

## ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Year in Cognitive Neuroscience***The porous boundaries between explicit and implicit memory: behavioral and neural evidence**

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*Explicit memory* refers to the conscious retrieval of past information or experiences, whereas implicit memory refers to an unintentional or nonconscious form of retrieval. Much of the literature in cognitive psychology and cognitive neuroscience has focused on differences between explicit and implicit memory, and the traditional view is that they rely on distinct brain systems. However, the potential interplay between implicit and explicit memory is not always clear. This review draws from behavioral and functional neuroimaging evidence to evaluate three areas in which implicit and explicit memory may be interrelated. First, we discuss views of familiarity-based recognition in terms of its relationship with implicit memory. Second, we review the challenges of distinguishing between implicit memory and involuntary aware memory, at both behavioral and neural levels. Finally, we examine evidence indicating that implicit and explicit retrieval of relational information may rely on a common neural mechanism. Taken together, these areas indicate that, under certain circumstances, there may be an important and influential relationship between conscious and nonconscious expressions of memory.

**Keywords:** explicit memory; recognition; implicit memory; priming; fMRI

**Introduction**

Over the past several decades, a substantial body of research in the experimental psychology, neuropsychology, and cognitive neuroscience literatures has been dedicated to characterizing and distinguishing between explicit and implicit memory retrieval. *Explicit memory* typically refers to the conscious, intentional retrieval of past information or events, and is measured with tasks such as recognition or free recall. In contrast, *implicit memory* typically refers to a nonconscious, unintentional form of memory retrieval and can be evidenced by priming, which is when performance on a cognitive task is facilitated for repeated relative to new stimuli. Priming can be characterized as perceptual in nature, such as when reading words facilitates later rapid perceptual identification of those words relative to baseline, new words. Priming can also be characterized as conceptual in nature, such as when reading words facilitates later performance on a task that requires meaningful judgments or classifications of

those words. *Semantic priming* refers to the indirect priming of related information, such as when reading words (e.g., the word *nurse*) facilitates later task performance on semantically related words (e.g., the word *doctor*). Implicit and explicit memory can be differentially affected by some of the same experimental variables and can be evidenced by different brain regions and different patterns of brain activity. As such, the literature has traditionally agreed that implicit and explicit memory reflect the operation of distinct brain systems.<sup>1,2</sup> The criteria traditionally used to dichotomize explicit and implicit forms of memory are highlighted in Table 1.

A substantial body of evidence has now accumulated, however, indicating that explicit and implicit memory do not consistently fit within these feature boundaries. As the remainder this review will suggest, the interrelationship between these forms of memory is not always certain. For instance, how and when might explicit versus implicit memory influence one another? Under what circumstances might implicit and explicit memory

**Table 1.** The traditional model, highlighting the critical features used to dichotomize explicit and implicit forms of memory

Feature	Memory phenomenon	
	Implicit	Explicit
System	Declarative/MTL-dependent	Nondeclarative/MTL-independent
Intention	Controlled	Automatic
Awareness	Conscious	Nonconscious
Measurement	Direct test	Indirect test
Behavior	Accuracy	Priming

Note: As the focus of the present review suggests, however, a substantial body of evidence now suggests that explicit and implicit memory do not consistently fit within these feature boundaries.

share processing characteristics or rely on the same mechanism?

This paper begins by briefly reviewing some of the dissociations that have been used to support clear distinctions between explicit and implicit memory. In the remainder of the review, we draw primarily from behavioral and functional magnetic resonance imaging (fMRI) evidence to evaluate the current state of three important questions. First, we review certain conditions under which implicit memory may influence explicit memory. Specifically, we discuss the ways that implicit memory may impact or operate concurrently with an explicit memory process known as familiarity memory. Second, we review conditions under which explicit memory may influence implicit memory. Specifically, we discuss the challenges of distinguishing implicit memory from involuntary or unintentional aware memory. Finally, we review conditions under which implicit and explicit memory may rely on a common mechanism. Specifically, we discuss a common role of medial temporal lobe (MTL) regions during explicit and implicit retrieval of relational information.

### Dissociating implicit and explicit memory

The experimental psychology literature has identified several manipulations that produce behavioral dissociations between implicit and explicit memory retrieval.<sup>3</sup> It is important to note at the outset that these dissociations have been found pri-

marily for the priming of perceptual information. (In contrast, overlaps between explicit memory and conceptual implicit memory are more frequently observed and will be considered in detail in the subsequent section.) Perceptual priming has been shown to be unaffected by levels of processing manipulations, despite noted differences in explicit memory performance between shallow and deeper levels of encoding.<sup>4</sup> Similarly, emotional, relative to neutral, processing of to-be-learned information enhances explicit memory, with little to no impact on perceptual implicit memory.<sup>5,6</sup> In contrast, changing perceptual modality from study to test affects perceptual priming but not recognition.<sup>7</sup>

Importantly, much of this evidence reflects single dissociations, where an encoding manipulation affects one form of retrieval but not the other. A limitation of such dissociations is that they can be alternatively explained by differential task sensitivity or memory strength.<sup>8</sup> To our knowledge, only one experimental manipulation has produced cross-over effects on explicit and implicit memory. In the generation paradigm, subjects read some words and generate others from meaningful cues. Generated items are typically better recognized than the read items, but have the reverse effect on tests of implicit memory.<sup>9</sup> The opposing effects of semantic generation on implicit versus explicit memory have been used to provide stronger evidence than single dissociations that explicit and implicit memory reflect fundamentally different forms of memory retrieval. However, such cross-over dissociations are rare in the explicit versus implicit memory literature.

In addition to functional dissociations, neuropsychological studies of patient populations have also been used as evidence that explicit and implicit memory reflect distinct forms of retrieval. For instance, patients with damage to the MTL typically show impaired explicit retrieval performance but relatively intact priming.<sup>10-12</sup> In addition to patients with MTL damage, a population dissociation is found among patients with schizophrenia, who have difficulty with explicit remembering compared to normal controls, yet retain normal implicit memory functioning.<sup>13</sup> Similarly, older adults demonstrate some loss of explicit memory but typically show no deficit on priming tasks when compared to younger adults.<sup>14-18</sup> In contrast with these populations, who show intact implicit despite impaired explicit memory, other populations show the reverse

pattern. For instance, patient M.S., who had lesions to occipital cortex, showed no priming on an implicit perceptual identification task, despite unimpaired explicit memory.<sup>19,20</sup> These patient studies have been critical in giving rise to the notion that implicit and explicit memory depend on distinct brain systems.<sup>21</sup> The ability of these dissociations to provide unambiguous evidence of multiple memory systems has been widely questioned, however.<sup>22</sup> One alternative account is that amnesic patients have a generalized learning deficit, whereas patients with occipital lobe damage are impaired in visual processing.<sup>23</sup> Deficits along these dimensions are not incompatible with single-system accounts of explicit and implicit memory, whereby both priming and recognition can be driven by the same memory source.<sup>8</sup>

Regarding the functional neuroimaging of normal subjects, some evidence has supported the view that explicit and implicit memory operate within distinct neural systems,<sup>24</sup> although the patterns of neural responses are complex and their interpretation continues to be debated. For instance, it has been well established that conscious, intentional memory retrieval involves an integrated series of cognitive processes linked with spatially distinct but functionally connected brain regions.<sup>25,26</sup> A thorough and targeted analysis of the multiple processes that comprise explicit memory is not the focus of this review. However, at a very broad level, explicit memory retrieval has been shown to involve controlled strategy and retrieval effort mediated by the prefrontal cortex (PFC),<sup>27–30</sup> top-down attention to retrieval goals mediated by dorsal posterior parietal cortex (PPC),<sup>31,32</sup> as well as bottom-up memory recovery processes mediated by the MTL<sup>33</sup> and bottom-up attentional capture in ventral PPC.<sup>31</sup>

The brain regions linked with implicit memory vary widely according to the type of stimuli and type of task. Neural priming is typically evident in areas of stimulus- or concept-specific processing, such as occipital cortex for visually perceived stimuli<sup>34–36</sup> fusiform cortex for object or face stimuli<sup>37</sup> or left inferior PFC for priming of lexical or semantic information.<sup>38,39</sup> (for review, see Refs. 40 and 41). However, a consistent pattern across different types of priming is the finding of decreased neural activity for repeated stimuli relative to new stimuli. (Although, there are a few examples of repetition-related increases in neural activity, par-

ticularly for novel stimuli; see Refs. 37, 40, and 42.) Several theories have been put forth to account for these repetition-related decreases in activity. Experiments using nonhuman animals have shown that single neurons exhibit a reduced firing rate for repeated stimuli,<sup>43</sup> a finding that gave rise to the term *repetition suppression*, although this term is not always used in reference to the neural priming effect in humans. An analogue of repetition suppression in humans posits a neural tuning, or sharpening, mechanism, in which only the most relevant neurons are selected to respond to a stimulus upon its reoccurrence, leading to faster mean firing rates.<sup>44,45</sup> Other accounts include fatigued neurons, which exhibit lower amplitudes, or a reduction in the duration of neural activity.<sup>46,47</sup> Reductions in gamma frequency oscillations, as measured by EEG, have also been recently linked with behavioral priming effects.<sup>48</sup> Despite this reliable pattern of decreased neural activity for repeated relative to new stimuli, the precise direction of the relationship between neural and behavioral priming effects is an ongoing topic of investigation.<sup>36,40,49,50</sup>

The differences observed between explicit and implicit memory in terms of both region and direction of neural response do suggest important distinctions between these memory phenomena. Yet we argue that the interpretation of these differences is not straightforward. One possible explanation is that explicit and implicit memory operate within distinct brain systems, divided on consciousness. Differences in brain activation patterns could alternatively be explained by differences along several other critical dimensions. Dimensions that can produce differences in neural activations may include, for example, differences in task demands, memory strength, memory representation, stimulus complexity, retrieval cues, processing mode, or control of retrieval. Sophisticated measures must be employed to isolate or control for the contributions of such variables, to yield unambiguous interpretations of neural activations (for a similar argument, see Ref. 51). Indeed, as the remainder of the review will suggest, when many of these input levels are carefully controlled—including contributions of perceptual versus conceptual processing, or the retrieval of item versus relational information—conscious and nonconscious forms of memory retrieval show clear overlaps in brain activity.

## Implicit memory versus familiarity memory

Explicit memory does not reflect a unitary function, but rather can be divided in memory for facts (semantic memory) versus events (episodic memory).<sup>52</sup> According to dual-process theories, episodic memory can be further subdivided into two processes, recollection and familiarity.<sup>53–59</sup> Recollection is typically characterized as a slow, intentional retrieval process whereby memories are retrieved along with rich contextual detail, such as an event that occurred at a particular time and place. In contrast, familiarity is a fast, unintentional retrieval process in which memories lack contextual detail; an example is when you recognize a person on the bus without memory of his name or where you met him.<sup>57</sup> Research from multiple methodological approaches, including the study of neuropsychological populations, ERP, and fMRI, has provided strong evidence that recollection and familiarity have different neural bases (cf. Ref. 60). Patients with selective damage to the hippocampus<sup>61,62</sup> or with amnesic MCI<sup>63</sup> have shown impaired recollection coupled with little or no impairments in familiarity. Using ERP, late positive-going 500–700 ms brain potentials in posterior scalp regions have been strongly linked to recollection, whereas early negative-going 300–500 ms frontal potentials (the N400 effect) have been linked to familiarity.<sup>64</sup> Using fMRI, recollection and familiarity have been dissociated in several brain regions.<sup>65–68</sup> For instance, within the medial temporal lobes, recollection has been shown to be more dependent on the hippocampus, while familiarity is more dependent on the adjacent rhinal cortex.<sup>69</sup> Within the posterior midline region, recollection has been linked with the retrosplenial cortex while familiarity has been linked with the precuneus.<sup>70</sup> Within lateral parietal cortex, recollection has been linked with more ventral regions, and familiarity, more dorsal regions.<sup>31,32,71</sup> Finally, hemispheric lateralization differences have been found within lateral frontal cortex, with recollection-related activity observed in the left hemisphere and familiarity-related activity observed in the right.<sup>72–74</sup> Taken together, these dissociations have been used as evidence that recollection and familiarity reflect distinct processes that occur in different neural regions. However, other lines of research argue against a dual-process perspective and instead suggest that at least some dissociations

that have been produced between recollection and familiarity have inadvertently captured differences in memory strength.<sup>12,60</sup> Consistent with this position is evidence showing a link between activity in the hippocampus and strong, high-confidence memories, regardless of whether these memories are accompanied by recollective, contextual detail.<sup>75,76</sup>

Overall, the characterization of recollection and familiarity, in terms of both their neural bases as well as component psychological processes, has long been a topic of investigation and debate.<sup>56</sup> One question of particular interest is the extent to which familiarity memory may be related to implicit memory. During standard recognition tests, previously studied words or objects are presented along with new items, and the subject evaluates each item for its previous occurrence. Given this stimulus repetition, several models have been put forth to account for how familiarity memory might be similar to, arise from, or operate concurrently with nonconscious repetition effects.<sup>56,77</sup> One model posits that, in contrast to a controlled memory search, familiarity arises from the uncontrolled activation of studied information, which can thereby support either (or both) conscious recognition judgments as well as performance on incidental or indirect tests of implicit memory.<sup>57</sup> This model emphasizes overlaps between familiarity memory and implicit memory, particularly conceptual implicit memory, and has been supported by evidence that they function similarly in response to numerous variables, including levels of processing manipulations, generation effects, and population dissociations (for review, see Ref. 56). The extent of these overlaps have even been used to question whether conceptual priming is perhaps better ascribed to a form of explicit, rather than implicit, retrieval.<sup>21</sup>

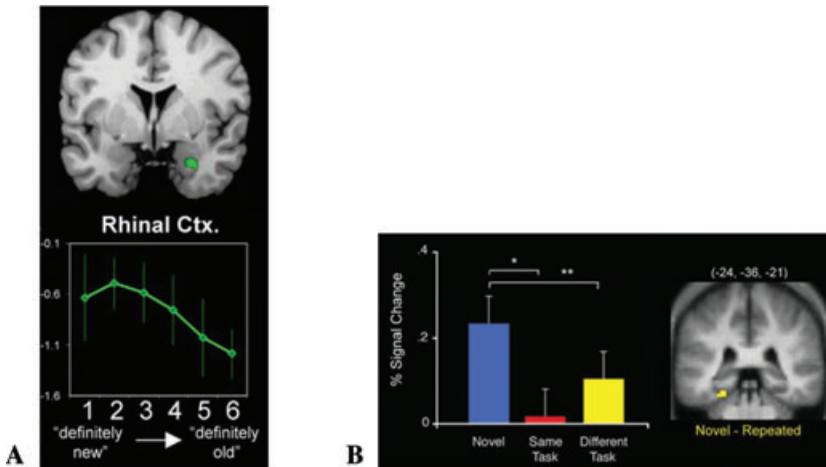
A second, related model posits that familiarity is a fast, automatic process in which memory judgments are in fact driven by the increased fluency of reprocessing studied information.<sup>4,53,59</sup> This possibility—that the increased fluency of processing that occurs during repeated items can influence recognition judgments—is arguably particularly likely for familiarity-based recognition, rather than recollection-based remembering, given that it lacks contextual detail and is driven by a general feeling of oldness.<sup>56,78,79</sup> The precise source of this increased fluency and its potential effect on recognition has been controversial. There is some evidence

that perceptually based fluency, which enhances implicit memory, can be used as a cue for recognition memory,<sup>80,81</sup> although other research suggests that the fluency supporting perceptual implicit memory is functionally distinct from the perceptual fluency that is operative during recognition.<sup>82,83</sup> In contrast to perceptual fluency, familiarity appears to be particularly sensitive to conceptual processing.<sup>82</sup> Indeed, the reengagement of meaningful features that gives rise to conceptual priming has been shown to influence or bias judgments of familiarity. For instance, familiarity-based responding has been increased by preceding test items with briefly presented semantically related primes.<sup>78,84</sup> There is recent convergent electrophysiological evidence that this type of masked priming manipulation may contribute to the memory signal used during familiarity judgments. Using ERP, the memory signal for words that were briefly preceded by the same word (i.e., primed) relative to a different word (i.e., unprimed) emerged at the earliest window (at approximately 200 ms) but then continued into the time window (approximately 400 ms) during which familiarity memory is evident.<sup>85</sup> Outside of this evidence, however, the neuroanatomical basis of such an influence of priming on recognition is still largely uncertain.

In contrast to models that propose that familiarity and implicit memory reflect the same process or share a common underlying mechanism, an alternative view is that implicit memory and recognition are distinct mnemonic processes that can operate concurrently in some circumstances.<sup>86</sup> A possible implication of this interplay between familiarity and conceptual priming is that it calls into question the putative neural basis of familiarity memory.<sup>87,88</sup> As described previously, a large body of ERP evidence has supported a distinction between late positive-going 500–700 ms brain potentials in posterior scalp regions linked with recollection, versus early negative-going 300–500 ms frontal potentials (N400 effect) linked with familiarity.<sup>64</sup> However, the role of concurrent conceptual priming during recognition testing has recently challenged these electrophysiological correlates of familiarity. One study used squiggle stimuli rated for meaningfulness and found that conceptual priming (which occurred only for high-meaningful stimuli) was in fact linked with the frontal N400 effect. In contrast, when controlling for the influence of conceptual

priming by using stimuli rated low on meaningfulness, familiarity memory was linked with a later parietal ERP effect.<sup>87,88</sup> Thus, the FN400 effect often observed during recognition memory may reflect conceptual priming rather than familiarity. There is some evidence against this interpretation: a study that manipulated familiarity by using famous versus nonfamous and common versus rare names found that the FN400 effect varied with familiarity but not priming.<sup>89</sup> Nonetheless, a considerable body of evidence has accumulated (reviewed by Ref. 90), suggesting that the FN400 effects traditionally attributed to familiarity memory may instead index a more general measure of semantic processing that is critical for both conceptual priming and familiarity memory.

In the fMRI literature, there is mixed but growing evidence that the putative neural correlates of familiarity might at least partly index a measure of concurrent conceptual priming. On the one hand, conceptual priming has been linked to decreases in neural activity in inferior PFC,<sup>38,39,91</sup> and at a general level it has been dissociated from explicit memory both in direction as well as region of response,<sup>92,93</sup> thus providing support for the position that familiarity and priming are distinct memory phenomena. However, familiarity—like priming—has also been associated with decreased neural activity, in particular in the rhinal cortex within the MTL.<sup>70,94–96</sup> A prominent interpretation of familiarity-related deactivations in rhinal cortex is the gatekeeper hypothesis, which posits that the rhinal cortex quickly directs cognitive and neural resources away from familiar and toward novel stimuli to promote efficient encoding and retrieval operations.<sup>97</sup> A key component of this hypothesis is that in order for the gatekeeper to operate efficiently, it is likely to code incoming information according to semantic or conceptual properties. Although the original gatekeeper hypothesis was interpreted in the context of explicit memory, the purported function of the rhinal cortex is arguably consistent with findings that conceptual implicit memory has also been shown to involve the rhinal cortex. Perirhinal cortex reductions have been observed for repeated relative to novel semantic decisions,<sup>98</sup> and the magnitude of conceptual priming on a speeded living/nonliving task has been directly linked to the magnitude of activity reductions in perirhinal cortex.<sup>99</sup> A recent study



**Figure 1.** Possible roles of the rhinal cortex in familiarity versus conceptual priming. (A) The rhinal cortex showed parametric decreases in activity as a function of perceived oldness during a recognition task.<sup>70</sup> This pattern suggests that the rhinal cortex may be sensitive to stimulus novelty. (B) Left perirhinal cortex showed reductions in activity for repeated relative to new objects during an incidental size judgment task, and particularly when the same semantic judgment was made during encoding.<sup>98</sup> These findings suggest a role of the rhinal cortex in the processing of semantic information. It is currently uncertain how reductions in neural activity in the rhinal cortex may be related to conscious versus nonconscious components of stimulus repetition.

has also shown that the magnitude of perirhinal activity during encoding predicts later conceptual priming.<sup>100</sup> Critically, these findings question whether the deactivations in rhinal cortex that are normally interpreted as a familiarity signal may instead index a measure of repetition-related conceptual fluency that occurs concurrently during recognition testing. One potentially important distinction relates to the level of perceived oldness that occurs during familiarity memory. Studies linking the rhinal cortex with familiarity have shown parametric decreases in activity as a function of conscious awareness of oldness.<sup>33,94</sup> However, conceptual priming can occur in the absence of conscious awareness.<sup>93</sup> Thus, a direct comparison of the role of the perirhinal cortex in conscious versus nonconscious expressions of oldness is a critical direction for future studies (Fig. 1).

One final note, given the subtraction logic of many fMRI investigations, where differences in brain activity are revealed by contrasting regions showing greater activation for one condition relative to a second condition, another possibility is that deactivations in rhinal cortex during repeated or relative to new stimuli in fact reflect novelty detection. It has been questioned whether there is a meaningful distinction between novelty and familiarity or whether they simply represent two sides

of the same coin.<sup>97,101</sup> On the one hand, interpreting decreased activity in rhinal cortex for repeated items as a measure of novelty detection would have important implications for the role of this region in episodic encoding.<sup>102</sup> However, new items do not consistently elicit rhinal cortex activity when compared with baseline,<sup>95,103</sup> and subregions along anterior versus posterior regions of MTL have been dissociated in terms of familiarity versus novelty when compared directly, such as by presenting items multiple times and measuring habituation<sup>104</sup> or by plotting magnitude of activity as a function of perceived oldness.<sup>43,65,70,94,105</sup>

In summary, models of familiarity memory have disagreed on the relationship between familiarity and implicit memory, in particular conceptual priming. Although there is some evidence that conceptual priming and familiarity-based recognition reflect distinct mnemonic processes, a clear distinction between them is difficult to discern given that priming has been shown to influence familiarity judgments, and that they may operate concurrently during standard recognition testing. These interactions challenge what is typically interpreted as the neural correlates of familiarity memory, especially in cases whereby the cognitive task employed does not control for influences of priming or generalized semantic processing. Although there

has been recent progress, much of the precise relationship between conceptual priming and familiarity and their associated brain activity is still to be determined.

### Implicit memory versus unintentional aware memory

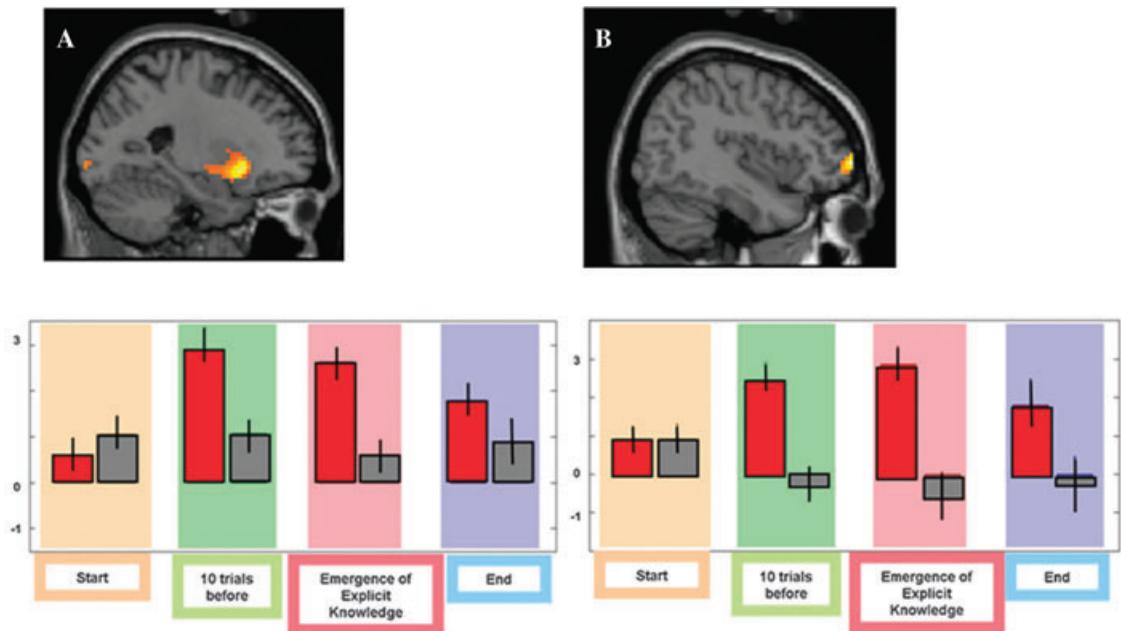
A common distinguishing feature between explicit and implicit memory centers on the control of retrieval. Although tests of explicit memory instruct subjects to think back to the studied information, tests of implicit memory make no mention of the study episode. Rather, they measure repetition-related learning on seemingly unrelated cognitive tasks, such as identifying words in noise or completing word fragments. Thus, the intention to retrieve has been a critical variable used to distinguish explicit from implicit memory. However, in contrast with research suggesting that the engagement of a controlled, PFC-mediated retrieval mode is necessary for explicit memory to occur,<sup>106</sup> an important subset of research within the both the explicit and implicit memory literatures highlights the occurrence of involuntary explicit memory.<sup>107–111</sup> That is, regardless of intention, subjects may incidentally become conscious, or aware, that an event or piece of information was previously experienced. This phenomenon has ecologically valid implications, such as when rich, autobiographical memories spontaneously come to mind in response to a salient cue in everyday life.<sup>112,113</sup> This phenomenon also has critical implications for the measure of implicit memory, as it offers an avenue through which explicit memory can affect the putative behavioral and neural correlates of priming.

The potential effects of unintentional memory awareness on priming have long been a topic of discussion in the behavioral experimental psychology literature.<sup>3,114</sup> A potentially common situation among cognitively intact subjects has been described,<sup>108</sup> in which, while completing the nominally implicit test of word stem completion, for example, subjects may become aware that some of the solutions can be completed with studied words. Importantly, although the pattern of behavioral priming performance has sometimes been unaffected by reported unintentional awareness,<sup>115–118</sup> in other cases priming is enhanced or is only produced by subjects who are aware of the study-test connection.<sup>119–123</sup> Thus, the potential impact of involun-

tary explicit awareness on implicit memory is of critical consideration when interpreting the mechanism of behavioral priming effects.

Arguably, the impact of involuntary explicit awareness on implicit memory is perhaps even more serious for functional neuroimaging. In behavioral studies, the results may remain unaffected if spontaneous awareness occurs after the participant's response to each trial, so long as this awareness does not encourage them to adopt a new, nonincidental strategy toward completing the task. In contrast, if spontaneous awareness occurs after a response in studies that use fMRI, the associated brain activity is still registered by the images, thus seriously confounding the interpretation of the neural basis of implicit memory. Despite this concern, the neural basis of involuntary aware memory has received relatively little attention in the cognitive neuroscience literature, and its precise relationship with implicit retrieval is still an ongoing topic of investigation. A prominent theoretical model based on neuropsychological data<sup>124</sup> posits that explicit memory can be initiated automatically by the hippocampus in response to either top-down or bottom-up signals. This notion has also been supported by studies using fMRI, which have shown that the MTL can predict an item's true oldness status independent from the subject's conscious experience of oldness.<sup>33</sup> Furthermore, the attention to memory (AToM) model<sup>32</sup> also posits a role of ventral PPC in bottom-up attentional capture to a previously experienced stimulus.<sup>125</sup> If both implicit and explicit memory can be initiated by stimulus-driven processing of repeated objects, then a critical question is whether there is a point at which neural priming transitions into a conscious signal of oldness.

One approach to addressing this question comes from a prominent a model of progressive differentiation from priming to item recognition to retrieval of contextual (e.g., source) detail.<sup>126</sup> This model posits that the presentation of a stimulus will give rise to a complex pattern of initial activation, and that over the timecourse of even a few milliseconds, this activation will not strengthen memories in a quantitative manner but rather may yield differentiated attributes or phenomenological experiences of memory, producing a transition from implicit memory to conscious item recognition, to the retrieval of perceptual or semantic detail. To date, there is little functional neuroimaging evidence as



**Figure 2.** BOLD signal changes preceding the emergence of explicit memory during an incidental stimulus–response learning task.<sup>127</sup> There was a significant increase in BOLD signal in the ventral striatum (A) and right ventrolateral PFC (B), 10 trials prior to when explicit awareness of a hidden regularity in the stimulus–response learning task was evident behaviorally. These findings suggest that increased neural activity in these regions can signal a transition from unconscious to conscious learning.

to whether, or how, this transition might occur over time. A recent combined EEG–fMRI investigation<sup>127</sup> showed that the emergence of explicit awareness during a contingent stimulus–response learning task was linked with an increase in neural activity in right ventromedial PFC and the ventral striatum, a region that has been implicated in feedback-based learning<sup>128</sup> and motivational learning.<sup>129</sup> These results therefore suggest a possible neural mechanism for how learning can transition from implicit to explicit (Fig. 2). Similarly, a recent ERP study<sup>130</sup> found that visual cortex activity associated with conscious (accurate) memory for spatial locations emerged later in time than visual cortex activity associated with nonconscious (forgotten) repetition effects, producing a temporal but not spatial distinction between conscious and nonconscious retrieval. Arguably consistent with these findings is evidence of an overlap in activity during encoding that predicts both implicit and explicit memory. One study instructed subjects to view novel scenes and then administered a surprise explicit memory test in which studied scenes were presented multiple times.<sup>131</sup> Activity in key regions typically linked with explicit scene memory (including bilateral parahippocam-

pal place area, bilateral fusiform gyrus, and right inferior PFC) predicted successful explicit memory, such that activity was greater for subsequently remembered than subsequently forgotten scenes. Activity in the same regions also predicted more neural attenuation, a measure of priming whereby peak activity decreases from first to second exposure of the encoded scenes during recognition testing. These findings emphasize an overlap in the initial stimulus representation that can produce both conscious and unconscious neural expressions of memory.

In contrast, other research emphasizes independence between explicit and implicit memory and suggests there is not a continuous transition from implicit to explicit memory. Rather, the repetition effects that lead to priming may stem from a different population of neurons than those that lead to involuntary aware memory. One study found that priming in the absence of explicit memory was linked with decreased neural activity in bilateral occipital and inferior temporal regions, whereas explicit remembering was linked with neural activations in parietal, frontal, and MTL regions.<sup>132</sup> Importantly, none of these regions interacted with retrieval intention, which was linked with

activation in bilateral superior frontal gyrus and right anterior PFC when compared with incidental retrieval. These results thus suggested that the neuroanatomical distinction between implicit and explicit memory does not reflect differences between incidental and intentional retrieval. A more recent study manipulated intentional versus incidental retrieval by asking subjects either to retrieve items intentionally, or to focus on categorizing items and then report whether they were also spontaneously recognized.<sup>133</sup> The authors found that while intentional retrieval was linked with increased activation in dorsolateral PFC, incidental retrieval was linked with reduced activity in extrastriate regions of occipital cortex as well as parahippocampal cortex (PHC), suggesting that involuntary explicit memory can be initiated by bottom-up signals in posterior brain regions. Given that this pattern of deactivations in posterior brain regions has frequently been associated with implicit memory,<sup>40</sup> the authors subsequently compared new, baseline trials with the repeated trials that were not spontaneously retrieved and did not find overlapping clusters of deactivation with the regions observed during incidentally aware trials. Thus, the specific clusters of activity observed during priming in the absence of awareness were distinct from those observed during involuntary explicit retrieval, despite both relying on bottom-up repetition effects.

Of note, although it has not been determined directly why these described studies<sup>132,133</sup> observed different regions associated with incidental retrieval, one possibility is that the difference is methodological: whereas the former study<sup>132</sup> compared overall differences between the intentional and incidental instruction conditions, the latter study<sup>133</sup> limited their incidental condition to trials in which subjects reported spontaneous retrieval. Importantly, however, what these studies both support is a neuroanatomical distinction between incidental explicit memory and implicit memory. In turn, they also suggest caution in interpreting the results of studies that do not distinguish between them, as brain activity attributed to priming effects may instead capture incidental awareness that an item has been previously experienced.

Finally, a growing topic of interest in the episodic memory literature is the relationship between successful explicit memory and the reactivation of encoding-related brain activity.<sup>134</sup> For instance, the

encoding of word-sound pairs has been linked with later reactivation of auditory cortex, even if the words are presented alone at test.<sup>135,136</sup> Although a thorough examination of the reactivation literature is beyond the scope of this review, one question of particular relevance is the extent to which reactivation occurs independently from consciousness. One study found that old hits and old misses engaged similar levels of activity in early-selection visual processing areas, suggesting that repetition priming for true (relative to false) memories was linked with reactivation of activity in perceptual stimulus processing areas.<sup>137</sup> Interestingly, priming was associated with increases in neural activity, rather than decreases. Increased activity for repeated relative to new stimuli has previously been observed in some cases, such as when using novel or unfamiliar stimuli that do not have a preexisting representation.<sup>37,40</sup> The pattern observed by the authors fits within those parameters, given their use of novel shape stimuli.<sup>137</sup> However, their findings do raise the question of whether reactivation during implicit retrieval is limited to cases that show repetition-related increases, rather than decreases in activity. A recent study reported encoding-retrieval overlaps in activations as well as overlaps in deactivations, in different regions.<sup>138</sup> Reductions in neural activity during a visual object search task were observed in the cuneus and precuneus during both encoding and implicit retrieval in study-test unaware subjects, producing a pattern of reactivations associated with implicit memory. In addition, however, successful implicit memory also involved reactivation of encoding-related increases in activity in bilateral occipital, fusiform, and lingual gyri, indicating a similarity in the operation of implicit and explicit memory systems. As the study did not employ a direct comparison between implicit and explicit retrieval-related reactivation, future research is needed to determine the precise extent of overlap in these two mechanisms, both spatial and temporal.

### **Explicit and implicit relational memory: a common role of MTL**

Despite cases in which implicit and explicit memory might influence each other—thus complicating the study and interpretation of either process—the majority of studies appear to agree that implicit and explicit memory often operate in the context

of different neurocognitive mechanisms. However, a common component within the studies described thus far is that they measure the retrieval (implicit or explicit) of individual items or stimuli. A separate line of research has focused on the retrieval of relational information; that is, the retrieval of links between items and their contextual environments. Critically, studies investigating relational retrieval have identified a common neural mechanism between implicit and explicit memory, centering on the MTL.

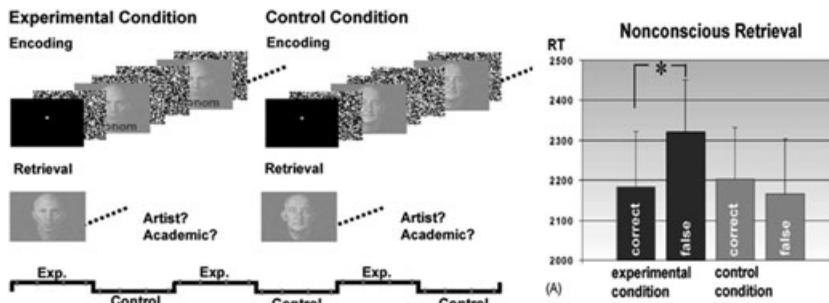
The role of the MTL in explicit memory has a long-standing history in the neuropsychological literature. The famous case-study of H.M., a patient who developed profound anterograde amnesia following surgical resection of major portions of his MTL, led to the development of a framework that distinguished between declarative memory and nondeclarative memory.<sup>139–141</sup> *Declarative memory* generally refers to a memory system dependent on the MTL and that supports the formation of new episodic and semantic memories (i.e., memories that can be “declared”). *Nondeclarative memory* generally refers to a system independent of the MTL and that supports the formation of varied learning functions such as motor, procedural and skill learning (i.e., functions that demonstrate learning but are not “declared” as memories).<sup>142</sup> Neuropsychological studies showing that patients with MTL damage were impaired in explicit memory but not priming<sup>10,143,144</sup> helped lead to the characterization of declarative memories as explicit (retrieved consciously) and nondeclarative memories as implicit (not retrieved consciously).<sup>107,114,145</sup>

Other evidence has accumulated that the precise role of the MTL in episodic memory is not consciousness per se, but rather in forming relationships among elements in a learning event. Indeed, episodic memories have long been described as not only conscious but also as fundamentally relational, composed of complex, contextually specific, representations.<sup>33,146,147</sup> Neuropsychological models based on lesion data suggest that the hippocampus in particular serves to bind elements together into memory traces and operates both incidentally and obligatorily.<sup>124</sup> This purported role of the MTL in relational processing supports a modification of the classic explicit/implicit distinction. A critical implication is that the MTL will be involved during the retrieval of relational in-

formation using both conscious tests of explicit memory as well as nonconscious tests of implicit memory.<sup>148,149</sup>

The idea that, in the case of relational retrieval, implicit and explicit memory can be driven by a common MTL mechanism has been supported by a large body of neuropsychological evidence. Chun and Phelps<sup>150</sup> employed the contextual cuing paradigm, a visual search task in which subjects are instructed to search for a visual target (e.g., a rotated T) among distracters (e.g., rotated Ls), and relational priming is demonstrated if subjects are faster to detect the target within a previously seen contextual configuration relative to a new configuration. Importantly, amnesic subjects demonstrated intact procedural learning in their general search abilities but demonstrated no relational priming, and performed at chance levels when asked to distinguish explicitly between previously seen visual configurations and randomly generated new configurations. This study provided critical and novel evidence that damage to the MTL produces a deficit in the ability to form new contextual associations or relationships, independent from the conscious/non-conscious distinction. A pattern of impaired implicit relational memory despite intact repetition priming has been found in several other investigations of MTL-amnesic patients.<sup>148,151,152</sup> (For a contrary result, see Ref. 153). Similarly, a similar pattern has been found by manipulating temporary, midazolam-induced, amnesia in healthy subjects.<sup>154,155</sup> Although some studies do emphasize a link between the MTL and consciousness,<sup>156–158</sup> the majority of current evidence appears to support the hypothesis that MTL structures are critical for the processing of relational information, independently from conscious awareness or intention.

Although an unambiguous distinction between implicit and explicit retrieval can be more difficult to discern in cognitively intact subjects relative to patient populations, a benefit of the functional neuroimaging approach is that it is typically better suited to identify more specific roles of subregions with the MTL during relational retrieval. Using fMRI, for instance, the hippocampus has been shown to make a unique contribution to episodic memory by linking together various aspects of a learning event into a bound memory representation<sup>66,159–161</sup> (but see Ref. 162). In particular, the hippocampus may be particularly important for the



**Figure 3.** Experimental design and behavioral index of nonconscious associative memory.<sup>164</sup> In the experimental condition, subjects viewed face-profession pairs between pattern masks. In the control condition, subjects viewed faces alone. Following encoding, the previously masked faces were presented again without masks, and subjects were instructed to guess the professional category of each face (artist or academic). Although accuracy for the category judgment was at chance, subjects were faster during correct relative to incorrect guesses, and only the experimental condition. The fMRI analysis showed that the degree of RT difference was correlated with activity in the right perirhinal cortex and left hippocampus, indicating a role of the MTL during implicit retrieval of novel semantic associations.

binding of flexible, nonunitized, between-domain associations,<sup>163</sup> where the binding of components A, B, and C can later be accessed as any variation of the original inputs. This type of binding can be contrasted with, unitized, inflexible, within-domain associations, such that binding of components A, B, and C can later be accessed only as the fused ABC.<sup>146,163</sup> Recent models suggest that the flexibility of binding does not center on the distinction between declarative and nondeclarative memory (i.e., consciousness) but rather on relative contributions of the hippocampus and adjacent MTL structures, such as the rhinal cortex. There has been relatively little evidence as to the role of the MTL during implicit relational retrieval, but the majority of studies thus far are consistent with neuropsychological models<sup>124</sup> that maintain that the hippocampus is critical for binding, regardless of consciousness.<sup>149</sup>

In one study,<sup>164</sup> subjects were instructed to view face-profession pairs that were flashed subliminally between visual masks. At test, subjects were asked to indicate whether the general semantic category of each face's profession had been an artist or academic. Accuracy for the categories test was at chance, yet subjects were faster to make correct guesses relative to incorrect guesses, producing a measure of unaware semantic associative retrieval. Neural activity associated with this contrast revealed increases in bilateral hippocampus as well as right perirhinal cortex (Fig. 3). The authors later extended these findings<sup>165</sup> by showing increased activity in anterior hippocampus and right perirhinal cortex dur-

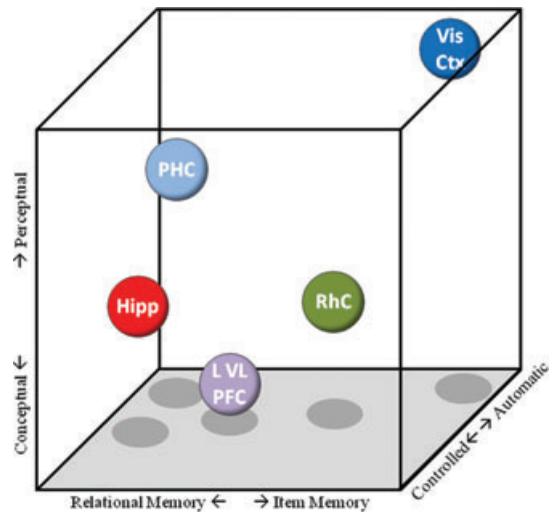
ing subliminal (nonconscious) associative encoding. Similarly, another study<sup>166</sup> used a sequence learning (serial reaction time) task, a form of spatiotemporal associative learning that produces faster response times to a cue for repeated sequences relative to randomly generated new sequences. After the serial reaction time task, subjects completed one of several explicit tests of the preceding sequences. Both implicit and explicit retrieval correlated with bilateral MTL activity (including hippocampus, entorhinal cortex, and parahippocampal cortex), although MTL activity correlated with PFC activity only the explicit test. Importantly, participants who were classified as unaware of the repeating patterns showed MTL activation that was indistinguishable from those classified as test-aware, and the MTL activity during implicit learning was uncorrelated with the successful performance on the explicit sequence tests. Finally, a recent investigation<sup>167</sup> used eye-tracking during fMRI to show that the activity in the hippocampus predicted eye movements in a visual relational configuration task even when explicit memory was at chance. Taken together, these studies maintain that the MTL, including the hippocampus, is critical during nonconscious formation and retrieval of relational information. A critical component of these studies is that they showed activations in hippocampus, not deactivations; thus, relational priming may reflect the engagement of an implicit memory system that is distinct from repetition priming not only in region but also in direction of neural response.

However, there are also recent findings that argue against activations in hippocampus during relational priming.<sup>168</sup> In one study, subjects viewed two Chinese characters (which were familiar word stimuli for the subjects) and judged their orthographic similarity. The implicit test measured reaction time to reading intact (i.e., presented together), recombined (presented at study but not together) and new character pairs, and relational priming was defined as the overlap in neural activations for intact-recombined and intact-new contrasts. In contrast to both the region and direction of neural activity found in prior studies,<sup>164</sup> relational priming was linked with decreased activity in right PHC, as well as anterior cingulate cortex, inferior frontal gyrus, and occipital cortex. Further research is needed to determine the extent to which the discrepancy in results between this study and prior fMRI studies of relational priming may be due to methodological differences.

One final note, even within the hippocampus, there is evidence that different regions along the anterior–posterior axis make different contributions to relational memory. Although posterior hippocampus has been shown to be involved in the structured reinstatement of perceptual information, anterior hippocampus has been shown to be involved in more flexible retrieval operations.<sup>169</sup> In turn, a critical question for future investigations is whether different regions along the hippocampal formation make a distinct contribution to implicit versus explicit relational retrieval. In psychological terms, this question links to whether explicit and implicit relational retrieval reflect access to the same or different features of an encoded memory representation.

## Conclusion

Although it has been well established that there are numerous critical distinctions between explicit and implicit memory at both behavioral and neural levels, recent research has also identified several ways in which these memory phenomena may be interrelated. Indeed, traditional constructs used to distinguish between explicit and implicit memory—including those centering on automaticity, consciousness or awareness, intention, control of retrieval, and the involvement of the MTL memory system—have been shown not to produce entirely straightforward or consistent dichotomies.



**Figure 4.** This model predicts that the brain regions associated with explicit or implicit memory do not divide on consciousness, but rather vary along the continua of several critical variables, including the cognitive process (conceptually or perceptually driven), the stimulus representation (item or relational), and the level of intention (controlled or automatic/involuntary). The model de-emphasizes the traditional systems view and leaves open the opportunity for neural regions to contribute uniquely as well as work in synchrony to support various memory phenomena. Hipp, hippocampus; LVL PFC, left ventrolateral prefrontal cortex; RhC, rhinal cortex; PHC, parahippocampal cortex; Vis Ctx, visual cortex.

Although parsimony should always be emphasized, it does appear that simple dichotomies between explicit and implicit memory are inadequate given the current state of the memory literature. We endorse the view that dissociations and interrelationships between explicit and implicit memory are equally critical and should both be represented in an effective model of memory and consciousness.

We have begun to approach this challenge by combining the literatures described in this review and plotting along intersecting axes the essential variables of memory representation, process, and intention (Fig. 4). Within this model, the brain regions operative during explicit or implicit memory do not divide on consciousness per se, but rather are predicted to vary along the continua of each of these variables. For instance, this model predicts that the relative contribution of visual cortex during a cognitive task of interest may be associated with intention (automatic greater than controlled), processing mode (perceptual greater than conceptual), as well as representation (item greater than relational). In

contrast, the predicted contribution of PHC may be more strongly associated with differences in process (perceptual greater than conceptual) and representation (relational greater than item) than intention. Importantly, the model leaves open the opportunity for neural regions to contribute uniquely as well as work in synchrony to support various memory phenomena. A challenge for further research will be to determine whether, and how, the conscious experience of memory can be captured within a model that de-emphasizes simple dichotomies. Ultimately, it remains to be seen: is there a specific point at which our memories become consciously experienced, and, if so, what power does cognitive neuroscience hold in identifying it?

### Conflicts of interest

The authors declare no conflicts of interest.

### References

1. Squire, L.R. 2004. Memory systems of the brain: a brief history and current perspective. *Neurobiol. Learn Mem.* **82**: 171–177.
2. Schacter, D.L., A.D. Wagner & R.L. Buckner. 2000. Memory systems of 1999. In *The Oxford Handbook of Memory*. E. Tulving & F.I.M. Craik, Eds.: 627–643. Oxford University Press, New York.
3. Roediger, H.L. & K.B. McDermott. 1993. Implicit memory in normal human subjects. In *Handbook of Neuropsychology*, Vol. 8. F. Boller & J. Grafman, Eds.: 63–131. Elsevier, Amsterdam.
4. Jacoby, L.L. & M. Dallas. 1981. On the relationship between autobiographical memory and perceptual learning. *J. Exp. Psychol. Gen.* **110**: 306–340.
5. Ramponi, C., G. Handelsman & P.J. Barnard. 2010. The memory enhancement effect of emotion is absent in conceptual implicit memory. *Emotion* **10**: 294–299.
6. Dillon, D.G. *et al.* 2007. Dissociable effects of conscious emotion regulation strategies on explicit and implicit memory. *Emotion* **7**: 354–365.
7. Hayman, C.A. & C. Rickards. 1995. A dissociation in the effects of study modality on tests of implicit and explicit memory. *Mem. Cognit.* **23**: 95–112.
8. Berry, C.J., D.R. Shanks & R.N. Henson. 2008. A single-system account of the relationship between priming, recognition, and fluency. *J. Exp. Psychol. Learn Mem. Cogn.* **34**: 97–111.
9. Jacoby, L.L. 1983. Remembering the data: analyzing interactive processes in reading. *J. Verbal Learn. Verbal Behav.* **22**: 485–508.
10. Carlesimo, G.A. *et al.* 1999. Lexical and conceptual components of stem completion priming in patients with Alzheimer's disease. *Neuropsychologia* **37**: 1049–1059.
11. Eichenbaum, H. & N.J. Cohen. 2001. *From Conditioning to Conscious Recollection: Memory Systems of the Brain*. Oxford University Press, New York.
12. Squire, L.R., C.E. Stark & R.E. Clark. 2004. The medial temporal lobe. *Annu. Rev. Neurosci.* **27**: 279–306.
13. Danion, J.M., T. Meulemans & F. Kauffmann-Muller. 2001. Intact implicit learning in schizophrenia. *Am. J. Psychiatry* **158**: 944–948.
14. Light, L.L. & A. Singh. 1987. Implicit and explicit memory in young and older adults. *J. Exp. Psychol. Learn Mem. Cogn.* **13**: 531–541.
15. Light, L.L. & S.A. Albertson. 1989. Direct and indirect tests of memory for category exemplars in young and older adults. *Psychol. Aging* **4**: 487–492.
16. Light, L.L. *et al.* 2000. Dual-process theories of memory in old age. In *Models of Cognitive Aging*. T.J. Perfect & E.A. Maylor, Eds.: 238–300. Oxford University Press, New York.
17. Jelicic, M. 1995. Aging and performance on implicit memory tasks: a brief review. *Int. J. Neurosci.* **82**: 155–161.
18. Wiggs, C.L., J. Weisberg & A. Martin. 2006. Repetition priming across the adult lifespan—the long and short of it. *Neuropsychol. Dev. Cogn. B Aging Neuropsychol. Cogn.* **13**: 308–325.
19. Gabrieli, J.D. 1995. A systematic view of human memory processes. *J. Int. Neuropsychol. Soc.* **1**: 115–118.
20. Schacter, D.L. & R.L. Buckner. 1998. Priming and the brain. *Neuron* **20**: 185–195.
21. Tulving, E. & D.L. Schacter. 1990. Priming and human memory systems. *Science*. **247**: 301–306.
22. Dunn, J.C. & K. Kirchner. 2003. What can we infer from double dissociations? *Cortex* **39**: 1–7.
23. Kinder, A. & D.R. Shanks. 2003. Neuropsychological dissociations between priming and recognition: a single-system connectionist account. *Psychol. Rev.* **110**: 728–744.
24. Schacter, D.L., R.L. Buckner & W. Koutstaal. 1998. Memory, consciousness and neuroimaging. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* **353**: 1861–1878.
25. Nyberg, L. *et al.* 1995. Functional brain maps of retrieval mode and recovery of episodic information. *Neuroreport* **7**: 249–252.
26. Rugg, M.D. & A.P. Yonelinas. 2003. Human recognition memory: a cognitive neuroscience perspective. *Trends Cogn. Sci.* **7**: 313–319.
27. Dobbins, I.G. *et al.* 2002. Executive control during episodic retrieval: multiple prefrontal processes subserved source memory. *Neuron* **35**: 989–996.
28. Donaldson, D.I., M.E. Wheeler & S.E. Petersen. 2010. Remember the source: dissociating frontal and parietal contributions to episodic memory. *J. Cogn. Neurosci.* **22**: 377–391.
29. Rugg, M.D. & E.L. Wilding. 2000. Retrieval processing and episodic memory. *Trends Cogn. Sci.* **4**: 108–115.
30. Wagner, A.D. *et al.* 1998. Prefrontal cortex and recognition memory. Functional-MRI evidence for context-dependent retrieval processes. *Brain* **121**(Pt 10): 1985–2002.
31. Cabeza, R. 2008. Role of parietal regions in episodic memory retrieval: the dual attentional processes hypothesis. *Neuropsychologia* **46**: 1813–1827.
32. Cabeza, R. *et al.* 2008. The parietal cortex and episodic memory: an attentional account. *Nat. Rev. Neurosci.* **9**: 613–625.

33. Daselaar, S.M. *et al.* 2006. The medial temporal lobe distinguishes old from new independently of consciousness. *J. Neurosci.* **26**: 5835–5839.
34. Badgaiyan, R.D. & M.I. Posner. 1996. Priming reduces input activity in right posterior cortex during stem completion. *Neuroreport* **7**: 2975–2978.
35. Badgaiyan, R.D. 2000. Neuroanatomical organization of perceptual memory: an fMRI study of picture priming. *Hum. Brain Mapp.* **10**: 197–203.
36. Zago, L. *et al.* 2005. The rise and fall of priming: how visual exposure shapes cortical representations of objects. *Cereb. Cortex* **15**: 1655–1665.
37. Henson, R.N., T. Shallice & R. Dolan. 2000. Neuroimaging evidence for dissociable forms of repetition priming. *Science* **287**: 1269–1272.
38. Buckner, R.L. *et al.* 2000. Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. *Brain* **123**(Pt 3): 620–640.
39. Wagner, A.D. *et al.* 1997. Semantic repetition priming for verbal and pictorial knowledge: a functional MRI study of left inferior prefrontal cortex. *J. Cogn. Neurosci.* **9**: 714–726.
40. Henson, R.N. 2003. Neuroimaging studies of priming. *Prog. Neurobiol.* **70**: 53–81.
41. Schacter, D.L., G.S. Wig & W.D. Stevens. 2007. Reductions in cortical activity during priming. *Curr. Opin. Neurobiol.* **17**: 171–176.
42. Soldan, A. *et al.* 2008. Neural mechanisms of repetition priming of familiar and globally unfamiliar visual objects. *Brain Res.* **1343**: 122–134.
43. Brown, M.W. & J.Z. Xiang. 1998. Recognition memory: neuronal substrates of the judgement of prior occurrence. *Prog. Neurobiol.* **55**: 149–189.
44. Wiggs, C.L. & A. Martin. 1998. Properties and mechanisms of perceptual priming. *Curr. Opin. Neurobiol.* **8**: 227–233.
45. Desimone, R. 1996. Neural mechanisms for visual memory and their role in attention. *Proc. Natl. Acad. Sci. USA* **93**: 13494–13499.
46. Grill-Spector, K., R. Henson & A. Martin. 2006. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* **10**: 14–23.
47. Henson, R.N. & M.D. Rugg. 2003. Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia* **41**: 263–270.
48. Moldakarimov, S., M. Bazhenov & T.J. Sejnowski. 2010. Perceptual priming leads to reduction of gamma frequency oscillations. *Proc. Natl. Acad. Sci. USA* **107**: 5640–5645.
49. Ghuman, A.S. *et al.* 2008. The effects of priming on frontal-temporal communication. *Proc. Natl. Acad. Sci. USA* **105**: 8405–8409.
50. Maccotta, L. & R.L. Buckner. 2004. Evidence for neural effects of repetition that directly correlate with behavioral priming. *J. Cogn. Neurosci.* **16**: 1625–1632.
51. Voss, J.L. & K.A. Paller. 2008. Brain substrates of implicit and explicit memory: the importance of concurrently acquired neural signals of both memory types. *Neuropsychologia* **46**: 3021–3029.
52. Tulving, E. 1983. *Elements of Episodic Memory*. Oxford University Press. Oxford, UK.
53. Jacoby, L.L. 1991. A process dissociation framework: separating automatic from intentional uses of memory. *J. Mem. Lang.* **30**: 513–541.
54. Yonelinas, A.P. 2001. Components of episodic memory: the contribution of recollection and familiarity. *Phil. Trans R. Soc. Lond. B Biol. Sci.* **356**: 1363–1374.
55. Yonelinas, A.P. 1999. The contribution of recollection and familiarity to recognition and source-memory judgments: a formal dual-process model and an analysis of receiver operating characteristics. *J. Exp. Psychol. Learn Mem. Cogn.* **25**: 1415–1434.
56. Yonelinas, A.P. 2002. The nature of recollection and familiarity: a review of 30 years of research. *J. Mem. Lang.* **46**: 441–517.
57. Mandler, G. 1980. Recognizing: the judgment of previous occurrence. *Psychol. Rev.* **87**: 252–271.
58. Atkinson, R., D.J. Hertmann & K.T. Wescourt. 1974. Search processes in recognition memory. In *Theories in Cognitive Psychology: The Loyola Symposium*. R.L. Solso, Ed.: 101–146. Erlbaum. Potomac, MD.
59. Jacoby, L.L. & C.M. Kelley. 1992. Unconscious influences of memory: dissociations and automaticity. In *The Neuropsychology of Consciousness*. A.D. Milner & M.D. Rugg, Eds.: 210–233. Academic Press. San Diego, CA.
60. Squire, L.R., J.T. Wixted & R.E. Clark. 2007. Recognition memory and the medial temporal lobe: a new perspective. *Nat. Rev. Neurosci.* **8**: 872–883.
61. Aggleton, J.P. *et al.* 2005. Sparing of the familiarity component of recognition memory in a patient with hippocampal pathology. *Neuropsychologia* **43**: 1810–1823.
62. Yonelinas, A.P. *et al.* 1998. Recollection and familiarity deficits in amnesia: convergence of remember-know, process dissociation, and receiver operating characteristic data. *Neuropsychology* **12**: 323–339.
63. Anderson, N.D. *et al.* 2008. Recollection- and familiarity-based memory in healthy aging and amnesic mild cognitive impairment. *Neuropsychology* **22**: 177–187.
64. Rugg, M.D. & T. Curran. 2007. Event-related potentials and recognition memory. *Trends Cogn. Sci.* **11**: 251–257.
65. Brown, M.W. & J.P. Aggleton. 2001. Recognition memory: what are the roles of the perirhinal cortex and hippocampus? *Nat. Rev. Neurosci.* **2**: 51–61.
66. Davachi, L., J.P. Mitchell & A.D. Wagner. 2003. Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. *Proc. Natl. Acad. Sci. USA* **100**: 2157–2162.
67. Ranganath, C. *et al.* 2004. Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia* **42**: 2–13.
68. Skinner, E.I. & M.A. Fernandes. 2007. Neural correlates of recollection and familiarity: a review of neuroimaging and patient data. *Neuropsychologia* **45**: 2163–2179.
69. Diana, R.A., A.P. Yonelinas & C. Ranganath. 2007. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends Cogn. Sci.* **11**: 379–386.
70. Daselaar, S.M., M.S. Fleck & R. Cabeza. 2006. Triple dissociation in the medial temporal lobes: recollection, familiarity, and novelty. *J. Neurophysiol.* **96**: 1902–1911.

71. Vilberg, K.L. & M.D. Rugg. 2008. Memory retrieval and the parietal cortex: a review of evidence from a dual-process perspective. *Neuropsychologia* **46**: 1787–1799.
72. Dobbins, I.G. *et al.* 2003. Memory orientation and success: separable neurocognitive components underlying episodic recognition. *Neuropsychologia* **41**: 318–333.
73. St Jacques, P. *et al.* 2008. The short and long of it: neural correlates of temporal-order memory for autobiographical events. *J. Cogn. Neurosci.* **20**: 1327–1341.
74. Henson, R.N. *et al.* 1999. Recollection and familiarity in recognition memory: an event-related functional magnetic resonance imaging study. *J. Neurosci.* **19**: 3962–3972.
75. Wais, P.E., L.R. Squire & J.T. Wixted. 2009. In search of recollection and familiarity signals in the hippocampus. *J. Cogn. Neurosci.* **22**: 109–123.
76. Wais, P.E. 2011. Hippocampal signals for strong memory when associative memory is available and when it is not. *Hippocampus*. **21**(1): 9–21.
77. Paller, K., J.L. Voss & C.E. Westerberg. 2009. Investigating the awareness of remembering. *Perspect. Psychol. Sci.* **4**: 185–199.
78. Rajaram, S. & L. Geraci. 2000. Conceptual fluency selectively influences knowing. *J. Exp. Psychol. Learn Mem. Cogn.* **26**: 1070–1074.
79. Wolk, D.A. *et al.* 2005. Patients with mild Alzheimer's disease attribute conceptual fluency to prior experience. *Neuropsychologia* **43**: 1662–1672.
80. Mulligan, N.W. & K. Osborn. 2009. The modality-match effect in recognition memory. *J. Exp. Psychol. Learn Mem. Cogn.* **35**: 564–571.
81. Johnston, W.A., K.J. Hawley & J.M. Elliott. 1991. Contribution of perceptual fluency to recognition judgments. *J. Exp. Psychol. Learn Mem. Cogn.* **17**: 210–223.
82. Wagner, A.D. & J.D. Gabrieli. 1998. On the relationship between recognition familiarity and perceptual fluency: evidence for distinct mnemonic processes. *Acta Psychol (Amst.)* **98**: 211–230.
83. Conroy, M.A., R.O. Hopkins & L.R. Squire. 2005. On the contribution of perceptual fluency and priming to recognition memory. *Cogn. Affect Behav. Neurosci.* **5**: 14–20.
84. Kinoshita, S. 1997. Masked target priming effects on feeling-of-knowing and feeling-of-familiarity judgments. *Acta Psychol (Amst.)* **97**: 183–199.
85. Woollams, A.M. *et al.* 2008. Event-related potentials associated with masked priming of test cues reveal multiple potential contributions to recognition memory. *J. Cogn. Neurosci.* **20**: 1114–1129.
86. Voss, J.L. & K.A. Paller. 2009. An electrophysiological signature of unconscious recognition memory. *Nat. Neurosci.* **12**: 349–355.
87. Voss, J.L. & K.A. Paller. 2007. Neural correlates of conceptual implicit memory and their contamination of putative neural correlates of explicit memory. *Learn Mem.* **14**: 259–267.
88. Voss, J.L., H.D. Lucas & K.A. Paller. 2010. Conceptual priming and familiarity: different expressions of memory during recognition testing with distinct neurophysiological correlates. *J. Cogn. Neurosci.* **22**(11): 2638–2651.
89. Stenberg, G. *et al.* 2008. Familiarity or conceptual priming: event-related potentials in name recognition. *J. Cogn. Neurosci.* **21**: 447–460.
90. Voss, J.L. & K.D. Federmeier. 2010. FN400 potentials are functionally identical to N400 potentials and reflect semantic processing during recognition testing. *Psychophysiology* Epub ahead of print. doi:10.1111/j.1469-8986.2010.01085.x.
91. Demb, J.B. *et al.* 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.
92. Donaldson, D.I., S.E. Petersen & R.L. Buckner. 2001. Dissociating memory retrieval processes using fMRI: evidence that priming does not support recognition memory. *Neuron* **31**: 1047–1059.
93. Levy, D.A., C.E. Stark & L.R. Squire. 2004. Intact conceptual priming in the absence of declarative memory. *Psychol. Sci.* **15**: 680–686.
94. Gonsalves, B.D. *et al.* 2005. Memory strength and repetition suppression: multimodal imaging of medial temporal cortical contributions to recognition. *Neuron* **47**: 751–761.
95. Henson, R.N. *et al.* 2003. A familiarity signal in human anterior medial temporal cortex? *Hippocampus* **13**: 301–304.
96. Montaldi, D. *et al.* 2006. The neural system that mediates familiarity memory. *Hippocampus* **16**: 504–520.
97. Fernandez, G. & I. Tendolkar. 2006. The rhinal cortex: 'gatekeeper' of the declarative memory system. *Trends Cogn. Sci.* **10**: 358–362.
98. O'Kane, G., R.Z. Insler & A.D. Wagner. 2005. Conceptual and perceptual novelty effects in human medial temporal cortex. *Hippocampus* **15**: 326–332.
99. Voss, J.L., K.K. Hauner & K.A. Paller. 2009. Establishing a relationship between activity reduction in human perirhinal cortex and priming. *Hippocampus* **19**: 773–778.
100. Wang, W.C. *et al.* 2010. The medial temporal lobe supports conceptual implicit memory. *Neuron* **68**: 835–842.
101. Habib, R. 2001. On the relation between conceptual priming, neural priming, and novelty assessment. *Scand J. Psychol.* **42**: 187–195.
102. Tulving, E. *et al.* 1996. Novelty and familiarity activations in PET studies of memory encoding and retrieval. *Cereb. Cortex* **6**: 71–79.
103. Herron, J.E., R.N. Henson & M.D. Rugg. 2004. Probability effects on the neural correlates of retrieval success: an fMRI study. *Neuroimage* **21**: 302–310.
104. Yassa, M.A. & C.E. Stark. 2008. Multiple signals of recognition memory in the medial temporal lobe. *Hippocampus* **18**: 945–954.
105. Poppenk, J. *et al.* 2010. Past experience modulates the neural mechanisms of episodic memory formation. *J. Neurosci.* **30**: 4707–4716.
106. Lepage, M. *et al.* 2000. Prefrontal cortex and episodic memory retrieval mode. *Proc. Natl. Acad. Sci. USA* **97**: 506–511.
107. Schacter, D.L. 1987. Implicit memory: history and current status. *J. Exp. Psychol. Learn Mem. Cogn.* **13**: 501–518.

108. Schacter, D.L., J. Bowers & J. Booker. 1989. Intention, awareness, and implicit memory: the retrieval intentionality criterion. In *Implicit Memory: Theoretical Issues*. S. Lewandowsky, J.C. Dunn & K. Kirsner, Eds. 47–65. Erlbaum. Hillsdale, NJ.
109. Kinoshita, S. 2001. The role of involuntary aware memory in the implicit stem and fragment completion tasks: a selective review. *Psychon. Bull. Rev.* **8**: 58–69.
110. Richardson-Klavehn, A., J.M. Gardiner & R.I. Java. 1994. Involuntary conscious memory and the method of opposition. *Memory* **2**: 1–29.
111. Richardson-Klavehn, A. et al. 1994. Intention and awareness in perceptual identification priming. *Mem. Cognit.* **22**: 293–312.
112. Berntsen, D. 1996. Involuntary autobiographical memories. *Appl. Cogn. Psychol.* **10**: 435–454.
113. Berntsen, D. 2010. The unbidden past: involuntary autobiographical memories as a basic mode of remembering. *Curr. Dir. Psychol. Sci.* **19**: 138–142.
114. Roediger, H.L. 1990. Implicit memory. Retention without remembering. *Am. Psychol.* **45**: 1043–1056.
115. Mulligan, N.W. 2003. Effects of cross-modal and intramodal division of attention on perceptual implicit memory. *J. Exp. Psychol. Learn Mem. Cogn.* **29**: 262–276.
116. Dew, I.T. & N.W. Mulligan. 2008. The effects of generation on auditory implicit memory. *Mem. Cognit.* **36**: 1157–1167.
117. Baques, J., D. Saiz & J. Bowers. 2004. Effects of working memory load on long-term word priming. *Memory* **12**: 301–313.
118. Lustig, C. & L. Hasher. 2001. Implicit memory is vulnerable to proactive interference. *Psychol. Sci.* **12**: 408–412.
119. Bowers, J. & D.L. Schacter. 1990. Implicit memory and test awareness. *J. Exp. Psychol. Learn Mem. Cogn.* **16**: 404–416.
120. Mace, J.H. 2003. Involuntary aware memory enhances priming on a conceptual implicit memory task. *Am. J. Psychol.* **116**: 281–290.
121. Mace, J.H. 2003. Study-test awareness can enhance priming on an implicit memory task: evidence from a word completion task. *Am. J. Psychol.* **116**: 257–279.
122. Barnhardt, T.M. 2004. Different involuntary mechanisms underlie priming and LOP effects in stem completion tests. *Memory* **12**: 614–636.
123. Geraci, L. & S. Rajaram. 2002. The orthographic distinctiveness effect on direct and indirect tests of memory: delineating the awareness and processing requirements. *J. Mem. Lang.* **47**: 273–291.
124. Moscovitch, M. 1992. Memory and working-with-memory: a component process model based on modules and central systems. *J. Cogn. Neurosci.* **4**: 257–267.
125. Lamontagne, P.J. & R. Habib. 2010. Stimulus-driven incidental episodic retrieval involves activation of the left posterior parietal cortex. *Neuropsychologia*. **48**(11): 3317–3322.
126. Johnson, M.K., S. Hashtroudi & D.S. Lindsay. 1993. Source monitoring. *Psychol. Bull.* **114**: 3–28.
127. Rose, M., H. Haider & C. Buchel. 2010. The emergence of explicit memory during learning. *Cereb. Cortex*. **20**(12): 2787–2797.
128. Shohamy, D. et al. 2004. Cortico-striatal contributions to feedback-based learning: converging data from neuroimaging and neuropsychology. *Brain* **127**: 851–859.
129. Seger, C.A. 2008. How do the basal ganglia contribute to categorization? Their roles in generalization, response selection, and learning via feedback. *Neurosci. Biobehav. Rev.* **32**: 265–278.
130. Slotnick, S.D. & D.L. Schacter. 2010. Conscious and non-conscious memory effects are temporally dissociable. *Cogn. Neurosci.* **1**: 8–15.
131. Turk-Browne, N.B., D.J. Yi & M.M. Chun. 2006. Linking implicit and explicit memory: common encoding factors and shared representations. *Neuron* **49**: 917–927.
132. Schott, B.H. et al. 2005. Redefining implicit and explicit memory: the functional neuroanatomy of priming, remembering, and control of retrieval. *Proc. Natl. Acad. Sci. USA* **102**: 1257–1262.
133. Kompus, K. et al. 2010. Multimodal imaging of incidental retrieval: the low route to memory. *J. Cogn. Neurosci.* **23**(4): 947–960.
134. Danker, J.F. & J.R. Anderson. 2010. The ghosts of brain states past: remembering reactivates the brain regions engaged during encoding. *Psychol. Bull.* **136**: 87–102.
135. Nyberg, L. et al. 2000. Reactivation of encoding-related brain activity during memory retrieval. *Proc. Natl. Acad. Sci. USA* **97**: 11120–11124.
136. Wheeler, M.E., S.E. Petersen & R.L. Buckner. 2000. Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proc. Natl. Acad. Sci. USA* **97**: 11125–11129.
137. Slotnick, S.D. & D.L. Schacter. 2004. A sensory signature that distinguishes true from false memories. *Nat. Neurosci.* **7**: 664–672.
138. Manelis, A., C. Hanson & S.J. Hanson. 2010. Implicit memory for object locations depends on reactivation of encoding-related brain regions. *Hum. Brain Mapp.* **32**(1): 32–50.
139. Corkin, S. 2002. What's new with the amnesic patient H.M.? *Nat. Rev.* **3**: 153–160.
140. Scoville, W.B. & B. Milner. 1957. Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatry* **20**: 11–21.
141. Eichenbaum, H. 2002. *The Cognitive Neuroscience of Memory*. Oxford University Press. New York.
142. Squire, L.R. 1992. Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychol. Rev.* **99**: 195–231.
143. Warrington, E.K. & L. Weizkrantz. 1970. Amnesic syndrome: consolidation or retrieval. *Nature* **274**: 972–974.
144. Shimamura, A.P. 1986. Priming effects in amnesia: evidence for a dissociable memory function. *Q. J. Exp. Psychol.* **38**: 617–644.
145. Schacter, D.L. & E. Tulving. 1994. What are the memory systems of 1994? In *Memory Systems 1994*. D.L. Schacter & E. Tulving, Eds.: 1–38. MIT Press. Cambridge, MA.
146. Cohen, N.J., R.A. Poldrack & H. Eichenbaum. 1997. Memory for items and memory for relations in the procedural/declarative memory framework. *Memory* **5**: 131–178.
147. Kirwan, C.B., Y. Shrager & L.R. Squire. 2009. Medial temporal lobe activity can distinguish between old and new

- stimuli independently of overt behavioral choice. *Proc. Natl. Acad. Sci. USA* **106**: 14617–14621.
148. Ryan, J.D. *et al.* 2000. Amnesia is a deficit in relational memory. *Psychol. Sci.* **11**: 454–461.
  149. Henke, K. 2010. A model for memory systems based on processing modes rather than consciousness. *Nat. Rev. Neurosci.* **11**: 523–532.
  150. Chun, M.M. & E.A. Phelps. 1999. Memory deficits for implicit contextual information in amnesic subjects with hippocampal damage. *Nat. Neurosci.* **2**: 844–847.
  151. Carlesimo, G.A. *et al.* 2005. Priming for novel between-word associations in patients with organic amnesia. *J. Int. Neuropsychol. Soc.* **11**: 566–573.
  152. Yang, J. *et al.* 2003. Involvement of the medial temporal lobe in priming for new associations. *Neuropsychologia* **41**: 818–829.
  153. Goshen-Gottstein, Y., M. Moscovitch & B. Melo. 2000. Intact implicit memory for newly formed verbal associations in amnesic patients following single study trials. *Neuropsychology* **14**: 570–578.
  154. Park, H. *et al.* 2004. The effect of midazolam on visual search: implications for understanding amnesia. *Proc. Natl. Acad. Sci. USA* **101**: 17879–17883.
  155. Chun, M.M. 2005. Drug-induced amnesia impairs implicit relational memory. *Trends Cogn. Sci.* **9**: 355–357.
  156. Smith, C.N., R.O. Hopkins & L.R. Squire. 2006. Experience-dependent eye movements, awareness, and hippocampus-dependent memory. *J. Neurosci.* **26**: 11304–11312.
  157. Smith, C.N. & L.R. Squire. 2008. Experience-dependent eye movements reflect hippocampus-dependent (aware) memory. *J. Neurosci.* **28**: 12825–12833.
  158. Smith, C.N. & L.R. Squire. 2005. Declarative memory, awareness, and transitive inference. *J. Neurosci.* **25**: 10138–10146.
  159. Eichenbaum, H., A.P. Yonelinas & C. Ranganath. 2007. The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.* **30**: 123–152.
  160. Giovanello, K.S., D.M. Schnyer & M. Verfaellie. 2004. A critical role for the anterior hippocampus in relational memory: evidence from an fMRI study comparing associative and item recognition. *Hippocampus* **14**: 5–8.
  161. Henke, K. *et al.* 1999. Human hippocampus associates information in memory. *Proc. Natl. Acad. Sci. USA* **96**: 5884–5889.
  162. Stark, C.E. & L.R. Squire. 2003. Hippocampal damage equally impairs memory for single items and memory for conjunctions. *Hippocampus* **13**: 281–292.
  163. Mayes, A., D. Montaldi & E. Migo. 2007. Associative memory and the medial temporal lobes. *Trends Cogn. Sci.* **11**: 126–135.
  164. Henke, K. *et al.* 2003. Nonconscious formation and reactivation of semantic associations by way of the medial temporal lobe. *Neuropsychologia* **41**: 863–876.
  165. Degonda, N. *et al.* 2005. Implicit associative learning engages the hippocampus and interacts with explicit associative learning. *Neuron* **46**: 505–520.
  166. Schendan, H.E. *et al.* 2003. An FMRI study of the role of the medial temporal lobe in implicit and explicit sequence learning. *Neuron* **37**: 1013–1025.
  167. Hannula, D.E. & C. Ranganath. 2009. The eyes have it: hippocampal activity predicts expression of memory in eye movements. *Neuron* **63**: 592–599.
  168. Yang, J. *et al.* 2008. Decreased parahippocampal activity in associative priming: evidence from an event-related fMRI study. *Learn. Mem. (Cold Spring Harbor, N.Y.)* **15**: 703–710.
  169. Giovanello, K.S., D. Schnyer & M. Verfaellie. 2009. Distinct hippocampal regions make unique contributions to relational memory. *Hippocampus* **19**: 111–117.