

On the Uniqueness of Episodic Memory

Endel Tulving

In his monumental *Principles of Psychology*, William James wrote a chapter on memory that even today makes for interesting and refreshing reading. In it James defined memory in the way in which it had become known in Western thought over the millennia, and in the way in which many people even now understand it. Memory for James then was equated with remembering what one has learned and experienced in the past. Formally, James wrote that memory is the knowledge of a former state of mind, or "*the knowledge of an event, or fact, of which meantime we have not been thinking, with the additional consciousness that we have thought or experienced it before*" (James, 1983, p. 610, emphasis in the original). A number of elements, James wrote, had to be present for a bit of knowledge to be acceptable as a memory: (i) revival in the mind of a "copy" of an original event, (ii) the requirement that the present image be held as standing for a "past original," and (iii) the requirement that the "pastness" refer not just to the past in general but rather to the personal past of the rememberer. Memory thus defined, James further elaborated, possesses the kind of subjectively experienced "warmth and intimacy" that mere conception, that is, mere thought about some previously learned fact, did not evoke.

Today, over a hundred years later, the concept of memory has changed in many ways even though its heart has not. Human memory, which James was writing about, has become much better understood, and infinitely more complex; the concept of memory has spread over vast domains of living organisms and their abilities to learn and benefit from their environments, from conditioning in nematodes to awareness of the past in humans; and the scientific study of memory now involves many different disciplines from molecular biology to cognitive science. But the progress in understanding memory has been more rapid in some respects than in others, and more rapid for some forms than others. The heart of Jamesian memory – one's awareness of the experienced past – was ignored for a long time by all students of memory. Only recently has it been declared to possess not only scientific interest but also being scientifically tractable. We now refer to it as episodic memory.

This chapter is about episodic memory, with especial emphasis on two key ideas that James had about memory and that characterize the thinking about episodic memory today. One idea is that memory has to do with the rememberer's own *personal* past. The other central idea is that the knowledge provided by episodic memory comes wrapped in the shell of a unique kind of conscious awareness that James tried to convey in terms of the notion of affective "warmth and intimacy" and that we today refer to as "*autonoetic*" awareness.

The central proposition of the chapter is that episodic memory is the only form of evolved memory that deals with the past and makes the personally experienced past accessible through autonoetic awareness. These two features – pastness of experiences and autonoetic awareness – differentiate episodic memory from all other forms of memory, and thereby make it unique. The central issue of the chapter has to do with the *neural correlates* of these two features of episodic memory: What, if anything, is known about the structures and circuits of the brain that subserve the awareness of the past? For a long time this question was completely beyond the pale of scientific methods. Today, thanks to the advances in theoretical thought about memory and to the recently developed techniques of functional brain imaging, we have available bits and pieces of fragmentary evidence that speak to the question. The chapter is a report of the initial progress that has been made.

What is Episodic Memory?

The concept of episodic memory has changed considerably since its introduction almost 30 years ago (Tulving, 1972). At that time it was thought of as an information processing system that (a) receives and stores information about temporally dated episodes or events, and about temporal-spatial relations among these events, (b) retains various aspects of this information, and (c) upon instructions transmits specific retained information to other systems, including those responsible for translating it into behavior and conscious awareness. It was contrasted with "semantic" memory to which it was assumed to be closely related and by which it was assumed to be influenced in its workings.

This conceptualization was largely shaped by the then dominant verbal learning orientation to memory (Tulving & Madigan, 1970), the nearly exclusive use of list-learning tasks and paradigms (Crowder, 1976), and the virtual absence of any directly relevant empirical evidence. The term "episodic memory" is widely used today, and many writers still think of it in terms similar to those proposed in 1972.

The meaning of "episodic memory" in this paper derives from the orienting

attitude that is known as “multiple memory systems” (Foster & Jelicic, 1999; Perani et al., 1993; Schacter & Tulving, 1994a). Episodic memory is one of several specific memory systems and subsystems. The criteria used for postulating, and defining memory systems, the distinction between systems and other classificatory concepts of memory – such as forms or kinds of memory, and memory tasks – and descriptions of currently known or assumed systems have been aired at some length elsewhere (Schacter & Tulving, 1994a, 1994b). The term “episodic memory” has also been used, and still is being used, in its earlier senses, but in this paper it always refers to its system-oriented concept.

Thus in this paper episodic memory refers to a memory system that makes possible mental “time travel” through subjective time, from the present to the past and to the future, a feat that other memory systems cannot perform. It does so by allowing the individual to re-experience, through autonoetic awareness, previous experiences as such, and to project similar experiences into the future. Episodic memory evolved more recently than other systems, it is probably unique to humans, and it develops late in childhood. Its operations depend on semantic and other forms of memory. Therefore, it shares neural mechanisms and cognitive processes with other systems, but in addition it is subserved by specific mechanisms and processes that are not components of any other system.

There are many other terms that are closely related even if not equivalent to episodic memory. Autobiographical memory, event memory, personal memory, source memory, memory for temporal-spatial context are the most frequently used ones. The choice of the terms reflects the user's knowledge, history, intention, and preference. Many of these other terms refer to the kind of remembered information rather than to any hypothetical memory system with specified properties, either of the kind specified by Schacter and Tulving (1994b) or any other kind. Thus, as mentioned, autobiographical memory, has to do with the recollection of significant events from a person's life. Source memory, and memory for “context,” refer to the subject's expressed knowledge concerning temporal, spatial, and other environmental conditions prevailing at the time of the acquisition of some particular information. Neither term implies the postulated existence of a special neurocognitive system, as does episodic memory, and neither refers to any unique recollective experience, as does episodic memory.

Episodic and Declarative (Semantic) Memory

The meaning of episodic memory can be clarified by contrasting it with semantic memory, because they are similar in many ways. Semantic memory – it has also been referred to as generic memory, or knowledge memory – is a memory

system that makes possible acquisition, retention, and use of factual information in the broadest sense. Despite its name it is not concerned with language or with verbal information, although much of human knowledge can be expressed linguistically. The knowledge acquired by, held in, and retrieved from semantic memory is about, or represents, the world as it is, or as it could be. This kind of knowledge provides the individual with the necessary material for thought, that is, for cognitive operations on the aspects of the world beyond the reach of immediate perception. Semantic-memory operations – encoding and retrieval – are accompanied by a state of conscious awareness that the individual can differentiate from other possible states of awareness familiar from experience, such as awareness that accompanies imaging visual scenes or auditory stimuli, daydreaming, dreaming, and remembering past happenings, as well as a considerable variety of affective states of awareness. We refer to the kind of awareness that accompanies semantic-memory operations as “noetic” awareness (Tulving, 1985c, 1993).

Episodic and semantic memory are in many ways very similar, and therefore many people, in the past and even today, have tended to think of them as basically the same kind of memory. Both are large and complex, capable of storing vast amounts of information of many different kinds. Both are cognitive (declarative, or representational) systems whose “contents” can be described in terms of propositions about objects and their relations. Information in both can, in a sense, be compared with the external world, and assertions made about the world on the basis of the stored information can be judged for their truth value. Encoding of new information into one of the two systems is difficult to distinguish from encoding of information into the other. There is no simple method that could be used, even in experimental settings, for adding new information to semantic knowledge of a normal adult, without corresponding information being encoded into episodic memory, or vice versa. Both episodic and semantic memory enable individuals to acquire factual information through different sensory modalities, and in both such acquisition can occur very rapidly, sometimes as a consequence of a single glimpse or sound of a relevant input. Both episodic and semantic memory can register, and hold information about, various states of the world, including the internal states of the individual, and both can form representations of the occurrence of events that have a beginning and an end in time. Stored information in both forms of memory is flexibly accessible, a given chunk or bundle of available information being ecphorizable (activatable, actualizable) by a variety of instructions, prompts, and cues. The operations of both memory systems obey the principles of encoding specificity and transfer appropriate processing: the effectiveness of given retrieval cues is determined not only by the nominal identity of target information in the memory

store, but also by its episodically and semantically encoded context. Finally, both systems can be thought of as being concerned with “remembering that” rather than “remembering how”: the results of acts of retrieval from either memory system can be expressed symbolically, in language or through graphic representations, unlike the skills mediated by procedural memory that can only be expressed through nonsymbolic behavior.

Episodic and semantic memory have been generally thought of as two “subsystems” of declarative memory. In some theories (Squire, 1987) they are assumed to be organized as two parallel branches of a hierarchy, in others (Tulving, 1984, 1993) their relation is one of “embeddedness”: the episodic system including the semantic but not vice versa. Recently, however, in order to better accommodate some new and intriguing findings from patients with early onset amnesia (Vargha-Khadem et al., 1997), a realignment in the organization of memory was proposed (Tulving & Markowitsch, 1998). The proposal was that “declarative memory” be equated with “semantic memory,” and defined in terms of properties and features that have been assumed to be *common* to semantic and episodic memory in previous formulations. Semantic memory would be retained as a term referring to declarative memory expressed through language. Episodic memory, in this new formulation, would then represent a system that has many features in common with declarative memory but also possess features, such as autonoetic awareness of the personal past, that declarative (semantic) memory does not possess.

Uniqueness of Episodic Memory

Despite the numerous similarities between episodic and declarative (semantic) memory – similarities that have made it difficult to separate the two – episodic memory does possess critical features not shared by the other systems. Some of these have already been mentioned or alluded to. A more detailed description is available elsewhere (Wheeler et al., 1997; Tulving & Markowitsch, 1998). I summarize episodic memory’s unique features here.

First and foremost, episodic memory is the only form of memory that, at the time of retrieval, is oriented towards the past: Retrieval in episodic memory means “mental time travel” through and to one’s past. All other forms of memory, including semantic, declarative, and procedural memory, are, at retrieval, oriented to the present. When an animal knows, whether “innately” or by virtue of the consequences of something learned in the past, what an appropriate response is in a given situation, it need not “think back to” earlier *experiences*. Even human beings who are capable of consciously recollecting past experiences seldom engage in such recollection when they make use of previously acquired “declarative” information and knowledge.

Second, and in many ways equally important, is the fact that episodic remembering (mental time travel) is accompanied by a special kind of "autonoetic" conscious awareness that is clearly different from the kind of conscious awareness ("noetic" awareness) that accompanies retrieval of declarative information (Tulving, 1993). The earlier experience remembered now may be hazy or fragmentary or even false by objective standards, but its phenomenal quality is not mistaken for any other kind of conscious awareness. A normal individual can distinguish between recollecting a personal experience and recalling an impersonal fact as readily as she can distinguish between, say, perceiving and imaging. This ability of humans makes possible an operational definition of autonoetic and noetic awareness in terms of the "remember"/"know" (R/K) paradigm (Dalla Barba et al. 1997; Gardiner & Java, 1993; Gardiner et al., 1998; Knowlton & Squire, 1995; Tulving, 1885), and the segregation of the two kinds of awareness at the level of electrophysiological activity of the brain (Düzel et al 1997).

Thus, combining the first two unique features, we can say that the function of episodic memory is conscious recollection of one's personal past. This is the crux of episodic memory: it has to do with conscious recollection of previous *experiences* of events, happenings, and situations. The emphasis is on "experience," rather than "event" or "happening." Declarative memory, on the other hand, is concerned with facts and events of the physical world, that is, with the acquisition and use of the knowledge of what is, or what could be, in the world, and what is appropriate behavior in a given situation.

Other features that characterize episodic memory are less striking, and some of them are more questionable, their verity still being evaluated and their reality debated. Thus, episodic memory lags behind declarative memory in human development (Perner & Ruffman, 1995; Pillemer & White, 1989). In general, it is more vulnerable than declarative memory to a number of pathological conditions of the brain (Bäckman & Small, 1998; Evans et al., 1993; Duffy & O'Carroll, 1994; Greene et al., 1996; Desgranges et al., 1998), as well as to the normal process of aging (Herlitz & Forsell, 1996; Nilsson et al., 1997). There are also clear gender differences: women consistently do better on episodic memory tasks than do men, although on tests of general knowledge, word knowledge, primary memory and perceptual priming both populations perform equally well (Herlitz, Nilsson, & Bäckman, 1997). Episodic memory probably evolved more recently than any other form of memory and there is no evidence that any other species possesses a similar kind of memory (Suddendorf & Corballis, 1997). Finally, although it is well established that episodic memory is like declarative memory in that both depend on MTL and diencephalic structures, it has also been suspected that episodic memory depends on the frontal lobes in a way that declarative and other forms of memory do

not (Schacter, 1987; Squire, 1987). Equally instructive have been the findings from functional neuroimaging studies of the kind that are discussed at some length in the second half of the present paper (Fletcher et al., 1995; Fletcher, Frith, & Rugg, 1997; Haxby et al., 1996; Kapur et al., 1994a; Nyberg, 1998; Nyberg et al., 1996).

In summary, episodic memory is unique in that it is the only form of memory that has the capability of registering and storing personally experienced happenings in subjective time, and making information about such experiences available in the form of a special form of conscious awareness, named autonoetic awareness. All other forms of evolved memory function to provide the individual with information as to how to respond to environmental contingencies and how to behave effectively in various situations.

Memory and Time

Because the uniqueness of episodic memory as described is not always appreciated, or not sufficiently appreciated, it may be worth while to discuss the issue a bit more fully. I do so next, dealing first with learning and memory that does not have much to do with remembering past experiences, and then with episodic memory, which has everything to do with it.

The behavior of organisms is always and inevitably shaped by heredity and environment. Many organisms, including human beings, begin life with biologically useful behavior patterns, or with the potential of postnatal maturation of such patterns that are "released" in appropriate situations. These innate capabilities can be very complex, as is the case in what is probably the most thoroughly studied human "instinct," namely language (Pinker, 1995). All these "instincts" are effective ways of coping with problems set by one's environment. They are built into the nervous systems of organisms independently of experience. For example, very young children, like the very young of many other species, do not crawl off a "visual cliff" when given an opportunity to do so, but cling to the safe side of the divide, even during the very first test (Gibson & Walk, 1960). Numerous other examples could be given how the genetically determined workings of an organism's brain guide the organism's behavior in a myriad life situations.

Environmentally shaped changes in behavior and cognition, that is learning and memory, represent another effective means of coping with the demands for survival. Learning something now that is useful for achieving desirable goals in the future complements genetically determined behavior patterns, and in higher organisms, such as many mammals, constitutes the source of the better part of the organism's knowledge about its world. Because young children lack innate knowledge about hot stoves, they must learn, through actual

experience or vicariously, about what are good and what are bad things to do around hot stoves. Because the world in which the children grow up is exceedingly complex, they must learn a myriad things to cope with it.

All forms of learning and memory, from the lowliest to the highest, serve very much the same function as do the "instincts": they provide the organisms with means of behaving more effectively than would have been possible in the absence of the relevant acquired knowledge or skill. An organism learns something today to behave more effectively in the future. In this sense, when learning occurs, it is oriented to the future; when its fruits are subsequently used, the memory is oriented to the present. The important criterion in judging the worth of any act of learning or memory has to do with their usefulness in guiding ongoing activity here and now.

Thus, all forms of learning and memory that are known throughout the whole animal kingdom could be said to be "proscopic," a term derived from Greek that means "forward-looking." From sensitization and habituation, through simple and complex classical and instrumental conditioning, through the learning of perceptual-motor and cognitive skills, through various forms of "implicit" memory, such as priming, through the imitative learning that occurs in higher animals, all the way to the immense quantities of concrete and abstract knowledge of the world that an adult human beings have accumulated throughout their lives, memory is proscopic: it is important solely because it shapes and effectively enhances the organism's interaction with its future environment. This basic truth holds as much for the *Aplysia* learning to withdraw its gill to a conditioned stimulus, the mouse learning the location of the sunken platform in a Morris water maze, for the monkey remembering the location of the peanut in a delayed non-matching-to-sample task, the child avoiding touching the hot stove, the pinch hitter hitting the ball out of the ball-park, the Scrabble player coming up with a clever word that astounds the opponents, the scientist thinking of a new kind of a distinction that is important in the study of the brain/mind, and so on, and on, and on, essentially *ad infinitum*.

In none of these future-oriented learning situations and the present-oriented memory situations does it matter how the knowledge was acquired. There is no necessity for any conscious access to the past, and no necessity to be consciously aware of past experiences. The only thing that matters is the efficacy of the current behavior. The child does not remember where and how she touched the hot stove in the past, but she knows how to treat the stove now; the amnesic patient does not remember that the examining physician hid a pin in his hand while shaking the patient's hand an hour ago, but she knows that it is not good to shake the doctor's hand now; the contestant in a TV show does not remember when or where or how she acquired the knowledge that Hannibal is associated with elephants, but she answers the question correctly and

profitably now. Because all these people can efficiently rely on their proscopic memory, remembering the past is irrelevant.

Thus, despite the traditional association between memory and the past, the remembering of the past, in the sense of conscious recollection of what happened on an earlier occasion, does not play any critical role in making use of what has been learned and how the fruits of the learning are used. Sometimes, of course, the expression of acquired skills and knowledge is accompanied by conscious recollections of past experiences, but these occurrences are epiphenomenal only. The circumstances surrounding the origin and creation of knowledge that guides effective behavior may be of interest to the scientist studying such behavior, but to the behaving organism it makes no difference.

The singular exception to all the ubiquity and evolutionary significance of the proscopic forms of learning and memory that serve the future without bothering about the past is episodic memory. Episodic memory does exactly what the other forms of memory do not and cannot do – it makes it possible for the individual to recollect previously experienced events as such. It enables the individual to mentally “travel back into her personal past.” It shares with proscopic memory the basic function – it provides the individual with useful information as to the effective courses of actions in various situations – but it goes beyond the proscopic function in that it does allow us to remember (to consciously recollect) what happened in the past. A child remembers what happened at a friend’s birthday party the day before, a young lover remembers the expression on the beloved’s face in the moonlight, the scientist remembers the first time when a speaker at a conference mentioned her name and work, and so on, and on. Because episodic memory is oriented towards the past, we can think of episodic memory as “palinscopic” (backward-looking) memory. An individual who “possesses” palinscopic memory can at Time 2 “mentally travel back” to Time 1.

In summary, then, the main points I make here are these. Despite common sense, most forms of memory have no special connection with the past. Events happen in time, of course, and this means that the learned behavior being made use of now (memory information being retrieved now) had its origin in the past, but the pastness of the origin is no more relevant to these “proscopic” forms of memory than, say, eating a meal “in the past” is relevant to the current feeling of satiation, in the short run, or physical growth and development, in the long run. The singular exception is episodic memory, which is “palinscopic” and unique in two senses: it makes it possible for the individual to remember personally experienced past happenings, and it makes it possible for the individual to experience such “mental time travel” in the form of autonoetic awareness.

The theory of episodic memory as summarized here naturally leads to the question of what is known about the brain side of the story. Are there any

specific brain regions that are involved in mediating autonoetic episodic remembering? Because we now have available techniques for identifying regional differences in brain activity, we can test this expectation empirically. We now turn to examine some available evidence provided by PET studies of memory.

PET Studies of Memory

Episodic Memory in the Laboratory

In the laboratory, episodic memory is studied by means of experimentally created "miniature events." One such event consists in the presentation by the experimenter, and perception by the subject, of a discrete stimulus object, such as a word, a simple sentence, a drawing of an object, a picture, a photographed face, and the like. When the subject perceives the appearance of a stimulus object on the display device (e. g., computer screen) for a short interval, usually measured in a few seconds, information about certain aspects of the event is encoded into different memory systems (Tulving, 1999). Some of this information is potentially retrievable under appropriate conditions. These conditions include experimental task instructions and the presentation of more or less specific retrieval cues (Tulving, 1983, Ch. 9). The subject needs to make no special effort to encode information about stimulus items into memory systems: encoding occurs automatically by virtue of the (situational) novelty of the occurrence of the miniature events. Less-than-perfect subsequent retrieval of the event information is usually attributable to the interference caused by the presence of other events in the presentation series, as well as inadequate retrieval cues. Various kinds of "encoding operations," usually consisting of subjects making specific judgments about presented items (Craik & Tulving, 1975), may "immunize" individual events against intralist interference and thus facilitate subsequent retrieval.

Retrieval means "utilization of stored information for the purpose of carrying out a task requiring the information." In a typical "explicit" memory task the subject has to demonstrate his or her knowledge of the previously encoded events by either recalling the name of the presented item, recognizing a copy of the item, or in some other fashion. The level of behavioral retrieval performance depends on a multitude of factors, including individual differences among subjects, the nature of to-be-remembered events, conditions under which encoding occurred, conditions prevailing at retrieval, and especially the relation between encoding and retrieval conditions (Roediger & Gynnn, 1996).

Modern neuroimaging studies of memory have been directed at various aspects of memory. One of the most popular approaches has turned out to be

studies of two kinds: (i) those comparing semantic and episodic retrieval, and (ii) those comparing episodic-memory encoding and retrieval. Because an act of retrieval of information from semantic memory in a typical memory experiment is a novel experience for the subject (Tulving, 1983), and because novel experiences are assumed to be automatically encoded into long-term memory (Tulving et al., 1996; Tulving & Kroll, 1995), semantic retrieval and episodic encoding are difficult to separate experimentally (Tulving et al., 1994a). Therefore, the two kinds of studies just mentioned are usually indistinguishable experimentally although they may differ in the interpretation of the obtained results. We now consider these studies.

The Logic of PET

The logic of PET "activation studies" of memory is straightforward. Different mental activities are supported by the activities in different brain regions. When the subject engages in a given cognitive task, PET provides information about the level of cerebral blood flow in different regions that are associated with the processes involved in the task. Because changes in blood flow are known to be correlated with changes in neuronal activity, their patterns (maps) provide information about neuronal activity in different brain sites that reflect these processes (Frackowiak & Friston, 1994; Posner & Raichle, 1995; Raichle, 1994).

Traditionally, PET data are presented in the form of "brain maps." A brain map reflects differences in the patterns of regional blood flow associated with two different tasks, A and B. The tasks are usually selected to differ from one another with respect to readily specifiable cognitive processes. A brain map shows regions in which blood flow, and hence neuronal activity, was higher in Task A than B, regions in which the level of blood flow could not be distinguished between the two tasks, as well as regions in which the level of blood flow was lower in task A than task B. The logic of PET studies holds that these "activation" maps reflect the differences between the two comparison tasks. The experimental challenge in such a situation is to describe the correlation between the functional neuroanatomy and the cognitive processes in a disciplined, systematic, and theoretically meaningful fashion. Although the "subtraction method" (Fox, 1991; Friston et al., 1995) of positron emission tomography (PET) that underlies these analyses has severe limitations (Friston et al., 1996; Jennings et al., 1997), it is widely used and, more important, it has yielded some surprisingly systematic data.

Encoding and Retrieval

The subtraction method used in PET studies can be illustrated with an example from a study done at Toronto involving a *direct comparison* between episodic encoding and retrieval in healthy young adults (Cabeza et al., 1997b; Kapur et al., 1996). Subjects' brains were scanned under two conditions. One condition involved encoding of novel verbal information into memory. Subjects were shown pairs of words, such as PENGUIN – TUXEDO, and they were instructed to think of some meaningful relation between the words of each pair. They were also told that their memory for these pairs would be tested. We know that at least two things occur in this situation. The first is semantic-memory retrieval: subjects have to make use of their semantic knowledge (general “knowledge of the world”) in relating the paired words to each other. Second, each miniature event of seeing a pair of words and thinking of a meaningful relation between them is encoded and stored in episodic memory: subjects can later on remember that such and such word pairs occurred in the study list. The other experimental condition involved retrieval of information thus encoded and stored. Subjects again saw pairs of words, such as PENGUIN – TUXEDO, but now they had to decide whether the pair had or had not appeared in the study list. This is an episodic-memory retrieval (recognition) condition. Responding correctly in this task requires that the subject be able to “think back” to a particular “period” in his life, the encoding trial, and make a decision about the relation between the present stimulus, the test pair, and the “contents” of the episode experienced earlier.

The two conditions are very similar in many ways: the subjects always saw a pair of words on the display screen, the pairs were presented at the same rate, they had to make a binary decision about each pair in both conditions, and the overt responses they made were also similar. The main difference had to do with the presentation history of the material (seen for the first time in encoding, and second time in retrieval) and the task instructions – encode versus retrieve.

The PET results of interest have to do with the differences in the patterns of regional cerebral blood flow, and hence neuronal activity, associated with the two tasks. There are two such difference patterns in this study. One results when the regional activation during retrieval is subtracted from the regional activation during encoding. This pattern shows brain regions more active during encoding than during retrieval. The other pattern results when the activation during encoding is subtracted from the activation during retrieval. This pattern shows brain regions more active during retrieval than during encoding. Note that areas that are activated to the same (high or low) extent during both encoding and retrieval will not show up in the comparison, because they are “subtracted out.”

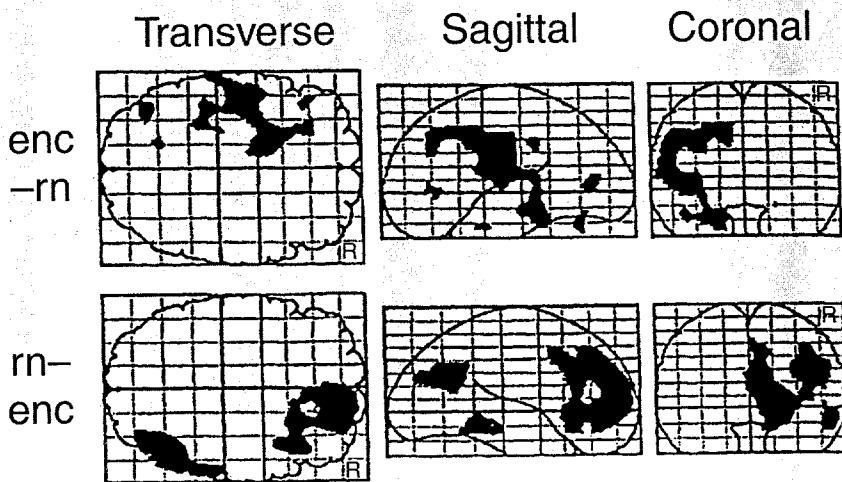


Figure 1. Brain maps illustrating differences in regional cerebral blood flow, and hence neuronal activity, in a PET study in which semantic retrieval (episodic encoding) of word pairs was directly compared with episodic retrieval of the same material. The blood flow data were averaged over all subjects and projected to three views – transverse, sagittal, and coronal – of a “see-through brain.” The maps in the upper bank show “encoding activations,” that is brain regions more active during encoding than during retrieval. The maps in the lower bank show “retrieval activations,” that is brain regions more active during retrieval than during encoding. (Figure reprinted from Nyberg, Cabeza, & Tulving, *Psychonomic Bulletin & Review*, 1996, 3, 135–148).

Figure 1 shows the results of the study. The blood flow data were averaged over all 12 subjects. The brain maps in the upper bank show “encoding activations,” that is brain regions more active during encoding than during retrieval. The brain maps in the lower bank show “retrieval activations,” that is brain regions more active during retrieval than during encoding.

Two observations are of interest regarding the data in Figure 1. First, there are considerable differences between the brain maps of encoding and those of retrieval. We can assume that there are common regions as well, activated during both encoding and retrieval, although they do not show in Figure 1, for reasons stated. Nevertheless, in light of the commonly held assumption that encoding and retrieval differ but little in psychological processes, and hence presumably in neuronal circuits, the extensive differences seen in Figure 1 are surprising. Second, the two sets of activation are heavily lateralized in the two hemispheres: encoding activations are all in the left hemisphere, and retrieval activations are all in the right hemisphere. Why such a striking hemispheric asymmetry? This second result becomes critical as we proceed.

The findings derived from any single study always have limited value, and the same is true of PET studies of memory. The problem is that the extent to which the observed results can be generalized to conditions other than those of the particular study is unknown. Conclusions regarding generalizability can only be drawn from larger collections of studies. We will consider such larger samples later in the paper.

HERA: Hemispheric Encoding/Retrieval Asymmetry

The hemispheric encoding/retrieval asymmetry shown in Figure 1 nicely complements similar data obtained in the frontal lobe regions in many other PET studies, including the very first ones designed to investigate encoding and retrieval processes in episodic memory. These studies were done at the Hammer-smith Hospital in London, England (Fletcher et al., 1995; Shallice et al., 1994), at Washington University in St Louis (Squire et al., 1992; Buckner et al., 1995), and at Toronto (Kapur et al., 1994a, 1994b; Moscovitch et al., 1995; Tulving et al., 1994a, 1994b). Taken together, the data from these studies suggested a surprising empirical regularity: Left prefrontal cortex seemed to be differentially more involved than right in encoding information into episodic memory, whereas right prefrontal cortex seemed to be differentially more involved than left in episodic memory retrieval.

This pattern is referred to as HERA: hemispheric encoding/retrieval asymmetry in the frontal lobes (Tulving et al., 1994a). Although initially unexpected, and therefore greeted sceptically (Roskies, 1994), the HERA pattern is now well established and indeed represents one of the most robust facts of the PET-memory literature. Figure 2 presents a schematic summary of the results from 25 different PET studies, available in May 1996, that had reported relevant data (Nyberg et al., 1996). The pattern of the data depicts the asymmetry: Episodic-memory encoding (intentional or incidental study) is associated with the activation of the left prefrontal cortex, and not with the right. Episodic-memory retrieval (recognition or recall) is associated predominantly with the activation of the right prefrontal cortex. Because in many cases episodic encoding involves semantically based judgments about the to-be-remembered information, the left-frontal activation associated with such encoding also reflects semantic memory retrieval. This is why the HERA model associates semantic-memory encoding also with the left frontal lobe.

The overall HERA pattern can be economically described in terms of the interaction among three pairs of concepts: (i) encoding versus retrieval, (ii) episodic versus semantic memory, and (iii) left and right frontal lobes. This overall regularity is largely unaffected by specific conditions of the relevant experiments. Available evidence suggests that it holds both for verbal and

The HERA Model

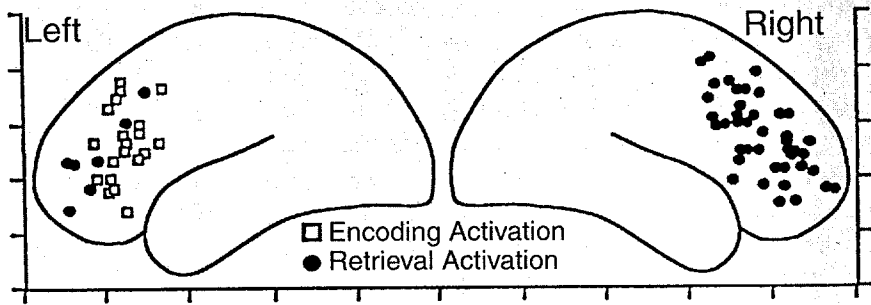


Figure 2. A schematic representation of the HERA model based on a meta-analysis of published data. Each data point, projected to the lateral surface of the cerebrum, represents the peak of an activation, obtained in one of the 25 studies in the data base, of encoding (on the left) or retrieval (on the right) against an appropriate reference condition. (Figure reprinted from Nyberg, Cabeza, & Tulving, *Psychonomic Bulletin & Review*, 1996, 3, 135–148).

nonverbal materials. For instance, encoding of human faces has been shown to activate the left prefrontal cortex, in the absence of comparable activation on the right, while recognition of previously studied faces has been shown to activate the right prefrontal cortex, in the absence of comparable activation on the left (Grady et al., 1995; Haxby et al., 1996; see also Andreasen et al., 1995). Relevant observations have also been reported for other nonverbal materials and line drawings of objects (Buckner et al., 1996; Köhler et al., 1998; Moscovitch et al., 1995; Owen et al., 1996). The encoding activations on the left have been observed under conditions of both intentional and incidental learning; the retrieval activations on the right have been observed in both recall and recognition tasks.

Before we ask the obvious question now, what does HERA mean theoretically, we raise two other issues that have been directly suggested by HERA. Once concerns refinement and elaboration of HERA: Is there regional specificity in prefrontal cortex that goes beyond the broad hemispheric asymmetry? The second has to do with extension of HERA: Are there other regions in the brain that are differentially involved in semantic-memory retrieval (episodic encoding) and episodic-memory retrieval?

Refinement of HERA

Although, as shown in Figure 2, the general left/right encoding/retrieval pattern is remarkably consistent, it is important to note that within this general regularity there exists considerable variability. Thus, the sites of retrieval-related activations seem to be distributed rather widely over the whole right prefrontal cortex, rather than concentrated in specific subregions. Why?

Because the experiments that yielded the data for HERA varied from one another in many respects – subjects, materials, retrieval tests, comparison (“baseline”) tasks, other specific details of the procedure, it is easy to speculate that the apparent variability of right frontal activations simply reflects the variability of the individual experiments. All this in addition to the difficulties attributable to the limitations in the spatial resolution of the PET method, and the limitations inherent in the typically used subtraction method (Friston et al., 1996; Jennings et al., 1997). As a result, there is nothing very much that can be done at this time by way of a more enlightened analysis and conclusions as to exactly why a given activation site is where it is rather than somewhere else. Future studies no doubt will clarify the issues.

Buckner (1996; see also Buckner & Petersen, 1996) did undertake a more detailed analysis of the HERA data, and suggested that there was indeed evidence for the involvement of different frontal regions in different kinds of encoding and retrieval tasks. He did his analysis at a time when the relevant data were still sparse. We now have a more extensive data base to work with, and can therefore address the issue with more adequate tools.

Recently, with the help of Martin Lepage at Rotman Research Institute, I conducted an “exercise” aimed at refinement of the neuroanatomical picture of HERA. Its purpose was to examine the extent to which the HERA-type pattern of activation is found in different subregions of prefrontal cortex, specified in terms of the classical Brodmann system in which brain areas are distinguished by their cytoarchitectonic differences and labelled numerically (Markowitsch, 1993).

We began with a data base consisting of a listing of 1131 cerebral activation sites that have been identified by PET as involved in memory-related processes in 56 published reports. It is a very slightly modified version of one that was described and used in a recent report of an empirical regularity, the so-called HIPER model, of PET activations in the hippocampal region (Lepage, Habib, & Tulving, 1998). For convenience, and in anticipation of its extension in the future, I refer to this modified version as the “June 98” memory data base. Each activation in the data base is specified in terms of the study it came from, the subtracted conditions, and Talairach and Tournoux (1988) stereotaxic coordinates, the “address” of a given site in the three-dimensional brain. A fuller

description of how PET studies of memory and other kinds of cognitive studies are conducted and their results described are available elsewhere (Buckner & Tulving, 1995; Posner & Raichle, 1994).

From the "June 98" data base we extracted an "encoding/retrieval" subset, consisting of all the activations that had been produced by "encoding conditions" and "retrieval conditions" in the original PET studies. Encoding conditions were defined as "subtractive" task comparisons in which the target task requires more elaborative processing of the materials than the (subtracted) reference task. Retrieval conditions were defined as subtractive task comparisons in which the target task produces a greater degree of recovery of previously experimentally encoded material than would the corresponding reference task. To qualify for the inclusion in the encoding/retrieval subset, the same stimulus materials had to be used in within any given comparison.

The "encoding/retrieval" subset of the data base thus constructed consisted of 280 activated sites produced by encoding conditions, and 516 activated sites produced by retrieval conditions. Of the 280 encoding activations, 195 were in the left hemisphere, and 85 in the right. Of the 516 retrieval activations, 230 were in the left hemisphere, and 286 in the right. (There is always some uncertainty in dealing with activations at or near the midline of the cerebrum, and therefore some corresponding error.)

The next step was the essential one. From the encoding/retrieval set of 796 activations we extracted all those that were located in or near prefrontal cortex, bilaterally. We included Brodmann area 6 in the analysis, although it is usually classified as "pre-motor" area. We did so because it has been frequently "sighted" in functional imaging studies of cognition.

This whole exercise is fraught with a number of difficulties and uncertainties, attributed to the random errors in the initial identification of an activated site in the original study, the identification of the Talairach and Tournoux coordinates of the activated site, the uncertainty, and inconsistency, of designations of Brodmann areas in the Talairach and Tournoux (1988) atlas, and the subjectivity of decisions involved in the assignment of an activation to a single Brodmann area (BA). The last source of uncertainty is especially vexing, because in many cases an activated cluster of voxels lies in a border region between two Brodmann areas, and sometimes even three areas. In carrying out the exercise, I assigned activations near two or more Brodmann areas to both, or to all. This means that there is some duplication of activations in the results.

The outcome of the exercise is summarized in Table 1. It shows the numbers of encoding and retrieval activations that were in or near various Brodmann areas. The bottom "total" line of the table shows the extent to which the overall HERA pattern held for this sample of data. The 117 encoding activations were distributed asymmetrically in the two hemispheres: 90 left, 27 right. The 198

Table 1. Distribution of frontal encoding and retrieval activations among Brodmann areas in the left and right hemispheres. Data pooled from 56 PET studies. Table entries are absolute frequencies of activations. See text for details. BA = Brodmann Area.

BA	Encoding		Retrieval	
	Left	Right	Left	Right
6	15	6	19	22
8	9	4	6	10
9	18	5	10	30
46	10	0	3	6
10	6	4	11	39
45	9	1	1	6
44	3	1	4	3
47	18	2	2	13
11	2	4	4	9
Total	90	27	60	138

retrieval activations were also distributed asymmetrically, although in the opposite pattern: 59 left, 139 right. These frequencies are in keeping with the HERA pattern. Because there was only partial overlap between the studies used by Nyberg et al. (1996) on which the data depicted in Figure 2 were based, and the studies that contributed data to the sample used here, the replication of the pattern speaks to its reliability.

Table 1 shows that different Brodmann areas contributed differently to the overall HERA pattern. When examining these data, and especially when comparing encoding and retrieval entries directly, one should keep in mind the fact that there are recorded in the table almost twice as many retrieval activations as encoding activations. Contrasts between the two hemispheres, left and right, within each of these two categories, encoding and retrieval, however, are not affected by differences in the base rates.

Distinctive HERA-type "symmetrical asymmetry" is seen in these data in the dorsolateral Brodmann area 9, and especially starkly in Brodmann area 47 on the prefrontal inferior convexity. Symmetrical asymmetry refers to the fact that in both these areas encoding is strongly left-lateralized whereas retrieval is strongly right-lateralized. In other regions data conform to HERA less symmetrically. Thus, Brodmann area 10 (anterior prefrontal cortex) shows clear HERA-type asymmetry for retrieval (11 left, 39 right), but not for encoding. And Brodmann areas 46 and 45 (lateral prefrontal cortex) show similarly clear HERA-type asymmetry for encoding (19 left, 1 right), but less convincingly so for retrieval. A surprising feature of the data in Table 1 is the relatively high overall involvement of Brodmann area 6 in encoding and especially retrieval, although in the latter case there is little evidence of HERA-type asymmetry.

These data thus do refine and clarify the HERA pattern of encoding and

retrieval activations in prefrontal cortex. Some of the subregions in the frontal lobes reflect the overall pattern, whereas others differ from it in specific ways. Thus, some regions (BA 47 and 9) are clearly "symmetrically asymmetric," while others show clearer asymmetry for only one of the two sets of processes (BA 46 and 45 for encoding, and BA 10 for retrieval).

Some of these findings confirm expectations based on the existing literature. Thus, the involvement of anterior prefrontal cortex (BA 10) and dorsolateral (BA 46 and 9) regions in encoding and retrieval has been frequently noted (Cabeza & Nyberg, 1996; Grady, 1998; MacLeod et al., 1998; Rugg et al., 1996; Nyberg et al., 1996). The data in Table 1 nicely corroborate these earlier impressions.

Another HERA-type regularity suggested by Table 1 is a bit more surprising, namely the strong "symmetric" encoding/retrieval laterality seen in area 47. The involvement of the *left* inferior prefrontal cortex in encoding-related processes is well known (Buckner, 1996), although activations are typically found at sites superior to area 47. Furthermore, the involvement of the homologous *right* region in episodic-memory retrieval has so far largely escaped systematic attention. Brodmann area 47 was discussed by Grady (1998) in a review of frontal activations observed in PET studies of cognition. She noted that the left area 47 "has more activations from semantic processing and language tasks than any other region" (Grady, 1998). It is of some interest that Talairach and Tournoux characterized it as one concerned with "vegetative functions" (Talairach & Tournoux, 1988, p 11).

In summary, then, there is some evidence that the well known functional heterogeneity of prefrontal cortex also shows up in the analysis of encoding and retrieval. Some regions, such as Brodmann areas 10, 9, 46, and 47 especially seem to contribute to the overall HERA pattern.

Extension of HERA

We now ask whether a HERA-type activation pattern extends to other, posterior parts of the brain? That is, is there any evidence of hemispheric encoding/retrieval asymmetry in regions other than prefrontal cortex?

Earlier in the paper we already saw a sample presented by the Cabeza-Kapur study. More important, reviews of the relevant studies show that in many cases intentional as well as incidental encoding in episodic memory activated left but not right temporal regions (Cabeza & Nyberg, 1996; Fletcher et al., 1995). As to retrieval, several studies have found increased activation in the parietal lobes. In some cases, the activation has been bilateral (e. g., Schacter et al., 1995; Tulving et al., 1994). In other cases, unilateral activation has been observed, and in these cases it has predominantly been located on the

right side (Grady et al., 1995; N. Kapur et al., 1995; Kapur et al., 1995; Moscovitch et al., 1995).

Again, however, individual studies are not sufficiently informative. One cannot draw strong conclusions from the results of isolated experiments or meta-analyses based on relatively small samples of data. The HERA pattern, after all, is nothing more than a statistical tendency. It survives by virtue of the fact that, and as long as, findings that conform to the pattern are observed more frequently than findings that seem to be exceptions to it. This means that if we wish to contemplate the extension of HERA seriously, we must examine a larger sample of data.

Using the "June 98" data base described above, I performed another exercise, this time aimed at the issue of hemispheric encoding/retrieval asymmetry in posterior regions. I chose, somewhat arbitrarily, two voxels in the temporal lobe bilaterally (Talairach xyz = 30 0 -10, and xyz = 32 -32 6), and drew a rectangular "volume of interest" (VOI) around each voxel. The VOIs had an overall extension of 64 mm in the left-right (x), 32 mm in the anterior-posterior (y), and 48 mm in the inferior-superior (z) dimension. These VOIs encompass not only cortical regions, but also subcortical ones. (Their separation would constitute one improvement of the method.) I then identified all the encoding and retrieval activations in the data base that were localized within the two VOIs thus specified. I repeated the same procedure for a voxel (bilaterally) in the parietal lobes. The stereotaxic coordinates of the two voxels, one left, one right, were -30 -66 36 and 30 -66 36, and the rectangular VOIs had extensions of 60, 36, and 48 mm in the x, y, and z dimensions, respectively. Finally, for purposes of comparison with HERA, I repeated the procedure for two frontal voxels (-18 30 16 and 18 30 16), with VOI extensions of 36 mm, 48 mm, and 72 mm in the x, y, and z dimensions, respectively. Given the extensions of the frontal, "temporal," and "parietal" VOIs, there was some overlap between them, with the consequence that some activations in the data base were assigned to more than one of these regions.

The procedure I used is admittedly quite gross; it is easy to think of ways in which it could be improved, and improved considerably. But refining the procedure would involve additional effort and time, and this is why it has to await for the future. What is lacking in refinement of the method, however, can be expected to be compensated for by the relatively large sample size, as there were a total of 280 encoding and 516 retrieval activations in the June 98 data base. The whole point of the exercise has to do with the question about hemispheric asymmetry, if any, in grossly defined brain areas other than the frontal lobes.

The results of this "HERA extension" exercise are summarized in Table 2 that shows the relative frequency of occurrence of encoding and retrieval activations in the three large areas mentioned – frontal, temporal, and parietal

Table 2. Relative density of encoding and retrieval activations in large and approximately designated cerebral regions in the left and right hemisphere. Pooled data from 56 different PET studies. Table entries are percentages of all encoding activations, and all retrieval activations, localized within the regions. See text for details.

	Frontal	Temporal		Parietal/ Occipital	Total
		Anterior	Posterior		
Encoding					
Left	14.3	9.6	11.1	7.1	42.1
Right	5.0	3.6	3.2	3.6	15.4
Retrieval					
Left	10.3	2.3	8.5	7.6	28.7
Right	19.9	1.7	7.8	9.3	38.7

— and in the two hemispheres. The percentages given in the table are expressed relative to the overall frequency of encoding and retrieval activations, separately for each. For example, the entry of 15.0 for left frontal encoding means that 42 (15.1 per cent) of the total of 280 encoding activations in the data base were found in the VOI for that region, as specified above. The entry of 19.8 for right frontal retrieval means that 102 activations (19.8 per cent) of the total of 516 retrieval activations in the data base were found in the VOI.

The major lesson to be learned from the data in Table 2 is that the HERA-like pattern of hemispheric encoding/retrieval asymmetry does extend towards posterior regions, although not as clearly as it holds in frontal regions. In the right temporal areas, encoding and retrieval activations occur more or less evenly. In the left temporal region, however, encoding activations predominate. A temporal encoding activation is about two and a half times more likely to occur in the left than the right hemisphere, whereas a temporal retrieval activation seems equally likely in the temporal regions in both hemispheres. The picture in the parietal area shows that the hemispheric asymmetry holds for the right hemisphere where retrieval activations are more likely to occur than encoding activations, but not for the left hemisphere where both are equally likely.

In summary, the overall picture that emerges from this exercise is that the two hemispheres show an overall disposition for specialization in episodic memory processes: the left more actively involved in encoding than the right, and the right more actively involved in retrieval than the left. The HERA-like pattern is not as striking in posterior regions as it is in prefrontal cortex, but it is discernible in the meta-analysis, and does describe a definite tendency. The future will tell how this tendency is related, if at all, to the specific conditions under which the data were generated, a problem that is too early to tackle now.

The Meaning of HERA

We now return to the original HERA model, in the frontal lobes, and pose the question: What does the right frontal retrieval activation mean? We are especially interested, of course, in the possible relevance of this activation for the theoretical concept of "mental time travel," the ability of individuals to hold in mind a temporally defined segment of their past life and to become auto-noetically aware of the happenings in it.

We know that retrieval is not a single process, as its label implies, but rather consists of a complex concatenation and combination of a number of component subprocesses. One way of tackling the question about the theoretical meaning of right-frontal activation therefore lies in the analysis of the overall retrieval process into subprocesses, and trying to find out to what extent these subprocesses are associated with right prefrontal cortex.

A major distinction within retrieval process can be made between retrieval "mode" and recovery of stored information. Retrieval mode is a necessary condition for any episodic retrieval to occur, it is a "set for treating stimulus events as cues to stored episodes" (Tulving, 1983, p. 170). It can be assumed to consist of several component processes.

One component process of *retrieval mode* allows the individual to actively hold, in the background of focal attention, a particular past segment of one's life that defines the temporal boundaries of the past events of interest. I refer to this component of retrieval mode as the "epoch set." When the individual answers a question about what she did "last night," or what she remembers from her first day in school, she is very clear in her mind about the period in question. Similarly, when a subject in an experiment tries to remember whether a certain word occurred in the first or the second half of the presented list, she is not confused about the temporal demands of the task – even if carrying out the task may be difficult and performance accuracy poor. In one of the "simplest" explicit memory tasks, yes/no recognition, the subject also must be able to somehow hold in mind the previously studied list if she is to perform the task. To a normal healthy person, to assume a particular epoch set comes easily and naturally. How this marvellous mental feat is accomplished at the neural level, however, is a deep mystery.

A second component process of retrieval mode involves assuming an orientation towards retrieval cues as pointers to past happenings rather than just current, here-and-now, occurrences. A cue represents a specific query about the "contents" of the epoch in question. Did an item like this one appear in the list? What item appeared in the list together with this item? This component of retrieval mode operates within the epoch set and reaches beyond it, in that it involves specific stimuli whereas epoch orienting can occur indepen-

dently of the contents of the sub-attended epochs. The two component processes further differ in that epoch set is a task-dependent variable, manipulated by instructions, whereas treating stimulus objects as retrieval cues an item-dependent variable (Düzel et al., 1999).

The second major constituent of the *retrieval process* is "ecphory," or actual recovery of stored information. According to theory, ecphory occurs when the retrieval cue "contacts" relevant stored information (Tulving, 1983, Ch. 9). Also according to theory, no recovery of episodic information can occur unless the system is in the appropriate state or mode. Whether or not such recovery occurs, as well as the specification of exactly what is recovered, depend critically on the nature of the relation between the information as encoded in the past and the retrieval cues as interpreted by the system in the present, the so-called encoding specificity principle (Tulving, 1983, Ch. 11). Ecphory too presumably embraces a number of as yet unanalyzed and unspecified component processes.

Given the known involvement of the frontal lobes, especially the right one, in episodic retrieval, and given the several hypothesized component processes of such retrieval, the obvious question to ask concerns the relations involved. Does the right-frontal activations signify retrieval mode, ecphory, both of these, or something else? A beginning has been made in answering this question using the PET and fMRI methods. The basic logic here can be put in the form of a question: Are there brain regions, especially in the frontal areas, that show activation during intentional retrieval independently of the degree of the extent to which studied items are recognized? If yes, the brain regions thus identified become candidate components of the neural circuits that are involved in the maintenance of the episodic retrieval mode.

Based on this logic and variations on the theme, a number of studies have been conducted that have addressed the issue (Buckner et al., 1998; Kapur et al., 1995, Nyberg et al., 1995, Schacter et al., 1996; Rugg et al., 1996, 1997; Wagner et al., 1998). The results of the initial experiments (Kapur et al., 1995, Nyberg et al., 1995) showed that when subjects have been set into the episodic retrieval mode through appropriate task instructions, a number of cerebral regions, especially prominently in the right prefrontal cortex, become activated regardless of the extent of ecphory, that is, actual recovery of the specific stored information. Other studies have largely confirmed these findings (Buckner et al., 1998; Rugg et al., 1997; Schacter et al., 1996; Wagner et al., 1998).

A particularly thorough examination of the whole issue of retrieval mode and right prefrontal cortex was recently conducted by Wagner and colleagues (Wagner et al., 1998). They identified five sites in the frontal lobes that showed activation associated with episodic retrieval mode. (They referred to the conditions as "retrieval attempt," a phrase descriptive of the subject's *task*). Three

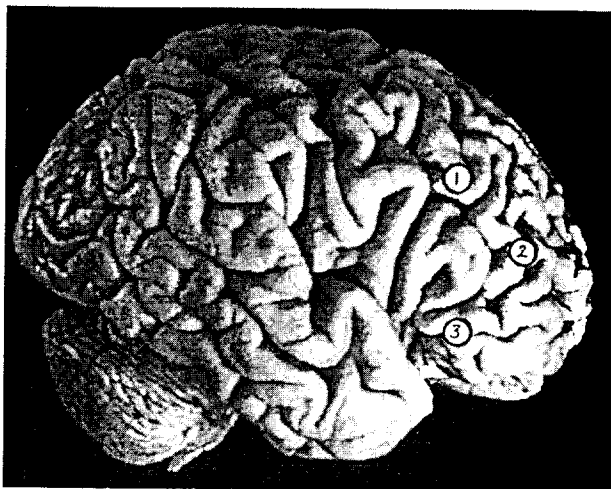


Figure 3. Approximate locations of three hypothetical right-frontal "epicenters" of episodic retrieval that are associated with "retrieval mode" projected onto the lateral surface of the brain.

of these were in the right prefrontal cortex. Their approximate location is schematically presented in Figure 3, projected onto the lateral surface of the right hemisphere. We can specify their locations in terms of Brodmann areas (BAs), and the Talairach and Tournoux stereotaxic coordinates) as follows. Site 1 is near the middle frontal gyrus (BA 46, xyz = 44 35 18), Site 2 is near the border of the middle frontal gyrus and precentral gyrus (BA 9, xyz = 40 14 34), and Site 3 is near the inferior frontal gyrus and the frontal operculum (BA 47, xyz = 35 21 -2).

These three right lateral sites turn out to be veritable "epicenters of retrieval" when they are compared with the data in our "June 98" data base. In that data base, there are 34 retrieval activations and only 2 encoding activations that are near (within 16 mm) of Site 1 as specified above, 31 retrieval and 2 encoding activations near (within 16 mm) Site 2, and 22 retrieval activations and a single encoding activation near Site 3.

Future research, no doubt, will illuminate the situation more fully. In the mean time, other evidence is converging on the relation between right prefrontal cortex and episodic retrieval. In a PET study specifically designed to distinguish between recovery of information about remembered items as such versus information about the time of their appearance in the learning list, retrieval of item information activated anterior medial temporal lobe regions bilaterally, whereas retrieval of item information activated frontal regions (Cabeza et al., 1997). The center of one of these "past time" regions was within a few millimeters of Site 2 in Figure 3 (BA 9, Wagner: xyz = 40 14 34; Cabeza: xyz = 48 18 32). The finding suggests that this area may be associated with "epoch set."

Also relevant is a finding reported by McIntosh et al (1997), using data from a previous study (Nyberg et al, 1995), that was produced by an analysis of functional connectivity of brain regions that are activated in retrieval. The analysis showed that Site 3 of Figure 3 (McIntosh's xyz = 32 22 0) participated in the prefrontal medial-temporal "retrieval circuit" only when the to-be-remembered words had originally been encoded at a "deep" semantic level, whereas more anterior regions (BA 10, xyz = 28 44 4) were a part of the circuit regardless of the type of prior encoding. This finding suggests that this area may be associated with retrieval mode for verbal semantic information.

Wagner and his colleagues (1998) concluded that the consistent prefrontal activation seen in tasks involving episodic retrieval signifies a general orientation of the subject towards the past. They further suggested, on the basis of their findings, that the specific brain regions associated with such an orientation depend on the "context," that is specific features of the retrieval task and subjects' "strategies" in carrying out the task. The other data we have briefly reviewed here support this idea of specificity of retrieval sets.

There are other findings that fit into the emerging picture. In a recent PET study it was found that subjects' thinking thoughts about themselves as compared to thinking similar thoughts about others is associated with right frontal activation (Craik et al., 1998). Also, clinical evidence suggests that patients who have suffered right anterior brain damage have difficulty in autonotically reminiscing about their premorbid personal experiences (Calabrese et al., 1996; Markowitsch et al., 1993; Markowitsch, 1995). In a particularly revealing PET activation study, in which recognition of recently heard sentences about others was compared with recognition of similar sentences taken out of the subjects' own autobiographical notes, Fink et al. (1996) found a largely right hemispheric activation that included temporal lobes, posterior cingulate insula, and prefrontal regions. They interpreted their results as suggesting that a right hemispheric network of brain areas, including prefrontal cortex, is engaged in the remembering of autobiographical information. And, in a remarkable convergence, Levine et al. (1997, in press) have provided a thorough analysis of the case of a young man who, subsequent to traumatic brain injury that resulted in a white-matter lesion in the same right frontotemporal region identified by Fink et al. (1996), lost his ability to autonotically recollect past events, although his learning and memory abilities otherwise were not adversely affected.

Frontal lobes are known or assumed to have many functions, summarized under concepts such as supervision, organization, integration, executive functions, working-with-memory, self-awareness, and the like (Moscovitch, 1994; Shallice, 1988; Stuss & Benson, 1986; Stuss, Eskes, & Foster, 1994). The data we have considered here, in search of the "meaning" of HERA, suggest several additions to the list: episodic retrieval mode, epoch set, and autonotetic aware-

ness of the past. The functions named are still fuzzy, and the relations among them not entirely clear. Nevertheless, we can think of retrieval mode as a specific form of the general “supervisory” function of the frontal lobes, and autonoetic awareness as a specific form (extension of) self awareness. A more complete account of these relations can be found elsewhere (Wheeler et al. 1997). For the present purposes, we can conclude that the right-frontal activations in PET studies of memory can be interpreted as reflecting some of the major components of mental time travel that make episodic memory unique.

Conclusions

Contrary to traditional thinking, most forms of learning and memory have little to do with has been in the past. Instead they are oriented towards what is to come: Present experiences allow more effective ways of behaving in the future. In these forms of memory and learning, the kind of conscious awareness of specific past happenings that we usually associate with the term “remembering” is irrelevant. The singular, and in many ways a most remarkable, exception to the future-oriented learning mechanisms and systems is episodic memory. Episodic memory makes possible a form of purely mental activity that is known as remembering of past experiences. This mental activity, highly familiar to all normal healthy humans, differs from other forms of mental activity, and is referred to a “autonoetic awareness.” Time-orientation towards the past and autonoetic awareness of what happened in the past differentiate episodic memory from all other forms of memory, and thereby make it unique.

In this chapter I have explored the issue of uniqueness of episodic memory at the level of brain activity. PET and other functional neuroimaging studies have begun to yield data that speak to the issue, by pointing to specific neuro-anatomical regions involved in episodic memory retrieval. An especially interesting finding, because completely unheralded by previous research, is the so called HERA (hemispheric encoding/retrieval asymmetry) pattern of neural activation in the frontal lobes: The *left* frontal lobe is more active in *semantic-memory retrieval* (and episodic-memory encoding), whereas the *right* frontal lobe is more active in *episodic-memory retrieval*. Results of meta-analyses of available data suggest that the frontal hemispheric asymmetry tends to be specific to particular subregions of prefrontal cortex – Brodmann areas 9, 46, 10, and 47 – and also that the HERA-type pattern extends posteriorly to temporal and parietal cortical areas.

Available evidence also suggests that the right-frontal activation, commonly seen in PET and fMRI studies, signifies the involvement of these regions in episodic “retrieval mode,” and that specific regions in prefrontal cortex may contribute to separate components of retrieval mode. These components

include the "epoch set," the neurocognitive operation that allows an individual to "tune into" a specific temporally extended period of past life. It is also reasonable to assume that right frontal regions play a critical role in enabling autooetic awareness, although the evidence on this issue is still fragmentary. In comparison with where we were only a few years ago in our understanding of episodic memory and its neural basis, however, we have come a long way.

Acknowledgments

My research is supported by the Natural Sciences and Engineering research Council of Canada (Grant A8632), and by an endowment in support of research in cognitive neuroscience by Anne and Max Tanenbaum. I thank Martin Lepage for help with data manipulation.

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Lars-Göran Nilsson
Hans J. Markowitsch
(Editors)

Cognitive Neuroscience of Memory



Hogrefe & Huber Publishers
Seattle · Toronto · Bern · Göttingen

Library of Congress Cataloging-in-Publication Data

is available via the Library of Congress Marc Database under the
LC Catalog Card Number 99-71722

Canadian Cataloguing in Publication Data

Main entry under title:

Cognitive neuroscience of memory

Based on a conference entitled Cognitive neuroscience and memory, held in
Lidingo, Stockholm, Sweden, June 13–15, 1997.

Includes index.

ISBN 0-88937-213-6

I. Memory – Congresses. 2. Cognitive neuroscience – Congresses.

I. Nilsson, Lars-Göran, 1944– . II. Markowitsch, Hans J., 1949– .

QP406.C63

1999

612.8'2

C99-930606-5

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Phone (416) 482-6339

SWITZERLAND:

Länggass-Strasse 76, CH-3000 Bern 9

Phone (031) 300-4500, Fax (031) 300-4590

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Printed and bound in Germany

ISBN 0-88937-213-6