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# The Hippocampus As a “Stupid,” Domain-Specific Module: Implications for Theories of Recent and Remote Memory, and of Imagination

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2007 CSBBC Donald O. Hebb Distinguished Award / Prix Donald O. Hebb 2007 de la SCCCSC

The hippocampus and surrounding regions of the medial temporal lobe play a central role in all neuropsychological theories of memory. It is still a matter of debate, however, how best to characterise the functions of these regions, the hippocampus in particular. In this article, I examine the proposal that the hippocampus is a “stupid” module whose specific domain is consciously apprehended information. A number of interesting consequences for the organisation of memory and the brain follow from this proposal and the assumptions it entails. These, in turn, have important implications for neuropsychological theories of recent and remote episodic, semantic, and spatial memory and for the functions that episodic memory may serve in perception, comprehension, planning, imagination, and problem solving. I consider these implications by selectively reviewing the literature and primarily drawing on research my collaborators and I have conducted.

*Keywords:* hippocampal module, episodic memory

I am honoured and very pleased and grateful to be the recipient of the Hebb Award. It would have been sufficient to know that I was worthy enough to have been nominated; receiving the award was a bonus. As will become clear from this article, my accomplishments would have been far less without generous and caring mentors, supportive and collaborative colleagues, and excellent students and postdoctoral fellows.

I have always benefited from sabbaticals and study leaves. They gave me time to gather scattered, inchoate ideas and examine and organise them, so that they could be formulated into a more coherent expression, a theory or framework, of what, until then, I only had intuited. After each sabbatical, I could tell a story that helped me, and I hope others, make sense of disparate facts and ideas. Though these stories may appear to be self-contained, they gain some of their legitimacy and power to enlighten or provoke from their associations with other people’s stories and facts, and departures from them.

Receiving the Hebb Award provides me with an occasion to tell yet another story. I hope that you will indulge me while I tell it. It is not entirely a new story, as may have been the case if the award included a sabbatical leave. Consequently, I will attempt to understand how I got here by using sabbaticals as signposts. I know enough about memory to appreciate that it is hopeless to try to recapture the past accurately. That is not my aim. Instead, I wish

to integrate aspects of my past research by highlighting some themes or elements of past stories whose full significance, and relation to one another, only became apparent in retrospect. I will focus on the role of the hippocampus in memory, taking into account its relation to the prefrontal cortex and posterior neocortex. Though this story resembles previous ones, I hope there are enough variations to sustain the reader’s interest, and to provide fresh insights into the cognitive neuroscience of memory that can illuminate the past and shine a light onto the future.

## Brief Personal History

Fittingly, the story begins with Professor Hebb, though permit me this short digression. I was born in Roumania in 1945, emigrated to Israel in 1950, and arrived in Montreal in 1953 where I spent my formative years. Like many Montrealers of my generation, I attended McGill University (1962–1966).

At that time, psychology courses were not offered until 2nd year. We could then take an introductory course that Hebb co-taught with Dr. Muriel Stern. In my 2nd year, the Psychology Department decided to experiment by allowing students to enter the honours’ program concurrently with their taking the introductory course. Although the class was large for the lecture portion, there were also weekly seminars in which groups of about 20 students met to discuss the material covered that week, or anything else the conference leader prepared. Typically, graduate students were the conference leaders, but for the honours’ class Hebb and Stern led the conferences. I was admitted to that honours’ class.

We all know that Hebb was a great psychologist whose empirical and theoretical contributions helped shape our thinking about brain and behaviour. *The Organization of Behavior* (Hebb, 1949), one of the most influential psychology books ever written, was the harbinger of behavioural and cognitive neuroscience that now holds dominion over the field. During his

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tenure at McGill, Hebb attracted excellent students and faculty, making it the best psychology department in Canada and one of the best in the world, where many students who became leaders of the field were educated.

I know all this now, but when I entered Hebb's conference I had no idea of his stature and eminence. So, I treated him much the way I treated our teachers in high school—I passed notes, talked, and giggled. And I was not the only one. At one point, Hebb left the class muttering, "Why am I doing this?" The experiment of an early honours' class began and ended with my year.

By the end of the 2nd year, I had come to appreciate Hebb more; and by 4th year, I wanted to work with him. I approached him to ask whether he would be the research supervisor for my honours' thesis, hoping that his memory of that honours' class would not colour his opinion. He agreed. After a couple of meetings in which we discussed a potential research project on phi phenomenon (apparent motion), whose purpose I never could grasp and that he declined to clarify, the meetings ended with his saying, "Mr. Moscovitch, I don't think we are going to get along." I think he would have been surprised to learn that I won an award that bore his name. I certainly was.

The upshot of that dismissal was that I worked with Peter Milner. My project was on memory consolidation in rats. It is a topic to which I returned 30 years later while spending a sabbatical at the University of Arizona with Lynn Nadel, with whom I had maintained a friendship since my undergraduate days at McGill where he was a graduate student.

Looking back, I now realize that being an undergraduate student in psychology at McGill in the early 1960s meant that I was born with an academic silver spoon in my mouth. Led by Hebb, the faculty in physiological psychology was very strong and included Peter and Brenda Milner, Dalbir Bindra, and Ronald Melzack, as well as Robert Malmo and Herbert Jasper, who were affiliated with the department. And, of course, there was Wilder Penfield, at the Montreal Neurological Institute, whose presence was felt not just at McGill but all over Montreal, and possibly the rest of Canada.

I have no doubt that coming from McGill helped to get me accepted to the Ph.D. program at the University of Pennsylvania, which then was in its heyday (1966–1971). Under the creative and exuberant supervision of Paul Rozin, and the tutelage of an extraordinary faculty, I completed my doctorate and joined a young and excellent faculty at Erindale College of the University of Toronto (now the University of Toronto at Mississauga) in 1971. It was part of the psychology department at Toronto, which arguably was the strongest in the world in research on human memory.<sup>1</sup>

If these riches were not enough, in 1987 I was appointed by Guy Proulx to the psychology department at Baycrest Hospital, and in 1989, by Don Stuss to the newly created Rotman research Institute as its first senior scientist. I now had ready access to patients and to functional neuroimaging. Most importantly, however, at Toronto and in all the other departments, the faculty attracted excellent graduate students and postdoctoral fellows who, together with the faculty, provided an intellectual environment that nurtured research and scholarship. The silver spoon never left by mouth.

This article, which charts the history of some of my contributions, is divided into six sections, with sabbatical and study leaves serving as signposts. The second and fourth sections describe the

component process model and the multiple trace theory (MTT), respectively, which were developed during two of the sabbatical leaves. The fifth section deals with new developments, followed by a concluding section.

## Signposts on the Sabbatical Road

### *Study Leave (1973–1974): Montreal Neurological Institute*

After only 2 years as an Assistant Professor at Erindale College of the University of Toronto, I was granted a leave of absence to work with Brenda Milner at the Montreal Neurological Institute (MNI). Though I had thought about memory since my undergraduate days in Peter Milner's lab, I had worked only on hemispheric specialisation since my third year in graduate school under the clever and exuberant direction of Paul Rozin. Inspired by a colloquium Brenda Milner gave on hemispheric specialisation, and lacking patients, I studied laterality in normal people by applying some of the new reaction time techniques being developed in the emerging field of cognitive psychology (Moscovitch, 1972, 1973). By combining response hand with visual-field presentation and varying the material and processing requirements, I could measure interhemispheric transfer time and hemispheric processing efficiency. In so doing, I could infer the specialisation of each hemisphere and how it shares information with its partner. By working with Brenda at the MNI, I hoped to pursue my interests in hemispheric specialisation, but now with a clinical population, and also study memory in patients with unilateral temporal or frontal lobectomy.

It was a wonderful year in which I learned much more than I had realised at the time. The year provided me not only with a foundation in neuropsychology but also with some of the scaffolding around which I could construct my stories. As well, I developed friendships that have lasted me to this day and a network of colleagues (everyone passed through the MNI) that may have been as invaluable as knowledge and productivity in establishing a career. I published an article with Arnold Wilkins based on the work we completed that year on semantic decisions in patients with unilateral temporal lobectomy (Wilkins & Moscovitch, 1978). However, it was the research I conducted on the frontal lobes that figured more prominently in my later work.

### *Sabbatical I (1978–1979): Hadassah Hospital and the Hebrew University, Jerusalem*

Most of what I learned at the MNI, however, did not bear fruit until my sabbatical in 1978–1979, which I spent in Shlomo Ben-tin's and Moshe Feinsod's lab at Haddasah Hospital in Jerusalem.

<sup>1</sup> In addition to Paul Rozin, the faculty at Penn included Richard Solomon, Phil Teitelbaum, Evelyn Satinoff, Frank Irwin, Leo Hurvich, Dorothea Jameson, Jack Nachmias, Duncan Luce, Robert Bush, Burt Rosner, Harris Savin, Henry and Lila Gleitman, Randy Gallistel, and Rochel Gelman, with Eliot Stellar, James Sprague, William Chambers, John Smith, Aaron Beck, and Alan Epstein being affiliated with the department. At Toronto, though the older faculty were now my colleagues, I also considered them my teachers and mentors: Endel Tulving, Gus Craik, Paul Kolers, Ben Murdock, and Norm Slamecka.

Shlomo and I were both just starting our careers (in fact, Shlomo had yet to receive his doctorate), our children were young, and all of us became fast friends and remained so to this day. My family also fell in love with Jerusalem, and with Israel in general, an affection that has not waned.

Taking some of the data I collected at the MNI and reflecting on some problems in research on amnesia, I wrote a chapter that identified some of the characteristics of amnesia and related disorders, particularly those affecting the prefrontal cortex. This work was presented at a conference organised by Laird Cermak at Lake Moray in 1979 and appeared as a chapter in the book on the proceedings of that conference (Moscovitch, 1982). I believe that conference was a watershed in memory research as it brought together researchers from cognitive psychology and neuropsychology and demonstrated to each how much they could learn from one another. Though commonplace now, that realisation had yet to penetrate the mainstream of either discipline.

*Lake Moray Conference, New Hampshire/Vermont  
(October 1979)*

A number of findings and ideas were discussed at the Lake Moray Conference, but three stood out for me (Moscovitch, 1982). The most exciting of them concerned memory without conscious awareness, because it was the newest and most provocative, and had the most far-reaching implications for theories of memory. Neuropsychologists showed that amnesic people could acquire and retain information about past events, as indicated by changes in performance on tests of perception and action, even though they had no conscious memory of the event or the relevant information. Cognitive psychologists showed the same thing in neurologically intact people. What was striking was the implication that although amnesic and normal people were worlds apart in retaining and retrieving memories with conscious awareness, what we now term *declarative* or *explicit memory*, they did not differ with respect to memory without awareness (termed *nondeclarative*, *procedural*, or *implicit memory*). It took two more decades of research to elucidate some of the basic characteristics of implicit memory and the neural substrates that mediate its different forms, and the enterprise is far from over (see later discussion). It already was obvious at that meeting that the structures considered crucial for memory, the medial temporal lobes and diencephalon, were really important for only one type—memory with conscious awareness.

The distinction between memories dependent on the medial temporal lobes and those dependent on other structures had been noted before in the human and animal literature, but consciousness was not considered to be a distinguishing feature. Indeed, in the animal literature it still is not, but it moved from the wings (or, more appropriately, the cellars and dressing rooms of psychology) to occupy centre stage in the human literature.

A second theme that emerged was that some memory disorders were associated with damage to the prefrontal cortex, though the nature of the disorder had more to do with memory organisation and interference rather than with memory loss per se, which many believed was the hallmark of medial temporal lobe amnesia. The implication of this observation was not fully appreciated until the advent of functional neuroimaging studies of memory where the involvement of the prefrontal cortex during memory encoding and retrieval seems to be ubiquitous.

The third theme was almost peripheral to the concerns of the conference but gained in importance for me only in retrospect. There was a controversy, ongoing since the early 1970s, as to whether remote memories were spared by amnesia or not. The view that memories take time to be consolidated dated back to the end of the 19th century with evidence showing that the extent to which memories can be disrupted by amnesic agents, such as brain damage, concussion, or electroconvulsive shock (ECS), is determined by their age, with decreasing vulnerability to disruption or loss from the most recent to the most remote. Such a temporal gradient also was observed following damage to the medial temporal lobes, leading investigators to conclude that the medial temporal lobes, and the hippocampus in particular, are temporary memory structures needed for retention and retrieval only until memories are consolidated elsewhere in the brain (Squire & Cohen, 1982). A number of investigators at the conference took issue with this formulation. They had shown that amnesia can extend for a lifetime (Sanders & Warrington, 1971; Warrington & Sanders, 1971) and argued that the hallmark of amnesia is loss of only episodic memory. Semantic memory is relatively spared (Kinsbourne & Wood, 1975; Wood, Ebert, & Kinsbourne, 1982). Despite this, the consensus was in favour of traditional consolidation theory.

Although the conference highlighted areas in which cognitive psychology and neuropsychology could make common cause, there were principles developed in the cognitive literature that could not be applied easily to studies of amnesic patients. One of these was levels of processing ( Craik & Lockhart, 1972), which held that memory is a byproduct of the perceptual and conceptual operations performed on a stimulus or event. The more deeply the information is processed, the better the memory for it. Intention to remember plays little or no role. Another was the encoding specificity principle (Tulving & Thompson, 1973) that states that for an item to be remembered the cues at retrieval must overlap with the information that was encoded. The reason that these principles could not be applied now seems obvious: The structures damaged in amnesia were necessary for the instantiation of these principles. With the loss of those structures, these principles could not operate and memory, accordingly, was impaired.

These findings and problems continued to preoccupy me, as they did much of the research community on memory. Between sabbaticals, I conducted experiments to solve some local problems that I hoped would provide me with some insight into the more global issues discussed at Lake Moray. How did everything fit together?

*Sabbatical II (1985–1986): Institute for Advanced Studies,  
Hebrew University, Jerusalem*

I made some more headway during my next sabbatical. Israel Nachshon convened a group of about a dozen Israeli and foreign scientists at the Institute for Advanced Studies at the Hebrew University in Jerusalem to spend a year discussing hemispheric specialisation. (In addition to Nachshon and me, the group included Asher Koriat, Harvey Babkoff, Elkhonon Goldberg, Sonny Kugelmass, Shlomo Bentin, Eran and Dahlia Zaidel, and Carlo Umiltà, with Michael Corballis joining us for a week. Gita Bendov and Gina Dvoretzky were senior graduate students who also participated). This sabbatical was as rewarding as the previous

one, not the least reason being that we were treated like royalty by the Institute. (For an idea of the variety of discussions, see the special issue of *Journal of Clinical & Experimental Neuropsychology*, 17; 1995).

We met weekly to discuss laterality, but soon the discussion broadened to include general theories of brain organisation and cognition. Jerry Fodor (1983) had just published his small, thought-provoking, but controversial, book, *The Modularity of Mind*, and it became the focus of our discussion. Like psychologists elsewhere, we could not agree about Fodor's definitions of modularity and central systems, let alone his views on how the mind was organised, some of us thought his enterprise was flawed beyond redemption, whereas others of us found merit in the fundamental dichotomy he proposed between modules and central systems, though we disagreed about details (although Fodor might say that we took exception with some of his basic principles).

Carlo Umiltà and I soon realised that we were often on the same side of most issues. We decided to meet almost daily for about 2 months and see how far we could get in applying Fodor's ideas to neuropsychology. To say we were grandiose in our ambitions would be an understatement: We examined the human neuropsychological literature from perception to action, with attention and memory included. The articles that emerged from our discussions (Moscovitch & Umiltà, 1990, 1991) helped organise our ideas and served as a general theoretical framework for my research since then.

We pared Fodor's criteria of modularity down to three: domain specificity, shallow output, and informational encapsulation. These were the only ones that seemed generally consistent with the neuropsychological literature. We proposed four functions of central systems, among them the assembling of lower order modules into higher order ones (automatization) and planning. Last, we tried to relate these ideas to brain structure and function. I will not dwell on our particular formulations, though it seems to me that our ideas and predictions have been vindicated more often than not by subsequent research. What I wish to do is show how we applied our notions of modularity and central systems to develop a component process model of memory to deal with those issues that figured so prominently at Lake Moray.

### The Component Process Model of Memory

Studies of memory in amnesia have indicated that memory is not unitary but rather consists of a variety of different forms, each mediated by different component processes, governed by different principles, and subserved by different neural mechanisms (Moscovitch, 1992; Witherspoon and Moscovitch, 1989). According to the component process model of memory, the posterior neocortex consists of domain-specific modules or representational systems that pick-up, analyse, and interpret stimulus input. Processing this information modifies the modules so that they store long-term perceptual and semantic records of the input. The records constitute nonconscious mnemonic representations that mediate performance on implicit tests of memory. The modules in the posterior neocortex can deliver the output of their analyses to consciousness so that we become aware of stimuli and their meaning.

To deal with explicit, episodic memory, we proposed that any information that is consciously experienced is picked up obligatorily by the hippocampus and related structures in the medial temporal lobes and diencephalon, which comprise the hippocam-

pal complex or system.<sup>2</sup> These structures bind into a memory trace those neural elements in the neocortex (and elsewhere) that mediate the conscious experience of an event. Thus, the episodic memory trace consists of an ensemble of hippocampal and neocortical neurons. The hippocampal component of this ensemble consists of a sparse neural representation of the trace that acts as an index or file entry pointing to the neural elements in the neocortex that represent both the content of the event and the conscious experience of it. *Consciousness*, therefore, is part of the memory trace. Retrieval occurs when an external or internally generated cue triggers the hippocampal index, which in turn activates the entire neocortical ensemble associated with it. In this way, we recover not only the content of an event but the consciousness that accompanied our experience of it. In short, when we recover episodic memories, we recover conscience experiences (Moscovitch, 1995<sup>b</sup>, 2000).

According to this model, both encoding and retrieval of consciously apprehended information via the hippocampus and related structures is obligatory, yet we know from experience and from experimental investigation that we have a measure of control over what we encode and what we retrieve from memory. Moreover, if encoding of consciously apprehended information is obligatory, the information cannot be organised. Indeed, according to the model, except for close temporal contiguity, memories are stored independently of each other, like beads in a jar. Nonetheless, memory appears to have some temporal and thematic organisation. How can we reconcile this model of memory with other facts we know about how memory works? One solution, elaborated with Gordon Winocur (Moscovitch & Winocur, 1992), my good friend and collaborator since 1975, is that other structures, particularly those in the frontal lobes, act as the "boss" of the memory system. They control the information delivered to the medial temporal and diencephalic system at encoding, initiate and guide retrieval, and monitor and help interpret and organise the information that is retrieved. By operating on the medial temporal and diencephalic system, the frontal lobes act as *working-with-memory* structures that control the more reflexive medial temporal and diencephalic system, and confer a measure of intelligence and direction on it. Such a complementary system is needed if memory is to serve functions other than mere retention and retrieval of past experiences (Moscovitch, 1992). In other words, the frontal lobes are needed to string the hippocampal/medial temporal lobe (HC/MTL) beads into different necklaces to be worn as befits the occasion.

In a nutshell, the hippocampal complex is essential for encoding, retaining, and recovering experiences, what we now term *recollection*, which the prefrontal cortex selects, organises, helps retrieve, monitors, and verifies. Because encoding and retrieval from the HC/MTL system are obligatory (once proximal cues are given) and storage by HC/MTL is random, all extended episodic memories are reconstructed.

### *The Hippocampal Complex or System Is Modular*

In retrospect, it seems to me that the key aspect of the component process model, what was original about it and distinguished it

<sup>2</sup> The hippocampal complex or system includes the hippocampus proper, the dentate gyrus and the subiculum, which comprise the hippocampal formation, and the parahippocampal, perirhinal, and entorhinal cortex of the medial temporal lobe.

from others, is the designation of the hippocampal complex or system as a domain-specific module. Its specific domain is consciously apprehended information and none other, and, being modular, the hippocampal complex picks up that information obligatorily and likewise delivers the stored information as output in response to a cue. The hippocampal complex is informationally encapsulated and cognitively impenetrable; we have no direct access to the intermediate processes between encoding and retrieval, nor any way to influence their operation. We are only aware of the output from the system. The output shallow in that the memory is not interpreted as to its significance or veridicality. It simply is designated a “memory” whose truth and meaning must be ascertained with the help of other parts of the brain.

Other aspects of the model, such as working-with-memory and perceptual and conceptual modules, may have been relatively novel when we proposed them, but they quickly were incorporated into the mainstream. So, too, was the idea that encoding and retrieval of memories depend on the interaction among prefrontal cortex, HC/MTL, and posterior neocortex. The idea that the hippocampal system is modular in the way we defined it, with all its inherent characteristics, I believe remains controversial and so retains its novelty.

Why place such a “stupid,” reflexive system at the core of memory? The best reason I could think of is that we (and by “we” I mean all organisms with a hippocampus) cannot predict the future with great certainty, so we cannot determine at any given moment what will be important to remember. It would place our minute-to-minute memory decisions at a level equivalent to that of students trying to determine what to study by predicting what will be on the exam or adults predicting the stock market. Even if we could predict the future with some confidence, events happen too quickly for us to decide what to remember, and working memory capacity is too small to retain large amounts of information until a decision is reached. By that time, crucial elements of the event may already have passed us by. There rarely is a “replay” button in real life. For that reason, we have to have a system that will encode obligatorily whatever we designate as sufficiently important at the moment it occurs to attend to it. As a result, the information comes to occupy our consciousness and thereby gains access to the HC/MTL.

Of course, as we noted, the price of having an efficient system that encodes everything in consciousness obligatorily and unselectively is that you need a control system at the front and back end. The prefrontal cortex, and likely other brain regions, serves latter function. Episodic memory that is organized and goal directed, therefore, arises from an interaction among the posterior neocortex, medial temporal lobes, and prefrontal cortex and is not the property of any one system.

What are the implications of having such an episodic memory module? The following discussion presents some of them briefly and provides some evidence to support our ideas.

#### *Modularity, Levels of Processing, and the Encoding Specificity Principle*

The idea that a stupid module lies at the heart of episodic memory provided some insight into two of the Lake Moray puzzles. It helps explain why memory is a byproduct of perception and comprehension, as levels of processing assert. Anything in con-

sciousness is picked up by the HC/MTL. The more deeply an item is processed, the richer and more distinctive is the conscious experience and the memory trace that ensues. As a result, the easier it is for any element in the trace to serve as a cue to reactivate it via the hippocampal index (Moscovitch & Craik, 1976). Damage to the HC/MTL impairs or obliterates a crucial component of the system on which level of processing depends; it prevents consciously experienced events from being encoded in long-term memory, so this framework has no means of operating normally in amnesic patients. As a result, levels-of-processing effects in episodic memory are severely reduced or eliminated, while intact implicit memory, which operated by different principles, is relatively spared (Moscovitch, Vriezen, & Goshen-Gottstein, 1993).

The interaction between the cue and the hippocampal index also underlies the encoding specificity principle. Because the index represents the information that is encoded, only cues at retrieval that have elements in common with the encoded information are capable of activating the index. *Ephory*, the automatic interaction of the cue with the HC/MTL components of the memory trace, is the basis of retrieval. The loss of the indexing function after HC/MTL damage means that the encoding specificity principle can no longer be implemented at the level of episodic memory, though similar principles may apply in semantic and implicit memory.

#### *Random Independent Storage, Shallow Output, Memory Reconstruction, and Confabulation*

If encoding anything in consciousness is obligatory, it is unlikely that memories will be organized by theme or temporal order, except for very close temporal contiguity (see Landauer, 1975). Information will just be dumped in and tagged according to elements of its content, to be sorted and organized at retrieval by prefrontal cortex and other structures into larger themes and, if need be, into a coherent narrative.

Though damage to the HC/MTL causes memory loss, insofar as some information is retained, memory for temporal order is not affected. Damage to the prefrontal cortex, however, does not affect memory for content or items but causes deficits in memory for temporal order, even if the information had been acquired long before the lesion (Milner, Corsi, and Leonard, 1991; Shimamura, Janowsky, and Squire, 1990).

Confabulation caused by damage to the ventromedial aspects of the prefrontal cortex provides the most dramatic evidence that memory storage is random, that output is shallow, and that memories are reconstructed (Moscovitch, 1989, 1995a; Moscovitch & Umiltà, 1991). People who confabulate do so without intending to deceive (“honest lying”) and are unaware of their memory deficit. Their confabulations are rife with information that often pertains to some event they experienced but that is recombined with elements of other events in a way that is inappropriate for the task at hand, often is implausible, and sometimes is internally inconsistent or bizarre. Though they sometimes are capable of detecting inconsistencies, people who confabulate lack the means to judge the veracity of the memory itself; they accept as true whatever memory is recovered from the HC/MTL in response to proximal cues that can activate the index. Memory is reconstructed on the fly without filters or monitors (see Moscovitch & Winocur, 2002, for

an updated discussion of working with memory functions of the prefrontal cortex, and Gilboa, et al., 2006; Gilboa & Moscovitch, 2002, for its most recent application to confabulation).

### *Obligatory Encoding and Retrieval: The Effects of Divided Attention*

The effects on episodic memory of divided attention at encoding and retrieval are asymmetrical. If the specific domain of HC/MTL is information in consciousness, which it obligatorily encodes, then distracting the individual by dividing attention while encoding should lead to severe impairment in episodic memory because consciousness is occupied by another task. This indeed is the case ( Craik, Govoni, Naveh-Benjamin, & Anderson, 1996).

At retrieval, however, output is obligatory once the proximal cue is apprehended. Consequently, in contrast to its effects at encoding, divided attention at retrieval has little effect on memory, though performance on the concurrent task drops because the recovered memory usurps attentional resources from it (see also Baddeley, Lewis, Eldridge, & Thompson, 1984). This latter finding has important implications for recent studies on the involvement of the parietal cortex in memory retrieval, which I consider in the following discussion.

There are two exceptions to the rule that divided attention does not affect memory at retrieval. If retrieval depends on strategic memory processes mediated by the prefrontal cortex (working with memory), then memory suffers under divided attention (Moscovitch, 1994). Conceiving and implementing those strategies is resource demanding, and allocating resources to a secondary task impairs performance.

Memory performance is also reduced if material specific processes and representations of the divided attention task overlap with those of the memory task (Fernandes & Moscovitch, 2000). Because the memory trace consists of an ensemble of HC-neocortical (NC) neurons, the temporary unavailability of the relevant neocortical representations prevent the memory trace from being recovered or expressed. Evidence from functional neuroimaging shows that reduction in HC/MTL activation is associated with increased activation in anterior and posterior neocortex during concurrent task performance (Fernandes, Moscovitch, Ziegler, & Grady, 2005).

### *Recovered Consciousness, Recollection, and Familiarity*

In 1985, Tulving proposed a distinction between two aspects of recognition memory, *remembering* and *knowing*, and the type of consciousness associated with each. Remembering involves re-experiencing or reliving a past event in the mind, what Tulving calls “mental time travel.” Characterised by recovering and recreating the context in which a stimulus or event occurred, it is a hallmark of true episodic memory. Knowing, on the other hand, is associated with a sense of recognising or experiencing a stimulus or event as old but with little or no information about the context in which it was encountered or occurred. Though knowing refers to recognition of a memory associated with an episode, it has much in common with semantic memory. Because remembering and knowing are not process pure, investigators refer to *recollection* and *familiarity*, respectively, as the processes that underlie them

(Jacoby, 1991; for reviews, see Roediger, Rajaram, & Geraci, 2007; Slotnick & Schacter, 2007; Yonelinas, 2002).

Recent investigations have linked recollection and familiarity to different regions of the medial temporal lobe; the hippocampus is linked with recollection, and the peri-rhinal cortex is linked with familiarity (for review, see Eichenbaum, Yonelinas, & Ranganath, 2007; Skinner & Fernandes, 2007). When we proposed the component process model, we did not distinguish between these different aspects of recognition or between different regions of the medial temporal lobe. To deal with the problem of explicit, conscious memory, however, we suggested that the HC/MTL binds consciousness into the memory trace so that what is recovered is not merely the content of the event but the conscious experience that went with it. In a later article, we argued that recovered consciousness is associated as much with medial temporal lobe function as with that of the prefrontal cortex, as others had argued (Wheeler, Stuss, & Tulving, 1997). In retrospect, the notion of *recovered consciousness* is very much akin to recollection and provides a neuropsychological account of why the process mediating recollection is associated specifically with the hippocampus.

Ours is not the only account of why recollection is linked to the hippocampus. The more common account is that the hippocampus is needed for relational binding, namely, the association of random elements with each other into a memory trace (Eichenbaum, 2004; Eichenbaum, Otto, & Cohen, 1994). Though relational binding may be a necessary component of recovered consciousness and, one could argue, makes it possible, relational binding does not provide a complete account of hippocampal function if consciousness is not taken into account. As yet, the evidence is not sufficient to distinguish between these two interpretations.

A third account derives from the cognitive map theory of hippocampal function (O’Keefe & Nadel, 1978; for updates, see Burgess, Maguire, & O’Keefe, 2002; Hassabis & Maguire, 2007). According to this account, the hippocampus is needed to form allocentric representations of space. Allocentric representations are defined according to the relations that different spatial elements bear to each other as compared, say, to an egocentric (viewer centred) representation. Such representations are central components of any episodic memory, because all episodes occur in a particular place. The hippocampus is necessary to construct the scenes in which events take place. Although there is much to recommend this view, studies of remote memory suggest that recovered consciousness captures more of the evidence (see later discussion). It is to the topic of remote memory that I now turn.

### *Signposts Along the Sabbatical Road, Continued*

#### *Sabbatical III (January–May 1996): The University of Arizona*

The distinctions among recollection, familiarity, and semantic memory (Tulving, 1972, 1983, 1985), are also crucial to our understanding of the literature on remote memory and consolidation. My collaborators and I did not arrive at our ideas about remote memory, however, from first principles based on the component process model. In hindsight, we could have, as we shall see, but because the model did not deal specifically with the problem, we did not turn to it for a solution. Instead, we arrived at our ideas empirically and, as usual, while I was on sabbatical.

The University of Arizona was a wonderful place to be on sabbatical. Tucson's weather for most of the year, and its terrain, are not very different from parts of Israel—and it has golf courses galore. I had the opportunity to renew my friendship with Lynn Nadel and work with him and a terrific group of people, some interested in memory and some in golf. Lynn and I had no idea on what we would collaborate, but we were confident that a project would materialise.

After I arrived in Arizona, I was invited by Michael Myslobodsky, a friend in Israel, to present a paper on consolidation at a conference at The University of Tel Aviv (May 1996). The only research I had done on consolidation was my undergraduate honours' thesis and an article I had written on the topic in my first year as a graduate student. I invited Lynn to join me in presenting the paper, as he was familiar with the topic, having coauthored an important chapter on consolidation (Squire, Cohen, & Nadel, 1984). We thought that we would update the literature but, with slight variation, stick with the standard model of consolidation (Milner, 1966; Squire & Alvarez, 1995).

That plan changed when we read a prepublication copy of an article by Rempel-Clower, Zola, Squire, and Amaral (1996). They reported remote memory performance in three patients whose lesions were restricted to the HC/MTL. It struck us that their retrograde amnesia for semantic memory (public events and famous people) was over 10 years long, and for autobiographical events it was over 35 years long. A survey of the literature indicated that such a long retrograde amnesia for autobiographical events was not unusual, if the HC/MTL lesion was large. That seemed to us well beyond the time the initial proponents of the standard model had in mind for the time course of consolidation. As we noted in the initial publication, before the 20th century the average human life span, at about 35 years, was not long enough for most people to consolidate any autobiographical memories and few semantic ones. Instead of updating the standard model, we decided to propose an alternative to it.

### *The Hippocampal Module in the Multiple Trace Theory of MTT of HC/MTL Neocortical (NC) Interactions*

The model had to account for what we considered to be the two major findings that argued against the standard model: (a) a distinction between the time course of autobiographical episodic and semantic memory, with the former extending up to a lifetime and the latter being restricted to about 10 years; and (b) the variation in the severity and extent of retrograde amnesia for episodic memory with the size of the HC/MTL lesion. For very large lesions, the retrograde amnesia encompasses most of a person's lifetime if not all of it. We proposed an MTT of HC/MTL–NC interaction whose basic tenets are listed in the following discussion and in which the conception of an HC/MTL module plays a leading role (Nadel & Moscovitch, 1997). I first present how the model deals with episodic, autobiographical memory and then turn to semantic memory.

*Autobiographical memory.* The HC/MTL automatically encodes all attended information. Memory traces in the HC/MTL are encoded in sparse, distributed representations that act as an index or pointers (see Teyler & DiScenna, 1986) to the neocortical ensembles that mediate the attended information. The full memory trace consists of the HC/MTL–NC ensemble. The HC/MTL and

neocortex are always jointly involved in the storage and retrieval of normal episodic memory—the combined regions together comprise the episodic memory system, regardless of the age of the memory.

Once we formulated this idea, it made eminent sense to us that the HC/MTL would always mediate autobiographical, episodic memories. Recovered consciousness or reexperiencing always depends on the HC/MTL and the hippocampus in particular, as stipulated in the component process model. If episodic memory (reexperiencing or recollection) of recently experienced events is dependent on the hippocampus by virtue of its organisation and operation, it did not seem reasonable or biologically plausible to relinquish that function, over time, to other regions that were less equipped to handle it.

Each reactivation of a memory trace (recollection or remembering) occurs in a different context and results in an altered trace. Because the hippocampus is a stupid module, as the component process model posits, it reencodes this information anew each time. This results in a new, sparsely distributed trace in HC/MTL and a new HC/MTL–NC link. Reactivation thus expands, modifies, and strengthens the initial HC/MTL trace and/or strengthens and elaborates the links between HC/MTL and neocortical traces.

The older the memory, the more likely it is that traces associated with it will be reactivated, leading to more numerous and widely distributed and/or stronger traces than more recent memories. This makes older memories more resilient to damage than recent memories, not by virtue of consolidation outside the HC/MTL but because of the nature and number of traces within the HC/MTL.<sup>3</sup>

*Semantic memory.* With respect to semantic memory, reactivation of memory traces accomplishes two things: Because each reactivated trace shares some neocortical representations with previous traces, reactivation slowly instructs the development of neocortical traces that reflect the statistical properties of the world and/or of memories—the *gist* or semantic core is extracted (see McClelland, McNaughton, & O'Reilly, 1995; Norman & O'Reilly, 2003). Reactivation of memory also facilitates formation of links between representations of elements of episodes.

The HC/MTL and neocortex are in constant interaction. Semantic and episodic memory are treated differently within the hippocampal and neocortical systems. Only episodic memory requires HC/MTL participation and storage. Semantic memory normally engages hippocampal involvement, and hence benefits from the presence of an intact hippocampal system, but it is not dependent on it. All aspects of semantic memory are typically stored outside

<sup>3</sup> It resembled, but was not identical, to other MTTs that, we later discovered, had been proposed to account for the literature on laboratory tests of anterograde memory in neurologically intact people (e.g. Estes, 1964; Hintzman, 1988). Aside from some assumptions being different, these theories had no neural component and did not address the neuropsychological literature.

<sup>4</sup> Another tenet is that the hippocampus is not merely an index to neocortical representations of memories but stores contextual information regarding the episode. Lynn and I differed on this last point. As the developer of the cognitive map theory of memory, Lynn believed that allocentric spatial information was represented in the hippocampus and provided a framework for all the other elements of the episode. I did not think that was the case. We settled on the neutral term *contextual information*, which allowed us wide scope for interpretation.



the hippocampal complex where semantic memories can be formed without reliance on the HC/MTL—albeit much more slowly and with less specificity, at least in adulthood (Westmacott & Moscovitch, 2001; Corkin, 2002; but see Gadian, Aicardi, Watkins, Porter, Mishkin, & Vargha-Khadem, 2000, for childhood).

This model, therefore, was able to account for the pattern of results observed in the literature. Because the hippocampus is needed for recollection no matter how long ago the event occurred, and because it only lends support to the formation of semantic memories outside the HC/MTL, damage to the HC/MTL leads to greater deficits in episodic than semantic memory. Because older, episodic traces are more numerous, widely distributed, and/or stronger than recent traces, and possibly with more neocortical links, the extent and severity of deficits in remote autobiographical impairment were related to extent of HC/MTL damage. With large HC/MTL lesions, severe retrograde amnesia sometimes extended to the person's entire life. When the lesion to HC/MTL is small, the deficits was minimal (Nadel and Moscovitch, 1997).

*Tests of MTT and modularity of the hippocampus.* Not content to rely on evidence already existing in the literature, we began collecting our own data because we thought that new methods were needed to test the predictions of the model more precisely. First, we needed better, more sensitive tests of remote memory for autobiographical events. If reexperiencing depends on the HC/MTL, as the component process model and MTT predict, then the tests need to capture that aspect of episodic memory. We chose to use narratives of past events because we believed that a narrative was best able to capture what the experience was like. We scored for the number of details, because we thought it was an objective measure of the richness of the remembered experience (Moscovitch, Yaschyshyn, Ziegler, & Nadel, 1999). We refined the measure further to distinguish details pertaining to the episode itself from those related to semantic and generic elements of the narrative (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). We developed this measure and tested its efficacy between my sabbaticals.

Second, we needed to assess the neural substrates of remote memory in neurologically intact people. One of the difficulties in conducting research on a clinical population, and one of the main sources of contention among rival theories of remote memory, is characterising the precise locus and extent of lesions. Though we continued to study patients, and to characterise their lesions as best we could, we also turned to functional neuroimaging studies of normal people. We realised that such studies would allow us to identify the neural substrates mediating performance on tests of remote memory and circumvent some of the problems posed by patient studies, while also providing converging evidence for our hypotheses.

#### *Sabbatical IV (1999–2000): Remote Memory and Functional Neuroimaging*

With Lee Ryan taking the lead, plans to conduct functional neuroimaging studies began toward the end of Sabbatical III, and the studies continued into Sabbatical IV. Participants were asked to relive in as much detail as possible experiences from different times in their life, ranging from childhood to the most recent past, while they were being scanned. The functional neuroimaging

evidence confirmed our hypothesis: As predicted by MTT, the hippocampus was active bilaterally when participants reexperienced past events, in comparison to control conditions, no matter how long ago the events occurred, with no evidence of a temporal gradient. As well, activation of the neocortex did not increase with time, as the standard consolidation model predicted; if anything, it was more active for recent than for remote events (Ryan et al., 2001).

By the middle of that sabbatical, we had already collected sufficient data from our various labs to test our hypotheses, and we consolidated the evidence from patient, neuroimaging, and computational models. We were encouraged by the findings that generally supported our position and made plans to design additional studies to extend and refine the model. Many of these studies have been completed and have been reviewed extensively in recent years (Fujii, Moscovitch, & Nadel, 2000; Moscovitch et al., 2005a, 2005b; 2006; Nadel, Ryan, Hayes, Gilboa, & Moscovitch, 2003; Nadel, Samsonovich, Ryan, & Moscovitch, 2000; Nadel, Winocur, Ryan, & Moscovitch, 2007; Rosenbaum, Winocur, & Moscovitch, 2001), so there is no need to describe the results in detail, though I will summarise them briefly.

In fairness, before I begin, I should note that there is not universal agreement either about the findings or their interpretation. The interested reader is invited to consult articles expressing these other views (e.g., Bright, Buckman, Fradera, Yoshimasu, Colchester, & Kopelman, 2006; Squire & Bayley, 2007; Kopelman & Kapur, 2001; for review, see Frankland and Bontempi, 2005) and references in our reviews where contrary evidence is considered in detail.

#### *Summary of Studies on Remote Memory*

*Autobiographical, episodic memory.* The functional neuroimaging evidence on episodic, autobiographical memory is consistent with Ryan et al.'s (2001) initial observation and overwhelmingly favours MTT. In more than a dozen studies from various laboratories that used a variety of techniques, the results confirmed that retrieval of autobiographical, episodic memories is associated with hippocampal activation no matter how long ago the events occurred, with no little or no evidence of a temporal gradient. Hippocampal activation almost always is associated with activation of a network of other regions that include the retrosplenial cortex, the posterior cingulate gyrus, the posterior parietal cortex, the precuneus, the anterior temporal cortex, the ventromedial and ventrolateral prefrontal cortex, and sometimes the frontal pole.

The precise contribution of these regions is not known, but presumably some regions, such as the prefrontal and posterior parietal cortex, are implicated in strategic search, guided attention, and monitoring. Addis and her colleagues (Addis, Moscovitch, Crawley, & McAndrews, 2004) found that activation in some of the regions is modulated by different aspects of autobiographical reexperiencing—personal significance, emotionality, and detail. Hippocampal activation is modulated in all cases, suggesting that the hippocampus acts as a hub linking these regions. Functional connectivity analysis in neurologically intact people supports this view. Once the hippocampus is damaged, activation and connectivity among the regions is reduced and sometimes eliminated (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, in press). These findings suggest that activation of this hippocampally cen-

tred network mediates the totality of the reexperienced event, as predicted by the component process model.

Though both recent and remote memories are associated with hippocampal activation, Gilboa et al. (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004) found that activations associated with more recent memories cluster at the anterior hippocampus, whereas those associated with more remote memories are distributed across its length. This finding is consistent with predictions from MTT that remote memories are more widely distributed than recent memories. What is intriguing is that other findings point to the anterior hippocampus as a region needed for acquisition and assimilation of new memories (Holahan, Rekart, Sandoval, & Routtenberg, 2006; Maguire, Nannery, & Spiers, 2007; Moser, Moser, Forrest, Anderson, & Morris, 1995).

Evidence from the lesion literature is less consistent, though on balance it favours MTT. Extensive damage to the HC/MTL is associated with a severe and extensive retrograde amnesia of episodic, autobiographical memory, sometimes lasting a lifetime, although proponents of the standard consolidation model claim that the most remote memories from adolescence and early adulthood are spared. Two effects have been observed following small lesions: either there is a less severe deficit across the entire life span, or the deficit is limited to recent years because the older traces may be sufficiently numerous, strong, and/or widely distributed to survive small lesions. In short, the extent of loss varies with the amount of damage to the HC/MTL but not to regions of the extra-HC/MTL cortex (Gilboa et al., 2005; Rosenbaum et al., in press). Indeed, bilateral lesions of the fornix, which carry the major, hippocampal projections, while leaving the hippocampus intact, have as severe an effect on recollection of autobiographical events across the life span as does extensive damage to the hippocampus (Poreh et al., 2006; Gilboa, Rosenbaum, Westmacott, Winocur, & Moscovich, in press). All these findings are consistent with MTT and the idea that the hippocampus is a module that is needed for reexperiencing the past (recovered consciousness).

For the most part, the functional neuroimaging and lesion literature are consistent with one another with one notable exception. Left lateralization of the autobiographical network is observed mainly in functional neuroimaging studies (Addis et al., 2004; Maguire, 2001); whereas in lesion studies, damage of the HC/MTL on either side leads to impairment in autobiographical memory (Viskontas, MacAndrews, & Moscovitch, 2000; St-Laurent, Moscovitch, Levine, & MacAndrews, 2007). This suggests that left-lateralization is related to the narrative-interpretative aspects of the task that are emphasised in neuroimaging studies and that often are associated with left-hemisphere dominance (Gazzaniga, 2000). The autobiographical memory itself is represented bilaterally, with each side presumably contributing to different aspects of it.

*Semantic memory.* With respect to semantic memory, such as vocabulary, public events, and names and faces of famous people, the loss is temporally limited following damage to HC/MTL and often is restricted to about 10 years. Once damage encroaches on the neocortex as well as the HC/MTL, as is the case in Alzheimer's disease, retrograde memory loss extends further back in time as the disease, and presumably the extent of damage, progresses (Westmacott, Freedman, Black, Stokes & Moscovitch, 2004). Functional neuroimaging studies of semantic memory are generally consistent with these findings (see Moscovitch, Nadel, Winocur, Gilboa, &

Rosenbaum, 2006; Moscovitch, Rosenbaum, et al., 2005; Moscovitch, Westmacott, et al., 2005;). Together, they suggest, as MTT predicted, that it takes time and repeated experience to enable the neocortex to extract the statistical regularities from experienced events to create semantic memories. The HC/MTL supports this process but is not necessary for it, as patients with HC/MTL damage can develop semantic memories, though likely not as quickly nor as detailed.<sup>5</sup>

## New Directions and New Controversies

### *The Hippocampus as a Cognitive Map or as the Substrate for Recovered Consciousness*

Studies of remote memory have posed a new challenge to the theory that the hippocampus is necessary for representing allocentric spatial information needed for navigation. Contrary to the cognitive map theory, damage to the HC/MTL does not lead to deficits in navigation of familiar neighbourhoods or locations either in humans or in rats, although acquisition of such spatial representation is dependent on the hippocampus (Rosenbaum, Gao, Richards, Black, & Moscovitch, 2005; Rosenbaum et al., 2000; Teng & Squire, 1999, and see reviews in Moscovitch et al., 2006; Nadel et al., 2007). Though navigation in familiar environments is spared, patients with hippocampal lesions, or even with lesions confined to the fornix (Rosenbaum, Gilboa, et al.), have difficulty in recovering perceptual details of the environment, preventing them from having a rich reexperience of navigating through it. In short, extrahippocampal structures seem sufficient to retain precisely what constitutes a map, cognitive or otherwise, namely, a schematic representation of an environment that is sufficient for navigation (or for whatever other purpose the map is created) without all the extraneous, incidental details that would only clutter it up. What the hippocampus provides is these details that make a rich, reexperience of the environment possible.

Studies of navigation in London seem to support this view, though proponents of cognitive map theory may take exception to my interpretation. Maguire, Woollett, & Spiers (2006) found that navigation on the main thoroughfares, the A routes, is preserved in a London taxi driver with large hippocampal lesions; navigation on the more tortuous side streets, B routes, is impaired precisely because such routes require detailed representations rather than schematic maps. A schematic representation would suffice for navigation in a city such as Toronto, where the roads are laid out in a grid (Spiers & Maguire, 2007).

The functional neuroimaging literature is generally consistent with this observation. Mental navigation in a familiar Toronto environment does not activate the hippocampus, even on allocentric spatial tasks (Rosenbaum, Ziegler, Winocur, Grady, & Mosco-

<sup>5</sup> It is very likely that the hippocampal contribution to acquisition of semantic memory is much less in childhood than it is in adulthood. The growth of vocabulary between the ages of 2 and 4 is so rapid that it is most likely mediated almost entirely by a neocortical system that is independent of the hippocampus. This conjecture receives some support from the studies of Vargha-Khadem and her colleagues (Gadian et al., 2000) who have shown that children with large hippocampal lesions from infancy can have a normal semantic memory even as their episodic memory is grossly impaired.

vitch, 2004; Rosenbaum, Winocur, Grady, Ziegler, & Moscovitch, in press) nor does navigation through a virtual reality representation of London (Spiers & Maguire, 2007). The region activated on those tasks is in the anterior aspects of the parahippocampal cortex, with the hippocampus being activated only when instructions are given to head to a particular location.

To determine whether the hippocampus is needed during acquisition of memory representations of a large-scale environment, Hirshhorn and her collaborators (Hirshhorn, Moscovitch, Winocur, Rosenbaum, & Grady, 2007) have begun a longitudinal study of students newly arrived to Toronto. Within the first year, there is clear hippocampal activation on the very same tasks in which experienced participants showed no activation. By the 2nd year, activation is tailing off in some participants but not others. These findings suggest that until they become familiar with an environment, participants rely on hippocampally based reexperiencing to aid navigation. With time, an extrahippocampal, schematic representation is created of the environment, that is, a spatial analogue of semantic memory, just as MTT predicts.

Similar results were obtained in rats that were reared in a large-scale (for rats), enriched environment—a rat village (Winocur, Moscovitch, Fogel, Rosenbaum, & Sekeres, 2005). Rats reared in the village could continue to navigate in it using allocentric environmental cues even after bilateral hippocampal lesions. By contrast, rats without rearing experience were severely impaired in navigating the village following such lesions.

### *The Coexistence of Episodic and Semantic Memory*

What happens to the detailed memory representations of environments and episodes once the semantic (context-free) representations are available? Are the former lost as the latter are gained, as some consolidation theories suggest (McClelland et al., 1995), or are both represented in neocortex, as other consolidation theories predict (Squire & Alvarez, 1995; Meeter & Murre, 2004; Murre, Graham, & Hodges, 2001)? According to MTT and the component process model, the HC/MTL and neocortex are in constant interaction and thus influence each other. Though undoubtedly episodic memories are lost over time, their loss is not necessarily linked to the development of semantic memories. Insofar as detailed, episodic memories are retained, they will continue to depend on the HC/MTL and coexist and interact with the neocortical, semantic memories (see Moscovitch et al., 2005; Westmacott and Moscovitch, 2003; Westmacott, Black, Freedman, & Moscovitch, 2004).

Ongoing studies of spatial navigation in human adults suggest that either detailed or schematic spatial representations can be used, depending on the demands of the task. Hirshhorn, Newman, Rosenbaum, Winocur, & Moscovitch (2008) compared young adults with older adults, because ageing is associated with hippocampal atrophy. The older adults performed as well as the younger adults on all tests of mental navigation that depended on schematic representation of large-scale environments. The older adults, however, were noticeably deficient if asked to describe in as much detail as possible what they “observe” as they mentally navigate along a route (which houses they passed, their appearance, idiosyncratic landmarks, etc.). They provided about half the number of details as young adults. For the young adults, and to a

lesser degree for older adults, the episodic memory is there and can be conjured up when the task requires it.

Similar findings are observed with respect to memory for public events and people (Petrican & Moscovitch, 2007). We asked neurologically intact individuals to indicate whether they were simply familiar with the events and people or whether they also recollected some personal episode associated with the names and events. We found that as the event receded in time, from the present to 50 years into the past, recollection diminished much more than familiarity, though recollection was present even for some of the most remote events. Recollection was reduced significantly in people with damage to the HC/MTL but not to the neocortex, even for the most remote events, as MTT would predict.

### *Transformation not Consolidation*

It is difficult to draw parallels between people and rats with regard to concepts such as recollection and familiarity, and episodic and semantic memory. Nonetheless, Winocur and his colleagues (Rosenbaum et al., 2001) proposed that context-dependent and context-independent memories in rats would provide a workable correspondence with episodic and semantic memory (or recollection and familiarity in people). Doing so would allow them to examine the fate of context-free and context-dependent memories over time in rats, with far greater control than one could have in studying people, and relate those findings to the literature on human memory. Using socially acquired food preferences and contextual fear conditioning as the memory tasks, Winocur, Moscovitch, and Sekeres (2007) showed that within a day after learning, memory in both tasks was disrupted by hippocampal lesions, whereas by 8 and 28 days, respectively, for the food and fear tasks, hippocampal lesions no longer had any effect. Such findings are usually interpreted as evidence in favour of consolidation theory, which states that with time the identical memory becomes independent of the hippocampus as it becomes consolidated in extrahippocampal structures. Consistent with MTT, however, Winocur et al. showed that the initial memory was transformed from one that represents context-specific information to a schematic representation that preserves only general contextual features that could be common to other environments. Hippocampal lesions eliminate only the context-specific memories that are evident shortly after learning but not the schematic memories that dominate performance at long delays.

Winocur et al. (2007) also found that the context-specific memories were not lost but were dormant and only relinquished control of behaviour to the more schematic memories by Day 28 in contextual fear conditioning. A reminder on Day 28 revived the context-specific memories, so that they once again dominated performance, making the context-specific memories vulnerable anew to hippocampal lesions (Winocur, Moscovitch, Frankland, & Sekeres, 2008). These findings provide a new perspective on systems consolidation and the reconsolidation phenomenon (Dudai, 2004, 2006). They suggest that it is the contextual specificity of the memory, not its lability, that determines its renewed vulnerability to hippocampal lesions during systems consolidation and reconsolidation.

*Rapid, Obligatory Hippocampal Activation and Recollection: Influence on Implicit and Semantic Memory*

If ecphory is obligatory to a proximal cue at retrieval, as the HC/MTL module hypothesis asserts, then recollection should also be obligatory and rapid, occurring without the participant's intention. Memories that pop into mind unbidden and sometimes even unwanted, are a common manifestation of this process. Evidence we collected, however, suggests that the phenomenon is more pervasive than that. Using names of famous people as stimuli, Westmacott and Moscovitch (2003) asked participants to make rapid fame judgements or simply to read the names as quickly as possible. Half the names held some personal significance to the participants, most often a recollection with an event or time of life; we termed these High-R names. The other half were Low-R names that were equated with High-R names for familiarity, frequency, and semantic facts but had no personal significance. We found that response times were on the order of about 1000 ms, with about a 100 ms advantage for High-R over Low-R names. The time at which the name became current had no bearing on the results, as MTT predicted. This recollection advantage was absent overall for patients with HC/MTL damage; but closer inspection of the data indicated that for those few names that held some personal significance, these patients also showed a recollection advantage (Westmacott, Black, Freedman, & Moscovitch, 2004).

This study was replicated by Park and her colleagues (Park & Moscovitch, 2007; Park, Westmacott, Moscovitch, & McAndrews, 2007). In a functional neuroimaging version of the study, they showed that making semantic decisions about these names was associated with rapid, hippocampal activation only for High-R names but not for equally familiar Low-R names.

In further investigations, Sheldon and Moscovitch (2008) have noted that similar effects can be obtained with ordinary words studied in the laboratory. On tests of lexical decision and stem completion, reaction times are faster to words associated with recollection than to words that are merely familiar. The advantage for the latter is no different than for words that have been studied but not recognised, and performance for both is superior to that of new words.

Together, these studies not only indicate that episodic and semantic memory associated with the same targets can coexist, as MTT predicts, but they also show that episodic memory can influence performance rapidly and automatically on ostensibly semantic and lexical tasks, as the HC/MTL modular hypothesis suggested. These findings have important implications for neuropsychological theories of implicit memory while raising new questions about the relation of recollection to consciousness and about some basic premises of the component process model. I discuss both issues in turn.

In attempts to show that implicit memory can be independent of explicit memory, investigators in the 1980s and 1990s were at great pains to ensure that performance on implicit tests was not contaminated by explicit memory (see Roediger & McDermott, 1993; Roediger, Rajaram, & Geraci, 2007). In doing so, they created an unnatural situation and prevented the typical interactions that episodic and implicit memory may have with one another. Sheldon and Moscovitch (2008) showed that recollection contributes to priming (implicit memory) over and above that of other studied words (familiar and misses).

This finding along with others showing that perceptual and response specificity effects in priming may be dependent on the HC/MTL suggest that the hippocampus contributes to performance on implicit tests of memory (Schacter, Dobbins, & Schnyer, 2004; Schnyer, Dobbins, Nicholls, Schacter, & Verfaellie, 2006). Likewise, the HC/MTL even influences performance on semantic tests such as classification, comprehension of metaphors, and semantic fluency but not phonemic tests, as attested from both functional neuroimaging and lesion studies (Gleissner & Elger, 2001; Pihlajamaki, Tanila, Hanninen, Kononen, Laakso, Partanen, Soininen, & Aronen, 2000). Such findings open a new chapter on research on implicit and explicit memory, and on episodic and semantic memory, in which the focus shifts from isolating one type of memory from the other to studying their interaction.

*Recollection as a Two-Stage Process: One Rapid and Unconscious, the Other Slower and Conscious*

Because the effects of recollection and HC/MTL lesions can be shown to influence semantic classification and even perceptual identification, they indicate that processes associated with recollection can occur rapidly. Perhaps they can even occur without the participant knowingly conjuring up recollections or even being aware they have them. This is consistent with predictions from the modular hypothesis that retrieval from HC/MTL (ecphory) is rapid and obligatory. On the surface, however, this conflicts with the idea that recovered consciousness is the output of the HC/MTL. It also argues against the view favoured by dual-process theorists (Yonelinas, 2002) who consider recollection to be a relatively slow, effortful process that requires cognitive control.

A possible solution to this puzzle is that recollection itself is at least a two-stage process. The first is a rapid, obligatory process (ecphory) whose output is not consciously apprehended but can contribute to performance on a variety of tasks, including those that are semantic or implicit, perceptual or conceptual. The second, slower stage, is one in which the individual becomes aware of the ecphoric output, making it explicit, and can use it consciously to guide behaviour (see discussion on the difference between ecphory and retrieval, Tulving, 1983). This might explain why divided attention at retrieval can lead to reduced recollection for both items and associations (Roediger et al., 2007). Future research, we hope, will illuminate these processes.

This two-stage solution, however, raises new problems, the chief of which is that it blurs the distinction between conscious and nonconscious processes in memory, and adds a nonconscious element to explicit memory (see Tulving, 1983, on this issue). Nonconscious processes, however, always figured prominently in the hypothesis that the hippocampus is modular. Ecphory, the cue-trace interaction, always was nonconscious and the output was shallow. This new, two-stage proposal, which borrows from Tulving's ideas, only specifies the parameters over which this nonconscious process operates and the means by which it can be detected. The observation that retrieval on some tests of implicit memory engages the hippocampus (Deslaar, Fleck, Prince, & Cabeza, 2006; Henke, Mondadori, Treyer, Nitsch, Buck, & Hock, 2003; Ryan, Althoff, Whitlow, & Cohen, 2000) is consistent with the hippocampal module hypothesis and its elaboration into the two-stage model of recollection.

### *The Influence of Memory on Attention*

I noted earlier that memory retrieval is associated with activation in the parietal cortex, structures that have been implicated in attention. Research on attention has shown that regions in superior parietal lobe (SPL), along the intraparietal sulcus (IPS), orient attention voluntarily to relevant aspects of the environment, whereas regions in the inferior parietal lobe (IPL) at the temporo-parietal junction (TPJ) mediate the automatic allocation of attention to task-relevant information. Ciaramelli, Grady, & Moscovitch (2008) proposed that the SPL and the IPL play conceptually similar roles in episodic memory retrieval (see also Cabeza, 2007). We hypothesised that the SPL implements voluntary retrieval attempts, whereas the IPL mediates the automatic allocation of attention to retrieved memory contents. It is the latter, we believe, that is associated with recovery of information from the hippocampus. The existing functional neuroimaging literature, and the few studies on patients with lesions in that area (see Davidson, Anaki, Ciaramelli, et al., in press; Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Simons, Peers, Hwang, Ally, Fletcher, & Budson, in press), suggest that this is the case. The IPL, in the region of the supramarginal gyrus, is consistently active when attentional capture by memory content is supposedly maximal, that is, for strong memories as compared to weak ones, for vividly recollected memories as compared to merely familiar ones, and for memories retrieved with high versus low confidence. Attentional capture by such memories seems to have priority even over the voluntary allocation of attention in perceptual tasks. Memory retrieval interferes with concurrent task performance in divided attention experiments, whereas the reverse effect is minimal ( Craik et al., 1996; Fernandes & Moscovitch, 2000, Fernandes et al., 2005). Because we have argued that there is a second stage to recollection that takes longer and is conscious, it is possible that a concurrent task at retrieval may interfere with this longer process. Indeed, Moroz (1998) and Cohn and Moscovitch (2007) have shown this to be the case in an associative memory task. A recent study by Skinner and Fernandes (2008) shows that the interference at retrieval only increases the number of false recollections, suggesting that it is the strategic, attribution process, rather than recovery of the material itself, that is affected.

### *Random, Independent Storage of Consciously Experienced Events Accounts for Flexibility of Memory*

One of the hallmarks of episodic memory is its flexibility. Many investigators have called attention to this property in people and in other organisms, insofar as one is willing to grant that other organisms with a hippocampus have at least the rudiments of episodic memory (Clayton, Bussey, & Dickinson, 2003). What is meant by flexibility is that memories are not tightly linked to each other in the sequence in which an event occurred. Instead, elements constituting memory for an event can be manipulated independently of one another and recombined in new ways, making episodic memory malleable and adaptive, ready to be put to whatever use the rememberer wishes.

Flexibility also is at the heart of reconstructive processes in memory. I want to argue that both flexibility and reconstruction arise from the modular nature of the hippocampus. They are byproducts of a memory system that stores information randomly

and independently and recovers it obligatorily in response to proximal cues. This type of storage and recovery is an essential feature of a memory system that obligatorily encodes all information in consciousness. If memories are stored randomly and independently of one another, all coherent memories of extended events must be reconstructed.

Reconstructive aspects of memory are difficult, though not impossible, to discern in laboratory studies of recall or recognition of single or paired items, because such items are inherently random themselves and do not lend themselves easily to reconstructive processes. Reconstruction is easily evident when narratives are used, as Bartlett (1932) noted in his seminal studies. Such reconstruction is especially noticeable in patients who confabulate. This raises a crucial question: What distinguishes confabulation from normal memory reconstruction that, for the most part, retains veridical information about an experienced event? Research from a number of domains, such as reality monitoring (Johnson, Foley, Suengas, & Raye, 1988), recovered memories of traumatic events (Loftus, 1993), and other types of memory distortion (Schacter, 2001), have provided interesting, but not definitive, answers.

*Temporal specificity or recollective experience?* The use of narrative in tests of remote memory has raised interesting questions about what constitutes the hippocampal contribution to episodic memory. Is temporal specificity, the marking of an event as specific to time and place, the crucial component of episodic memory, or are other features, such as the richness of the memory, equally important or even more so? In functional neuroimaging experiments, Addis et al. (2004) asked participants to retrieve memories of unique, past events (a particular vacation or a celebration) and of repeated events (holiday dinners or shovelling snow) while they were being scanned. What Addis et al. discovered is that the pattern of activation was essentially similar in the two cases; both activated the hippocampus and the related autobiographical network to an equal extent, and the pattern of activation was modulated by experiential qualities such as vividness, emotion, and personal significance.

In a follow-up study, St-Laurent and her colleagues (2007) showed that patients with unilateral temporal lobe epilepsy or lobectomy were equally and similarly impaired in describing repeated events as unique ones. What distinguished the narratives of patients from healthy controls was the paucity of details, particularly perceptual ones. This finding is consistent with Addis et al.'s neuroimaging study and also with Hirshhorn et al.'s (2007) finding that older adults provide fewer perceptual details when describing, from memory, their surroundings as they travel a familiar or new route.

These studies suggest that the hippocampal contribution to memory is not simply temporal and spatial specificity, the specification of the time and place where an event occurred, but rather the richness of the memory, the extent to which the event can be reexperienced. Though the memory may be reconstructed, the hippocampus provides the details that make reconstruction possible, as suggested by the component process model.

*The hippocampal module and imagining the future.* Tulving (2002; Wheeler et al., 1997) has referred to the reexperiencing of events as mental time travel, and he reasoned, along with others (Ingvar, 1985), that it should be as easy to travel mentally into the future as into the past (Spreng & Levine, 2006). Following Tulving and picking up on the conclusion drawn from Addis's findings on

memory for unique and repeated events, Addis, Schacter, and their colleagues (Addis, Wong, & Schacter, 2007; Schacter & Addis, 2007a, 2007b) and others (Okuda et al., 2003; Szpunar, Watson, & McDermott, 2007) showed that imagining possible future events in detail activates, with some minor exceptions, the same regions of the autobiographical network, including the hippocampus, as recalling events from the past. Likewise, in a behavioural study, they showed that older adults have a paucity of episodic (internal) details in their memories of the future in comparison to young adults (Addis, Wong, & Schacter, in press). The number of episodic details was correlated with the performance of these adults on a standard test of anterograde explicit memory, which is sensitive to hippocampal function, but not with phonemic or letter fluency, a standard test of frontal function.

*The hippocampal module and imagination.* Taking the reconstructive aspects of episodic memory and hippocampal function a step further, Hassabis, Kumaran, Vann, and Maguire (2007; see also Rosenbaum, McKinnon, Levine, & Moscovitch, 2003) asked healthy controls and people with HC/MTL damage to imagine a scene (e.g., sitting on a beach or in a bar) and describe the scene in as much detail as possible without resorting to a specific past memory. As in the previous studies, the description of patients with HC/MTL lesions was noticeably poorer in detail and in spatial coherence among the details they did report; they reported that the scene consisted of fragments, isolated features or snapshots, without being integrated into a spatial “narrative.” This last observation led Hassabis and Maguire (Hassabis et al., 2007; Hassabis & Maguire, 2007) to propose that the hippocampus is needed not only for memory of perceptual details but also for providing the spatial coherence that is a crucial element of an episodic memory and around which rich memories are built; it provides the context in which the content of events occur, much as Nadel had argued (see footnote 4). Such lack of coherence, however, may be a byproduct of a memory impoverished in detail specific to the event at hand, rather than an impairment in scene construction per se.

*The hippocampal module and problem solving.* Building on these studies, Sheldon, Ramos, and Moscovitch (2008) reasoned that the flexibility and richness of episodic memory may contribute to problem solving, particularly of those problems for which there are no set of rules to arrive at a solution. Case-based problem solving is of this type and occurs often in social situations. No event is quite like another, and, therefore, many social problems require creative solutions. Because episodic memories capture co-occurring, often unrelated, elements of consciously experienced events in a single memory trace, the memory trace is informationally rich and ideal for cross-domain pattern matching and completion, as would be needed to solve such social problems. Because episodic memories are flexible, those elements of the “template” that are identified as pertaining to a solution can be isolated or modified to allow the person to imagine a scenario that may lead to a solution. Using the Means End Problem Solving Test (Platt & Spivack, 1975), Beaman, Pushkar, Etezadi, Bye, and Conway (2006) found that older adults provided fewer viable solutions than younger adults to social problems, such as how to make up after an argument with a friend. Most interesting, as in the Addis et al. (2008) study on imagining the future, the older adults’ performance was correlated with their scores on a standard test of episodic memory but not of phonemic fluency. In a subsequent

study, Sheldon et al. (2008) showed that the older adults’ performance correlated very highly with number of details related specifically to the problem that needed to be solved, as it did with the number of internal details in their narrative of an unrelated event they experienced in the past. Again, there was no correlation with phonemic fluency or other tests of frontal function.

The studies on social problem solving and imagining the future are important because they suggest that the HC/MTL’s capacity for representing and recovering detailed information about past experiences, and the flexibility built into that capacity, contributes crucially to solving problems in the present and to planning for the future. These studies, as well as those on imagination, open up new areas of research in which memory is not studied primarily for its own sake, as was the case for most of memory research in the past, but for the uses to which memory can be put in such diverse fields as decision making and problem solving, scientific discovery, and artistic creation.

### Conclusion: Memory, Hebb Synapses, Cell Assemblies, and Phase Sequences

The recent studies on reconstructive processes in memory and on reconsolidation suggest that we cannot think of memory as an immutable, free-standing entity waiting to be discovered and retrieved, but as a representation that is created from the interaction of retrieval cues and processes with stored knowledge (Bartlett, 1932; Moscovitch, 2007; Tulving, 1983). Such a notion suggests that it is necessary to distinguish between the memory trace or engram on the one hand, and the memory we experience, on the other. The former refers to the stored information that results from neural changes that occur at encoding, whereas the latter refers to the reexperience we have of the past that is influenced by the retrieval environment, past retrievals of the same memory, and so on. Though we use stored information to construct memories, the two are not the same.

Hebb’s (1949, 1958) discussion of learning and memory, the creation of cell assemblies, and phase sequences has some bearing on this issue. Cell assemblies are a group of neurons that are arranged as a set of closed pathways, and phase sequences are a series of cell assemblies firing in sequence. These cell assemblies are formed as a result of activity at the synapse among the neurons that form the assembly. In an often quoted passage, which I memorised as a student when I took his course, Hebb (1958) speculated:

The fundamental physiological assumption of learning is that whenever an impulse crosses a synapse, it become easier for later impulses to do so. More precisely: when a neuron A fires, or takes part in firing another neuron B, some change occurs in A or B or both, which increases A’s capacity to fire B in the future. The change might be an enlargement of a synaptic knob...; or it might be some chemical change. (p. 103)

In his discussion of the formation of cell assemblies, Hebb was concerned more with perception of objects, but his lessons apply equally to memory (Hebb, 1949, pp. 62, 227–230; Hebb, 1958, pp. 100–107, 147–150).

Neuroscientists and modellers of computational networks have focused more on the Hebb synapse, which is concerned with the formation of links between two neurons, than on cell assemblies

and phase sequences that are created as a result of that activity. Often, neuroscientists assume that understanding how the Hebb synapse works, or identifying the changes that occur there, is equivalent to understanding the nature of memory. What they uncover, however, are the necessary neural changes that make creation of the memory trace or engram, but not the memory itself. Neuron A can be part of assembly A-B-C-D-E or A-B-C-D-X, which may represent different objects or memories; knowing that Hebb synapse A-B has changed will tell you little about the difference between them (Hebb, 1958, p. 105). In an extended discussion of the relation of memory, as we have defined reexperiencing the past, Hebb (p. 150) shows that he is sensitive to the distinction and notes that memories are mutable and subject to distortion, partly because the synaptic connections may weaken and partly because different experiences and our thoughts about them may modify them. Indeed, his discussion bears such an uncanny similarity to aspects of MTT that I begin to wonder whether Nadel and I had been influenced more than we realised by our unconscious memories of those passages. What these discussions make clear is that the unit of memory is not the Hebb synapse but the cell assembly and the phase sequence.

In considering these issues, I suggested that if we follow them to a logical conclusion, then “memory is a lasting, internal representation of a past event or experience (or some aspect of it) *that is reflected in thought or behavior*. It follows, therefore, that *memory does not exist until it is recovered*.” (Moscovitch, 2007, pp. 17) To illustrate this point, let me quote at length from the following passage (Moscovitch, 2007) on memory being analogous to looking for a book in a library:

Suppose you think a particular book is in the library. You go to the shelf where you believe it was located and it is not there. Does the book exist in the library or not? One possibility is that you looked in the wrong place. You now look up its call number but you discover that the book is not at the location the call number specified. There are now two possibilities: The book is somewhere in the library but you can't find it, or the book has disappeared. For all intents and purposes, as long as you do not recover the book, you cannot know whether it exists. Saying it is there because there is a record that it possibly existed once (the call number) does not solve the problem, but begs the question.

There are a number of problems with that analogy, but far from undermining the conclusion that a memory does not exist until it is recovered, they only reinforce it. The first problem is that the engram is not like a book. Once written, a book is immutable. That is not true of an engram. Though the engram is the representation of an encoded event, it too is subject to change. Moreover, though the book is a bound entity existing in a single location, the engram may consist of information that is not tightly bound, if it is bound at all, and is distributed over many locations. Recovering a memory, therefore, is not like finding a book at a particular single location, but it is more like assembling the pages of a book that may be scattered in different locations in the library. Finally, unlike a call number, which is distinct from the book itself, retrieval cues and processes interact with the engram and influence the memory that is recovered. Depending on the interaction, some “pages” of the memory may be missing, others may be placed in the wrong sequence, still others may be imported from other books that are related in some way to the cues and the engrams, and some of the cues themselves may be incorporated into the memory that is recovered and change the engram on which it was based (Schacter, 1996, 2001). These findings that memory is a product of a recovery process, rather than a free-standing entity awaiting discov-

ery, and that it is distinguishable from an engram that itself may be mutable, have a number of implications for the science of memory. (pp. 18–19)

The only implication I will consider is the one that concerned us regarding the reconstructive processes in memory. What exactly is the role of the hippocampus in such processes? Is it to provide the core of memory, those details of past experiences that serve as the building blocks that other regions, such as the prefrontal cortex, assemble into a coherent structure or narrative—a recollection of the past, an imagined future, or a scenario of possible solutions to a problem? Or does the hippocampus itself not only provide the building blocks but also assemble them during retrieval, much as it binds elements of an experience together at encoding? These observations, and the questions they arouse, potentially alter how we think about the neuropsychological basis of memory and how we investigate it. Neither Hebb nor Bartlett wrote about the hippocampus in their major works, but in science, as in life, the past informs the present, which in turn, interprets the past, in its own light, and helps shape the future.

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## Résumé

L'hippocampe et les régions voisines du lobe temporal médial jouent un rôle clé dans les théories neuropsychologiques de la mémoire. Toutefois, on ne s'entend toujours pas sur la meilleure façon de définir les fonctions de ces régions, et celle de l'hippocampe en particulier. Dans le présent article, j'étudie l'idée selon laquelle l'hippocampe serait un module « stupide » dont l'objet se limite à l'information appréhendée consciemment. De cette idée découlent un certain nombre d'implications et d'hypothèses intéressantes. Ces hypothèses ont, à leur tour, des implications importantes pour les théories neuropsychologiques s'appliquant à la mémoire épisodique récente et à long terme, ainsi qu'à la mémoire sémantique et spatiale, et pour les fonctions que joue la mémoire épisodique dans la perception, la compréhension, la planification, l'imagination et la résolution de problèmes. Pour examiner ces implications, je m'appuie sur certaines publications, mais j'utilise surtout les résultats des recherches que mes collaborateurs et moi avons menées.

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