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The cognitive neuroscience of memory: perspectives from neuroimaging research

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SUMMARY

Cognitive neuroscience approaches to memory attempt to elucidate the brain processes and systems that are involved in different forms of memory and learning. This paper examines recent research from brain-damaged patients and neuroimaging studies that bears on the distinction between explicit and implicit forms of memory. Explicit memory refers to conscious recollection of previous experiences, whereas implicit memory refers to the non-conscious effects of past experiences on subsequent performance and behaviour. Converging evidence suggests that an implicit form of memory known as priming is associated with changes in posterior cortical regions that are involved in perceptual processing; some of the same regions may contribute to explicit memory. The hippocampal formation and prefrontal cortex also play important roles in explicit memory. Evidence is presented from recent PET scanning studies that suggests that frontal regions are associated with intentional strategic efforts to retrieve recent experiences, whereas the hippocampal formation is associated with some aspect of the actual recollection of an event.

1. INTRODUCTION

Cognitive neuroscience is an interdisciplinary enterprise that draws on data from studies of brain-damaged patients, functional neuroimaging techniques, computational models and research with non-human animals (for reviews, see Gazzaniga 1995; Kosslyn & Koenig 1992). Cognitive neuroscience approaches to memory have grown explosively in recent years. During the past two decades impressive progress has been made in elucidating the functional properties of memory and in relating them to underlying neuroanatomical substrates (for reviews and discussion, see Damasio 1989; Schacter 1996; Moscovitch 1994; Squire *et al.* 1993; Thompson & Krupa 1994)

One of the most important new developments in the cognitive neuroscience of human memory involves the advent of functional neuroimaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (functional MRI). These 'windows on the brain' (Posner & Raichle 1994) provide new tools for probing different aspects of memory; they have led to an explosion of recent studies and a rapid accumulation of novel information (for reviews, see Buckner & Tulving 1995; Ungerleider 1995). In this paper I relate findings and ideas from neuroimaging studies to an issue that has assumed paramount importance in recent research: the notion that memory is not a unitary or monolithic entity, but instead can be fractionated into a number of distinct but interacting component processes and systems (for review and discussion, see Schacter & Tulving (1994)). This conclusion has been based largely on converging evidence from studies of human amnesic patients and lesion studies of experimental animals. I consider recent neuroimaging research that has begun to illuminate the nature of the relations among various memory processes and systems.

2. FORMS OF MEMORY AND FUNCTIONAL NEUROIMAGING

The past two decades worth of research in cognitive neuroscience have pointed towards a fundamental distinction between an explicit or declarative form of memory that is critically dependent on the integrity of medial temporal lobe and diencephalic brain structures, and an implicit or non-declarative form of memory that involves a variety of systems outside the medial temporal/diencephalic region (cf. Eichenbaum 1994; Schacter 1987, 1994; Squire 1992; Squire & Zola-Morgan 1991). Explicit memory is reflected by conscious recall and recognition of recent information and events. Implicit memory is reflected by non-conscious effects of past experience on subsequent behaviour, as expressed by such phenomena as priming (Tulving & Schacter 1990), skill learning (Cohen & Squire 1980; Salmon & Butters 1995) and habit formation (Knowlton & Squire 1993; Mishkin 1984).

While conclusions about brain systems and forms of memory have relied heavily on research concerning human patients and experimental animals with brain lesions, the advent of functional neuroimaging techniques provides a new opportunity to map the

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component processes and systems underlying implicit and explicit forms of memory. In studies using PET and functional MRI, estimates of regional cerebral blood flow are obtained in different experimental conditions. Ideally, experimental conditions are constructed so that they are similar in all respects except for a critical feature that differs between conditions. Comparisons are then made between conditions of interest by subtracting estimates of blood flow in one condition from estimates of blood flow in another. The logic of this approach holds that any resulting differences in regional cerebral blood flow are associated with the critical feature that distinguishes one condition from another. Because the inferences that one draws about memory or any other cognitive processes in such a study depends crucially on the specific subtraction that is performed, it is important in PET studies to hold constant between conditions all variables except for the key parameter of interest (for further discussion of the logic of PET studies of memory, see Buckner & Tulving (1995)).

3. IMPLICIT AND EXPLICIT MEMORY FOR WORDS: STEM COMPLETION AND CUED RECALL

An important early PET study of explicit and implicit memory was reported by Squire *et al.* (1992). Subjects in Squire *et al.*'s experiment initially studied a list of familiar words prior to PET scanning (e.g. garden). 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; during one scan stems could be completed with study list words (priming) and during another scan stems could only be completed with new words (baseline). In a separate scan, subjects were given a cued recall task in which they were provided with three-letter stems of study-list words and were asked to think back to the study list (explicit memory). The priming versus baseline comparison revealed decreased blood flow in extrastriate occipital cortex. This finding is important theoretically, because a number of investigators have argued that visual word priming depends on posterior cortical regions (Gabrieli *et al.* 1995; Keane *et al.* 1995; Schacter 1990, 1994; Squire 1992; Tulving & Schacter 1990). However, Squire *et al.* (1992) also reported significant blood flow increases in the right hippocampal formation in the priming condition compared to the baseline condition. This finding was surprising because previous research with amnesic patients characterized by medial temporal lobe damage has shown clearly that such patients typically exhibit normal priming (for reviews, see Bowers & Schacter 1993; Schacter *et al.* 1993*a*,*c*; Squire 1992; Shimamura 1986). Based on these findings, various investigators have argued that priming occurs independently of the hippocampal formation (cf. Gabrieli *et al.* 1995; Keane *et al.* 1995; Moscovitch 1994; Schacter 1990, 1994; Squire 1992, 1994). In addition, Squire *et al.* (1992) observed right parahippocampal gyrus blood flow increases in the cued recall versus baseline comparison, implicating the hippocampal region in some aspect of explicit recall.

Why was the hippocampal region active during priming in Squire *et al.*'s (1992) experiment, given previous results from amnesic patients indicating that normal priming can occur even when the hippocampal formation is damaged? Consideration of Squire *et al.*'s behavioural data revealed unusually high levels of priming. In fact, the percentage of stems completed with study list targets in the priming condition (72%) was nearly identical to the percentage of stem completed with study list targets in the explicit recall condition (76%). These findings raise the possibility that priming was 'contaminated' by explicit memory for study list words. It is known that subjects sometimes explicitly remember target items on nominally implicit memory tasks, particularly when the targets are easily accessible (cf. Jacoby 1991; Schacter *et al.* 1989). Consistent with this idea, during the study phase of the experiment, subjects saw all target words twice and performed a 'deep' encoding task (pleasantness rating) that promotes high levels of explicit memory. Because short study lists and brief study-test delays were used, all of these factors operating together may have led to the evident contamination from explicit memory.

Given the theoretical importance of the idea that priming can occur independently of hippocampal activation, we have recently conducted two PET experiments that examine issues raised by the Squire *et al.* findings (Schacter *et al.* 1996). Our first experiment addressed the possible role of 'contamination' from explicit memory in the hippocampal activation that Squire *et al.* (1992) observed in their priming condition. To evaluate the issue, we conducted an experiment in which we used a 'shallow' or non-semantic study task—counting the number of t-junctions in a word—in an attempt to eliminate explicit contamination. Previous studies of stem completion priming have shown that the t-junction counting task can support robust priming even when subjects have little or no explicit memory for the target items (Bowers & Schacter 1990; Graf & Mandler 1984). Accordingly, if the priming-related hippocampal activation observed by Squire *et al.* (1992) reflects contamination from explicit memory, using the t-junction encoding task should eliminate both the explicit contamination and the associated hippocampal blood flow increases.

After carrying out the t-junction task (no scanning was performed during the encoding task), two separate scans were conducted during which subjects completed three-letter stems with the first word that came to mind. One scan consisted of stems that could be completed with study list words (priming); the other consisted of stems that could not be completed with study list words (baseline). To maximize the likelihood of detecting relevant blood flow changes, the same series of non-scanned study list, baseline stem completion and primed stem completion—what we call a 'study-test unit'—was carried out three times. Order of conditions and assignment of items to conditions was completely counterbalanced.

The experiment yielded three key results. First, analysis of behavioural data indicated that we

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successfully eliminated explicit contamination: the absolute magnitude of the priming effect was comparable to priming in previous experiments in which explicit contamination could be ruled out (Bowers & Schacter 1990; Graf & Mandler 1984). Also, there was no indication that priming increased across the three study-test units, which would have been expected had subjects 'caught on' to the nature of the experiment and begun to engage in explicit retrieval more frequently as the experiment progressed. Second, there was no evidence of blood flow increases in the vicinity of the hippocampal formation associated with priming. Third, we replicated Squire *et al.*'s (1992) finding of decreased blood flow in extrastriate occipital cortex in association with priming. In addition, we observed a variety of other priming-related blood flow increases and decreases (see Schacter *et al.* (1996), for additional findings, details on PET scanning procedures and other methodological information).

These findings have potentially important theoretical and methodological implications. On the theoretical side, the data support the position that perceptual priming occurs independently of the hippocampal formation. On the methodological side, the Squire *et al.* (1992) and Schacter *et al.* (1996) results indicate that PET scanning experiments on priming that use stem completion or similar tasks that are easily contaminated by explicit memory must also use procedures that minimize the possibility of explicit contamination, such as non-semantic study tasks. However, both of these conclusions are compromised somewhat by the fact that the failure to observe hippocampal activity during priming must be viewed cautiously. Negative findings in PET studies do not carry the force of positive findings (e.g. Buckner & Tulving 1995). More importantly, as noted earlier, various studies of explicit retrieval have failed to observe hippocampal activation (cf. Andreason *et al.* 1995; Shallice *et al.* 1994; Tulving *et al.* 1994*b*). Moreover, in studies that followed-up the initial Squire *et al.* (1992) finding of hippocampal activation during stem cued recall (explicit memory), Buckner *et al.* (1995) failed to observe hippocampal blood flow increases when modality changed between study and test (i.e. auditory study-visual cued recall test) or when the typecase of target stimuli changed between study and test (i.e. study words in lower case-test in upper case). If activity in the hippocampal formation is not reliably increased during explicit retrieval, then it may not be surprising that we failed to detect hippocampal activity during primed stem completion performance.

In view of these considerations, we performed a second experiment that examined explicit retrieval on the stem cued recall test to determine whether we could observe hippocampal activation. Subjects studied a list composed of two different types of words. Words in the high recall condition appeared four times and subjects made semantic encoding judgements about them (judging the number of meanings associated with each word); words in the low recall condition appeared once and subjects made a non-semantic judgement about them (judging the number of t-junctions in a word). After seeing study lists in which both types of words were presented for 5 s each in a random order (no PET scanning was performed during the encoding task), stem cued recall was tested during separate scans for high recall words and low recall words. Three such study-test units were carried out to maximize the sensitivity of our procedure. The study-test units were preceded and followed by two separate scans during which subjects were given word stems that could not be completed with study-list targets and were asked to respond with the first word that came to mind. This baseline condition provided a control for simple perceptual, motor and lexical activities.

Behavioural data showed, as expected, that subjects remembered many more words in the high recall condition (79%) than in the low recall condition (35%). Results revealed clear evidence of blood flow increases in the hippocampal formation in the high recall condition, but not in the low recall condition. In the high recall minus baseline comparison, we observed bilateral hippocampal activation; in the high recall minus low recall condition, we observed right-sided hippocampal blood flow increases. These results confirm earlier findings of hippocampal activation during stem cued recall (Squire *et al.* 1992). The fact that we observed hippocampal activation during the high but not the low recall condition suggests 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 trying to remember a past event. In the low recall condition, subjects tried to remember study-list words, but successfully recalled relatively few of them. Instead, hippocampal activation may be related to the level or type of recall in a particular situation: some aspect of the actual recollection of a past event, as opposed to the effort involved in attempting to remember the event. These observations are consistent with Buckner *et al.*'s (1995) failure to observe hippocampal activation in different modality and different case conditions. Although subjects were trying to recall study list words in both conditions, the way in which they remembered those words may have differed from the way in which they remembered words in the same case condition. For example, their recollections may have been less vivid or less confident in the different case or modality conditions compared to the same case condition. Consistent with these suggestions, our findings are further supported by results from another PET study showing that activity in the left medial temporal lobe and hippocampal region is positively correlated with level of successful retrieval in individual subjects (Nyberg *et al.* 1996).

Schacter *et al.* (1996) also reported that, in contrast to the hippocampal activations in the high recall condition, prefrontal cortex was selectively activated in the low recall condition. More specifically, Brodmann areas 10/46 showed bilateral blood flow increases in the low recall minus baseline comparison and left-sided increases in the low recall minus high recall comparison. As noted earlier, these prefrontal regions have been activated frequently in PET studies of explicit retrieval. Our data raise the possibility that blood flow increases in prefrontal cortex during stem-cued recall

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primarily reflect the effort involved in attempting to remember past events, as opposed to the actual experience of recollection. The fact that right prefrontal activity was observed in the low recall minus baseline comparison, but not in the low recall minus high recall comparison, is also noteworthy. As Tulving and colleagues have emphasized, right prefrontal regions appear to be especially involved in explicit retrieval (e.g. Tulving *et al.* 1994*a*). Our results suggest that right prefrontal regions may be specifically implicated in attempting to generate contextual information that guides episodic or explicit retrieval. The left prefrontal region, by contrast, may be involved in other aspects of effortful search, such as generating candidate responses under low recall conditions. One curious feature of our findings, however, is that the right prefrontal region did not show a significant blood flow increase in the high recall minus baseline comparison. We suggested that this might have occurred because retrieval was so easy in the high recall condition that we could not detect significant blood flow increases compared to baseline. Consistent with this idea, there were indeed trends for blood flow increases in right prefrontal cortex in the high recall minus baseline comparison, but they failed to reach the statistical threshold set prior to the experiment.

4. IMPLICIT AND EXPLICIT MEMORY FOR NOVEL OBJECTS

In a related PET experiment (Schacter *et al.* 1995) we examined implicit and explicit memory for novel objects using an experimental paradigm that we had explored extensively in previous behavioural work (for review, see Cooper & Schacter 1992). In this paradigm, subjects are first exposed to line drawings of novel objects. Some of the objects are structurally possible; they could exist in three-dimensional form. Others are structurally impossible: they contain local edge and surface violations that would prohibit them from actually existing in three dimensions. After encoding a series of possible and impossible objects during the study phase of the experiment, priming is assessed on an object decision task: subjects make possible/impossible decisions about studied and non-studied objects that are flashed briefly (e.g. 50–100 ms). Explicit memory is assessed with a recognition test in which subjects make yes/no decisions about old and new objects.

Priming on the object decision tests exhibits a number of consistent characteristics: it is (i) observed for possible but not for impossible objects; (ii) dependent on encoding the overall shape of an object; (iii) little affected by semantic encoding operations that enhance explicit memory; (iv) preserved in amnesic patients with explicit memory deficits; and (v) insensitive to study-to-test changes in size and left/right reflection of objects that impair explicit memory (e.g. Cooper *et al.* 1992; Schacter *et al.* 1990; Schacter & Cooper 1993; Schacter *et al.* 1993*b*). This overall pattern of findings has led us to propose that priming depends on a structural description system (Riddoch & Humphreys 1987) that represents information about the global structure of an object independently of its retinal size and left/right orientation (for an alternative interpretation, see Ratcliff & McKoon 1995; see also, Schacter & Cooper 1995).

Schacter *et al.* (1991) noted that numerous lesion studies and experiments using electrophysiological recordings implicate regions of inferior temporal cortex in the identification of complex visual stimuli (for reviews, see Plaut & Farah 1990; Tanaka 1993). Studies of animals with lesions to inferior temporal regions suggest that this region participates in the size- and reflection-invariant representation of global object structure. Accordingly, Schacter *et al.* (1991) speculated that priming of, and object decisions about, structurally possible objects may involve inferior temporal regions. By contrast, Schacter *et al.* (1991) suggested that explicit recognition of novel objects depends on an episodic memory system involving the hippocampus and other medial temporal lobe structures (e.g. Squire & Zola-Morgan 1991; Squire 1992).

The PET study provided a direct test of these ideas. We used a variant of the usual object decision/recognition paradigm to accommodate the requirements of PET scanning. During each of the first two one-minute scans, subjects saw a series of either 20 possible or 20 impossible objects for 50 ms each, and pushed a button when an object disappeared from the screen. The purpose of this no-decision baseline condition was to control for visual stimulation and movement. Subjects next studied 20 possible and 20 impossible objects for 5 s each in the absence of a scan, and carried out an encoding task that has previously been shown to result in significant priming. During each of the next four scans, subjects made possible/impossible decisions about four separate blocks of objects: old possible (possible objects that had appeared on the study list), new possible (possible objects that had not appeared at any previous point in the experiment), old impossible and new impossible. During the final four scans, subjects made yes/no recognition decisions about old possible, new possible, old impossible and new impossible objects. Individual objects were presented for 50 ms each during each of the eight object decision and recognition scans.

Despite the fact that separating objects into distinct categories for each scan (e.g. old possible, new impossible) constitutes a major departure from the usual procedure of intermixing different object types during testing, behavioural data in the PET lab were indistinguishable from previous behavioural data: there was priming for possible but not impossible objects, and recognition accuracy was higher for possible than impossible objects (Schacter *et al.* 1995). On the object decision task, several key comparisons were made. First, the new object decision minus baseline comparison allowed us to examine which brain regions are especially active when people focus on the global shape of an object by making a possible/impossible decision, relative to when they simply look at the object. According to the ideas outlined earlier, we would expect to see blood flow increases in inferior temporal regions during this comparison for possible objects, which have a globally coherent structure, but

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not for impossible objects, which do not. Second, in the old object decision minus new object decision comparison, the task is held constant and only prior exposure to the object varies. Therefore, in this comparison we would expect to see blood flow changes in brain regions that are associated with priming, which, according to our hypothesis, should include the inferior temporal region for possible objects only. Finally, in the old object decision minus baseline comparison, activity related both to priming and object decisions should be evident, so once again we expected to see changes in inferior temporal regions for possible but not impossible objects. Our hypotheses were supported: analysis of PET data revealed significant blood flow increases in inferior temporal/fusiform regions for possible objects during each of the three preceding comparisons, together with no corresponding increases for impossible objects.

On the recognition test, our main interest centred on the old minus new recognition comparison, in which the task is held constant (subjects try to remember whether they have seen an object in each condition), but subjects recollect more objects in the old than in the new recognition condition. Here we found blood flow increases in the right parahippocampal gyrus for possible objects but not for impossible objects. Because possible objects were remembered more accurately than impossible objects, this finding provides a nice parallel to the results discussed earlier in the high versus low recall procedure. Again, the evidence suggests that activation of the hippocampal formation during retrieval is related to the level or type of recollection. Pertinent information is also provided by the new recognition minus baseline comparison. Here, subjects try to remember whether an object appeared previously on the study list. However, because all of the objects are new, subjects cannot 'remember' any items from the study list. In this comparison, then, subjects are making efforts to remember but are not retrieving episodic memories. Here we found blood flow increases in prefrontal cortex bilaterally for both possible and impossible objects, which probably reflects retrieval effort. Interestingly, however, we also observed activations in the left hippocampal formation for both possible and impossible objects. These blood flow increases do not reflect episodic memory for previously studied objects. One possibility is that they reflect retrieval effort, in contrast to our findings from the high versus low recall procedure. Another possibility is that they reflect encoding of the novel or unusual features of our objects. Previous experiments have shown blood flow increases in the hippocampal formation during encoding of novel pictures (e.g. Tulving *et al.* 1994*c*).

In summary, the results of the object memory study converge with the results of the high/low verbal recall study insofar as both studies revealed hippocampal activation in conditions that yielded high levels of episodic memory (high recall, possible objects) relative to conditions that yielded lower levels of episodic memory (low recall, impossible objects). In addition, both studies yielded evidence of prefrontal activations in association with retrieval effort or attempt.

Both studies also implicated extrastriate visual cortex in verbal and non-verbal priming, respectively. However, whereas priming was accompanied by blood flow decreases in the word stem completion study, it was accompanied by blood flow increases in the object decision study. The reasons for these discrepancies are not entirely clear. One possibility is that blood flow increases in old object decision minus new object decision comparison are related to some process other than priming. For instance, Schacter *et al.* (1995) pointed out that more objects are perceived as structurally coherent in the old than the new object decision condition, and that this difference between the two conditions, as opposed to the process of priming *per se*, could have produced inferior temporal blood flow increases in the old minus new object decision comparison.

The finding that stem completion priming was accompanied by blood flow decreases suggests that the processing of primed stimuli requires less metabolic activity and possibly fewer neurons than priming of non-primed stimuli. This idea also receives support from experiments with non-human primates, showing that when they passively view stimuli that become increasingly familiar, the responses of some neurons in the inferior temporal cortex gradually decrease (for a review of these studies, see Desimone *et al.* 1995). Interestingly, Desimone *et al.* (1995) note that some inferior temporal neurons show enhanced responses to repeated stimuli, particularly when monkeys are required to actively respond to the targets items. Analogously, it is conceivable that priming in humans may be accompanied by either blood flow increases or decreases, depending on task demands (see Ungerleider, 1995, for a helpful discussion of priming-related blood flow decreases in relation to animal studies, and also in relation to blood flow increases and decreases in skill learning experiments).

5. CONCLUDING COMMENTS

Functional neuroimaging studies of human memory are in their infancy, and we are just now beginning to address the complex methodological issues surrounding such studies, and to consider the nature of the theoretical inferences that can be drawn from them. However, the early research reviewed in this paper suggests that the neuroimaging approach constitutes a valuable addition to the methods of cognitive neuroscience. Of course, neuroimaging studies alone are unlikely to be sufficient for understanding the complex aspects of brain activity that are involved in various forms of memory. Although neuroimaging experiments can inform us about which brain regions are active during the performance of various kinds of memory tasks, they cannot indicate which structures are necessary for task performance. To obtain this latter kind of information, it is still important to study memory deficits in patients with localized lesions and specific forms of memory loss, as well as non-human animals with experimentally induced lesions (cf. Squire 1992; Thompson & Krupa 1994). By combining results from brain imaging and lesion studies, it should be possible to attain a broader understanding of the various regions and connections that together comprise the memory systems of the brain.

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REFERENCES

Andreasen, N. C., O'Leary, D. S., Arndt, S. *et al*. 1995 Short-term and long-term verbal memory: a positron emission tomography study. *Proc. Natn. Acad. Sci. USA* **92**, 5111–5115.

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

Bowers, J. S. & Schacter, D. L. 1993 Priming of novel information in amnesic patients: issues and data. In *Implicit memory: new directions in cognition, development, and neuropsychology* (ed. P. Graf & M. E. J. Masson), pp. 303–326. New York: Academic Press.

Buckner, R. L., Petersen, S. E., Ojemann, J. G. *et al*. 1995 Functional anatomical studies of explicit and implicit memory retrieval tasks. *J. Neurosci*. **15**, 12–29.

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.

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

Cooper, L. A. & Schacter, D. L. 1992 Dissociations between structural and episodic representations of visual objects. *Curr. Direc. Psychol. Sci*. **1**, 141–146.

Cooper, L. A., Schacter, D. L., Ballesteros, S. *et al*. 1992 Priming and recognition of transformed three-dimensional objects: effects of size and reflection. *J. Exp. Psychol. Learn. Mem. Cogn* **18**, 43–57.

Damasio, A.R. 1989 Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition* **33**, 25–62.

Desimone, R., Miller, E. K., Chelazzi, L. *et al*. 1995 Multiple memory systems in the visual cortex. In *The cognitive neurosciences* (ed. M. S. Gazzaniga), pp. 475–486 Cambridge, MA: MIT Press.

Eichenbaum, H. 1994 The hippocampal system and declarative memory in humans and animals: experimental analysis and historical origins. In *Memory systems 1994* (ed. D. L. Schacter & E. Tulving), pp. 147–202. Cambridge, MA: MIT Press.

Gabrieli, J. D. E., Fleischman, D. A., Keane, M. M. *et al*. 1995 Double dissociation between memory systems underlying explicit and implict memory in the human brain. *Psychol. Sci*. **6**, 76–82.

Gazzaniga, M. (ed.) 1995 *The cognitive neurosciences*. Cambridge, MA: MIT Press.

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

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

Keane, M. M., Gabrieli, J. D. E., Noland, J. S. *et al*. 1995 Normal perceptual priming of orthographically illegal nonwords in amnesia. *J. Int. Neuropsychol. Soc*. **5**, 425–433.

Knowlton, B. J. & Squire, L. R. 1993 The learning of categories: parallel brain systems for item memory and category level knowledge. *Science* **262**, 1747–1749.

Kosslyn, S. M. & Koenig, O. 1992 *Wet mind: the new cognitive neuroscience*. New York: The Free Press.

Mishkin, M., Malamut, B. & Bachevalier, J. 1984 Memories and habits: two neural systems. In *Neurobiology of learning and memory* (ed. G. Lynch, J. L. McGaugh & N. M. Weinberger), pp. 65–77. New York: Guilford Press.

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.

Nyberg, L., McIntosh, A. R., Houle, S. *et al*. 1996 Activation of medial temporal structures during episodic memory retrieval. *Nature* **380**, 715–717.

Plaut, D. C. & Farah, M. J. 1990 Visual object representation: interpreting neurophysiological data within a computational framework. *J. Cogn. Neurosci*. **2**, 320–343.

Posner, M. I. & Raichle, M. E. 1994 *Images of the mind*. New York: Scientific American Library.

Ratcliff, R. & McKoon, G. 1995 Bias and explicit memory in priming of object decisions. *J. Exp. Psychol. Learn. Mem. Cogn* **21**, 754–767.

Riddoch, M. J. & Humphreys, G. W. 1987 Visual object processing in optic aphasia: a case of semantic access agnosia. *Cogn. Neuropsychol*. **4**, 131–186.

Salmon, D. P. & Butters, N. 1995 Neurobiology of skill and habit learning. *Curr. Opin. Neurobiol*. **5**, 184–190.

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

Schacter, D. L. 1990 Perceptual representation systems and implicit memory: toward a resolution of the multiple memory systems debate. *Ann. NY Acad. Sci*. **608**, 543–571.

Schacter, D. L. 1994 Priming and multiple memory systems: perceptual mechanisms of implicit memory. In *Memory systems 1994* (ed. D. L. Schacter & E. Tulving), pp. 244–256. Cambridge, MA: MIT Press.

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

Schacter, D. L. & Cooper, L. A. 1993 Implicit and explicit memory for novel visual objects: structure and function. *J. Exp. Psychol. Learn. Mem. Cogn* **19**, 995–1009.

Schacter, D. L. & Cooper, L. A. 1995 Bias in the priming of object decisions: logic, assumption, and data. *J. Exp. Psychol. Learn. Mem. Cogn* **21**, 768–776.

Schacter, D. L. & Tulving, E. 1994 What are the memory systems of 1994? In *Memory systems 1994* (ed. D. L. Schacter & E. Tulving), pp. 138. Cambridge, MA: MIT Press.

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: Erlbaum.

Schacter, D. L., Cooper, L. A. & Delaney, S. M. 1990 Implicit memory for unfamiliar objects depends on access to structural descriptions. *J. Exp. Psychol. Gen*. **119**, 5–24.

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

Schacter, D. L., Cooper, L. A. & Treadwell, J. 1993*b* Preserved priming of novel objects across size transformation in amnesic patients. *Psychol. Sci*. **4**, 331–335.

Schacter, D. L., Alpert, N. M., Savage, C. R. *et al*. 1996 Conscious recollection and the human hippocampal formation: evidence from positron emission tomography. *Proc. Natn. Acad. Sci. USA* **93**, 321–325.

Schacter, D. L., Cooper, L. A., Tharan, M. *et al*. 1991 Preserved priming of novel objects in patients with memory disorders. *J. Cogn. Neurosci*. **3**, 118–131.

Schacter, D. L., Kihlstrom, J. F., Kaszniak, A. W. *et al*. 1993*c* Preserved and impaired memory functions in elderly adults. In *Adult information processing: limits on loss* (ed. J. Cerella, W. Hoyer, J. Rybash & M. Commons) pp. 327–350. New York: Academic Press.

Schacter, D. L., Reiman, E., Uecker, A. *et al*. 1995 Brain regions associated with retrieval of structurally coherent visual information. *Nature* **376**, 587–590.

Shallice, T., Fletcher, P., Frith, C. D. *et al*. 1994 Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature* **368**, 633–635.

Shimamura, A. P. 1986 Priming effects in amnesia: evidence for a dissociable memory function. *Q. J. Exp. Psychol*. A **38**, 619–644.

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

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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. & Zola-Morgan, M. 1991 The medial temporal lobe memory system. *Science* **253**, 1380–1386.

Squire, L. R., Knowlton, B. & Musen, G. 1993 The structure and organization of memory. *A. Rev. Psychol.* **44**, 453–495.

Squire, L. R., Ojemann, J. G., Miezin, F. M. *et al.* 1992 Activation of the hippocampus in normal humans: a functional anatomical study of memory. *Proc. Natn. Acad. Sci. USA* **89**, 1837–1841.

Tanaka, K. 1993 Neuronal mechanisms of object recognition. *Science* **262**, 685–688.

Thompson, R. F. & Krupa, D. J. 1994 Organization of memory traces in the mammalian brain. *A. Rev. Neurosci.* **17**, 519–549.

Tulving, E., Kapur, S., Craik, F. I. M. *et al.* 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. *et al.* 1994*b* Neuroanatomical correlates of retrieval in episodic memory: auditory sentence recognition. *Proc. Natn. Acad. Sci. USA* **91**, 2012–2015.

Tulving, E., Markowitsch, H. J., Kapur, S. *et al.* 1994*c* Novelty encoding networks in the human brain: positron emission tomography data. *Neuroreport* **5**, 2525–2528.

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

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

Downloaded from http://rstb.royalsocietypublishing.org/ on November 22, 2014