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# Episodic memory and common sense: how far apart?

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Research has revealed facts about human memory in general and episodic memory in particular that deviate from both common sense and previously accepted ideas. This paper discusses some of these deviations in light of the proceedings of The Royal Society's Discussion Meeting on episodic memory. Retrieval processes play a more critical role in memory than commonly assumed; people can remember events that never happened; and conscious thoughts about one's personal past can take two distinct forms—'auto-noetic' remembering and 'noetic' knowing. The serial—dependent—-independent (SPI) model of the relations among episodic, semantic and perceptual memory systems accounts for a number of puzzling phenomena, such as some amnesic patients' preserved recognition memory and their ability to learn new semantic facts, and holds that episodic remembering of perceptual information can occur only by virtue of its mediation through semantic memory. Although common sense endows many animals with the ability to remember their past experiences, as yet there is no evidence that humanlike episodic memory—defined in terms of subjective time, self, and auto-noetic awareness—is present in any other species.

**Keywords:** auto-noetic awareness; false memory; recognition memory; remembering and knowing; retrieval; SPI model

## 1. INTRODUCTION

Much of science begins as exploration of common sense, and much of science, if successful, ends if not in rejecting it then at least going far beyond it. The science of memory, although still in its early formative years, is no exception to the general rule. Many findings yielded by research, and theoretical interpretations of them that were brought up at the Royal Society discussion meeting on episodic memory and appearing in print here, neatly illustrate this point. They transcend traditional thought.

Here I organize my comments on the discussion meeting around the theme of how the science of memory has departed, or is in the process of distancing itself, not only from common sense but also from what have been standard views of memory—what Alan Baddeley in his introductory paper refers to as 'status quo' or 'received wisdom'. In doing so I rely heavily on a simple model—the serial-parallel-independent (SPI) model—of the relations among three memory 'systems' because it embodies a number of active issues around which the battle of old versus newer ideas about memory currently revolves.

## 2. WHAT IS EPISODIC MEMORY?

Let us begin with the very theme of the meeting, 'episodic memory'. Episodic memory, very roughly speaking, is the kind of memory that allows one to remember past happenings from one's life. The definition implies that there are other 'kinds' of memory that do not have the

same properties that episodic memory does, and that do not serve the same function.

The (postulated) existence of different 'kinds' of memory (or 'memory systems') represents the first departure from traditional thought because in traditional thought, as in common sense, memory is 'unitary' in the sense that there is only one 'kind' of memory, as there is only one kind of water, or blood or forget-me-nots. In the world of memory, for a long time, just about everyone accepted the idea of a fundamental unity of learning and memory as a basic given. It was seldom questioned and, when it was, it was affirmed without hesitation. At an unusual, small conference in 1962 that had been explicitly organized to consider the 'taxonomy' of learning, most participants blithely ignored the central issue of the meeting: the possibility of different kinds of learning. Only Benton Underwood, one of the pre-eminent verbal learning researchers of the era, confronted it and succinctly put the credo of the field as follows:

'Are we to accept a conclusion that we will have different principles of learning for different species? Most of us would not accept this any more than we would accept the idea that we will have fundamentally different principles for different forms of human learning.' (Underwood 1964, p. 74).

Alan Baddeley, in his introductory paper in this issue, provides a pithy summary of how the idea of 'unitary' memory was shattered. The first breach came with the revelation that the laws and principles governing primary ('short-term') memory are not quite the same as those

that apply to secondary ('long-term') memory (Waugh & Norman 1965; Atkinson & Shiffrin 1968). Although the split between primary and secondary memory was initially vigorously resisted by Underwood and others, it was not long before it was considered standard fare in all textbooks. Today, the break between primary memory, or its more theoretically meaningful successor, 'working memory' (Baddeley & Hitch 1974), on the one hand, and secondary memory ('long-term memory') on the other, is as sharp as one can find anywhere in nature.

The second breach took the form of the division of secondary memory into 'episodic' and 'semantic' (Tulving 1972). The division did not emerge out of the blue; similar ideas had been proposed before. These earlier ideas about different kinds of memory, however, were largely ignored. As pointed out by Baddeley, the idea of episodic memory stayed alive, grew, changed, matured and is now under intense scrutiny. It is one member of the family of 'multiple memory systems' (Foster & Jelicic 1998; Schacter & Tulving 1994). It has traditionally been categorized as one of the two subsystems of 'declarative' (or 'cognitive' or 'explicit') memory, semantic memory being the other one (Squire 1992; Tulving & Markowitsch 1998; Griffiths *et al.* 1999).

Episodic memory is 'memory for *personally experienced events*' or '*remembering* what happened where and when', whereas semantic memory is 'memory for *general facts* of the world.' A somewhat more elaborate definition holds that episodic memory has to do with one's 'autonoetic' awareness of one's experiences in the continuity of subjectively apprehended time that extends both backward into the past in the form of 'remembering' and forward into the future, in the form of 'thinking about' or imagining or 'planning for' the future. This definition emphasizes the conjunction of three ideas: self, autonoetic awareness, and subjectively sensed time. The definition of semantic memory at the corresponding level would refer to 'one's "noetic" awareness of the existence of the world and objects, events, and other regularities in it', independently of self, autonoetic awareness and (subjective) time. In this case, the less familiar terms used—such as autonoetic awareness and subjective time—then need to be explicated, as has been done elsewhere (Tulving 1993; Wheeler *et al.* 1997).

Critics have persistently questioned the concept of episodic memory, for a variety of reasons (for a summary, see Tulving 2002a). In this issue, Conway has taken the more constructive step of refining the concept by drawing a substantial distinction between episodic and autobiographical memory. Until now most students of memory have thought of autobiographical memory in the way that Kopelman and Kapur do:

Autobiographical memory refers, characteristically, to a person's recollection of past incidents and events, which occurred at a specific time and place. Episodic memory is a somewhat broader term, encompassing autobiographical memories as well as performance on certain learning tasks such as recall of a word-list. However, the terms "autobiographical" and "episodic" are often used interchangeably. (Kopelman & Kapur 2001.)

Conway's concept of autobiographical memory (see also Conway & Pleydell-Pearce 2000) retains some

features previously associated with episodic memory, but also includes some novel ideas—such as the temporal duration of episodic memory (short) and autobiographical memory (long), and different kinds of recollective experience: recollection and familiarity in episodic, and feelings of 'knowing' in autobiographical memory. Conway's proposal is wide in scope and rich in detail. It should generate a lively debate in the future.

### 3. STORAGE AND RETRIEVAL

Common sense and everyday thinking about memory, honouring a long tradition that goes back all the way to Plato's aviary metaphor of memory, conceptualize memory in terms of a single measurable capacity, frequently identified with memory 'storage'. Thus, when a lay person, or even an expert, speaks of encoding information 'into' memory, the 'memory' in the expression designates the metaphorical 'store' in which 'memories' are held. 'Good memory' is a store with a large capacity for holding information. Once the remembered stuff ('memories') has been effectively acquired, or stored, it can be used ('retrieved') at will.

In the science of memory too, there is, of course, a great deal of interest in encoding and storage, but these two concepts are only a part of the story. Another part, some go as far as to say a more important part (Roediger 2000), has to do with the problem of how the successfully encoded information can be used ('retrieved'). Retrieval consists in a complex and elaborate set of processes; it is not simply a matter of 'reading the contents of memory store'. Every educated person, to give a homely example, knows the names of two capital cities in Europe which have two initial letters and three final letters in common. Although the required memory information is clearly 'in' the memory store, few people can produce the names thus described. This kind of a retrieval failure points to the existence of the 'problem' of retrieval in both semantic and episodic memory, which is independent of the 'problem' of storage, and leads to experiments in which the two sets of processes can be examined and measured separately (Brown & Craik 2000; Koriat 2000). The earlier tradition, which still rules supreme in some quarters, consisted in measuring 'memory' in memory 'tasks' and psychometric 'tests' in which encoding, storage and retrieval were thoroughly conflated (Tulving 1983, pp. 219–220).

Because of the historical tendency to identify memory with information storage, the problem of retrieval escaped the attention of memory researchers for a long time. In some branches of the science of memory it still does. But the concept of retrieval, and its relation to storage (and encoding), played a central role in the proceedings of the discussion meeting, and were especially prominent in the papers in this issue by Conway 2001; Gardiner 2001; Kopelman & Kapur 2001; Maguire 2001; Mayes 2001; and Yonelinas 2001. Without the distinction between storage and retrieval, many ideas that one can have about episodic memory would not arise. This simple even if surprising fact shows again how the science of memory goes beyond common sense.

Consider two relevant examples. The first one is provided by neuropsychological research on retrograde

amnesia—severe impairment in the ability to remember or make use of knowledge acquired before the onset of the brain damage that causes such amnesia. The topic is thoroughly aired in the papers by Kopelman & Kapur (2001) and elsewhere (Wheeler & McMillan 2001). In the absence of the concept of retrieval one would necessarily have to conclude that retrograde amnesia stems from the loss of relevant information from the memory store. Now an interesting and serious possibility is that we are dealing with a special kind of failure of retrieval, and the existence of alternative explanations provides the kind of guidance for research that would not exist otherwise.

Second, in research designed to explore the similarities and differences in functional neuroanatomy of episodic and semantic memory—a topic of central concern in Maguire's paper (2001), and actively pursued in a number of laboratories in a number of countries—it turns out that it has been difficult to differentiate between encoding and storage processes in episodic and semantic memory but relatively easy to do so with respect to retrieval. This whole rich research area, which has contributed greatly to the neuroanatomical differentiation of episodic from semantic memory, either would not exist or would have been quite different in the world of 'memory tests', i.e. in the absence of the concept of retrieval.

#### 4. FALSE MEMORIES

Let us next consider another departure from conventional wisdom, put in the form of a question: 'If a person clearly and vividly remembers a particular event, does that mean that the event in fact happened?' In other words, can we make safe inferences about the past on the basis of what people remember about it? Common sense says 'yes', of course, and wonders how it could be otherwise. Is it not self-evident? Surely we make use of this simple truth—'I remember it, therefore it happened'—all the time. Much of our legal system operates on the premise that eyewitness's testimony, if given in good faith, provides true evidence of what happened. Physicians take a patient's history and believe that the patient correctly remembers when a symptom first appeared. People take great delight in telling stories of what they did, saw or heard, and others take equal delight in listening to them. Storytelling and listening are some of the oldest and most common forms of entertainment. The listeners naturally believe that the storyteller describes what actually happened. The element of entertainment would be marred if one had no idea whether the story was true or just so much imagination.

Scientific research has clearly established that it is not always possible to determine what happened in the past on the basis of a person's recollection, regardless of whom the person is, and regardless of how strongly—and genuinely—the person believes that he or she is telling the truth. This research shows that it is perfectly possible for even completely sane, intelligent and honest people to clearly remember and strongly believe something that never happened. Such 'false memories' or 'memory illusions' do not happen all the time, of course. Usually what we remember is true to a larger or smaller extent. Memory can also be absolutely veridical—think of all the memorized poems, speeches, dates, addresses, phone

numbers and passwords that we can recall (most of the time). Nevertheless, a good part of the activity of memory consists not in reproduction, or even in reconstruction, but in sheer construction. And constructed memories do not always correspond to reality. One need not suffer from any neurological or psychiatric dysfunction, nor need one be very young or very old, to have false memories and to remember events that never happened. Thus, thanks to research, we now know something that does not readily fit into common sense: sometimes people remember events, say the 'miniature' event of a word or picture having appeared in a visually presented to-be-remembered list, that in fact did not appear. This is a fact. The relevant research is discussed in this issue at some length by Schacter & Dodson (2001) and touched on by Gardiner (2001).

Now, however, what about the situation where there is available completely objective verification of the fact that an event did happen, and the person being tested (the 'subject' participant in the experiment) correctly indicates his or her knowledge of the fact. Can we infer that the subject now actually does remember seeing the word? Again, for an outsider, it must be very difficult not to say 'yes,' and imagine why anyone would want to even raise the question. Yet research shows that the question is appropriate and the answer to it more complex than what was suspected in traditional thinking. Much of the relevant data come from a widely used method of observing and measuring retrieval known as the yes–no recognition test.

#### 5. REMEMBERING AND KNOWING

Recognition tests are no doubt the most frequently used tests of memory today. The reason for their popularity lies in their apparent common-sense face value, assumed theoretical simplicity, ease of administration and employability across different kinds of stimulus materials as well as subject populations. What is a more direct way of testing someone's memory than presenting a stimulus item now for (intentional or casual) study or inspection and then later on asking the subject to indicate whether it is an item that was previously encountered? The 'remembered' item is responded to in one way, a 'non-remembered' item in another. All sorts of items can be used: words, pairs of words, line drawings, photographs of scenery or faces, actual three-dimensional objects. The test subjects can be people—infants, young, old, healthy, brain damaged or whatever—as well as non-human animals of a great variety—goldfish, rats, pigeons, monkeys and many others. Subjects in recognition tasks can be instructed about the rules of the game through verbal instructions, if they possess language, or through appropriate training procedures if they do not.

Common sense and traditional thought about yes–no recognition is that it measures memory, or, with the advent of the episodic–semantic distinction, that it measures episodic memory: 'Did you see this item in the list that you studied earlier?'. Again, it is a perfectly natural assumption to make. How well the experimental subject can distinguish between old and new test items clearly depends on, and hence reflects, how well the subject remembers what she or he previously studied. As with much if not all

wisdom inherent in common sense, there seems nothing debatable about these kinds of thoughts.

However, research suggests that the idea that 'episodic' recognition tests assess episodic memory is only partially correct. The relevant research has been carried out under the banner of the remember-know (RK) paradigm. It is of central concern in Gardiner's paper (2001; see also Gardiner & Richardson-Klavehn 2000; Knowlton & Squire 1995; Rajaram & Roediger 1997). The RK paradigm is also involved in the evaluation of Yonelinas's (2001) dual-signal detection model of recognition that he discusses in his paper in this issue.

In a typical application of the RK paradigm, experimental subjects participate in a standard yes-no recognition test, with an additional twist: whenever they judge a test item to be 'old' (they think it was a member of the studied collection) they make a further judgement about whether they 'remember' the event of the item's occurrence in studied collection or whether they have some other grounds (such as a feeling of 'familiarity') for 'knowing' that the item did occur in the collection.

There is surprisingly good agreement between the conclusions drawn by Gardiner and Yonelinas, despite several differences in their overall approach to the issue. Thus, Gardiner concentrates on the RK paradigm, Yonelinas includes Jacoby's process-dissociation procedure (Jacoby 1991) in his analyses. Gardiner is interested in the conscious aspects of recognition, whereas Yonelinas keeps his focus on measurement of behaviour. Gardiner is very much in tune with the idea of multiple memory systems; Yonelinas concentrates on processes and can do without multiple systems. Gardiner roams over a wide territory in his coverage of empirical evidence, Yonelinas sticks more closely to traditional cognitive psychology and neuropsychological procedures.

Given all these differences, it is most satisfying to see how well the conclusions drawn by the two converge on a common bottom line: there are indeed two, rather different components (modes of retrieval, processes, memory systems) that feed into performance on yes-no recognition tests. This means that the standard measures of recognition memory that have served the field so well for a very long time—hit rates, false alarm rates and their derivatives—can no more be regarded as sufficiently analytical. Anyone who wishes to study nature, rather than theories about nature, will have to start worrying about the meaning of old-fashioned recognition tests.

Additional convergent evidence for the existence of two component processes of recognition is provided by event related potential (ERP) studies (Düzel *et al.* 1997; Mangels *et al.* 2001) and functional magnetic resonance imaging (fMRI) studies (Henson *et al.* 1999; Eldridge *et al.* 2000) that have revealed neural correlates of the two processes. Especially interesting converging evidence is provided by the ERP findings on the young amnesic patient Jon, who has a severely impaired episodic memory but performs quite normally on standard yes-no recognition tests. These findings show that he has a normal N400 ERP effect, which is known to be associated with the familiarity component of recognition, whereas the late-positive effect, known to reflect episodic recollection, is completely absent in Jon's ERP waveform (Düzel *et al.* 1999). These findings suggest that, unlike healthy

people, Jon relies largely if not wholly on his intact, perhaps enhanced, ability to distinguish between novel and familiar test items in performing the recognition test.

A new idea about recognition memory is that, in addition to reflecting 'remembering' and 'knowing,' it can also reflect familiarity that is purely perceptual. Aggleton & Pearce (2001) as well as Morris (2001), in their respective papers in this issue, cogently argue in considerable detail that recognition tests may, but need not, depend on episodic memory. Many animals do perfectly well on a variety of recognition tests and one need not assume that they have episodic memory.

The idea that successful performance on recognition tests can occur at different levels of memory—episodic, semantic, and perceptual—may help to clarify outstanding issues and help understand a number of memory phenomena.

## 6. KNOWLEDGE THROUGH EXPERIENCE? THE SPI MODEL

In everyday thinking about memory it is often assumed that new facts about the world are learned through experience, i.e. through observing happenings in everyday life, through being exposed to statements about the facts (as in learning from teachers or books), or observing happenings in real life and drawing appropriate conclusions about the 'facts of the world' from them. This means that when we wonder which came first—episodic memory (experiences) or semantic memory (facts)—common sense tells us that the answer is episodic memory. Information gets into semantic memory 'through' episodic memory: first an individual has a particular experience in the course of which he, say, learns a new fact, and later on he can use the knowledge thus acquired independently of any remembering of the original learning episode as such.

This is what many experts in the area of memory have believed (and many still do) ever since the distinction between episodic and semantic memory was drawn. The careful reader of papers in this issue will be able to spot statements to this effect in various chapters. Nevertheless, although the jury is still out on this question, and although the final answer may turn out to be of a kind that almost always is reached at the end of debates ('well, it all depends'), I believe that the correct view is the reverse of common sense: information gets into episodic memory through semantic memory.

This belief has been formalized in a very simple model of the relations among memory systems. The central idea is that the relations among systems are process-specific: encoding is serial (S), storage is parallel (P) and retrieval is independent (I); hence the model is referred to as SPI (Tulving 1995; Tulving & Markowitsch 1998). Figure 1 presents a sketch of the SPI model, applied to three kinds of memory or memory systems: perceptual, semantic and episodic. The three memory systems are arranged hierarchically (or 'monohierarchically'). The perceptual system is at the lowest level and episodic at the highest. The perceptual system (also called 'perceptual representation system' or PRS; Tulving & Schacter 1990) receives, stores and makes available to other systems information

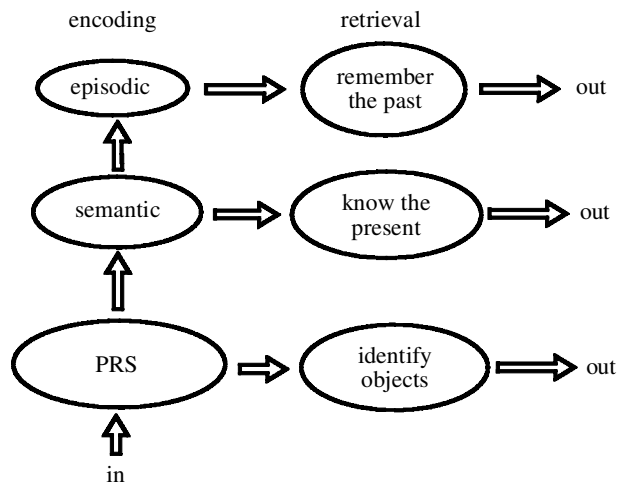


Figure 1. A schematic rendering of a model of process-specific relations (serial-parallel-independent; SPI) among three large memory systems—perceptual (PRS), semantic and episodic.

about perceptual features of physical objects. It makes possible associative (e.g. stimulus–response) learning by furnishing one ingredient (the stimulus) for the basic unit of such learning. The perceptual system is also assumed to be involved in ‘perceptual priming’ in that experience-based changes in it may manifest themselves as enhancement in the perceptual identification of objects (Tulving & Schacter 1990). The other two levels are as already specified: the semantic system does with ‘facts’ what PRS does with perceptual features of objects, and the episodic system extends the processing of objects and facts to the ‘self’ in ‘subjective time’. (Note that semantic memory concerns knowledge of the world in general; despite its label it does not require language for its operations.)

Encoding of information into these systems proceeds serially. At any level of the monohierarchy, the products of processing of a given system can be either transmitted to the next higher level, or ‘stored’ at that level, or both. Whatever is stored at a given level of processing is potentially retrievable at that level, provided that the other conditions of efficient retrieval are fulfilled. Thus, information from the perceptual system can be, but need not be, transmitted to the semantic system and stored ‘in’ the perceptual memory system.

Not all perceptually processed information, of course, needs to ‘reach’ the semantic system, and not all of the information processed at the semantic level needs to reach the episodic system. It all depends on other factors that influence encoding: ‘bottom-up’ factors, such as novelty of the incoming information (Tulving *et al.* 1994); and ‘top-down’ factors, such as ‘levels of processing’ ( Craik & Lockhart 1972).

The parallel storage assumption of SPI holds that different aspects of incoming information are stored separately in different systems: information about the perceptual features of the input are stored in the perceptual system, information about conceptual and semantic aspects is stored in the semantic system, and information about the involvement of the self in the experiencing of the input is stored in the episodic system. This assumption

also goes against traditional thought, and perhaps common sense, which holds that a single event leaves a ‘single’ trace in the memory store. The idea in SPI is that the trace is a ‘bundle’ of widely but systematically dispersed features organized hierarchically.

The third process in SPI, retrieval, is assumed to be independent between the systems. This assumption follows directly from the assumption of parallel storage. It holds that what is retrieved from one system need not have any implications for retrieval of information from any other system. Frequently, the information from different systems is used jointly in a given act of retrieval, or separately but additively on individual components of a task. However, because of separate storage, it is perfectly possible, although not necessary of course, for retrieval to occur from only one system.

The SPI model goes against traditional thought in several ways. But because it is not only testable but falsifiable, it is worth attention and analysis.

## 7. SPI AND TRADITIONAL THOUGHT

It may be worth emphasizing five points about this simple model that illustrate how what was held by many to be true for a long time (and by some still is) should no more be so, or how at least it is now being challenged.

First, the organizational structure of SPI makes explicit that ‘memory’ can operate perfectly well at lower levels independently of higher levels in a given kind of brain—as well as in brains in which higher levels do not exist, either because they never evolved or in which they have been lost through brain damage. Thus, learning and memory may occur at the perceptual level alone, in the absence of any intervention by semantic and episodic memory. A great deal of memory research in non-human animals, for example, is essentially concerned with perceptual (recognition) memory (Aggleton & Pearce 2001), as is research done with pre-verbal human infants (Rovee-Collier & Hayne 2000). The widely used delayed non-matching to sample (DNMS) and other kinds of ‘object recognition’ tasks can be effectively executed without relying on semantic memory. It is this feature that allows a meaningful comparative analysis of ‘memory’ across species at the same level (Wright *et al.* 1985). Because comparisons in situations where memory operates at non-corresponding levels in different species are difficult to interpret, it is always important to establish what level of memory in species *X* is compared with what level of memory in species *Y*.

A great deal of learning and memory may occur at the semantic (general knowledge) level alone, without any intervention by episodic memory. Young children can acquire knowledge about the world efficiently and rapidly long before they develop the ability to recollect specific happenings from their past (Nelson 1993; Perner & Ruffman 1995; for more detailed discussion see Wheeler *et al.* 1997). Some amnesic patients, who have severely impaired or no functional episodic memory, can nevertheless acquire new semantic information (Hamann & Squire 1995; Kitchener *et al.* 1998; Tulving *et al.* 1991), especially when associative interference in learning is minimized (Hayman *et al.* 1993) or when ‘errorless learning’ procedures are used (Baddeley & Wilson 1994).

An especially striking demonstration of massive semantic learning in the absence of episodic memory is provided by cases of developmental amnesia, such as the young man Jon, described by Vargha-Khadem *et al.* 1997; 2001). Such cases present a serious challenge to conventional theory (Squire & Zola 1998; Tulving & Markowitsch 1998). The important point in the present context, however, is that all these cases illustrate how memory can successfully work below the level of episodic, even in the human brain.

Second, there is no provision in SPI for 'direct' encoding of perceptual information into episodic memory: the information must first go 'through' the semantic memory system. This proposal goes very much against common sense and against my own earlier thinking (Tulving 1972). Recently, the assumption that there is 'no direct line' from perceptual to episodic memory has been questioned by Simons and his colleagues in Cambridge (Graham *et al.* 2000; Simons *et al.* 2001). The issue represents one of the central topics of the paper by Hodges & Graham (this issue). I will return to it later in this paper.

Third, the SPI model explicitly allows—one might even say 'predicts'—double dissociations between episodic and semantic memory in retrograde amnesia (RA). If an individual suffers brain damage that causes RA, it can consist only (or at least primarily) in impairment of episodic memory (Kitchener *et al.* 1998; Kapur 1999; Tulving *et al.* 1988; Wheeler & McMillan 2001), only (or primarily) in semantic memory (De Renzi *et al.* 1987; Grossi *et al.* 1988; Wheeler & McMillan 2001; Yasuda *et al.* 1997), or more or less evenly in both, as in the majority of reported cases of amnesia. This feature of SPI is directly contrary to the widely accepted views of amnesia, advocated by Squire and Zola and their colleagues (Squire 1992; Squire & Zola 1998), which do not readily allow for exceptions to the more-or-less even impairment of memory for facts (semantic memory) and memory for events (episodic) memory.

Fourth, although double dissociations are allowed in RA or even 'predicted' by SPI, because of the serial encoding assumption they are strictly ruled out in anterograde amnesia (AA). When a healthy individual suffers brain damage and develops AA, it can consist in impairment of both semantic and episodic memory (the 'standard' form of AA) or impairment in episodic memory alone. What cannot happen, according to SPI, is AA in semantic memory alone. The matter is of considerable interest because, according to a widely accepted alternative view, anterograde memory for facts (semantic memory) and memory for events (episodic memory) are expected to be impaired more-or-less evenly (Squire 1992; Squire & Zola 1998).

Finally, SPI can be used to account for the many facts generated by the RK paradigm, which constitutes the central theme of Gardiner's paper (this issue) and figures prominently in Yonelinas's dual-process model of signal detection in recognition memory (this issue), as discussed in §8.

The SPI model, when first proposed, was meant to be a purely 'psychological theory', an abstract model in keeping with the hypothetical, abstract nature of the concepts of episodic and semantic memory. No suggest-

ions were offered about its neural correlates. Some recent developments, however, allow us to postulate parallels between the abstract SPI model and conclusions drawn from neuropsychological studies of both humans and animals. Aggleton & Brown (1999; see also Aggleton & Pearce, this issue) point out that, in animals, the brain structures involved in spatial memory are surprisingly different from those involved in recognition memory. In Aggleton's model, two partially overlapping medial-temporal and diencephalic systems mediate performance on different memory tasks. Recall, and episodic memory, depend on the hippocampus, the fornix and several structures in the diencephalon, whereas non-episodic recognition and familiarity are highly dependent on the perirhinal cortex and the medial dorsal nucleus of the thalamus, and do not require the hippocampus. The logic of this model would fit SPI if we assumed that the performance on recognition memory tests, in animals, is mediated by the perceptual (PRS) systems whereas performance on spatial memory tests is mediated by the declarative ('semantic' in Tulving & Markowitsch, 1998) system.

Mishkin and his colleagues (Mishkin *et al.* 1997; Vargha-Khadem & Mishkin, this issue) have suggested a hierarchical model of the organization of medial-temporal lobe structures in the service of episodic and semantic memory that also agrees neatly with the abstract SPI model. In Mishkin's model, the hippocampus operates at the highest level of the medial-temporal lobe (MTL) hierarchy and is associated with episodic memory, whereas the subjacent cortical regions operate at lower levels and are associated with semantic memory. The model is compatible with what is known about the psychology and neuroanatomy of the case of Jon and other perinatal amnesia patients (Vargha-Khadem *et al.* 1997) who fit SPI.

The idea that episodic recollection is not needed for recognition of 'old' and 'new' items is relevant to two other issues discussed at the meeting. First, the test of one of the most counter-intuitive features of the SPI model discussed earlier, namely the idea that there is no direct encoding of perceptual information into episodic memory and that perceptual information can enter episodic memory only through semantic memory. Second, the question of whether animals have episodic memory. I discuss these two issues in the remainder of this paper.

## 8. IS THERE DIRECT ENCODING OF PERCEPTUAL INFORMATION INTO EPISODIC MEMORY?

The SPI model, as already mentioned, rules out any direct encoding of perceptual information into episodic memory. As shown in figure 1, for perceptual information to be stored in episodic memory it needs to be processed not only in the perceptual system but also in the semantic system. The idea that it is not possible for people to recollect consciously what they have perceived unless it has been first 'interpreted' by semantic memory sounds counter-intuitive, perhaps even strongly so. However, the matter is testable and therefore the model is capable of being rejected in its present form. Surprisingly, the demonstration of direct entry of perceptual information into episodic memory has turned out to be difficult.

Recently, Jon Simons and his colleagues in Cambridge (Graham *et al.* 2000; Simons *et al.* 2001) have questioned the validity of the assumption of serial encoding in the SPI model. This assumption implies that individuals with dysfunctional semantic memory should have difficulty storing information in episodic memory. Even if such individuals have intact perceptual systems, their remembering of recent experiences should be deficient because there is no direct input from perceptual systems to episodic memory. Simons and his colleagues have tested this assumption with their semantic dementia patients who are selectively deficient in semantic memory, attributed to (usually asymmetrical) temporal lobe atrophy (Graham *et al.* 1997, 1999, 2000).

In one experiment, Simons and his colleagues (2001, experiment 2) tested two such patients for their ability to recognize recently seen faces. Two kinds of faces were initially presented for inspection: celebrities that were known and celebrities who were not known to the patients. After study, the patients were given two kinds of yes–no episodic recognition tests. In one, the test faces were identical with those seen initially; in the other, the test faces of the celebrities encountered at encoding were presented in different orientations.

The logic of the experiment rested on two assumptions: (i) the subjects' semantic memory would contribute to the recognition of known celebrities but not, or less so, to the recognition of unknown faces, and (ii) the problem of recognizing faces presented in the same orientation at study and test could be solved by relying on perceptual features alone, whereas recognizing faces in changed orientations would require, or at least would benefit from, semantic knowledge of the people whose faces were shown.

In the experimental situation used by Simons *et al.* (2001), the SPI model implies that the patients' impaired semantic memory should make it impossible, or at least more difficult, to remember the previous (virtual) encounter with unknown individuals than the encounter with known celebrities. The findings of this study agreed with this implication in the test condition in which different views of faces were used, but not in the condition in which test faces were changed. Simons and colleagues claimed this latter finding to be contrary to the SPI model, and proposed, therefore, that the SPI model, needs to be rejected and replaced with a more appropriate model, one they call 'multiple input' (MI) model or hypothesis. According to this revised model, episodic memory normally receives information from both the perceptual and conceptual (semantic) systems of the brain. These sentiments were echoed by Andrew Mayes and Neil Roberts (2001).

The Cambridge group's suggested revision of the SPI is attractive for several reasons:

- (i) The SPI model is currently very crude. It is difficult to imagine that as such it could capture the essence of the encoding–retrieval relations of complex memory systems, such as PRS, semantic and episodic.
- (ii) All good scientists know that all current models and theories are wrong—in the sense that sooner or later they all will be modified or replaced by better

ones—and therefore any explicitly proposed revision of the crude SPI model represents a step in the right direction.

- (iii) The proposed MI model makes good common sense. What could be more natural than to believe that a person can remember 'purely perceptual' events?

It is to be hoped, therefore, that the MI model of the Cambridge group will turn out to be a better idea about the encoding relations of PRS, semantic memory and episodic memory than the SPI model. There are, however, a couple of problems that need attention before we can certify the MI as the current 'front runner'.

One problem has to do with the claimed critical finding that patients with semantic dementia show equally good recognition memory for semantically familiar and unfamiliar faces (Simons *et al.* 2001), or recognition memory comparable with that of healthy controls (Graham *et al.* 2000), when test items have the same format as studied items. The validity of the claim is uncertain because of the observed ceiling effects in relevant conditions in both experiments. Thus, in the Simons *et al.* (2001) study, it is simply not known whether the critical interaction between type of recognition test (identical versus perceptually different test objects) and type of test items (familiar versus unfamiliar faces) came about because of the processes postulated in the MI model or because of ceiling effects. The Cambridge group are aware of the problems caused by ceiling effects but are willing to overlook them and to assume that the interaction would occur even in the absence of the ceiling effects. Nevertheless, the matter requires attention especially because other experiments have shown that even healthy individuals (young, old and very old) show better recognition memory for familiar than unfamiliar faces tested in their original form (Bäckman 1991; see also Bäckman & Herlitz 1990). A clear demonstration of the absence of the same effect in patients with semantic dementia, under conditions where the patients' recognition performance is free to vary, would settle this particular matter convincingly, leaving only the second problem.

This second problem has to do with the discrepancy between the concepts of episodic memory in the SPI and the MI models. In the formulation of the SPI model, 'episodic memory' refers to the episodic 'system', which has a certain set of process-specific relations to other systems. The critical findings that Simons and his colleagues use to reject the SPI model were obtained in yes–no recognition memory tests. Although such tests are frequently treated as 'tests of episodic memory'—I myself have done it regularly—as mentioned earlier, we now know that this is an oversimplification. The current understanding is that the extent to which episodic memory influences performance on recognition tests can vary, sometimes greatly, with conditions. In the absence of corroborating evidence there is no need to assume that semantic dementia patients relied on their episodic memory in the recognition test for faces. It is conceivable that they relied on their perceptual memory alone.

The assumption is that it is quite possible for any kind of subjects to do well on recognition memory tests in the absence of episodic memory. The most glaring example is

provided by recognition memory tests in experiments with non-human animals as subjects.

### 9. DO ANIMALS REMEMBER PAST EVENTS?

Do animals, such as rats, cats, dogs and monkeys, have episodic memory? That is, do they remember their own life experiences the same way that humans do? Common sense would say 'yes' and perhaps again be perplexed at the questions. Surely there could be no doubt that they do. Surely, all one needs to do is watch one's pet cat or dog to be convinced that the cat has excellent episodic memory. Why even bother raising the question?

Indeed, more often than not, the question has not been raised—because the answer to it has been clear without any need for thought. The earlier quote by Underwood said it all. Besides, there have been literally thousands of research reports on the close similarity of learning and memory data for non-human animals and humans. So, what is the reason for wanting to raise the question about episodic memory in animals?

The question about episodic memory in animals is a part of a larger issue—the nature of continuity of forms of learning and memory across the species. On the one hand, it is an unassailable fact that humans share a very large proportion of their genome with other animals, that their brains are built on the same basic plan as those of rats and monkeys and other mammals, and that, as far as we know, the molecular mechanisms and synaptic changes assumed to underlie learning and memory are the same across the species. These facts make thinking of continuity natural and non-controversial. On the other hand, the fact that humans engage in many unique forms of learned behaviour that are found in no other species—language and literature, art and music, religion and philosophy, science and technology, to mention the most obvious ones—should also encourage thoughts about differences in learning and memory. It would be unreasonable to assume that these uniquely human forms of self-expression are based on features of the evolved human brain that it shares with other animals.

The issue of episodic memory in animals is discussed thoroughly by three sets of authors: Aggleton & Pearce (2001; Aggleton & Brown 1999); Clayton and her colleagues (2001; Clayton & Dickinson 1998; Griffiths *et al.* 1999); and Morris (2001; Morris & Frey 1997). All three come to the conclusion, put by Clayton *et al.* (2001), as follows. In many of the tasks used in studies of animal memory, presumably including various 'recognition' tasks:

'... the animal does not need to recall the "what, where and when" of an event. Instead, the task may be solved by discriminating on the basis of relative familiarity, a process which is dissociable both psychologically (Mandler 1980; Jacoby & Dallas 1981; Jacoby 1991) and neurobiologically (Aggleton & Brown 1999) from episodic memory recall.' (Clayton *et al.* 2001, § 1).

More broadly, the common verdict is that the answer to the question about episodic memory in animals is not obvious and it cannot be settled by common sense. At the present time, all agree that the weight of evidence seems to lie with the absence of human-like episodic memory in

animals. However, because interesting analogues of episodic memory exist in non-human animals ('episodic-like' memories), future research may topple the current received wisdom.

The ingenious and convincing demonstrations of the 'what, where, when' memory in scrub jays by Clayton and her colleagues come very close to clinching the case for the jays' episodic memory. The only thing missing is evidence that they have human-like conscious recollections of their worm and nut caching activities. They may just 'know' what kind of food is where, and what state it is in—fresh or rotten—without knowing how or why they know it; hence, most appropriately, the use of the term 'episodic-like' memory. Clayton's scrub jay experiments clearly take us beyond what was known about non-human animals' ability to handle the 'when?' part of episodic memory—the 'what' and 'where' in animal learning and memory has been known for a long time (e.g. Shettleworth 1998). However, the nature of the information—is it 'remembered' or just 'known'—remains an open question. Richard Morris, in his talk at the meeting, expressed his hope (conviction?) that this question will be answered through the ingenuity of comparative psychologists who may be able to invent ways of communicating with animals that are almost as good as Dr Doolittle's. A wise scientist would not even dream of doubting the reality of the hope.

It is interesting, as Clayton *et al.* (2001) point out, that scrub jays do have episodic memory by the standards of 1972: their performance in the various tasks that Clayton and her team have posed for them clearly implies that they remember what happened where and when. In 1972, I (and I suspect just about everybody else) was convinced that remembering particular events, such as occurrences of words in a list, necessarily depended on remembering the general event of which the particular ones had been a part, namely the learning the list. For example, for a subject in a verbal learning experiment to be able to respond with the word 'gallant' to the word 'legend', which she had learned in a paired-associate learning task, she had to remember that she had learned the list. I and others thought it was impossible to remember that 'legend' and 'gallant' appeared together in the list if one did not remember having learned the list. This is very similar to the demonstrated capabilities of scrub jays.

The scrub jays' problem, therefore, is that our concept of episodic memory has changed since 1972. Unlike then, the main emphasis is now on three concepts: subjectively apprehended time, self and auto-noetic consciousness. The combination of the three supports activities that can be subsumed under the category of 'mental time travel', activities such as remembering past experiences as such and imagining possible future personal happenings as such. It is the uncertainty about the animals' possession of these kinds of experiential capabilities that makes it difficult to attribute human-type episodic memory to them.

Another feature of episodic (as well as semantic) memory that has been mentioned but has not been systematically explored, but which may turn out to be relevant to the issue of episodic and episodic-like memories in animals, is that retrieval of information 'from' episodic memory does not oblige the rememberer to any kind of overt behaviour. Any 'conversion' (Tulving



1983) of retrieved ('ecphoric') information is optional rather than obligatory: there is no fixed relation between thought and action. This fact is sometimes said to illustrate a property of cognitive or declarative memory called 'flexibility,' although the term has been used in other senses as well.

In animal studies of episodic-like memory, it would be interesting to see whether it would be possible to persuade the subjects to demonstrate their ability to act 'flexibly' upon the information that they have about a given 'what-where-when'. For example, could Clayton and her colleagues (or someone else) get their scrub jays, who remember what kind of food is where, to do something other with that information than act on it 'inflexibly', i.e. something other than approach the preferred food in order to eat it? Could the internally generated knowledge of a state of the world ('rotten worms on the left') serve as a Skinnerian discriminative stimulus for some other behaviour that produces some other reward that the birds appreciate? Convincing demonstrations of the decoupling of what appears a hard-wired connection between fixed behaviour prompted by fixed knowledge would constitute another step in the emancipation of birds, or other animals, as episodic creatures.

Another kind of a situation that is unrelated to mediation by or communication through language, and which, if it yielded appropriate results, I would find supportive of the idea of 'real' episodic (not just episodic-like) memory in animals is the following. Systematic observation shows that animals, at some point  $T_1$  in their 'spare time,' engage in a given behaviour  $X$  which is not controlled (instigated and maintained) by any physiological stimulus, external or internal, but which can be shown to be of benefit to the animal at some future time  $T_2$ . The argument here is, first, that humans engage in these kinds of (foresightful, 'planning') behaviours all the time—indeed, a surprisingly large proportion of all human activities is orientated towards the future—and, second, at the root of such an ability to travel mentally into the future is an 'autonoetic' time sense of episodic memory (for more on these kinds of ideas see Tulving 2002*a,b*). Therefore, if animals would also exhibit intelligent and purposeful behaviour that is not prompted by present stimuli, it becomes reasonable to assume that they are doing so on the same basis as humans. Lloyd Morgan's canon, emphasized by both Morris (2001) and Aggleton & Pearce (2001) would no longer apply.

At the present time the rational consensus is that episodic memory is unique to humans. Lest someone worry about the current political correctness of such an assertion, let me hasten to remind such a person that many behavioural and cognitive capabilities of many non-human species are equally unique to those species: echolocation in bats, electrical sensing in fish and genetically determined navigational capabilities of migratory birds are examples that come quickly to mind, but there are many, many others. Indeed, it is these kinds of abilities—unfathomable by common sense, but very real in fact—that allow one to remain a sceptic about episodic memory in birds and animals: evolution is an exceedingly clever tinkerer who can make its creatures perform spectacular feats without necessarily endowing them with sophisticated powers of conscious awareness.

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## REFERENCES

- Aggleton, J. P. & Brown, M. W. 1999 Episodic memory, amnesia and the hippocampal–anterior thalamic axis. *Behav. Brain Sci.* **22**, 425–444.
- Aggleton, J. P. & Pearce, J. M. 2001 Neural systems underlying episodic memory: insights from animal research. *Phil. Trans. R. Soc. Lond.* **B 356**, 1467–1482.
- Atkinson, R. C. & Shiffrin, R. M. 1968 Human memory: a proposed system and its control processes. In *The psychology of learning and motivation: advances in research and theory*, vol. 2 (ed. K. W. Spence & J. T. Spence), pp. 89–195. New York: Academic Press.
- Bäckman, L. 1991 Recognition memory across the adult life span: the role of prior knowledge. *Mem. Cogn.* **19**, 63–71.
- Bäckman, L. & Herlitz, A. 1990 The relationship between prior knowledge and face recognition memory in normal aging and Alzheimer's disease. *J. Gerontol. Psychol. Sci.* **45**, 94–100.
- Baddeley, A. D. & Hitch, G. J. 1974 Working memory. In *Recent advances in learning and motivation*, vol. 8 (ed. G. H. Bower), pp. 47–89. New York: Academic Press.
- Baddeley, A. & Wilson, B. A. 1994 When implicit learning fails—amnesia and the problem of error elimination. *Neuropsychologia* **32**, 53–68.
- Brown, S. C. & Craik, F. I. M. 2000 Encoding and retrieval of information. In *The Oxford handbook of memory* (ed. E. Tulving & F. I. M. Craik), pp. 93–107. New York: Oxford University Press.
- Clayton, N. S. & Dickinson, A. 1998 Episodic-like memory during cache recovery by scrub jays. *Nature* **395**, 272–274.
- Clayton, N. S., Griffiths, D. P., Emery, N. J. & Dickinson, A. 2001 Elements of episodic-like memory in animals. *Phil. Trans. R. Soc. Lond.* **B 356**, 1483–1491.
- Conway, M. A. & Pleydell-Pearce, C. W. 2000 The construction of autobiographical memories in the self memory system. *Psychol. Rev.* **107**, 261–288.
- Conway, M. A. 2001 Sensory-perceptual episodic memory and its context: autobiographical memory. *Phil. Trans. R. Soc. Lond.* **B 356**, 1375–1384.
- Craik, F. I. M. & Lockhart R. S. 1972 Levels of processing: a framework for memory research. *J. Verbal Learn. Verbal Behav.* **11**, 671–684.
- De Renzi, E., Liotti, M. & Nichelli, P. 1987 Semantic amnesia with preservation of autobiographic memory: a case report. *Cortex* **23**, 575–597.
- Düzel, E., Yonelinas, A. P., Mangun, G. R., Heinze, H. J. & Tulving, E. 1997 Event-related brain potential correlates of two states of conscious awareness in memory. *Proc. Natl Acad. Sci. USA* **94**, 5973–5978.
- Düzel, E., Vargha-Khadem, F., Heinze, H. J. & Mishkin, M. 1999 ERP evidence for recognition without episodic recollection in a patient with early hippocampal pathology. *Soc. Neurosci. Abstr.* **25**, 259.11.
- Eldridge, L. L., Knowlton, B. T., Furmanski, C. S., Bookheimer, S. Y. & Engel, S. A. 2000 Remembering episodes: a selective role for the hippocampus during retrieval. *Nature Neurosci.* **3**, 1149–1152.
- Foster, J. K. & Jelicic, M. (eds) 1998 *Memory: systems, process or function?* pp. 31–65. Oxford University Press.
- Gardiner, J. M. & Richardson-Klavehn, A. 2000 Remembering and knowing. In *The Oxford handbook of memory* (ed. E. Tulving & F. I. M. Craik), pp. 229–244. New York: Oxford University Press.
- Gardiner, J. M. 2001 Episodic memory and autonoetic consciousness: a first-person approach. *Phil. Trans. R. Soc. Lond.* **B 356**, 1351–1361.

- Graham, K. S., Becker, J. T. & Hodges, J. R. 1997 On the relationship between knowledge and memory for pictures: evidence from the study of patients with semantic dementia and Alzheimer's disease. *J. Int. Neuropsychol. Soc.* **3**, 534–544.
- Graham, K. S., Patterson, K. & Hodges, J. R. 1999 Episodic memory: new insights from the study of semantic dementia. *Curr. Opin. Neurobiol.* **9**, 245–250.
- Graham, K. S., Simons, J. S., Pratt, K. H., Patterson, K. & Hodges, J. R. 2000 Insights from semantic dementia on the relationship between episodic and semantic memory. *Neuropsychologia* **38**, 313–324.
- Griffiths, D. P., Dickinson, A. & Clayton, N. S. 1999 Declarative and episodic memory: what can animals remember about their past? *Trends Cogn. Sci.* **3**, 74–80.
- Grossi, D., Trojano, L., Grasso, A. & Orsini, A. 1988 Selective 'semantic amnesia' after closed-head injury. A case report. *Cortex* **24**, 457–464.
- Hamann, S. B. & Squire, L. R. 1995 On the acquisition of new declarative knowledge in amnesia. *Behav. Neurosci.* **109**, 1027–1044.
- Hayman, C. A. G., Macdonald, C. A. & Tulving, E. 1993 The role of repetition and associative interference in new semantic learning in amnesia. *J. Cogn. Neurosci.* **5**, 375–389.
- Henson, R. N. A., Rugg, M. D., Shallice, T., Josephs, O. & Dolan, R. J. 1999 Recollection and familiarity in recognition memory: an event-related functional magnetic resonance imaging study. *J. Neurosci.* **19**, 3962–3972.
- Jacoby, L. L. 1991 A process dissociation framework: separating automatic from intentional uses of memory. *J. Mem. Lang.* **30**, 513–541.
- Jacoby, L. L. & Dallas, M. 1981 On the relationship between autobiographical memory and perceptual learning. *J. Exp. Psychol. Gen.* **3**, 306–340.
- Kapur, N. 1999 Syndromes of retrograde amnesia: a conceptual and empirical analysis. *Psychol. Bull.* **125**, 800–825.
- Kitchener, E. G., Hodges, J. R. & McCarthy, R. 1998 Acquisition of post-morbid vocabulary and semantic facts in the absence of episodic memory. *Brain* **121**, 1313–1327.
- Knowlton, B. J. & Squire, L. R. 1995 Remembering and knowing: two different expressions of declarative memory. *J. Exp. Psychol. Learn. Mem. Cogn.* **21**, 699–710.
- Kopelman, M. D. & Kapur, N. 2001. The loss of episodic memories in retrograde amnesia: single-case and group studies. *Phil. Trans. R. Soc. Lond.* **B 356**, 1409–1421.
- Koriat, A. 2000 Control processes in remembering. In *The Oxford handbook of memory* (ed. E. Tulving & F. I. M. Craik), pp. 333–346. New York: Oxford University Press.
- Maguire, E. A. 2001 Neuroimaging studies of autobiographical event memory. *Phil. Trans. R. Soc. Lond.* **B 356**, 1441–1451.
- Mandler, G. 1980 Recognizing: the judgment of previous occurrence. *Psychol. Rev.* **97**, 252–271.
- Mangels, J. A., Picton, T. W. & Craik, F. I. M. 2001 Attention and successful episodic encoding: an event-related potential study. *Cogn. Brain Res.* **11**, 77–95.
- Mays, A. R. & Roberts, N. 2001 Theories of episodic memory. *Phil. Trans. R. Soc. Lond.* **B 356**, 1395–1408.
- Mishkin, M., Suzuki, W. A., Gadian, D. G. & Vargha-Khadem, F. (1997) Hierarchical organization of cognitive memory? *Phil. Trans. R. Soc. Lond.* **B 352**, 1461–1467.
- Morris, R. G. M. & Frey, U. 1997 Hippocampal synaptic plasticity: role in spatial learning or the automatic recording of attended experience? *Phil. Trans. R. Soc. Lond.* **B 352**, 1489–1503.
- Morris, R. G. M. 2001 Episodic-like memory in animals: psychological criteria, neural mechanisms and the value of episodic-like tasks to investigate animal models of neurodegenerative disease. *Phil. Trans. R. Soc. Lond.* **B 356**, 1453–1465.
- Nelson, K. 1993 The psychological and social origins of autobiographical memory. *Psychol. Sci.* **4**, 7–14.
- Perner, J. & Ruffman, T. 1995 Episodic memory and autoethic consciousness: developmental evidence and a theory of childhood amnesia. *J. Exp. Child Psychol.* **59**, 516–548.
- Rajaram, S. & Roediger III, H. L. 1997 Remembering and knowing as states of consciousness during recollection. In *Scientific approaches to the question of consciousness* (ed. J. D. Cohen & J. W. Schooler), pp. 213–240. Hillsdale, NJ: Erlbaum.
- Roediger III, H. L. 2000 Why retrieval is the key process in understanding memory. In *Memory, consciousness and the brain: the Tallinn conference* (ed. E. Tulving), pp. 52–75. Philadelphia: The Psychology Press.
- Rovee-Collier, C. & Hayne, H. 2000 Memory in infancy and early childhood. In *The Oxford handbook of memory* (ed. E. Tulving & F. I. M. Craik), pp. 267–282. New York: Oxford University Press.
- Schacter, D. L. & Dodson, C. S. 2001 Misattribution, false recognition and the sins of memory. *Phil. Trans. R. Soc. Lond.* **B 356**, 1385–1393.
- Schacter, D. L. & Tulving, E. 1994 What are the memory systems of 1994? In *Memory systems 1994* (ed. D. L. Schacter & E. Tulving), pp. 1–38. Cambridge, MA: MIT Press.
- Shettleworth, S. 1998 *Cognition, evolution, and behavior*. New York: Oxford University Press.
- Simons, J. S., Graham, K. S., Galton, C. J., Patterson, K. & Hodges, J. R. 2001 Semantic knowledge and episodic memory for faces in semantic dementia. *Neuropsychology* **15**, 101–114.
- Squire, L. R. 1992 Memory and the hippocampus: a synthesis from findings with rats, monkeys and humans. *Psychol. Rev.* **99**, 195–231.
- Squire, L. R. & Zola, S. M. 1998 Episodic memory, semantic memory, and amnesia. *Hippocampus* **8**, 205–211.
- Tulving, E. 1972 Episodic and semantic memory. In *Organization of memory* (ed. E. Tulving & W. Donaldson), pp. 381–403. New York: Academic Press.
- Tulving, E. 1983 *Elements of episodic memory*. Oxford: Clarendon Press.
- Tulving, E. 1993 What is episodic memory? *Curr. Persp. Psychol. Sci.* **2**, 67–70.
- Tulving, E. 1995 Organization of memory: quo vadis? In *The cognitive neurosciences* (ed. M. S. Gazzaniga), pp. 839–847. Cambridge, MA: MIT Press.
- Tulving, E. 1998 Study of memory: processes and systems. In *Memory: systems, process, or function?* (ed. J. K. Foster & M. Jelicic), pp. 11–30. Oxford University Press.
- Tulving, E. 2002a Episodic memory: from mind to brain. *Ann. Rev. Psychol.* (In the press.)
- Tulving, E. 2002b Chronesthesia: awareness of subjective time. In *Principles of frontal lobe function* (ed. D. T. Stuss & R. C. Knight). New York: Oxford University Press. (In the press.)
- Tulving, E. & Markowitsch, H. J. 1998 Episodic and declarative memory: role of the hippocampus. *Hippocampus* **8**, 198–204.
- Tulving, E. & Schacter, D. L. 1990 Priming and human memory systems. *Science* **247**, 301–306.
- Tulving, E., Schacter, D. L., McLachlan, D. R., & Moscovitch, M. 1988 Priming of semantic autobiographical knowledge: a case study of retrograde amnesia. *Brain Cogn.* **8**, 3–20.
- Tulving, E., Hayman, C. A. G. & Macdonald, C. A. 1991 Long-lasting perceptual priming and semantic learning in amnesia: a case experiment. *J. Exp. Psychol. Learn. Mem. Cogn.* **17**, 595–617.
- Tulving, E., Markowitsch, H. J., Kapur, S., Habib, R. & Houle, S. 1994 Novelty encoding networks in the human brain: positron emission tomography data. *Neuroreport* **5**, 2525–2528.
- Underwood, B. J. 1964 The representativeness of rote verbal learning. In *Categories of human learning* (ed. A. W. Melton), pp. 48–78. New York: Academic Press.

- Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W. & Mishkin, M. 1997 Differential effects of early hippocampal pathology on episodic and semantic memory. *Science* **277**, 376–380.
- Vargha-Khadem, F., Gadian, D. G. & Mishkin, M. 2001 Dissociations of cognitive memory: the syndrome of developmental amnesia. *Phil. Trans. R. Soc. Lond. B* **356**, 1435–1440.
- Waugh, N. C. & Norman, D. A. 1965 Primary memory. *Psychol. Rev.* **72**, 89–104.
- Wheeler, M. A. & McMillan, C. T. 2001 Focal retrograde amnesia and the episodic–semantic distinction. *Cogn. Affect. Behav. Neurosci.* **1**, 22–37.
- Wheeler, M., Stuss, D. T. & Tulving, E. 1997 Toward a theory of episodic memory: the frontal lobes and autonoetic consciousness. *Psychol. Bull.* **121**, 331–354.
- Wright, A. A., Santiago, H. C., Sands, S. F., Kendrick, D. F. & Cook, R. G. 1985 Memory processing of serial lists by pigeons, monkeys, and people. *Science* **229**, 287–289.
- Yasuda, K., Watanabe, O. & Ono, Y. 1997 Dissociation between semantic and autobiographical memory: a case report. *Cortex* **33**, 623–638.
- Yonelinas, A. P. 2001 Components of episodic memory: the contribution of recollection and familiarity. *Phil. Trans. R. Soc. Lond. B* **356**, 1363–1374.