



J. Tubbs

EPISODIC MEMORY: From Mind to Brain

Endel Tulving

Rotman Research Institute of Baycrest Centre, Toronto, Canada, M6A 2E1;
e-mail: tulving@psych.utoronto.ca

Key Words semantic memory, memory systems, amnesia, history of memory, functional neuroimaging, patient K.C.

■ **Abstract** Episodic memory is a neurocognitive (brain/mind) system, uniquely different from other memory systems, that enables human beings to remember past experiences. The notion of episodic memory was first proposed some 30 years ago. At that time it was defined in terms of materials and tasks. It was subsequently refined and elaborated in terms of ideas such as self, subjective time, and auto-noetic consciousness. This chapter provides a brief history of the concept of episodic memory, describes how it has changed (indeed greatly changed) since its inception, considers criticisms of it, and then discusses supporting evidence provided by (a) neuropsychological studies of patterns of memory impairment caused by brain damage, and (b) functional neuroimaging studies of patterns of brain activity of normal subjects engaged in various memory tasks. I also suggest that episodic memory is a true, even if as yet generally unappreciated, marvel of nature.

CONTENTS

INTRODUCTION	1
EARLY HISTORY	3
EPISODIC MEMORY TODAY	5
CRITICISMS OF EPISODIC MEMORY	8
BIOLOGICAL REALITY OF EPISODIC MEMORY	11
THE CASE OF K.C.	12
FUNCTIONAL NEUROIMAGING OF MEMORY	16
CONCLUSION	19

INTRODUCTION

With one singular exception, time's arrow is straight. Unidirectionality of time is one of nature's most fundamental laws. It has relentlessly governed all happenings in the universe—cosmic, geological, physical, biological, psychological—as long as the universe has existed. Galaxies and stars are born and they die, living creatures are young before they grow old, causes always precede effects, there is no return to yesterday, and so on and on. Time's flow is irreversible.

The singular exception is provided by the human ability to remember past happenings. When one thinks today about what one did yesterday, time's arrow is bent into a loop. The rememberer has mentally traveled back into her past and thus violated the law of the irreversibility of the flow of time. She has not accomplished the feat in physical reality, of course, but rather in the reality of the mind, which, as everyone knows, is at least as important for human beings as is the physical reality. When Mother Nature watches her favorite creatures turning one of her immutable laws on its head, she must be pleased with her own creativity.

How did Mother Nature do it? We do not yet know, not only because the question has seldom been raised by those who study Mother Nature's ways but also because the brain/mind science that could throw some light on the question is still in its early formative years and many important issues to be explored have not yet been discovered. It will be all a bit clearer a hundred years from now, or a thousand. But there are some clues available even now, and we can make use of them.

The first clue is offered by a perceived absence. There is no evidence that any nonhuman animals—including what we might call higher animals—ever think about what we could call subjective time. Animals are as capable as humans have been at the game of producing more of their kind. They have minds, they are conscious of their world, and they rely as much on learning and memory in acquiring the skills needed for survival as we do (Weiskrantz 1985), but they do not seem to have the same kind of ability humans do to travel back in time in their own minds, probably because they do not need to. The clue suggests that one's sense of subjective time is not a biological necessity. If humans have it, it is an evolutionary frill, necessary for mental time travel. No sense of subjective time, no mental time travel.

A second clue is provided by the realization that, when we do travel back in time, our conscious awareness of our experience is different from our ordinary "on-line" awareness of our environment. We seldom confuse the feeling that we are remembering a past event with the feeling that we are looking at the world, that we are imagining what is on the other side of the mountain, or that we are dreaming. These and other mental activities are conscious, too, but the consciousness is plainly and recognizably different. The term *autonoetic* has been used to refer to this special kind of consciousness that allows us to be aware of subjective time in which events happened. *Autonoetic awareness* (or *autonoesis*) is required for remembering. No *autonoesis*, no mental time travel.

A third clue is that mental time travel requires a traveler. No traveler, no traveling. The traveler in this case is what is referred to as "self." But an ordinary self will not do. By some criteria at least—the well known Gallup mirror test, for example—some nonhuman primates (chimpanzees and gorillas) also have minds in which their own selves exist as entities different from the rest of the world, but if one assumes that they are not quite capable of the human-type time travel, their selves exist only in the present, whereas ours exist in subjective time.

The three clues—sense of subjective time, *autonoetic awareness*, and self—point to three central components of a neurocognitive (mind/brain) system that

makes mental time travel possible. This (hypothetical) system is called episodic memory, and in this essay I tell its story. Like psychology, episodic memory has a long past but a short history. The concept was first proposed some 30 years ago (Tulving 1972), but it has changed drastically since then and has now reached a stage at which one can, as I am doing now, muse about it as a true marvel of nature.

In this essay I first say a few words about the history of the concept of episodic memory, then describe its current status as not just a psychological but rather a neurocognitive (brain/mind) entity, review criticisms, and end by discussing some evidence. The emphasis in this discussion is squarely on the brain side of the mind/brain equation. The early problems with the concept of episodic memory were largely rooted in the lack of relevant evidence. Moreover, as is almost always the case with purely behavioral data, it was frequently possible to account for relevant findings without invoking the distinction between episodic and semantic memory. Evidence for the separate status of episodic memory at the level of brain activity, however, is more difficult to dismiss or discount. In recent years this kind of evidence (summarized below) has become available.

EARLY HISTORY

The early formulation of the distinction between episodic and semantic memory (Tulving 1972) centered on different kinds and sources of to-be-remembered information (personally experienced events versus general facts). The distinction was readily accepted by the psychological world and regarded by many as a useful heuristic distinction. The initial difficulties consisted of the constraints imposed by the then-prevailing verbal learning tradition as well as the total absence of any relevant data.

By the time I wrote *Elements of Episodic Memory* (Tulving 1983), it had become possible to entertain the thought that the heuristic distinction was useful for the simple reason that it corresponded to biological reality. I proposed, therefore, that episodic and semantic memory represented two functionally separable memory systems. In *Elements* I also made a confession: I had been wrong in 1972 when I had assumed that the traditional, Ebbinghaus-inspired, study/test laboratory experiments of verbal learning and memory had dealt with episodic memory. They had not. Two important features of episodic memory were missing.

One had to do with the contents of what the subjects in the experiments had to learn. Episodic memory is about happenings in particular places at particular times, or about “what,” “where,” and “when” (Clayton & Dickinson 1998, Nyberg et al. 1996). Traditional laboratory experiments, however, were almost invariably concerned with “what.” Subjects are asked, “What do you remember of the presented material?” They report their knowledge in tests such as free recall, cued recall, or recognition. Subjects’ memory for “where” and “when” was hardly ever examined. Just about the only exception was provided by studies of “memory judgments,” (Hintzman 2000) which, however, were largely ignored by most students

of memory, presumably because they did not fit readily into any appropriate theoretical framework. Subsequent history corrected this oversight. There are now on record literally hundreds of studies that are concerned with “what,” “where,” and “when.”

The other missing feature was what I referred to in *Elements* as “recollective experience,” or conscious awareness of what had happened in the past. In traditional experiments the experimenter assumes that the overt behavioral response reflects the subject’s mental state; that is, that behavior is a faithful index of cognition. The reasoning goes something like this: Surely, if the subject recognizes an item in a recognition test, it means that he remembers it from the list, that is, that he has a conscious recollection of the item’s occurrence in the study list. How could it possibly be otherwise?

As subsequent history showed, it could be otherwise. Research on implicit memory (Roediger & McDermott 1993, Schacter 1987a), or so-called nonconscious memory (Jacoby 1991, Toth 2000), has overwhelmingly proved that one and the same behavioral response in a study/test experiment could represent conscious awareness of the retrieved item’s experimental history as readily as it could represent total lack of such awareness. In a further development it turned out that when subjects were consciously aware of an item’s earlier occurrence in the study list, the awareness could be one of two different kinds. One was referred to as “autonoetic,” the other as “noetic.” The former, as already mentioned, was used to describe the experiential “flavor” of remembering, or recollection; the latter was used to describe the conscious state that accompanies thinking about (knowing) the world. Thus, even in such sterile situations as list-learning experiments, subjects could either remember the event of an item’s appearing in the study list, or know that it occurred, without remembering, and make appropriate experiential judgments (Gardiner 1988, Gardiner & Richardson-Klavehn 2000, Knowlton & Squire 1995, Rajaram 1993, Tulving 1985b). The news here was a further extension of the lessons learned from the studies of implicit memory: One and the same behavioral response (correctly recalled item, or old response in the recognition test) could reflect either of two different states of conscious awareness about the past. The general point made by all these studies, which barely existed at the time of *Elements*, is that there is no necessary correlation between behavior and conscious experience (Tulving 1989) and that in that sense the traditional research was not concerned with episodic memory.

This essay is partly about how the concept of episodic memory came to be what it is today, partly about what it is today, and mainly about how we know or think we know what it is today. The scope of a short essay allows us to discuss only the highlights of what, for want of a better expression, I call the theory of episodic memory, or simply episodic theory, although we are here dealing mostly with conceptual rather than theoretical issues. The theory represents an attempt to formulate a set of interrelated ideas about memory that are internally consistent and reasonably closely tied to the basic empirical facts about memory. A fuller account of the theory of episodic memory is found in Wheeler et al.

(1997); a reasonably up-to-date tabulation of episodic memory's similarities to and differences from semantic memory is found in Tulving & Markowitsch (1998), as well as in Griffiths et al. (1999); one possible extension of the theory, into the relation between the domain of subjective time and evolution of human culture, has been offered elsewhere (Tulving 2001b).

EPISODIC MEMORY TODAY

Today we think of episodic memory as one of the major neurocognitive memory systems (Schacter & Tulving 1994) that are defined in terms of their special functions (what the system does or produces) and properties (how they do it). It shares many features with semantic memory, out of which it grew (Tulving 1984), but it also possesses features that semantic memory does not (Tulving & Markowitsch 1998).

Episodic memory is a recently evolved, late-developing, and early-deteriorating past-oriented memory system, more vulnerable than other memory systems to neuronal dysfunction, and probably unique to humans. It makes possible mental time travel through subjective time, from the present to the past, thus allowing one to re-experience, through auto-noetic awareness, one's own previous experiences. Its operations require, but go beyond, the semantic memory system. Retrieving information from episodic memory (remembering or conscious recollection) is contingent on the establishment of a special mental set, dubbed episodic "retrieval mode." Episodic memory is subserved by a widely distributed network of cortical and subcortical brain regions that overlaps with but also extends beyond the networks subserving other memory systems. The essence of episodic memory lies in the conjunction of three concepts—self, auto-noetic awareness, and subjectively sensed time.

Let us briefly expand on some of the constituent ideas in this definition of episodic memory.

First, episodic memory is a hypothetical memory system. It is not a particular kind of memory task or test. According to episodic theory, there exist few if any memory tasks used in the laboratory or the clinic that involve a single memory system. In terms of memory systems, all tasks are "multiply determined" (Tulving 1991). The systems' ideas may be assessed in terms of outcomes of tasks, but the logic is a bit more subtle than that inherent in the assumption of the one-to-one mapping of tasks to systems (see Tulving 1983, pp. 55, 77–78). Episodic memory is not just a particular type of retained and retrieved information, and it is not just a particular kind of mental experience, although it is systematically related to both of these. These distinctions may be subtle, but they are important. For instance, if one accepts them, one would not ask a question such as, "... how does a systems theorist unambiguously identify a particular memory as being in one system or another...?" (Toth & Hunt 1999, p. 233). The answer is that a systems theorist would not, because such questions are uninteresting and lead nowhere.

The concept of memory system, like any other live concept in a developing branch of science, is fluid, and its specific features change over time. But some early ideas are still quite relevant. Because one of my criticisms of the criticisms of multiple systems in general, and episodic memory in particular, is that the critics have misconstrued what they criticize, it is useful here to repeat what I said on the topic when the concept of multiple systems was introduced. In an article entitled, "How many memory systems are there?" I said the following about what memory systems are:

Memory systems are organized structures of more elementary operating components. An operating component of a system consists of a neural substrate and its behavioral or cognitive correlates. Some components are shared by all systems, others are shared only by some, and still others are unique to individual systems. Different learning and memory situations involve different concatenations of components from one or more systems Although there is no one-to-one correspondence between tasks and systems . . . they are nonetheless systematically related: A given memory system makes it possible for organisms to perform memory tasks that entail operating components unique to that system. This means, among other things, that intervention with the operation of a system—even if it occurs through a single component of the system—affects all those learning and memory performances that depend on that system Different systems have emerged at different stages in the evolution of the species, and they emerge at different stages in the development of individual organisms. Thus, they can be ordered from 'lower' to 'higher' systems (or from less to more advanced), provided that it is clearly understood that such attributions are meaningful only with respect to comparisons between combinations of systems, on the one hand, and individual systems alone, on the other When a new memory system with specialized novel capabilities evolves or develops, it enables the organism to increase the number, and the sophistication, of its memory functions." (Tulving 1985a, pp. 386–87).

More recent and more detailed formulations of systems are available elsewhere (Sherry & Schacter 1987, Schacter & Tulving 1994; see also Schacter et al. 2000).

Episodic memory is oriented to the past in a way in which no other kind of memory, or memory system, is. It is the only memory system that allows people to consciously re-experience past experiences. Its special, and unique, relationship to time, surprisingly, is not widely known. Nor is it, I think, adequately appreciated. Most people naturally associate all memory with the past and are astonished to learn that this is not so.

The theory holds that episodic memory evolved out of semantic memory: Semantic memory appeared long before episodic memory. Many nonhuman animals, especially mammals and birds, possess well-developed knowledge-of-the-world (declarative, or semantic, memory) systems and are capable of acquiring vast amounts of flexibly expressible information. Early humans were like these animals,

but at some point in human evolution, possibly rather recently, episodic memory emerged as an “embellishment” of the semantic memory system. The details of this emergence are unknown, and one can only speculate about them (Tulving 2001b). It is not even certain that the evolution of episodic memory was a part of (neo)Darwinian evolution. Episodic memory may represent an instance of the so-called Baldwin effect (Baldwin 1902, Richards 1987).

For nature, the famous tinkerer, to have produced neurocognitive machinery that brings the past into the present is clearly a much greater achievement than evolving the (marvelous) visual system. Many animals have eyes and visual systems, and some of them have been “invented” independently several times in the course of evolution. A system that turns time’s arrow into a loop has evolved only once, in only one species, although other species would presumably benefit from it as much as do humans. The singular rarity of the existence of episodic memory in nature presumably reflects the complexity and biological cost of such a system, in terms of both structural components and their operations.

The hypothesis that episodic memory was built on top of the earlier systems, including semantic memory, is in agreement with other ideas and facts about memory. One such is the SPI (serial, parallel, independent) model that postulates process-specific relations among the memory systems (Tulving 1995). Another is the now well-known fact that people can have mental access to their personal past not only in terms of auto-noetic remembering but also in terms of nonauto-noetic knowing. This state of affairs is reflected in the title of an article by Suparna Rajaram (1993): “Remembering and knowing: two means of access to the personal past.”

The notion here is that even before episodic memory emerged in human evolution, humans were capable of acquiring and making use of knowledge about their personal experiences, in the absence of auto-noesis, and possibly without a precise temporal “tag.” The same scenario holds for nonhuman animals. They too are capable of learning about and from experiences of the past, but without auto-noetic awareness that they are doing so (Suddendorf & Corballis 1997). An especially interesting example of the operations of this type of episodic-like memory by food-caching scrub jays has recently been described by Clayton & Dickinson (1998), thereby helping to fill the evolutionary gap between humans, happy possessors of the sophisticated system of episodic memory, and many other animals, capable learners of impersonal and timeless facts of their worlds.

The late (ontogenetic) development of the episodic system is meant to be true in a relative sense. Everyone knows that young children are amazingly efficient learning machines from birth on, and perhaps even earlier, not only with respect to language but many other skills and knowledge as well. According to theory, such learning occurs in the absence of auto-noesis and does not require any sense of self in subjective time (cf. McCormack & Hoerl 1999). The late development of episodic memory provides another hint at the complexity of the system. Although it is difficult to put a specific figure on the age when children acquire a more-or-less fully functioning episodic memory system, a rough rule of thumb is that children younger than 4 years of age do not yet have such a system (Perner & Ruffman

1995, Nelson 1993). Wheeler et al. (1997) discuss the issue of development of episodic memory from the perspective of episodic theory at greater length.

CRITICISMS OF EPISODIC MEMORY

As mentioned, most psychologists were happy to use the term episodic memory in a purely descriptive sense, referring to the kinds of experiments that psychologists had been doing since Ebbinghaus: Subjects study some material, and the experimenter tests them for their retention of the material. The suggestion made in *Elements* (Tulving 1983) that episodic and semantic memory are two “functionally different memory systems,” however, quickly became controversial, as the saying goes. A controversial idea in science, as everyone knows, means that some people love it, some could not care less, and some are highly opposed to it. Whereas some students of memory were quite willing to begin exploring the hypothesis that there exist real differences between episodic and semantic memory, many others, including those who had had no problem with the heuristic distinction, rejected the hypothesis out of hand.

Critics did not like the thought that there was anything special about episodic memory. The idea was vague, they claimed, it did not follow the established procedure, and it violated the law of parsimony. There was no need to make up imaginary memory systems in order to get on with the task of making theoretical sense of memory facts and phenomena, the critics said. Some did not like the “metaphysics of identifying hidden systems” and the burden of having to try to figure out “in what complex arrangements they may be ordered” (Roediger et al. 1989, p. 36). Some complained that post-hoc dissociations, used to argue for differences between systems, are meaningless because they are not “predicted by a theory” (Hintzman 1984, p. 241). Some did not see any reason to draw any kind of sharp distinction between two kinds of facts: facts about the world and facts about the self (Kihlstrom 1984, p. 244). Some were alarmed at the possibility that many other kinds of memory might be proposed in addition to episodic, and thought it essential to nip the threat of “proliferation of memories” in the bud, lest we end up with the kind of an intellectual disaster that evolved out of the story of instincts (Roediger & Blaxton 1987, pp. 370–71).

Along similar lines, some questioned the wisdom of the misguided believers in separate memory systems, suggesting that our field should show “the maturity to attempt to incorporate a new finding into its abiding viewpoint before offering a proliferation of additional memory stores to account for a few new data points” (Gorfein 1987, p. 383). Some were suspicious of classification of memories because it might be “detrimental to theory” (Ratcliff & McKoon 1986, pp. 312–13). Some believed in multiple memory systems but had doubts about episodic memory: “. . . although a dissociation between autobiographical and nonautobiographical memory is intuitively sensible, the critical question is whether such a dissociation is of a natural kind. One could just as easily split the memory system

into . . . memories for all things with sharp boundaries versus all things with fuzzy boundaries . . ." (Cohen 1984, p. 99). Others reviewed the evidence for discrete neurobiological mechanisms that might underlie episodic and semantic memory and concluded that the evidence "does not indicate that episodic and semantic memory are mediated by discrete neural subsystems" (Horner 1990, p. 281).

Skepticism was expressed about the neuropsychological and the then-barely-existing brain-imaging methods I had suggested would be necessary to get beyond futile psychological arguments (Tulving 1986). These methods were thought to be no more useful for exploring memory than would be the attempts to understand the workings of a computer by smashing it with a sledgehammer to create "lesions" (Ratcliff & McKoon 1986, pp. 312–13). Finally, some critics did not want to give the newborn even a chance at life. Only a year after the proposal of a separate episodic memory system had appeared in print, critics told the world that episodic memory's time had "come and gone" (Hintzman 1984).

These critical comments date from the earlier days of the efforts to work out an acceptable set of ideas about episodic memory. Many of them were pertinent and justifiable, because the evidence at the time was scanty at best, and I said so (Tulving 1986). Other comments were perfectly understandable in light of tradition and well-established practices in the field. Traditions always die hard, and the traditional, unquestioned, and unanalyzed view of memory was unitary.

In terms of practice, as already mentioned, memory research was extremely restricted: lists, verbal materials, measurement of the amount recalled or recognized, and the single-minded focus on the contents of lessons, the "what" component of the information. In this kind of an environment there clearly is little need for any kind of a classification of memory, because memory is highly uniform. Given the emphasis on "what," rather than "where" and "when," given the emphasis on behavior and the irrelevance of experience, given the strangeness of the central concepts of episodic memory, and especially the strangeness of some of the terms (such as *autonoetic* and *noetic*), it is not surprising that an intelligent practitioner in traditional memory research would not find anything of interest in the concept of episodic memory. Rejection of the idea as an unparsimonious and unnecessary complication made perfect sense—as long as one kept close to the tradition.

It is more puzzling that even today there are many who have no use for the idea of different memory systems in general and the episodic/semantic distinction in particular. For example, Howe, in a monograph on memory development in young children, dismissed the whole idea of multiple memory systems and advocated the status quo of unitary memory: "Because there is little evidence to support the idea (a) that there are separate memory systems or, (b) that they come on line at different developmental junctures . . . it is perhaps still more parsimonious to view memory as a unitary system that supports a variety of modes of remembering" (Howe 2000, p. 87). Others express similar views: "I am explicitly equating episodic and semantic memory in the sense that there are no separate episodic and semantic memory systems, hierarchically arranged . . . or otherwise" (Glenberg 1997, p. 8). Glenberg thinks that what is (mistakenly) attributed to two separate systems reflects

differential use of different memories, methods used to assess them, and different information. Craik (2001) too thinks there is no division between episodic and semantic memory. Like Glenberg, he believes semantic information is usually more accessible than episodic because, by being more general, it receives “more practice.” Others in a long list who deny or doubt the reality of multiple systems include McClelland et al. (1995), Toth & Hunt (1999), and Weldon (1999).

What does one do about such criticism? The rules of the game here are the same in episodic memory as they are in the rest of science. If a weakness or flaw of the theory pointed out by a critic is justified, one takes it into account, one way or another, and is grateful to the critic for his or her contribution to the refinement and improvement of the theory. The theory of episodic memory has benefited greatly from such constructive criticism. The situation is different when a criticism essentially reduces to an expression of lack of interest in, no perceived need for, or simple temperamental antagonism to structural as opposed to functional concepts. In such cases one simply agrees to disagree with the critic and proceeds with business on hand. The same solution is usually adopted when the critic complains that all the problems inherent in the new approach have not yet been solved, or even tackled. These kinds of criticism are comparable to complaints about young children not being as strong and smart as adults. In a rational world, there is nothing much one can do about them, other than remember what Benjamin Franklin said about electricity, when asked what use it was, and wait.

I do not attempt to deal with the critics in this article, because there is not enough room. However, I briefly touch on one category of criticism because it is prevalent, because it is a waste of time, and because it can be avoided. These are criticisms based on misconceptions of the subject of the criticism, as mentioned earlier. This kind of criticism takes several forms. I consider only one of these. (I must mention parenthetically that in this matter, as in everything else covered in this essay, I can only speak for myself, and for my own understanding of the issues. There are many other students of memory who believe in multiple memory systems whose ideas need not be the same as mine.)

In an article I know has not been totally ignored, I discussed two kinds of primary concepts of memory, having to do with processes and systems. To minimize the probability of misunderstanding, I said that “the classification approach *complements* the process-oriented approach to memory; it is not an alternative to it” (Tulving 1991; emphasis in original). I have not had any reason to change this understanding of the relation between processes and systems. A recent book chapter dealing with the topic was entitled “Study of Memory: Processes and Systems” (Tulving 1999). Nevertheless, a surprisingly large number of people who wish systems would go away think they were introduced to provide rival, alternative ways of explaining experimental and other empirical findings, especially task dissociations (e.g., Roediger et al. 1989, Toth & Hunt 1999, Craik 2001). In a recent collection of papers, entitled *Memory: Systems, Process, or Function?* (Foster & Jelicic 1999), the central question discussed was whether long-term memory is “best regarded as comprising multiple independent systems . . . , as a processing framework . . . , or as a complex function which can be used in a flexible and

task-appropriate manner?” (p. 1). In both the title and the guiding question the operative word is “or.” The possibility that the correct answer to the question is, “at the very least all of the above,” is ignored, for reasons unknown.

BIOLOGICAL REALITY OF EPISODIC MEMORY

By the standards of mature sciences, the amount of relevant evidence in support of episodic memory is still small. In this respect, much remains to be done. However, by the standards of psychology, or cognitive neuroscience, the amount of evidence is respectable. In this respect, the situation has changed greatly from the early days of episodic memory. Most satisfying is the trend one can discern in the accumulation of pertinent data; not only the quantity but, more importantly, the quality of the data is clearly on the upswing.

In the remainder of this essay I discuss evidence related to the issue of biological reality of episodic memory. Is episodic memory just a category in an abstract organizational scheme applied to memory, that is, a figment of a classifier’s imagination, or does something like it actually exist as a separate structure/function in the brain?

The question, of course, does not, and cannot at this time, have a complete answer. The issue is far too complex to have been solved in a few years. Therefore, what follows are examples of a progress report. None of the evidence I discuss below, like the evidence I mentioned above, was available in 1983 when I wrote *Elements of Episodic Memory*, and there is a good deal more recent evidence in the literature.

A number of approaches can be, and have been, taken to this issue. I discuss two. One lies in the neuropsychological study of consequences of the kind of brain damage that selectively involve memory processes. The other has to do with functional neuroimaging of healthy young people.

Case studies of neurological patients who, as a result of brain damage caused by accident or disease, suffer from memory impairment frequently provide information useful to the issue of the biological reality of episodic memory. The history of the relevant research neatly illustrates the dictum, “It is difficult for an explorer to find something that he does not know exists.” Even serendipity fails in a situation in which a scientist looks at a pattern but does not see it. Even when one scientist sees it and informs others of it, others may not hear the message.

In 1958, in summarizing his extensive clinical neurological investigations of memory and amnesia, Nielsen, a neurologist at UCLA, reported that

A study of pathways of memory formation has revealed a basic fact not suspected when this study began—there are two separate pathways for two kinds of memories. The one is memories of life experiences centering around the person himself and basically involving the element of time. The other is memories of intellectually acquired knowledge not experienced but learned by study and not personal. (Nielsen 1958, p. 25)

Corresponding to these two kinds of memories, Nielsen said, are two types of amnesia: “Amnesia is of two types: (1) loss of memory for personal experiences (temporal amnesia), and (2) loss of memory for acquired facts (categorical amnesia). Either may be lost without the other.” (Nielsen 1958, p. 15). This was one year after the appearance of a report of bilateral resection of large chunks of the medial temporal lobe tissue from the brain of a young man with epileptic seizures, H.M., who became the world’s most famous amnesic (Scoville & Milner 1957).

Thus, Nielsen, looking at many patients, saw the separation between what we now call episodic and semantic memory, told the world about it, and essentially nobody heard him. Milner, and later many others, looking initially at a single patient, did not, and, because H.M.’s amnesia was different, possibly could not, see the separation, and so they lumped episodic and semantic memory together. It was only very recently that a distinction between “episodic amnesia for personally experienced events and semantic retrograde amnesia for components of knowledge” (Kapur 1999, p. 800) was again taken under serious scrutiny.

In the meantime, the case of H.M., suffering from the impairment of declarative (now also called explicit) memory, i.e., memory for personal events and memory for general facts (Squire 1992), has dominated the minds of researchers of amnesia, although the possibility is now being considered that the episodic memory impairment in medial temporal lobe amnesic patients is associated with hippocampal damage, whereas semantic memory problems reflect the damage of cortical tissue (Aggleton & Brown 1999, Mishkin et al. 1997).

If episodic memory is a separate entity—anatomical, hodological, physiological, or in some as yet unknown fashion—in the normal brain, it is possible for damage to the brain to occur in such a way that it is deleteriously affected while other kinds of memory are not, or are less affected. Because there are good reasons to believe that the operations of all memory systems are supported by widely distributed and intricately interconnected regions of the brain (Mesulam 1990, Nyberg et al. 2000), the probability of the kind of brain damage that neatly cleaves the brain function along the lines of such complex systems is small. Most of the time the damage affects the components of a number of systems, resulting in the typical, diffuse impairment of memory for facts and memory for events (Squire 1992). But every now and then the low-probability event materializes. The important point is that it is difficult to imagine how, for instance, brain pathology could occur in which the patient loses all episodic memory functions while retaining those that rely on other systems unless there exists the potentiality for such a division in the healthy brain. But such cases, although rare, do occur.

THE CASE OF K.C.

At University of Toronto we have studied one such individual, K.C., over a number of years (Figure 1). His episodic memory is totally dysfunctional and he has no autoeotic consciousness. Otherwise, all his intellectual functions are close to those of an ordinary, normal, healthy person.



Figure 1 K.C., a man who lost his episodic memory as a result of traumatic brain injury in 1981, photographed in 1986 when he was 35 years of age.

K.C. was born in 1951. At the age of 30 he suffered serious closed head injury in a motorcycle accident, with extensive brain lesions in multiple cortical and subcortical brain regions, including medial temporal lobes (Rosenbaum et al. 2000), and consequent severe amnesia (Tulving et al. 1988, Tulving 2001a). As is the case, by definition, with all amnesics, most of K.C.'s cognitive capabilities are intact and indistinguishable from those of many healthy adults. His intelligence and language are normal; he has no problems with reading or writing; his ability to concentrate and to maintain focused attention are normal; his thought processes are clear; he can play the organ, chess, and various card games; his ability to visually imagine things is intact; and his performance on primary (short-term) memory tasks is normal. He knows many objective facts concerning his own life, such as his date of birth, the address of his home for the first 9 years of his life, the names of the some of the schools he attended, the make and color of the car he once owned, and the fact that his parents owned and still own a summer cottage. He knows the location of the cottage and can easily find it on a map of Ontario. He knows its distance from his home in Toronto and how long it takes to drive there in weekend traffic. He also knows that he has spent a lot of time there.

Like many other typical amnesic patients, K.C. is impaired in his ability to pick up novel generic information from his everyday world and in his ability to remember ongoing experiences: He has deep anterograde amnesia for both personal experiences and semantic information. However, his retrograde amnesia

is highly asymmetrical: He cannot recollect any personally experienced events, whether one-time or repeated happenings, whereas his semantic knowledge acquired before the critical accident is still reasonably intact. His knowledge of mathematics, history, geography, and other "school subjects," as well as his general knowledge of the world is not greatly different from others' at his educational level.

The outstanding fact about K.C.'s mental make-up is his utter inability to remember any events, circumstances, or situations from his own life. His episodic amnesia covers his whole life, from birth to the present. The only exception is the experiences that, at any time, he has had in the last minute or two. It does not matter how much and how specific information is given to him about any particular event from further back in the past, how memorable the event is by ordinary standards, how long its duration, or how many times he has been asked about it before. He always denies any recollection and does not even acknowledge any sense of familiarity with the event (Tulving et al. 1988).

K.C. has no particular difficulty apprehending and discussing either himself or physical time. He knows many true facts about himself; he also knows what most other people know about physical time: its units, its structure, and its measurement by clocks and calendars. It is his apprehension of subjectively experienced time, the auto-noetic (self-knowing) consciousness, that is grossly impaired. The impairment does not encompass only the past; it also extends to the future. Thus, when asked, he cannot tell the questioner what he is going to do later on that day, or the day after, or at any time in the rest of his life. He cannot imagine his future any more than he can remember his past. This aspect of the syndrome he presents suggests that the sense of time with which auto-noetic consciousness works covers not only the past but also the future (Tulving 1985b).

The profile of K.C.'s cognitive capabilities suggests that his brain damage greatly impaired his episodic memory and auto-noetic consciousness while leaving his semantic memory and noetic consciousness largely intact. There are problems with this interpretation, of course. An obvious one is that his apparently greater ability to retrieve pre-morbidly acquired semantic compared to episodic information reflects the differential effects of overlearning or rehearsal of the two kinds of information, rather than the operations of different memory systems. Against this possibility are instances in which he can recall factual information that he is unlikely to have rehearsed repeatedly, such as his knowledge of the difference between stalactites and stalagmites, but he cannot bring back to mind memorable happenings lasting for many days, such as his having been evacuated from his home, along with tens of thousands of others following the nearby derailment of a train carrying deadly chemicals. Nevertheless, the hypothesis of more often repeated versus less often repeated experiences, rather than impersonal and personal ones, popular with critics (e.g., Craik 2001), is logically possible.

We did two extensive case experiments with K.C. to compare his episodic and semantic abilities under better controlled conditions. The question was whether he could learn new factual information presented a number of times, for a few seconds

each time, despite his inability to bring back to mind the hours-long occasions on which such learning took place. In one experiment (Tulving et al. 1991) we taught him 64 3-word sentences (such as “reporter sent review,” and “student withdrew innuendo”) over a number of widely distributed learning trials and then tested him with sentence frames (e.g., “reporter sent—”) for the missing word. In the second experiment (Hayman et al. 1993) we taught him 96 amusing definitions (such as “mates live in, employees outside: prison” and “performs a daily massage: toothbrush”) and tested him with definitions (e.g., “a servant in name only”) for the target word (e.g., bridesmaid). Both experiments showed that he was able to learn, slowly but surely, substantial portions of the material and retain the information normally over weeks and months, while not being able to recollect any visits to the laboratory where the learning took place.

Thus, we know that K.C. can learn new factual information in the total absence of any episodic remembering, under conditions in which there is no confounding between the kind of retrieval (episodic versus semantic) and the amount of learning or rehearsal. Other cases have been described in which new semantic learning by densely amnesic patients has been demonstrated (Hamann & Squire 1995, Schacter et al. 1984, Shimamura & Squire 1987). Note again, however, that, as one might expect, there is a good deal of variability in such learning in amnesic patients (Hamann & Squire 1995, Rajaram & Coslett 2000).

The overall pattern of memory impairment shown by K.C.—much more severe for personal, autobiographical experiences than generic, factual knowledge—has been described by others. A case strikingly similar with respect to the clinical picture of K.C., although of different etiology (herpes simplex encephalitis) and different brain pathology, was described in considerable detail by Kitchener et al. (1998). Their patient, R.S., did not reveal any signs of functioning episodic memory, lost as a result of a bout of herpes simplex encephalitis, but he had nevertheless been able to postmorbidity acquire considerable amounts of factual information about people and news events.

Especially interesting in this context are the cases of three young people, described by Vargha-Khadem and her collaborators (1997), who became amnesic at very early ages as a result of anoxic accidents that produced severe bilateral hippocampal atrophy. They too show striking differences between the impaired episodic memory and relative preservation of semantic memory. None of them can reliably remember ongoing experiences and recollect past personal happenings. They also perform in the amnesic range on most standard psychometric memory tests. Remarkably, however, all three have made and are making normal or near-normal progress in school, and all three have acquired normal or near-normal semantic knowledge about the world.

There have been other cases of impaired episodic and largely spared semantic memory. Most of these are less striking than K.C.’s, but the asymmetry has always been easy to detect (Calabrese et al. 1996, Cermak & O’Connor 1983, DellaSala et al. 1993, Kopelman et al. 1999, Levine et al. 1998, Markowitsch et al. 1993, Rousseaux et al. 1997, Viskontas et al. 2000). Summaries of these and other relevant

cases, together with discussion, are available in Kapur (1999) and Wheeler & McMillan (2001).

Although all these cases can be understood in terms of the distinction between episodic and other kinds of memory, there have been, of course, as there always are, different interpretations of them. For example, Squire & Zola (1998) think the slow and laborious learning of new factual information by amnesic patients with impaired hippocampally dependent declarative memory, including Vargha-Khadem's young people who learn at school, is made possible by a small, difficult-to-detect degree of preserved episodic memory.

Clinical cases of the kinds summarized here can be quite convincing, especially to those who have met the patients and studied them extensively. But there are problems, too. A major one is that those who have not met such patients and have not worked with them, usually find the reports difficult to believe and tend to simply dismiss the evidence contained in them. At a distance it is easy to imagine all sorts of reasons why any given case might not quite be what it is claimed to be, all the way from malingering on the part of the patient to sloppy methods on the part of the investigator. Another problem has to do with the fact that studies of specially selected patients are deficient in one of the main conditions of science—independent verification. Most researchers do not have access to the kinds of patients they can read about in specialty journals, and even if they did, their patients might behave differently. The rarity of interesting and truly informative cases allows a sceptic to ignore them. Finally, there is Hughling Jackson's famous dictum about what one can and cannot learn about the normal brain from observing the effects of its damage. Under the circumstances, lessons about memory taught by neuropsychology seep into the awareness of outsiders slowly.

FUNCTIONAL NEUROIMAGING OF MEMORY

Functional neuroimaging techniques [such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI)] as well as electrophysiological recording, from both the scalp and implanted electrodes, make it possible to examine brain activity associated with mental activity. These techniques have many problems, but they represent an immense advance over the situation that prevailed before their development.

The general logic of functional neuroimaging studies is straightforward, although the interpretation of the data yielded by them is not. Different mental activities are supported by the activities in different brain regions. When the subject engages in a given cognitive task, PET or fMRI provide information about the level of cerebral blood flow (PET) or blood oxygenation level (fMRI) in different brain regions. Because changes in blood flow or oxygenation level are known to be correlated with changes in neuronal activity, their patterns (brain maps) provide information about neuronal activity in different brain sites that reflect these processes (Raichle 1994).

In the most popular method used in “imaging cognition,” the subtraction method, the brain maps associated with performance on two cognitive tasks are compared. The differences between the two brain maps are assumed to reflect the differences between the two cognitive tasks. The value of such knowledge clearly depends on what is known, or can be reasonably assumed, about the differences between two tasks. As every cognitive task involves a large number of (frequently interacting) processes, the interpretation of the brain maps yielded by the subtraction method is constrained by the goodness of one’s knowledge of the cognitive “ingredients” of the compared tasks. (For a more detailed analysis on the method and limitations of neuroimaging studies, see Buckner & Tulving 1995, Cabeza & Nyberg 2000, Raichle 1994)

The vagaries of the functional neuroimaging techniques and the problems inherent in the interpretation of the obtained results can be mitigated by relying on the traditional scientific standbys of converging results from many studies and guidance by theory. Any given individual study can always be interpreted in many ways. Interpretation of empirical regularities that emerge from a larger number of studies is necessarily more constrained.

One such empirical regularity that has been yielded by PET and FMRI studies of episodic memory is referred to as the HERA (hemispheric encoding/retrieval asymmetry) model: Left prefrontal cortex is differentially more involved than right in encoding information into episodic memory, whereas right prefrontal cortex is differentially more involved than left in episodic memory retrieval. Because episodic encoding processes usually involve semantic memory retrieval, the HERA model assigns semantic-memory retrieval also to the left frontal lobe. The empirical regularity is called a model, because it is described in terms of cognitive-memory concepts of encoding and retrieval, as well as the concepts of episodic and semantic memory. Without these concepts, it would be awkward to describe the regularity.

HERA emerged from initial PET studies investigating encoding and retrieval processes in episodic memory, done in Toronto (Kapur et al. 1994; Moscovitch et al. 1995; Tulving et al. 1994a,b), the Hammersmith Hospital in London (Shallice et al. 1994, Fletcher et al. 1995), and Washington University (Squire et al. 1992, Buckner et al. 1995). A large number of subsequent studies have confirmed the initial findings. The HERA pattern holds not only for verbal materials but also for nonverbal ones (Buckner et al. 1996, Haxby et al. 1996, Köhler et al. 1998, Moscovitch et al. 1995, Nyberg et al. 1996a, Owen et al. 1996; see also Andreasen et al. 1996). This is despite the fact that, orthogonally to the HERA pattern, there are other data showing hemispheric asymmetry for cognitive processing of different kinds of information: Words are processed predominantly in the left hemisphere, whereas unfamiliar faces are processed in the right hemisphere (Kelley et al. 1998, Wagner et al. 1998b).

The HERA model implies that frontal lobes are heavily involved in episodic memory processes, thus confirming earlier suggestions that this might be the case (Schacter 1987, Squire 1987). The relations among episodic memory, autoegetic consciousness, and the frontal lobes have been discussed at some length by Wheeler

et al. (1997). At any rate, in addition to telling us something about what brain regions are involved in memory processes such as encoding and retrieval, HERA also provides support to the biological reality of the distinction between episodic and semantic memory. The fact that semantic retrieval seems to be localized largely to the left, whereas episodic retrieval involves additional processes subserved by regions in the right hemisphere (Buckner 1996) points to basic differences in the neuroanatomy of the two memory systems (Desgranges et al. 1998; Fletcher et al. 1995, 1997).

The right frontal activation associated with episodic retrieval stands in striking contrast to semantic-memory retrieval, which is seldom observed in the right hemisphere (Cabeza & Nyberg 2000, Nyberg 1998). In studies designed to further specify the meaning of such a contrast, it was found that the frontal activation, especially on the right, is associated not necessarily with successful remembering of previously studied material but rather, or additionally, with the episodic memory retrieval mode, mentioned above. The data from these studies (Buckner et al. 1998, Kapur et al. 1995, Nyberg et al. 1995, Rugg et al. 1997, Schacter et al. 1996, Wagner et al. 1998a) showed frontal activation not only when subjects successfully recognized previously studied items but also when they tried to do so but failed, because the test items had not been encountered before.

This pattern of data points to the possibility that the right frontal activation reflects retrieval attempt or episodic retrieval mode (Tulving 1983) rather than, or perhaps in addition to, retrieval success.

Retrieval mode represents a mental (neurocognitive) state, a “set,” required for remembering earlier experiences as well as for remembering that something did not happen. In a recent analysis of PET data pooled over several different studies in which subjects had been given episodic recognition tests, involving a total of 53 subjects (Lepage et al. 2000), we succeeded in identifying 6 different “retrieval mode sites” in the brain. A retrieval mode site was defined as any brain region that is significantly more active during episodic retrieval than during episodic encoding (or semantic retrieval), and that is equally active when recovery succeeds and when it fails. These sites were all in the frontal lobes: five in prefrontal cortex, three strong ones in the right and two weaker ones in the left hemisphere, and one in the medial anterior cingulate. No similar sites were seen in any other part of the brain.

Episodic retrieval mode involves a number of different processes (Lepage et al. 2000), but because of the limitations of the study we do not know which, or which combination, of these was associated with activation observed at which retrieval mode site. In keeping with the episodic theory, it is possible to imagine that at least some of these frontal activations reflect the mental time travel component of the recognition test. In order for the subject to actually remember that he saw, or did not see, a test item in the study list he must “travel back” to the study episode. Future work no doubt will clarify the matter. However, it is encouraging to see the data point to the likelihood that the frontal lobes, recent appearances on the evolutionary scene, are centrally involved, presumably in close interaction

with other regions (McIntosh 1999), in the execution of episodic memory's most distinguishing feature, mental time travel.

CONCLUSION

Is the issue of the special status of episodic memory settled now? In at least one way it is, and in some others it will probably never be settled. In my 1983 monograph, when I posed a similar question, I wrote,

An issue as complex as the one with which we are concerned is unlikely to be resolved on the basis of a handful of experiments and clinical observations. The debate will undoubtedly continue, and more evidence will be generated that bears on the issue. The consensus that eventually will emerge is going to be shaped by the outcome of a large number of systematic studies, empirical observations, evaluation of the evidence, and rational thought. In the process, the original question, too, is likely to be changed; it is not just the relation between episodic and semantic systems that is going to be studied but also the relation of these two systems on the one hand to other memory systems on the other." (Tulving 1983, p. 99)

At that time we were indeed talking about a handful of half-relevant experiments and a few pertinent clinical observations. Now we have available what by comparison could be thought of as masses of data but that in the bigger reality of living and developing science is still a mere pittance. This is why the debate will continue, and it is in this sense that the matter is not yet settled.

However, it is settled in the sense that the concept of episodic memory is here to stay. It is now a permanent fixture in the thinking about memory in the minds of many memory researchers all over the world, in a way in which memory for things with firm versus fuzzy boundaries or other comparable notions is not. No more is it just an idea about how memory is organized; it now has become a concept that has a home, even if still a hidden one, in the brain. It is thereby a part of the objective reality.

Finally, what about time's arrow that is bent into a loop by episodic memory? Does episodic memory, or the fact that healthy humans can think about their own past, violate the law of unidirectionality of time? Is it really a marvel of nature? Surely this story line is too dramatic, even absurd. An event happens, a person experiences it, memory traces are laid down representing the event, the past vanishes and is replaced by the present. The memory traces of the event continue to exist in the present, they are retrieved, and the person remembers the event. This, in a nutshell, has been the understanding of how memory works. It is simple and straightforward; there is no need or room for magic, or marvel. There is certainly no violation of any law of time.

The common sense reflected in this theory is seduced by the word 'remember' which, in everyday usage, does not distinguish between re-experiencing the past

on one hand and all other, temporally neutral, consequences of acts of learning on the other. Moreover, every person's possession of the capability of mental time travel works against the appreciation of the rarity of this capability. A barn owl, were it to reflect on its mental powers, probably would not think much of anyone's ability to catch mice in the dark, just as people in some erewhon where all children, in the course of growing up, learn to walk on water would not give the matter a second thought. Because everyone does it, there is nothing marvelous about it.

If there is hope for a more appropriate assessment of the uniqueness of episodic memory and auto-noetic consciousness, it may come through the realization that mental time travel involves awareness not only of what has been but also of what may come. This awareness allows auto-noetic creatures to reflect on, worry about, and make plans for their own and their progeny's future in a way that those without this capability possibly could not. *Homo sapiens*, taking full advantage of its awareness of its continued existence in time, has transformed the natural world into one of culture and civilization that our distant ancestors, let alone members of other species, possibly could not imagine.

It took biological evolution a long time to build a time machine in the brain, and it has managed to do it only once, but the consequences have been enormous: By virtue of their mental control over time, human beings now wield powers on earth that in many ways rival or even exceed those of nature itself. It is difficult to imagine a marvel of nature greater than that.

Visit the Annual Reviews home page at www.AnnualReviews.org

LITERATURE CITED

- Aggleton JP, Brown MW. 1999. Episodic memory, amnesia and the hippocampal-anterior thalamic axis. *Behav. Brain Sci.* 22:425–44
- Andreasen NC, O'Leary DS, Arndt S, Cizadlo T, Hurtig R, et al. 1996. Neural substrates of facial recognition. *J. Neuropsychiatry Clin. Neurosci.* 8:139–49
- Baldwin JM. 1902. *Development and Evolution*. New York: Macmillan
- Buckner RL. 1996. Beyond HERA: contributions of specific prefrontal brain areas to long-term memory. *Psychonom. Bull. Rev.* 3:149–58
- Buckner RL, Koutstaal W, Schacter DL, Dale AM, Rosen BR. 1998. Functional-anatomic study of episodic memory retrieval II. Selective averaging of event-related fMRI trials to test the retrieval success hypothesis. *NeuroImage* 7:163–75
- Buckner RL, Petersen SE, Ojemann JG, Miezin FM, Squire LR, Raichle ME. 1995. Functional anatomical studies of explicit and implicit memory retrieval tasks. *J. Neurosci.* 15:12–29
- Buckner RL, Raichle ME, Miezin FM, Petersen SE. 1996. Functional anatomical studies of memory retrieval for auditory words and visual pictures. *J. Neurosci.* 16:6219–35
- Buckner RL, Tulving E. 1995. Neuroimaging studies of memory: theory and recent PET results. In *Handbook of Neuropsychology*, ed. F Boller, J Grafman, 10:439–66. Amsterdam: Elsevier
- Cabeza R, Nyberg L. 2000. Imaging cognition. II. An empirical review of 275 PET and fMRI studies. *J. Cogn. Neurosci.* 12:1–47
- Calabrese P, Markowitsch HJ, Durwen HF, Widlitzek H, Haupts M, et al. 1996. Right temporofrontal cortex as critical locus for the

- ecphory of old episodic memories. *J. Neurol. Neurosurg. Psychiatry* 61 (3):304–10
- Cermak LS, O'Connor M. 1983. The anterograde and retrograde retrieval ability of a patient with amnesia due to encephalitis. *Neuropsychologia* 21:213–34
- Clayton NS, Dickinson A. 1998. Episodic-like memory during cache recovery by scrub jays. *Nature* 395:272–74
- Cohen NJ. 1984. Preserved learning capacity in amnesia: evidence for multiple memory systems. In *Neuropsychology of Memory*, ed. LR Squire, N Butters, pp. 83–103. New York: Guilford
- Craik FIM. 2001. Human memory and ageing. *Proceedings of the 27th International Congress of Psychology, Stockholm, August 2000*. In press
- DellaSala S, Laiacona M, Spinnler H, Trivelli C. 1993. Autobiographical recollection and frontal damage. *Neuropsychologia* 31 (8):823–39
- Desgranges B, Baron JC, Eustache F. 1998. The functional neuroanatomy of episodic memory: the role of the frontal lobes, the hippocampal formation, and other areas. *NeuroImage* 8:198–213
- Fletcher PC, Dolan RJ, Frith CD. 1995. The functional anatomy of memory. *Experientia* 51:1197–207
- Fletcher PC, Frith CD, Rugg MD. 1997. The functional neuroanatomy of episodic memory. *Trends Neurosci.* 20:213–18
- Foster JK, Jelicic M, eds. 1999. *Memory: Systems, Process, or Function?* Oxford: Oxford Univ. Press
- Gardiner JM. 1988. Functional aspects of recollective experience. *Mem. Cogn.* 16:309–13
- Gardiner JM, Richardson-Klavehn A. 2000. Remembering and knowing. See Tulving & Craik 2000, pp. 229–44
- Glenberg AM. 1997. What memory is for. *Behav. Brain Sci.* 20:1–55
- Gorfein DS. 1987. Functional dissociation: comments on the chapter by Roediger and Blaxton. See Gorfein & Hoffman 1987, pp. 381–83
- Gorfein DS, Hoffman RR, eds. 1987. *Memory and Learning: The Ebbinghaus Centennial Conference*. Hillsdale, NJ: Erlbaum
- Griffiths DP, Dickinson A, Clayton NS. 1999. Declarative and episodic memory: What can animals remember about their past? *Trends Cogn. Sci.* 3(2):74–80
- Hamann SB, Squire LR. 1995. On the acquisition of new declarative knowledge in amnesia. *Behav. Neurosci.* 109:1027–44
- Haxby JV, Ungerleider LG, Horwitz B, Maisog JM, Rapoport SL, Grady CL. 1996. Face encoding and recognition in the human brain. *Proc. Natl. Acad. Sci. USA* 93:922–27
- Hayman CAG, Macdonald CA, Tulving E. 1993. The role of repetition and associative interference in new semantic learning in amnesia. *J. Cogn. Neurosci.* 5:375–89
- Hintzman DL. 1984. Episodic versus semantic memory: a distinction whose time has come—and gone? *Behav. Brain Sci.* 7:240–41
- Hintzman DL. 2000. Memory judgements. See Tulving & Craik 2000, pp. 165–77
- Horner MD. 1990. Psychobiological evidence for the distinction between episodic and semantic memory. *Neuropsychol. Rev.* 1:281–321
- Howe ML. 2000. *The Fate of Early Memories*. Washington, DC: Am. Psychol. Assoc.
- Jacoby LL. 1991. A process dissociation framework: separating automatic from intentional uses of memory. *J. Mem. Lang.* 30:513–41
- Kapur N. 1999. Syndromes of retrograde amnesia: a conceptual and empirical analysis. *Psychol. Bull.* 125:800–25
- Kapur S, Craik FIM, Jones C, Brown GM, Houle S, Tulving E. 1995. Functional role of the prefrontal cortex in retrieval of memories: a PET study. *NeuroReport* 6:1880–84
- Kapur S, Craik FIM, Tulving E, Wilson AA, Houle S, Brown GM. 1994. Neuroanatomical correlates of encoding in episodic memory: levels of processing effect. *Proc. Natl. Acad. Sci. USA* 91:2008–11
- Kelley WM, Miezin FM, McDermott KB,

- Buckner RL, Raichle ME, et al. 1998. Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. *Neuron* 20:927–36
- Kihlstrom JF. 1984. A fact is a fact is a fact. *Behav. Brain Sci.* 7:243–44
- Kitchener EG, Hodges JR, McCarthy R. 1998. Acquisition of post-morbid vocabulary and semantic facts in the absence of episodic memory. *Brain* 121:1313–27
- Knowlton BJ, Squire LR. 1995. Remembering and knowing: two different expressions of declarative memory. *J. Exp. Psychol.: Learn. Mem. Cogn.* 21:699–710
- Köhler S, Moscovitch M, Winocur G, Houle S, McIntosh AR. 1998. Networks of domain-specific and general regions involved in episodic memory for spatial location and object identity. *Neuropsychologia* 36:129–42
- Kopelman MD, Stanhope N, Kingsley D. 1999. Retrograde amnesia in patients with diencephalic, temporal lobe, or frontal lesions. *Neuropsychologia* 37:939–58
- Lepage M, Ghaffar O, Nyberg L, Tulving E. 2000. Prefrontal cortex and episodic memory retrieval mode. *Proc. Natl. Acad. Sci. USA* 97:506–11
- Levine B, Black SE, Cabeza R, Sinden M, McIntosh AR, et al. 1998. Episodic memory and the self in a case of isolated retrograde amnesia. *Brain* 121:1951–73
- Markowitsch HJ, Calabrese P, Liess J, Haupts M, Durwen HF, Gehlen W. 1993. Retrograde amnesia after traumatic injury of the frontotemporal cortex. *J. Neurol. Neurosurg. Psychiatry* 56 (9):988–92
- McClelland JL, McNaughton BL, O'Reilly RC. 1995. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychol. Rev.* 102:419–57
- McCormack T, Hoerl C. 1999. Memory and temporal perspective: the role of temporal frameworks in memory development. *Dev. Rev.* 19:154–82
- McIntosh AR. 1999. Mapping cognition to the brain through neural interaction. *Memory* 7:523–48
- Mesulam MM. 1990. Large-scale neurocognitive networks and distributed processing for attention, language, and memory. *Ann. Neurol.* 28:597–613
- Mishkin M, Suzuki WA, Gadian DG, Vargha-Khadem F. 1997. Hierarchical organization of cognitive memory. *Philos. Trans. R. Soc. London B* 352:1461–67
- Moscovitch M, Kapur S, Köhler S, Houle S. 1995. Distinct neural correlates of visual long-term memory for spatial location and object identity: a positron emission tomography (PET) study in humans. *Proc. Natl. Acad. Sci. USA* 92:3721–25
- Nelson K. 1993. The psychological and social origins of autobiographical memory. *Psychol. Sci.* 4:7–14
- Nielsen JM. 1958. *Memory and Amnesia*. Los Angeles: San Lucas
- Nyberg L. 1998. Mapping episodic memory. *Behav. Brain Res.* 90:107–14
- Nyberg L, Cabeza R, Tulving E. 1996a. PET studies of encoding and retrieval: the HERA model. *Psychonom. Bull. Rev.* 3:135–48
- Nyberg L, Habib R, Tulving E, Cabeza R, Houle S, et al. 2000. Large scale neurocognitive networks underlying episodic memory. *J. Cogn. Neurosci.* 12:163–73
- Nyberg L, McIntosh AR, Cabeza R, Habib R, Tulving E. (1996b). General and specific brain regions involved in encoding and retrieval of events: what, where, and when. *Proc. Natl. Acad. Sci. USA* 93:11280–11285
- Nyberg L, Tulving E, Habib R, Nilsson L-G, Kapur S, et al. 1995. Functional brain maps of retrieval mode and recovery of episodic information. *NeuroReport* 7:249–52
- Perner J, Ruffman T. 1995. Episodic memory and auto-noetic consciousness: developmental evidence and a theory of childhood amnesia. *J. Exp. Child Psychol.* 59:516–48
- Raichle ME. 1994. Images of the mind: studies

- with modern imaging techniques. *Annu. Rev. Psychol.* 45:333–56
- Rajaram S. 1993. Remembering and knowing: two means of access to the personal past. *Mem. Cogn.* 21:89–102
- Rajaram S, Coslett HB. 2000. New conceptual associative learning in amnesia. *Mem. Lang.* 43:291–315
- Ratcliff R, McKoon G. 1986. More on the distinction between episodic and semantic memories. *J. Exp. Psychol.: Learn. Mem. Cogn.* 12:312–13
- Richards RJ. 1987. *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior*. Chicago: Univ. Chicago Press
- Roediger HL III, Blaxton TA. 1987. Retrieval modes produce dissociations in memory for surface information. See Gorfein & Hoffman 1987, pp. 349–79
- Roediger HL III, McDermott KB. 1993. Implicit memory in normal human subjects. In *Handbook of Neuropsychology*, ed. H Spinnler, F Boller, pp. 63–131. Amsterdam: Elsevier
- Roediger HL III, Weldon MS, Challis BH. 1989. Explaining dissociations between implicit and explicit measures of retention: a processing account. In *Varieties of Memory and Consciousness: Essays in Honour of Endel Tulving*, ed. HL Roediger III, FIM Craik, pp. 3–42. Hillsdale, NJ: Erlbaum
- Rosenbaum RS, Priselac S, Köhler S, Black S, Gao F, et al. 2000. Remote spatial memory in an amnesic person with extensive hippocampal lesions. *Nat. Neurosci.* 3:1044–48
- Rousseaux M, Godfrey O, Cabaret M, Bernati T, Pruvo JP. 1997. Retrograde memory after rupture of aneurysms of the anterior communicating artery. *Rev. Neurolog.* 153 (11):659–68
- Rugg MD, Fletcher PC, Frith CD, Frackowiak RS, Dolan RJ. 1997. Brain regions supporting intentional and incidental memory: a PET study. *NeuroReport* 8:1283–87
- Schacter DL. 1987a. Implicit memory: history and current status. *J. Exp. Psychol.: Learn. Mem. Cogn.* 13:501–18
- Schacter DL. 1987b. Memory, amnesia, and frontal lobe dysfunction. *Psychobiology* 15:21–36
- Schacter DL, Alpert NM, Savage CR, Rauch SL. 1996. Conscious recollection and the human hippocampal formation: evidence from positron emission tomography. *Proc. Natl. Acad. Sci. USA* 93:321–25
- Schacter DL, Harbluk J, McLachlan D. 1984. Retrieval without recollection: an experimental analysis of source amnesia. *J. Verb. Learn. Verb. Behav.* 23:593–611
- Schacter DL, Tulving E. 1994. What are the memory systems of 1994? In *Memory Systems*, ed. DL Schacter, E Tulving, pp. 1–38. Cambridge, MA: MIT Press
- Schacter DL, Wagner AD, Buckner R. 2000. Memory systems of 1999. See Tulving & Craik 2000, pp. 627–43
- Scoville WB, Milner B. 1957. Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatry* 20:11–21
- Shallice T, Fletcher P, Frith CD, Grasby P, Frackowiak RSJ, Dolan RJ. 1994. Brain regions associated with acquisition and retrieval of verbal episodic memory. *Nature* 368:633–35
- Sherry DF, Schacter DL. 1987. The evolution of multiple memory systems. *Psychol. Rev.* 94:439–54
- Shimamura AP, Squire LR. 1987. A neuropsychological study of fact memory and source amnesia. *J. Exp. Psychol.: Learn. Mem. Cogn.* 13:464–73
- Squire LR. 1987. *Memory and Brain*. New York: Oxford Univ. Press
- Squire LR. 1992. Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychol. Rev.* 99:195–231
- Squire LR, Ojemann JG, Miezin FM, Petersen SE, Videen TO, Raichle ME. 1992. Activation of the hippocampus in normal humans: a functional anatomical study of memory. *Proc. Nat. Sci. USA* 89:1837–41
- Squire LR, Zola S. 1998. Episodic memory, semantic memory, and amnesia. *Hippocampus* 8:205–11
- Suddendorf T, Corballis MC. 1997. Mental time travel and the evolution of the human

- mind. *Genet. Soc. Gen. Psychol. Monogr.* 123:133–67
- Toth JP. 2000. Nonconscious forms of memory. See Tulving & Craik 2000, pp. 245–61
- Toth JP, Hunt RR. 1999. Not one versus many, but zero versus any: structure and function in the context of the multiple memory systems debate. See Foster & Jelicic 1999, pp. 232–72
- Tulving E. 1972. Episodic and semantic memory. In *Organization of Memory*, ed. E Tulving, W Donaldson, pp. 381–403. New York: Academic
- Tulving E. 1983. *Elements of Episodic Memory*. Oxford: Clarendon
- Tulving E. 1984. Relations among components and processes of memory. *Behav. Brain Sci.* 7:257–68
- Tulving E. 1985a. How many memory systems are there? *Am. Psychol.* 40:385–98
- Tulving E. 1985b. Memory and consciousness. *Can. Psychol.* 26:1–12
- Tulving E. 1986. What kind of a hypothesis is the distinction between episodic and semantic memory? *J. Exp. Psychol. Learn. Mem. Cogn.* 12:307–11
- Tulving E. 1989. Memory: performance, knowledge, and experience. *Eur. J. Cogn. Psychol.* 1:3–26
- Tulving E. 1991. Concepts of human memory. In *Memory: Organization and Locus of Change*, ed. L Squire, G Lynch, NM Weinberger, JL McGaugh, pp. 3–32. New York: Oxford Univ. Press
- Tulving E. 1995. Organization of memory: Quo vadis? In *The Cognitive Neurosciences*, ed. MS Gazzaniga, pp. 839–47. Cambridge, MA: MIT Press
- Tulving E. 1999. On the uniqueness of episodic memory. In *Cognitive Neuroscience of Memory*, ed. L-G Nilsson, HJ Markowitsch, pp. 11–42. Göttingen: Hogrefe & Huber
- Tulving E. 2001a. The origin of autoevidence in episodic memory. In *The Nature of Remembering: Essays in Honor of Robert G. Crowder*, ed. HL Roediger, JS Nairne, I Neath, AM Suprenant, pp. 17–34. Washington, DC: Am. Psychol. Assoc.
- Tulving E. 2001b. Chronesthesia: awareness of subjective time. In *The Age of the Frontal Lobes*, ed. DT Stuss, RC Knight. In press
- Tulving E, Craik FIM, eds. 2000. *The Oxford Handbook of Memory*. New York: Oxford Univ. Press
- Tulving E, Hayman CAG, Macdonald CA. 1991. Long-lasting perceptual priming and semantic learning in amnesia: a case experiment. *J. Exp. Psychol.: Learn. Mem. Cogn.* 17:595–617
- Tulving E, Kapur S, Craik FIM, Moscovitch M, Houle S. 1994a. Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. *Proc. Natl. Acad. Sci. USA* 91:2016–20
- Tulving E, Kapur S, Markowitsch HJ, Craik FIM, Habib R, Houle S. 1994b. Neuroanatomical correlates of retrieval in episodic memory: auditory sentence recognition. *Proc. Natl. Acad. Sci. USA* 91:2012–15
- Tulving E, Markowitsch HJ. 1998. Episodic and declarative memory: role of the hippocampus. *Hippocampus* 8:198–204
- Tulving E, Schacter DL, McLachlan DR, Moscovitch M. 1988. Priming of semantic autobiographical knowledge: a case study of retrograde amnesia. *Brain Cogn.* 8:3–20
- Vargha-Khadem F, Gadian DG, Watkins KE, Connelly A, Van Paesschen W, Mishkin M. 1997. Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* 277:376–80
- Viskontas IV, McAndrews MP, Moscovitch M. 2000. Remote episodic memory deficits in patients with unilateral temporal lobe epilepsy and excisions. *J. Neurosci.* 20:5853–57
- Wagner AD, Desmond JE, Glover G, Gabrieli JDE. 1998a. Prefrontal cortex and recognition memory: fMRI evidence for context-dependent retrieval processes. *Brain* 121:1985–2002
- Wagner AD, Poldrack RA, Eldridge LL, Desmond JE, Glover G, Gabrieli JDE. 1998b. Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. *NeuroReport* 9:3711–17

-
- Weiskrantz L, ed. 1985. Animal intelligence. *Proceedings of a Royal Society Discussion Meeting*. Oxford, UK: Clarendon
- Weldon MS. 1999. The memory chop shop: issues in the search for memory systems. See Foster & Jelicic 1999, pp. 162–204
- Wheeler MA, Stuss DT, Tulving E. 1997. Toward a theory of episodic memory: the frontal lobes and autonoetic consciousness. *Psychol. Bull.* 121:331–54
- Wheeler MA, McMillan CT. 2001. Focal retrograde amnesia and the episodic-semantic distinction. *Cogn. Affect. Behav. Neurosci.* 1:22–37