, 404–416.

Buckner, R. L. 1996 Beyond HERA: contributions of specific prefrontal brain areas to long-term memory retrieval. *Psychonom. Bull. Rev.* **3**, 149–158.

Buckner, R. L. & Koutstaal, W. 1998 Functional neuroimaging studies of encoding, priming, and explicit memory retrieval. *Proc. Natn. Acad. Sci. USA* **95**, 891–898.

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

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

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. *J. Neurosci.* **15**, 12–29.

Buckner, R. L., Bandettini, P., O'Craven, K., Savoy, R., Petersen, S. E., Raichle, M. E. & Rosen, B. R. 1996*a* Detection of cortical activation during averaged single trials of a cognitive task using functional magnetic resonance imaging. *Proc. Natn. Acad. Sci. USA* **93**, 14 878–14 883.

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

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 *Cognitive Neuroscience Society, 4th Annual Meeting Abstract Program*, p. 67. Cambridge, MA: MIT Press.

Buckner, R., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B., and Dale, A. M. 1998*a* Functional–anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron* **20**, 285–296.

Buckner, R. L., Koutstaal, W., Schacter, D. L., Dale, A. M., Rotte, M. & Rosen, B. 1998*b* Functional–anatomic study of episodic retrieval: selective averaging of event-related fMRI trials to test the retrieval success hypothesis. *NeuroImage* **7**, 151–162.

Buckner, R. L., Koutstaal, W., Schacter, D. L., Wagner, A. D. & Rosen, B. R. 1998*c* Functional–anatomic study of episodic retrieval using fMRI: retrieval effort versus retrieval success. *NeuroImage* **7**, 163–175.

Cabeza, R. & Nyberg, L. 1997 Imaging cognition: an empirical review of PET studies with normal subjects. *J. Cogn. Neurosci.* **9**, 1–26.

Cabeza, R., Kapur, S., Craik, F. I. M., McIntosh, A. R., Houle, S. & Tulving, E. 1997 Functional neuroanatomy of recall and recognition: a PET study of episodic memory. *J. Cogn. Neurosci.* **9**, 254–265.

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

Cohen, N. J. & Squire, L. R. 1980 Preserved learning and retention of pattern analysing skill in amnesics: dissociation of knowing how and knowing that. *Science* **210**, 207–210.

Curran, T., Schacter, D. L. & Bessenoff, G. 1996 Visual specificity effects on word stem completion: beyond transfer appropriate processing? *Can. J. Exp. Psychol.* **50**, 22–33.

Dale, A. M. & Buckner, R. L. 1997 Selective averaging of rapidly presented individual trials using fMRI. *Hum. Brain Mapp.* **5**, 329–340.

Demb, J. B., Desmond, J. E., Wagner, A. D., Vaidya, C. J., Glover, 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. *J. Neurosci.* **15**, 5870–5878.

Duzel, E., Yonelinas, A. P., Mangun, G. R., Heinze, H.-J. & Tulving, E. 1997 Event-related brain potential correlates of two states of conscious awareness in memory. *Proc. Natn. Acad. Sci. USA* **94**, 5973–5978.

Eich, E. 1984 Memory for unattended events: remembering with and without awareness. *Mem. Cogn.* **12**, 105–111.

Evans, R. & Thorn, W. A. F. 1966 Two types of posthypnotic amnesia: recall amnesia and source amnesia. *Int. J. Clin. Exp. Hypnosis* **14**, 162–179.

Fiez, J. A. 1997 Phonology, semantics, and the role of the left inferior prefrontal cortex. *Hum. Brain Mapp.* **5**, 79–83.

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 Neurosci.* **20**, 213–223.

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

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

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. *Psychol. Sci.* **7**, 278–283.

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.

Gardiner, J. M. & Java, R. I. 1993 Recognising and remembering. In *Theories of memory* (ed. A. Collins, M. A. Conway, S. E. Gathercole & P. E. Morris), pp. 163–188. Hove, UK: Lawrence Erlbaum.

Graf, P. & Mandler, G. 1984 Activation makes words more accessible, but not necessarily more retrievable. *J. Verb. Learn. Verb. Behav.* **23**, 553–568.

Graf, P. & Schacter, D. L. 1985 Implicit and explicit memory for new associations in normal subjects and amnesic patients. *J. Exp. Psychol. Learn. Mem. Cogn.* **11**, 501–518.

Graf, P., Mandler, G. & Haden, P. E. 1982 Simulating amnesic symptoms in normal subjects. *Science* **218**, 1243–1244.

Graf, P., Squire, L. R. & Mandler, G. 1984 The information that amnesic patients do not forget. *J. Exp. Psychol. Learn. Mem. Cogn.* **10**, 164–178.

Hamann, S. B. & Squire, L. R. 1997 Intact perceptual memory in the absence of conscious memory. *Behav. Neurosci.* **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., Fischman, A. J. & Alpert, N. M. 1998 Impaired recruitment of hippocampus during conscious recollection in schizophrenia. *Nature Neurosci.* **1**, 318–323.

Jacoby, L. L. 1991 A process dissociation framework: separating automatic from intentional uses of memory. *J. Mem. Lang.* **30**, 513–541.

Jacoby, L. L. & Dallas, M. 1981 On the relationship between autobiographical memory and perceptual learning. *J. Exp. Psychol. Gen.* **110**, 306–340.

Jacoby, L. L. & Witherspoon, D. 1982 Remembering without awareness. *Can. J. Psychol.* **36**, 300–324.

Janowsky, J. S., Shimamura, A. P. & Squire, L. R. 1989 Source memory impairment in patients with frontal lobe lesions. *Neuropsychologia* **27**, 1043–1056.

Johnson, M. K. & Raye, C. L. 1981 Reality monitoring. *Psychol. Rev.* **88**, 67–85.

Johnson, M. K., Hashtroudi, S. & Lindsay, D. S. 1993 Source monitoring. *Psychol. Bull.* **114**, 3–28.

Johnson, M. K., Nolde, S. F., Mather, M., Kounios, J., Schacter, D. L. & Curran, T. 1997 The similarity of brain activity associated with true and false recognition memory depends on test format. *Psychol. Sci.* **8**, 250–257.

Johnson, R. 1995 Event-related potential insights into the neurobiology of memory systems. In *Handbook of neuropsychology*, vol. 10 (ed. J. C. Baron & J. Grafman), pp. 135–164. Amsterdam: Elsevier.

Josephs, O., Turner, R. & Friston, K. 1997 Event-related fMRI. *Hum. Brain Mapp.* **5**, 243–248.

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.

Keane, M. M., Gabrieli, J. D. E., Mapstone, H. C., Johnson, K. A. & Corkin, S. 1995 Double dissociation of memory capacity after bilateral occipital-lobe or medial temporal-lobe lesions. *Brain* **118**, 1129–1148.

Kihlstrom, J. F. 1997 Hypnosis, memory and amnesia. *Phil. Trans. R. Soc. Lond.* B **352**, 1727–1732.

Kihlstrom, J. F. & Schacter, D. L. 1995 Functional disorders of autobiographical memory. In *Handbook of memory disorders* (ed. A. Baddeley, B. Wilson & F. Watts), pp. 337–364. Chichester, UK: Wiley.

Klein, D., Olivier, A., Milner, B., Zatorre, R. J., Johnsrude, I., Meyer, E. & Evans, A. C. 1997 Obligatory role of the LIFG in synonym generation: evidence from PET and cortical stimulation. *NeuroReport* **8**, 3275–3279.

Kolers, P. 1973 Remembering operations. *Mem. Cogn.* **1**, 347–355.

Koutstaal, W., Buckner, R. L., Schacter, D. L. & Rosen, B. R. 1997 An fMRI study of item repetition during auditorily cued word generation. In *Cognitive Neuroscience Society, 4th Annual Meeting Abstract Program*, p. 68. Cambridge, MA: MIT Press.

McIntosh, A. R., Nyberg, L., Bookstein, F. L. & Tulving, E. 1997 Differential functional connectivity of prefrontal medial temporal cortices during episodic memory retrieval. *Hum. Brain Mapp.* **5**, 323–327.

MacLeod, A. K., Buckner, R. L., Miezin, F. M., Petersen, S. E. & Raichle, M. E. 1998 Right anterior prefrontal cortex activation during semantic monitoring and working memory. *NeuroImage* **7**, 41–48.

Mandler, G. 1980 Recognizing: the judgment of previous occurrence. *Psychol. Rev.* **87**, 252–271.

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. 1997 Modulation of human medial temporal lobe activity by form, meaning, and experience. *Hippocampus* **7**, 587–593.

Milner, B., Corkin, S. & Teuber, H.-L. 1968 Further analysis of the hippocampal amnesic syndrome: 14-year follow-up study of H.M. *Neuropsychologia* **6**, 215–234.

Morris, C. D., Bransford, J. P. & Franks, J. J. 1977 Levels of processing versus transfer appropriate processing. *J. Verb. Learn. Verb. Behav.* **16**, 519–533.

Moscovitch, M. 1982 Multiple dissociations of function in amnesia. In *Human memory and amnesia* (ed. L. S. Cermak), pp. 337–370. Hillsdale, NJ: Lawrence Erlbaum.

Moscovitch, M. 1994 Memory and working with memory: evaluation of a component process model and comparisons with other models. In *Memory systems 1994* (ed. D. L. Schacter & E. Tulving), pp. 269–310. Cambridge, MA: MIT Press.

Moscovitch, M., Goshen-Gottstein, Y. & Vriezen, E. 1994 Memory without conscious recollection: a tutorial review from a neuropsychological perspective. In *Attention and performance*, vol. 15 (ed. C. Umilta & M. Moscovitch), pp. 619–660. Cambridge, MA: MIT Press.

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* **7**, 249–252.

Nyberg, L., Cabeza, R. & Tulving, E. 1996*a* PET studies of encoding and retrieval: the HERA model. *Psychonom. Bull. Rev.* **3**, 135–148.

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

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

Paller, K. A., Kutas, M. & McIsaac, H. K. 1995 Monitoring conscious recollection via the electrical activity of the brain. *Psychol. Sci.* **6**, 107–111.

Petrides, M., Alivisatos, B. & Evans, A. 1995 Functional activation of the human ventrolateral frontal cortex during mnemonic retrieval of verbal information. *Proc. Natn. Acad. Sci. USA* **92**, 5803–5807.

Price, C. J., Moore, C. J., Humphreys, G. W. & Wise, R. J. S. 1997 Segregating semantic from phonological processes during reading. *J. Cogn. Neurosci.* **9**, 727–733.

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. *Cerebr. Cortex* **4**, 8–26.

Richardson-Klavehn, A. & Bjork, R. A. 1988 Measures of memory. *A. Rev. Psychol.* **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 *Handbook of neuropsychology*, vol. 8 (ed. H. Spinnler & F. Boller), 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 *Varieties of memory and consciousness: essays in honor of Endel Tulving* (ed. H. L. I. Roediger & F. I. M. Craik), pp. 3–41. Hillsdale, NJ: Lawrence Erlbaum.

Rosen, B. R., Buckner, R. L. & Dale, A. M. 1998 Event related fMRI: past, present, and future. *Proc. Natn. Acad. Sci. USA* **95**, 773–780.

Rugg, M. D. 1994 Event-related potential studies of human memory. In *The cognitive neurosciences* (ed. M. S. Gazzaniga), pp. 789–801. Cambridge, MA: MIT Press.

Rugg, M. D. 1995 Cognitive event-related potentials: intracranial and lesion studies. In *Handbook of neuropsychology*, vol. 10 (ed. J. C. Baron & J. Grafman), pp. 165–186. Amsterdam: Elsevier.

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. 1985 Priming of old and new knowledge in amnesic patients and normal subjects. *Ann. NY Acad. Sci.* **444**, 41–53.

Schacter, D. L. 1987*a* Implicit memory: history and current status. *J. Exp. Psychol. Learn. Mem. Cogn.* **13**, 501–518.

Schacter, D. L. 1987*b* 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. 1997 The cognitive neuroscience of memory: perspectives from neuroimaging research. *Phil. Trans. R. Soc. Lond.* B **352**, 1689–1695.

Schacter, D. L. & Buckner, R. L. 1998*a* Priming and the brain. *Neuron* **20**, 185–195.

Schacter, D. L. & Buckner, R. L. 1998*b* On the relations among priming, conscious recollection, and intentional retrieval: evidence from neuroimaging research. *Neurobiol. Learn. Memory.* (In the press.)

Schacter, D. L. & Kihlstrom, J. F. 1989 Functional amnesia. In *Handbook of neuropsychology*, vol. 3 (ed. F. Boller & J. Grafman), pp. 209–231. Amsterdam: Elsevier.

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

Schacter, D. L., Harbluk, J. L. & McLachlan, D. R. 1984 Retrieval without recollection: an experimental analysis of source amnesia. *J. Verb. Learn. Verb. Behav.* **23**, 593–611.

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

Schacter, D. L., Chiu, C. Y. P. & Ochsner, K. N. 1993 Implicit memory: a selective review. *A. Rev. Neurosci.* **16**, 159–182.

Schacter, D. L., Church, B. & Treadwell, J. 1994 Implicit memory in amnesic patients: evidence for spared auditory priming. *Psychol. Sci.* **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., Alpert, N. M., Savage, C. R., Rauch, S. L. & Albert, M. S. 1996*a* Conscious recollection and the human hippocampal formation: evidence from positron emission tomography. *Proc. Natn. Acad. Sci. USA* **93**, 321–325.

Schacter, D. L., Curran, T., Galluccio, L., Milberg, W. P. & Bates, J. F. 1996*b* False recognition and the right frontal lobe: a case study. *Neuropsychologia* **34**, 793–808.

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

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

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

Schacter, D. L., Norman, K. A. & Koutstaal, W. 1998 The cognitive neuroscience of constructive memory. *A. Rev. Psychol.* **49**, 289–318.

Seger, C. A., Rabin, L. A., Zarella, M. & Gabrieli, J. D. E. 1997 Preserved verb generation priming in global amnesia. *Neuropsychologia* **35**, 1069–1074.

Senkfor, A. J. & Van Petten, C. 1996 ERP measures of source and item memory in young and elderly subjects. *Psychophysiology* **33** (suppl. 1), S77 [Abstract.]

Shimamura, A. P. & Squire, L. R. 1987 A neuropsychological study of fact memory and source amnesia. *J. Exp. Psychol. Learn. Mem. Cogn.* **13**, 464–473.

Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E. & Petersen, S. E. 1997 Common blood flow changes across visual tasks. II. Decreases in cerebral cortex. *J. Cogn. Neurosci.* **9**, 648–663.

Smith, M. E. 1993 Neurophysiological manifestations of recollective experience during recognition memory judgments. *J. Cogn. Neurosci.* **5**, 1–13.

Smith, M. E. & Halgren, E. 1989 Dissociation of recognition memory components following temporal lobe lesions. *J. Exp. Psychol. Learn. Mem. Cogn.* **15**, 50–60.

Spencer, W. D. & Raz, N. 1994 Memory for facts, source, and context: can frontal lobe dysfunction explain age-related differences? *Psychol. Aging* **9**, 149–159.

Spencer, W. D. & Raz, N. 1995 Differential effects of aging on memory for content and context: a meta-analysis. *Psychol. Aging* **10**, 527–539.

Squire, L. R. 1987 *Memory and brain.* New York: Oxford University Press.

Squire, L. R. 1992 Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychol. Rev.* **99**, 195–231.

Squire, L. R. 1994 Declarative and nondeclarative memory: multiple brain systems supporting learning and memory. In *Memory systems 1994* (ed. D. L. Schacter & E. Tulving), 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. *Proc. Natn. Acad. Sci. USA* **89**, 1837–1841.

Tendolkar, I., Doyle, M. C. & Rugg, M. D. 1997 An event-related potential study of retroactive interference in memory. *NeuroReport* **8**, 501–506.

Teyler, T. J. & DiScenna, P. 1986 The hippocampal memory indexing theory. *Behav. Neurosci.* **100**, 147–154.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K. & Farah, M. J. 1997 Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a re-evaluation. *Proc. Natn. Acad. Sci. USA* **94**, 14 792–14 797.

Trott, C. T., Friedman, D., Ritter, W. & Fabiani, M. 1997 Item and source memory: differential age effects revealed by event-related potentials. *NeuroReport* **8**, 3373–3378.

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

Tulving, E. 1985 Memory and consciousness. *Can. Psychol.* **26**, 1–12.

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

Tulving, E., Schacter, D. L. & Stark, H. 1982 Priming effects in word-fragment completion are independent of recognition memory. *J. Exp. Psychol. Learn. Mem. Cogn.* **8**, 336–342.

Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M. & Houle, S. 1994*a* Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. *Proc. Natn. Acad. Sci. USA* **91**, 2016–2020.

Tulving, E., Kapur, S., Markowitsch, H. J., Craik, F. I. M., Habib, R. & Houle, S. 1994*b* Neuroanatomical correlates of retrieval in episodic memory: auditory sentence recognition. *Proc. Natn. Acad. Sci. USA* **91**, 2012–2015.

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. 1997*a* An fMRI study of within- and across-task item repetition during semantic classification. In *Cognitive Neuroscience Society, 4th Annual Meeting Abstract Program*, p. 68. Cambridge, MA: MIT Press.

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

Wagner, A. D., Desmond, J. E., Glover, G. H. & Gabrieli, J. 1998 Prefrontal cortex and recognition memory: fMRI evidence for context dependent retrieval processes. *Brain*. (In the press.)

Warrington, E. K. & Weiskrantz, L. 1968 New method for testing long-term retention with special reference to amnesic patients. *Nature* **217**, 972–974.

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. *J. Int. Neuropsychol. Soc.* **1**, 525–533.

Wheeler, M. A., Stuss, D. T. & Tulving, E. 1997 Toward a theory of episodic memory: the frontal lobes and autonoetic consciousness. *Psychol. Bull.* **121**, 331–354.

Wilding, E. L. & Rugg, M. D. 1996 An event-related potential study of recognition memory with and without retrieval of source. *Brain* **119**, 889–905.

Wilding, E. L. & Rugg, M. D. 1997 Event-related potentials and the recognition memory exclusion task. *Neuropsychologia* **35**, 119–128.

Wilding, E. L., Doyle, M. C. & Rugg, M. D. 1995 Recognition memory with and without retrieval of context: an event-related potential study. *Neuropsychologia* **33**, 743–767.

Zarahn, E., Aguirre, G. & D'Esposito, M. 1997 A trial-based experimental design for fMRI. *NeuroImage* **6**, 122–138.