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MEMORY CONCEPTS - 1993

BASIC AND CLINICAL ASPECTS

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Editors:

Per Andersen
Department of Neurophysiology, Institute of Basic Medical Sciences, University of Oslo, N-0317 Oslo, Norway

Øivind Hvalby
Department of Neurophysiology, Institute of Basic Medical Sciences, University of Oslo, N-0317 Oslo, Norway

Ole Paulsen
Department of Neurophysiology, Institute of Basic Medical Sciences, University of Oslo, N-0317 Oslo, Norway

Bernt Hökfelt
Department of Endocrinology, Malmö General Hospital, S-214 01 Malmö, Sweden

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Human Memory

Endel Tulving

Rotman Research Institute of Baycrest Centre
3560 Bathurst Street, Toronto M6A 2E1, Canada

INTRODUCTION

The short history of scientific study of human memory can be divided into three periods. The first was inaugurated with the publication of Ebbinghaus's "Über das Gedächtnis" (1) in 1885, and lasted some 75 years, to around 1960. Problems of memory were pursued by experimental psychologists under the general rubric of "verbal learning." Emphasis was on experimental design and precise measurement of basic phenomena of learning and forgetting. List-learning methods were almost exclusively used. The concept of association, with its single property of "strength," was pressed into service of accounting for just about all of the experimental findings.

Around 1960 the associative verbal-learning framework was largely replaced by the "information processing" paradigm. A wider variety of problems, issues, approaches, methods, and theoretical interpretations were adopted. Paired-associate and serial learning procedures were largely abandoned in favour of free and cued recall, as well as recognition and various kinds of memory judgments--recency, frequency, and the like. Experimental studies of short-term memory led to theoretical distinction between primary (short-term) and secondary (long-term) memory. Units of analysis shifted from lists to single items. Single items were thought of as "events" whose occurrence subjects remembered. The distinction between storage and retrieval became a significant experimental and theoretical concern. Influential concepts such as levels of processing, encoding specificity, and encoding/retrieval interactions emerged during this stage, as did "context" and "context effects." Connections were established between the previously isolated disciplines of cognitive psychology and neuropsychology. Empirical new findings about memory were interpreted in terms of a variety of processes.

The current era of research, beginning some time around 1980, could be labelled cognitive neuroscience of memory. It is characterized by further expansion and liberalization of methods, techniques, and choices of questions and problems. The domain of "memory" has expanded considerably. The central concepts of the era so far have been priming and memory systems. There has been a steadily growing convergence between cognitive psychology and neuropsychology, interest has deepened in the study of memory in memory-impaired patients, more attention is being paid to memory in life-span development, theoretically motivated and precisely controlled psychopharmacological studies of memory have appeared on the scene, computer modelling of memory processes has become increasingly sophisticated, and neuroimaging approach to the study of memory is rapidly overcoming its initial difficulties. The multidisciplinary study of memory has taken off with a flourish.

This paper reviews some of the recent work that has been done under the banner of cognitive neuroscience of memory. It focuses on the issue of different forms of human memory, with special emphasis on perceptual priming, semantic memory, and episodic memory. It also presents a sketch of a general abstract model of organization of human memory. This so-called SPI model helps to organize empirical facts into a simple but general scheme in which memory processes (a focus of interest of the information processing era) are related to memory systems (a focus of interest of the current era).

HUMAN MEMORY SYSTEMS

Over the recent years empirical support has been adduced for the separability, on either functional or physiological grounds, or both, among different "forms" of learning and memory. Five major categories of human memory, or "systems," together with some subcategories or subsystems, for which reasonably good evidence is available now, are listed in Table 1 (2-6).

Table 1 --Major Categories of Human Learning and Memory

System	Other terms	Subsystems	Retrieval
1. Procedural	Nondeclarative	Motor skills Cognitive skills Simple conditioning Simple associative learning	Implicit
2. PRS	Priming	Structural description Visual word form Auditory word form	Implicit
3. Semantic	Generic Factual Knowledge	Spatial Relational	Implicit
4. Primary	Working Short-term	Visual Auditory	Explicit
5. Episodic	Personal Autobiographical Event memory		Explicit

The evidence for the biological and functional separability of the categories and subcategories listed in Table 1 is still fragmentary, largely indirect, and of variable quality and quantity. It is more than likely that the overall classificatory scheme will be elaborated, refined, and perhaps even radically modified as relevant research unfolds.

The ordering of the major systems in the overall classification scheme corresponds roughly to their presumed developmental sequence, with the procedural system the earliest, and the episodic the latest. The ordering of the systems also reflects the conjectured relations among the systems: many operations of the later ones depend on, and are supported by, the operations of the earlier ones, whereas earlier systems can operate essentially independently of the later ones.

The scheme in Table 1 does not include primitive forms of learning, such as sensitization and habituation, because little work has been done with them in humans, and sensory (iconic and echoic) memory, because little is known about their relation to forms of memory other than short-term memory. Two entries in Table 1, semantic and episodic memory are sometimes categorized together as <u>declarative</u> (7) or <u>propositional</u> memory (8), as they share a number of features. Another frequently used distinction is that between implicit and explicit memory (9-11). Implicit memory designates the <u>expression</u> of stored information without awareness of its acquisition coordinates in space and time, that is, expression of what the individual has learned, without necessarily remembering how, when, or where the learning occurred. Explicit memory, on the other hand, refers to the expression of what the person is consciously aware of as a personal experience (9, 10). Retrieval (use or expression of acquired information) operations in the earlier systems as shown in Table 1 (procedural, PRS, and semantic) can be said to be "implicit," whereas in the later systems (primary, working, and episodic) it is "explicit." Typical implicit tests are priming tests, discussed below; typical explicit tests are recall or recognition of previously encountered ("studied") items or events.

The procedural system is an <u>action</u> system, its operations are expressed in the form of skilled behavioral and cognitive procedures, independently of any cognition. Skilful performance of perceptual-motor tasks, conditioning of simple stimulus-response connections, and execution of cognitive skills such as reading are examples of tasks that depend heavily on the procedural memory system.

The other four are <u>cognitive</u> systems. They mediate changes in cognition, or thought. In the course of normal everyday activity, the computational outputs of the cognitive memory systems typically guide overt behavior, but such conversion of cognition into behavior is not an obligatory part of memory. Rather it is an optional post-retrieval process. The ultimate output of cognitive memory systems is expressed in conscious awareness of the individual, which can, but need not, be converted into overt behavior such as verbal expression. Indeed, in the laboratory the products of cognitive memory systems are analyzed in the form of "pure" experience or thought, with behavioral responses serving merely as indicators of properties of cognitive processes.

Perceptual priming is a specific form of learning that is expressed in enhanced identification of objects as structured physical-perceptual entities. A perceptual encounter with an object on one occasion primes or facilitates the perception of the same or a similar object on a subsequent occasion, in the sense that the identification of the object requires less stimulus information or occurs more quickly than it does in the absence of priming.

Semantic memory makes possible the acquisition and retention of factual information in the broadest sense; the structured representation of this information, semantic knowledge, models the world. Semantic 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. An example of the capabilities of semantic memory is knowledge of location of objects in the nonperceived space, another is classification of objects, events, or situations--or symbolic descriptions of them--into higher-order conceptual categories depending upon their functions and uses.

Primary memory, also referred to as short-term memory, or working memory (2) registers and retains incoming information in a highly accessible form for a short period of time after the input. Primary memory, like other memory systems, is identified through dissociations of its products from those of other systems. It makes possible a lingering impression of the individual's present environment beyond the duration of the physical presence of the stimulus information emanating from the environment.

Episodic memory enables individuals to remember their personally experienced past, that is, to remember experienced events as embedded in a matrix of other personal happenings in subjective time. It depends on but transcends the range of the capabilities of semantic memory. The most distinctive aspect of episodic memory is the kind of conscious awareness that characterizes recollection of past happenings. This awareness is unique and unmistakably different from the kinds of awareness that accompany perceptual experiences, imagining, dreaming, solving of problems, and retrieval of semantic information. To distinguish the episodic-memory awareness from these other kinds, it has been referred to as autonoetic consciousness (12, 13).

The forms of memory in Table 1 are listed in order of their assumed emergence, from the earliest to the latest, both with respect to the phylogenetic and ontogenetic development, and with respect to the dependence relations that govern their operations. Thus, procedural forms of learning and memory probably evolved first and develop early in human infants, and episodic memory evolved last and develops later in human children. It is also assumed that the earlier systems can exist and function relatively independently of the later systems, whereas complete operations of the later systems necessarily depend on the earlier ones.

The hypothesis that perceptual priming, semantic memory, and episodic memory, like other major categories of memory, represent different neurocognitive systems and subsystems is supported by experiments conforming to the task-comparison methodology (14). Outcomes of different memory tasks that are known or assumed to be differentially weighted by contributions of different systems are systematically compared. Dissociations among these outcomes are regarded as providing support for the hypothesis of separability of systems. Outcomes of tests are said to be dissociated if they differ as a function of an independent variable, or if they differ for different groups of subjects or patients, or for different brain states. Dissociations contrast with "parallel effects," observations that the manipulation of an independent variable or a treatment produces similar changes in the outcomes of different tasks, or different measures of memory performance.

When a number of different dissociations--yielded by different kinds of subjects, different tasks and situations, and different techniques--are seen as converging on the same classificatory scheme, it becomes reasonable to hypothesize the existence of separate memory systems. Examples of such convergence will be presented later in this paper. Although dissociations of interest are usually observed first at the level of behavior, behavioral data on their own are seldom sufficiently compelling to allow exclusion of alternative interpretations of empirical facts. Classification of memory into different systems and subsystems requires a broad-based multidisciplinary approach. Functional analyses of task performance must be integrated with relevant neuroanatomical, neurochemical, and neurophysiological evidence.

Perceptual priming was identified as a distinct form of memory only recently, although the basic phenomena have been known for some time (15). Perceptual priming is observed and measured in experimental situations in which the observers' task is to identify target objects (frequently familiar words) on the basis of incomplete stimulus information. In these experiments the identification of target objects (naming, or assignment to a category) is rendered difficult by reducing the amount of relevant stimulus information available to the observer. In the priming test, incomplete or otherwise impoverished test stimuli (cues) are presented to the observer with the instructions to read, name, label, or in some other way identify (classify) the corresponding object (11). Experimental parameters are selected in such a manner that the observer can identify only a certain proportion of target objects in the test sample. Priming is said to have occurred if an earlier presentation of the target objects results in an increased probability that the objects can be identified.

A typical perceptual priming experiment is very similar to a typical "explicit" study/test memory experiment. It consists of two phases. The first phase consists of "study": the subject is asked to inspect a large number of objects in one or more categories, such as familiar words, pseudowords, line drawings of objects, pictures of objects, photographs of faces, and the like. The second phase is the "test": the subject is presented with "cues" representing incomplete or impoverished perceptual information about both previously studied and previously not studied "target" objects. The test may follow the study phase immediately, or after a delay. The subject's task is to identify the cued target. Thus, for example, in the "fragment-completion" test, the word ASSASSIN may be presented in the form of a graphemic fragment such as A---SS-N, or -SS--SI-, or AS----IN, and the subject is asked to say what the word is. In the "stem-completion" test, the target words are cued with their initial letters. For example, FRAGMENT would be cued with FRA-----. At test, the subject is presented with the three-letter "stem" and asked to produce the first word that "comes to mind." Other kinds of cues have also been used (11).

Although most work on priming has been done with visually and auditorily presented words, the effects are by no means limited to these materials. Many different kinds of nonverbal materials and tasks have been used, producing effects similar to those observed with verbal items (16-19). It is reasonable to assume that priming of verbal materials represents a more recently evolved specialization of perceptual learning capabilities that originally emerged in the domain of identification of real objects. The juxtaposition of the presumed ubiquity of perceptual priming and its late discovery is probably responsible, at least in part, for the great interest it now holds for students of human memory.

In laboratory experiments it is the retrieval instructions--the question, "What is it?"--that distinguishes priming tests from tests of explicit retrieval. In these instructions, no reference is made to any previous study phase of the experiment, and the subject need not "think back to" the study phase in order to exhibit priming. In explicit memory tests the retrieval instructions always include some version of the question, "What was the item in the presented list?" thus requiring explicit reference to a particular study episode.

Perceptual priming differs from two other major forms of priming, semantic priming (20, 21), and conceptual priming (22, 23). Perceptual priming is concerned with the perceptible form and structure (or appearances) of objects, or with lexical properties of words, and has little to do with their function or meaning, whereas both semantic and conceptual priming operate at the level of function and meaning, and are not greatly influenced by the perceptible features of words. In this paper, "priming" without qualifiers always refers to perceptual priming.

The priming effect is measured in terms of the difference between the probabilities of identifying target objects that were presented in the study phase and those that were not. For example, in an early experiment (24) subjects saw a list of 96 English words in the study phase, presented at the rate of 5 s per word. An hour later, subjects completed 46 per cent of the fragments of studied words and 31 per cent of the fragments of nonstudied words. The difference between these two quantities represents the priming effect. Experimental design assured that the "old" and "new" target words were equivalent in every respect save one--previous occurrence or non-occurrence in the study phase. Thus, the priming effect could be unequivocally attributed to the presentation of the word in the study list.

At first blush, the finding that subjects show a priming effect as described seems uninteresting: Surely it has been known for a long time that subjects can "remember" all kinds of things they have seen, including words in a list. On the basis of the information stored in memory during the study episode the subjects can answer the "What is this item?" question as readily as the "What was the item in the list?" question. Answers to both questions are presumably influenced by the information encoded during the presentation of the item in the study episode; both priming and explicit recall or recognition represent similar aftereffects of the same original event. Why is yet another demonstration that people remember words in a list noteworthy?

If priming were regarded as a form of "remembering"--and it should not be, because the term "remembering" designates the function of episodic memory--it is a rather peculiar form of remembering, because it behaves quite differently from the more conventional forms of "remembering" of the sort that were studied in the past. A great deal of evidence has been accumulated to suggest that the principles of operation of priming are substantially different from those governing standard tests of recall and recognition. These differences provide the basis for postulating the existence of a separate "priming system" that has evolved for the special purpose of fast identification of objects in the world to which the organism seeks survival. The system subserving perceptual priming has been referred to as the perceptual representation system, or PRS (24, 25). PRS consists of a number of different subsystems, each of which processes particular type of information (10, 15).

The properties of the PRS, and its operating principles, are suggested and delineated by the outcomes of experiments in which priming is compared with explicit forms of retrieval such as recall and recognition. Thorough reviews of priming experiments done with both normal subjects (11) and amnesic patients (10) have recently appeared. A selected list of differences between priming and explicit retrieval is shown in Table 2.

Table 2

A selected list of features differentiating perceptual priming and explicit retrieval.

Feature	Priming	Explicit
Perceptual exposure	Sufficient	Insufficient
Perceptual features	Relevant	Irrelevant
Sensory modality	Sensitive	Insensitive
Size changes	Insensitive	Sensitive
Language shift	Sensitive	Insensitive
Encoding operations	Irrelevant	Relevant
Massed repetition	Ineffective	Effective
Consciousness	Anoetic	Autonoetic
Contingency relation	Independent	Positive
Access	Hyperspecific	Flexible
Duration	Longer	Shorter
Development	Invariant	Variant
Drugs	Less sensitive	More sensitive
Anterograde amnesia	Preserved	Impaired
Evoked potentials	No P300	P300

The evidence speaking to many of these features is extensive. A summary is presented in what follows.

Perceptual exposure. Mere perceptual exposure of an object to the observer is sufficient to produce priming, but it is not always sufficient for subsequent explicit retrieval (11).

Perceptual (structural) features. Priming is sensitive to the compatibility between the perceptual format of the studied item and the test cue. Priming effects may be considerably reduced if the perceptual format at test is changed from that used at study, whereas similar shifts in structural features have little effect on explicit memory (19), or sometimes opposite effects (26).

Sensory modality. Priming effects are reduced, and sometimes eliminated, when the sensory modality at test does not match the modality at study, whereas similar mismatching of modalities has little effect on explicit memory (27).

Size changes. Changing the physical size of the target object from study to test results in the reduction of explicit memory performance but has no effect on priming (16, 28).

Language shift. Priming does not transfer across languages. Little priming is found when bilingual subjects study the material in one language and are then tested for priming for the same words in the other language (29, for an exception see 30).

Encoding operations. The cognitive format of encoding an item at study, manipulated experimentally through different "encoding operations," invariably produces large effects in explicit memory (31, 32). But similar variations in the encoding operations performed on target items at study have little or no effect on priming (33, 34).

Massed repetition. At least some forms of priming seem to be impervious to the effects of massed repetition of target items at study. Priming effect is as large when the target item is seen on a single study trial as it is when the target item is seen on 16 immediately successive study trials (35).

Conscious awareness. Unlike the expression of other kinds of cognitive memory, expression of priming is nonconscious. An observer in a priming situation need not be aware that he has been exposed to the target object on a previous occasion in order to benefit from the exposure (36-38).

Contingency relation. Priming effects are as large for the target items that the subjects consciously recognize as having occurred in the study list as they are for the study-list items that the subject does not recognize (23, 39). This kind of stochastic independence between facilitated perceptual identification and unawareness of prior occurrence, in a situation in which the observer is aware of the previous study phase, provides another objective basis for the claim that priming is a "nonconscious" form of memory.

Access. There is some evidence that access to the information that supports priming may be rather rigidly hyperspecific. Observed priming effects are the largest, and sometimes occur only, when the cues at test fit the previously primed object precisely (19, 40). Moreover, success or failure of performance on the priming test through one cue is independent of the success or failure through a different cue, although the tests are otherwise highly reliable (23). Such "configural hyperspecificity" represents an extreme example of the determination of priming by perceptible "surface features" of objects.

Duration. Some priming effects decay very slowly over time, not only in normal subjects (26, 41) but also in amnesic patients. In one experiment (42) it was found that the primed fragment-completion performance by the amnesic patient K.C. showed practically no decline over a 12-month period during which he was not exposed to the target items.

Development. Perceptual priming is largely invariant across developmental stages though childhood, adulthood, and old age, whereas explicit memory may show large systematic changes (43-46). Priming effects shown by three-year old children may be as large as those shown by adults (47).

Drug effects. Priming effects are less adversely affected, or not affected at all, by amnestic drugs such as diazepam, which can substantially impair learning and retention on explicit tasks (48, 49). However, another benzodiazepine, lorazepam has been claimed to impair priming more than explicit retrieval (50).

Anterograde amnesia. Priming is preserved in most cases of anterograde amnesia. Amnesic patients who have great difficulty learning new associative knowledge frequently show normal priming effects (51-53).

Evoked potentials. Evidence has been reported that evoked potentials elicited by studied items differ depending upon their subsequent recallability (explicit retrievability) whereas no similar patterns has so far been found for studied items depending on their subsequent production or nonproduction in priming tests (54, 55).

The evidence summarized here illustrates how different forms of memory are influenced differently by independent variables, and how their expressions vary when subjected to identical treatments. It is this kind of evidence that encourages the search for their separate neural substrates. So far neuroanatomical and neurophysiological correlates of PRS have remained elusive. The fact that severely amnesic patients frequently show perfectly normal priming implies that priming is mediated by neuronal pathways that lie outside the medial temporal and diencephalic regions whose damage frequently results in amnesia. It can be conjectured that priming involves cortical regions that are closely connected to primary sensory areas. For example, identification of visual words involves bilateral extrastriate regions of the occipital lobes (56), and it can be surmised that the same regions play a role in priming of word identification. On similar grounds it can be assumed that priming of object identification depends on the right posterior cortical regions (57), and that neural computations underlying priming of face recognition are performed in the same region that is involved in identification of faces (17). Direct evidence is still lacking.

One complicating factor standing in the way of identification of the neural substrates of priming lies in the absence of relevant data from animal experiments. Memory processes and memory systems of other animals are both similar to and different from those of humans. It can be assumed that the earlier forms of learning and memory are similar in many animals, whereas the later forms are either different or lacking altogether in sub-human species. It is also reasonable to hypothesize that the neuronal substrates and the operating principles of the earlier evolved systems overlap considerably across species, whereas some of the more recently evolved structures and mechanisms are unique to humans. As perceptual priming represents a rudimentary capability whose biological utility seems to be obvious, we would expect it to be ubiquitously represented in many species. Interestingly, priming is yet to be demonstrated experimentally in any of the nonhuman species.

What about the "other" system, the one that subserves explicit retrieval? To answer this question we must turn to another distinction. At the level of cognitive analysis it is described as a distinction between knowing and remembering; at the level of conceptual analysis, it will be identified with semantic and episodic memory systems.

SEMANTIC KNOWING AND EPISODIC REMEMBERING

The idea that people sometimes just know about things they have experienced whereas on other occasions they explicitly remember them is an old one. It was well known to Ebbinghaus, who referred to the difference between "simple return of recurring ideas" and the accompanying "knowledge of their former existence and circumstances" (1, p. 58). This latter form of memory, Ebbinghaus thought, was a manifestation of "higher mental life." William James, too, in his classic "Principles of Psychology" (58) clearly differentiated between conceptions and memory. James defined memory in terms of the "warmth and intimacy" that thoughts about one's personal past bring to mind. The proverbial person in the street, when thinking about memory, usually has in mind Ebbinghaus's "knowledge of the former existence and circumstances" of ideas, or the Jamesian memory. We refer to this form memory as episodic memory, and think of its function as "remembering."

In the past, observations about knowing and remembering were usually interpreted within a unitary framework of human memory. The two cognitive functions were seen as separate aspects of the workings of one and the same complex system. It has been only over the last 20 years or so that the possibility has been raised that these two forms of cognition--knowing and remembering--represent the end-products of different neurocognitive systems. When the old idea about the two distinctive forms of cognitive memory was resuscitated under the labels of semantic and episodic (59) there was little hard, systematic, empirical evidence available to support it. Therefore the distinction was initially presented merely as a possibly useful heuristic or classificatory device. Over the subsequent years more relevant empirical evidence has come to light, and the hypothesis that these two forms of memory represent separable neurocognitive systems is on a firmer footing now. As frequently happens, the concepts have also changed, especially that of episodic memory. The story of these changes has been recorded in greater detail elsewhere (5, 8, 13).

Semantic memory is concerned with general knowledge; its basic function is to enable knowing. The designation is somewhat misleading: semantic memory is not necessarily tied either to language or to meaning. A better label would be "generic" memory, or "knowledge of the world," but the appellation in use is retained for historical reasons. Semantic memory allows organisms to acquire, and internally represent, information about complex states of the world that are not present to the senses, that is, states of the world that exist elsewhere, either in a concrete or abstract form. Semantic memory models the complex world outside the individual, or acts as a surrogate for it, thus allowing for vicarious cognitive operations to be performed on the world prior to, or as a substitute for, corresponding overt operations. The organism possessing a semantic memory system can think about things that are not here now. There are excellent reasons for supposing that many animals have semantic memory: they possess their own specific knowledge of the world, much of it learned through experience, and much of it shaped by and closely tied to the perceptual capabilities of the species. Excellent knowledge of space, and of spatial relations, for example, is well established in mammals and birds. Semantic memory in humans transcends semantic memory capabilities of other animals by virtue of the fact that human beings, aided by language, can encode, process, and express abstract and symbolic knowledge in ways not possible for other animals.

Episodic memory is concerned with experienced events; its basic cognitive function is to enable remembering (or conscious recollection) of personal happenings from the past. Its operations are assumed to be subserved by a neurocognitive system specialized for that purpose. Episodic memory grows out of but remains supported by semantic memory. This hierarchical (or monohierarchical) arrangement means that an organism possessing a fully functional episodic memory system must also possess an intact semantic system. Episodic memory transcends semantic memory by being self-referential: its contents include a reference to the self in subjective space and time. As semantic memory allows individuals to process information about objects and their relations in space, and abstractions derived from space, so episodic memory enables people to remember personally experienced events and their temporal relation in time. Those who possess episodic memory are not only capable of thinking about things not present in the immediately perceptible environment, they are also capable of "mental time travel." In their own awareness they can transport themselves into their previously experienced past, as well as into the future. These kinds of neurocognitive achievements are not possible for organisms who do not possess episodic memory. There are reasons to believe that other animals, young human children, and patients suffering from certain kinds of brain damage may be deficient, sometimes grossly deficient, in this kind of ability.

The idea that semantic and episodic memory represent different neurocognitive systems has been slow to gain support, probably because at first glance the two putative systems seem to be more similar than different. Both are large, complex, long-term, structures that render feasible acquisition and retention of factual information about the world. The operations of both systems can occur independently of overt behavior: both are cognitive systems. Both process "declarative" (7) or "propositional" (8) information that has truth value. Both are "representational": they represent (complex) states and relations "in the world." That is, both "model" the environment, including aspects of the internal environment, of the individual. Both are capable of storing new, intricate information as a result of a single exposure to the information. The operation of encoding information into episodic and semantic memory seem to be highly similar and governed by the same general rules. Finally, episodic and semantic memory resemble each other with respect to flexibility of access to the stored infirmation, and by virtue of the possibility of expressing retrieved information through language or in some other symbolic form. Because of all these correspondences, the parsimonious position that memory mechanisms subserving knowing of facts and remembering of personal events are essentially the same has appeared and remained attractive to many.

Nevertheless a closer look reveals differences that can be seen as basic and fundamental.

THE CASE OF K.C.

It is difficult to separate semantic and episodic processes in normal human adults. But the separability is revealed by special cases of brain damage in which the neural systems subserving the two forms of memory are differentially impaired. As an illustration, consider the case of K.C.

K.C., a man born in 1951, suffered a motorcycle accident in 1981 that extensively but highly selectively damaged his brain. Although his other cognitive functions--perception, short-term memory, language, thought--are quite normal, he cannot remember, in the sense of episodic memory (bringing back to autonoetic awareness) a single thing that he has ever done or experienced in the past (13). His short-term memory allows him access to happenings from the last few minutes of his life. Beyond this very narrow temporal window his anterograde amnesia for personal events is as severe as that observed in any amnesic patient, including H.M. (60). In addition, K.C.'s retrograde amnesia for personal happenings extends back all the way to his birth. (The case has been described in more detail elsewhere, 12, 42, 61, 62).

Yet K.C.'s semantic memory is reasonably intact. He does know many things about the world: the semantic knowledge he had acquired before his accident is largely intact. He knows who Louis Armstrong was, where the Sahara desert is, why dark-colored clothes are warmer than light-colored clothes, the difference between stalagmites and stalactites, the definition of "spiral mandrel," and thousands of other such "facts of the world." Part of his preserved knowledge has to do with his own past life: He knows things about himself and his past. Thus, not only does he know that his family owns a summer cottage, its location, and the fact that he has spent many summers and weekends there; he also knows that he owned a personal car, and its make and year. But this kind of "autobiographical" knowledge is all impersonal knowledge. It is knowledge of aspects of one's life from the point of view of an observer rather than that of a participant. It is rather similar to the knowledge one possesses about other people and their lives.

These kinds of dissociations between episodic remembering and semantic knowing originating in the patient's premorbid life support the idea that the two functions are subserved by separate neurocognitive systems. But they are not decisive, because the observations can be accounted for without recourse to the postulation of different underlying systems. Experimental findings regarding the acquisition of new information by memory--impaired patients are more telling.

In one extensive study of the amnesic patient K.C., we obtained highly consistent evidence of his ability to learn new semantic knowledge and to retain it, as far as we could tell, normally over a long interval of time (42). In another experiment (61), we also caught a glimpse of the reasons why in many previous investigations such new semantic learning has been declared to be beyond the capabilities of amnesic patients. In the study of K.C.'s ability to learn new semantic information (42), we taught him 64 three-word sentences (such as STUDENT WITHDREW INNUENDO) over a number of widely distributed learning trials. We then tested K.C. for his learning over a number of sessions, with both word fragments (IN - U - - D - for INNUENDO) and with the two-word "sentence frame" (e.g. STUDENT WITHDREW ---------). It is important to keep in mind that at no time did K.C. remember any of the previous learning sessions or the visits to the laboratory. When we gave him the sentence frames at test, we did not ask him to produce the third word that he had previously learned, because he could neither remember any previous learning of the sentences nor could he recognize the sentences as familiar. Instead we simply asked him to provide a third word that would represent a meaningful completion of the whole sentence.

At the end of the training, K.C. could complete 70 per cent of the graphemic fragments of the 64 target words. This high level contrasts with the 12 per cent completion performance before training, and illustrates his capabilities in perceptual priming. His primed fragment completion performance remained at a high 69 per cent over the following 12-month period, in the absence of any interpolated training or testing. His sentence completion performance at the end of the training was 59 per cent, and a year later it was still 39 per cent, suggesting rather normal forgetting.

An important finding from the study just described (42), apart from K.C.'s demonstrated capability of learning new facts, was that of stochastic independence between perceptual priming and semantic learning: the target words that he had learned to complete to fragments were different from those that he had learned to produce in the sentence completion test.

Data from another experiment with K.C. (61) suggested that the success of K.C.'s semantic learning was at least partly attributable to the method we used. The tests administered to K.C. during the multiple distributed learning trials were such that they largely eliminated incorrect, potentially interfering, responses to sentence frames, resulting in "errorless" learning. As normal subjects suffer less from interference than do memory-impaired individuals, these results suggest that normal subjects' intact episodic memory allows the learner to overcome interference and to correct errors in a fashion not possible for amnesic subjects. At any rate, minimization of interference seems to be an important determinant of semantic learning by amnesics. (It is worth mentioning that in a study that Suzanne Corkin and I conducted at MIT with H.M., a study comparable in many ways to that done with K.C., H.M. did not show any evidence of new semantic learning.)

The single-case experiments with K.C. provide a graphic illustration of a three-way dissociation among (1) remembering of events (totally lacking in K.C.), (2) acquisition of new "facts of the world" (possible for K.C., even if much more slowly and laboriously than in normal learners), and (3) perceptual priming (K.C. at least as proficient as average university students). What is especially relevant here is the sharp contrast between semantic learning and retention on the one hand, and the absence of any episodic remembering on the other hand, because the implications of these kinds of dissociations are not yet fully appreciated. In support of the findings with K.C., other evidence has been reported that speaks to the issue of the separability of, and the relation between, semantic and episodic forms of memory (4, 13), and there are reports of other patients who have exhibited similar dissociations between more impaired remembering of personal events and less impaired general knowledge (63-65). Perhaps the most significant observation is that there is considerably more relevant evidence available today than there was only ten years ago (42). It is the slow but steady increase in this kind of evidence that encourages us to entertain thoughts that the distinction between episodic and semantic memory is biologically real.

It is assumed here that the medial temporal lobe and diencephalic structures--damage to which frequently produces amnesia (3, 66)--are critical for operations such as encoding and consolidation of information in the semantic memory system, even if they are not critical for retrieval. To the extent that episodic memory depends on the semantic system they are also critical for the corresponding episodic memory operations. It is also assumed that certain prefrontal cortical areas play a special additional role in remembering of aspects of personal experiences, such as temporal sequencing of events (67-69). At Toronto we are currently exploring the hypothesis that the frontal pole regions (Brodmann Area 10) are involved in episodic memory. Area 10 is a promising candidate region in the quest for localization of episodic memory, because, like episodic memory, it has evolved recently, it is rather different in humans than monkeys, it has appropriate connections to the limbic system, including the amygdala, and its function or functions are largely unknown (D. Pandya, personal communication, May 20, 1993). Ontogenetically, myelination is completed last in association areas, including the prefrontal cortex (70).

SPI MODEL OF ORGANIZATION OF MEMORY

The kinds of findings that have been briefly reviewed in this paper, and ideas that have emerged from them, allow us to speculate about a problem that has recently moved to the center stage: What is the nature of the interrelations between and among different memory systems?

The problem demands a reconciliation between two sets of seemingly conflicting ideas that many people, justifiably, now hold about different memory systems. One set concerns the separability, distinctness, or independence of systems. A certain degree of autonomy is a necessary precondition of the separate functions that different memory systems serve (71). Such presumed autonomy also implies separability at the level of neural substrates. The other set of ideas, equally reasonable and sensible, has to do with the interaction among the systems. It is an almost universal belief that most, if not all, memory tasks that are continually carried out in the course of ongoing behavior of the individual are accomplished through the close cooperation among many systems. Interaction and cooperation imply interdependence? So, are different systems independent or interdependent?

On the basis of the kinds of data reported in this paper and a good deal of other evidence, it is possible to suggest a simple, general, abstract model of organization of memory that takes us a step closer to answering this question. It is referred to as the SPI model. SPI stands for "serial, parallel, and independent." Its central assumption is that the nature of relation among different cognitive systems is process-specific: the relations among systems depend on the nature of the processes involved. Specifically it is assumed: (1) Information is encoded into systems serially, with encoding in one system being contingent on the successful processing of the information in some other system, that is, with the output from one system providing the input into another. (2) Information is stored in different systems in parallel. The information in each system and subsystem, even if it all originates in one and the same act of perception, or a "study episode," is different from that in others, its nature being determined by the nature of the original information and the properties of the system. Thus, what appears to be a single act of encoding--a single glance at a visual display, or a single short learning trial--produces multiple mnemonic effects, in different regions of the brain, all "existing" (available for potential access) in parallel. (3) Information from each system and subsystem can be retrieved without any necessary implications for retrieval of "corresponding" information in other systems. In this sense retrieval is independent.

Table 3

Process-specific relations among cognitive memory systems

Process	Relation
Encoding	Serial
Storage	Parallel
Retrieval	Independent

The SPI model holds that when an event such as the presentation of an unfamiliar but meaningful sentence occurs, information about different aspects of it is registered in multiple memory systems. Information embodying the structural features of constituent stimulus objects (words) is registered in the perceptual representation (word form) systems: this information tells the brain about the kinds of objects that are "out there." The products of the processing in PRS can be retrieved, as happens in priming experiments, or they can be forwarded to the semantic systems for more elaborate processing of the relations among the words and their meaning. The output of the semantic system tells the brain about the contingencies of the world. This output is normally also forwarded to the episodic system, that further elaborates the information by computing its temporal-spatial contextual co-ordinates in relation to already existing episodic information, or the "self."

Thus, the overall information generated by a "single" event is distributed throughout the brain, with different aspects of the information coded in their own specific, possibly unique, form in different regions. Whether or not the information within a given system is tightly localized or more widely distributed remains a moot point.

The SPI model providers tentative answers to a number of questions that can be asked about the relation between and among systems: In what sense are memory systems and subsystems independent? In what sense are they interdependent? How dow they interact? Do they operate in series? Is information entered into, or retrieved from, one system through another? Do they operate in parallel? The model proposes that different systems are dependent on one another in the operations of interpreting, encoding, and initial storing of information. (Interpreting and encoding here apply to all incoming information, including that held by retrieval instructions and retrieval cues.) And it proposes that once encoding has been completed, information is held in many different systems "in parallel" and can be retrieved from different systems independently of what happens in other systems.

The SPI model helps us to make sense out of a number of known facts. Some of the examples are: (1) Various dissociations between priming and explicit tests of memory, including observations of stochastic independence. (2) The impossibility of certain kinds of double dissociations in situations involving acquisition of information, coupled with the possibility of corresponding double dissociations in situations involving retrieval of already existing information. (3) The possibility of new semantic learning in the absence of remembering of the learning. (4) The fact that neural structures necessary for acquisition of new information are not always necessary for retrieval. (5) The fact that certain pharmacological agents affect acquisition of new knowledge but not retrieval of existing knowledge. The evidence for all of these and many other comparable statements is extensive, but its discussion is beyond the scope of the present paper.

The SPI model is highly abstract. No specific neuroanatomical or neurophysiological implications are claimed. It is compatible with many possible more concrete neurobehavioral and neurocognitive models. We can replace any one of the abstract "systems" in the model with a corresponding (known or assumed) neural structure--such as the hippocampal structure--without changing the basic logic. The basic assumptions of process-specific relations among systems should remain valid: encoding is serial, storage is parallel, and retrieval can be independent.

The SPI model represents an extension and elaboration of earlier ideas concerning the relations among memory systems, especially the conjecture that, contrary to popular views, episodic memory evolves and develops later than, and in its operations depends on, semantic memory (4). It has a number of affinities to other theories of organization of memory. Thus, to give just a few of many possible examples, it shares with Weiskrantz (6) the current concept of five major systems, with Squire (3) the ideas of earlier ("nonhippocampal") and later ("hippocampal") systems, with Johnson (72) the notion of multiple entries of information into different systems, and with Moscovitch (73) the emphasis on the nature of interrelations among memory processes and components.

The SPI model is probably most closely related to Lynch and Granger's (74) "assembly line" model. In this model, too, operations occur in a serial fashion, leading, among other things, to "the expectation that late functions can be dissociably removed without affecting early functions, but that damage to early functions will also damage late functions" (74, p. 196). Lynch and Granger come to their views on the basis of work on long-term potentiation as a possible storage mechanism of olfactory memory in rats, whereas the (mono)hierarchical features of the SPI model were suggested, among other things, by observed dissociations between forms of awareness associated with retrieval of personal and impersonal information in memory pathology. Such a convergence of ideas from "bottom-up" reasoning based on work with animals and "top-down" reasoning based on work with humans may be just an interesting coincidence. But there is a possibility that it will turn out to be more than that, perhaps even a genuine insight into how evolution has built the complex machinery of biological memory and organized its operations.

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REFERENCES

1 Ebbinghaus H. Über das Gedächtnis. Leipzig: Duncker & Humblot, 1885. (Transl. Dover Publ 1964).

2 Baddeley AD. Working memory. Oxford: Clarendon Press, 1986.

3 Squire LR. Science 1986; 232: 1612-1619.

4 Tulving E. Human Neurobiol 1987; 6: 67-80.

5 Tulving E. In: Squire L, Lynch G, Weinberger NM, McGaugh JL, eds. Memory: Organization and locus of change. New York: Oxford University Press, 1991; 3-32.

6 Weiskrantz L. Human Neurobiol 1987; 6: 93-105.

7 Squire LR. Ann Rev Neurosci 1982; 5: 241-273.

8 Tulving E. Elements of episodic memory. Oxford: Clarendon Press, 1983.

9 Graf P, Schacter DL. J Exp Psychol Learn Mem Cognit 1985; 11: 501-518.

10 Schacter DL, Chiu CYP, Ochsner KN. Ann Rev Neurosci 1993; 16: 159-182.

11 Roediger HL III, McDermott KB. In: Boller F, Grafman J, eds. Handbook of Neuropsychology. Amsterdam: Elsevier, 1993; 63-131.

12 Tulving E. Can Psychol 1985; 25: 1-12.

13 Tulving E. Curr Direct Psychol Sci 1993; 2: 67-70.

14 Richardson-Klavehn A, Bjork RA. Annu Rev Psychol 1988; 39: 475-543.

15 Schacter DL, Tulving E. In: Schacter DL, Tulving E, eds. Memory Systems 1994. Cambridge, MA: MIT Press, in press.

16 Biederman I, Cooper EE. J Exp Psychol Learn Mem Cognit 1992;18: 121-133.

17 Ellis AW, Young AW, Flude BM. Q J Exp Psychol 1990; 42A:495-512.

18 Schacter DL, Cooper LA, Tharan M, Rubens AB. J Cognit Neurosci 1991; 3: 117-130.

19 Srinivas K. J Exp Psychol Learn Mem Cognit 1993; 19: 582-602.

20 Meyer DE, Schvaneveldt RW. J Exp Psychol 1971; 90: 227-234.

21 Neely JH. J Exp Psychol Gen 1977; 106: 226-254.

22 Challis BH, Chiu CY, Kerr SA, Law J, Tulving E. Memory, in press.

23 Tulving E, Schacter DL. Science 1990; 247: 301-306.

24 Tulving E, Schacter DL, Stark HA. J Exp Psychol Learn Mem Cognit 1982; 8: 352-373.

25 Schacter DL. Ann NY Acad Sci 1990; 608: 543-571.
26 Roediger HL III, Weldon MS, Stadler MA, Riegler GH. J Exp Psychol Learn Mem Cognit 1992; 18: 1251-1269.
27 Bassili JN, Smith MC, MacLeod CM. Q J Exp Psychol 1989; 41A:439-453.
28 Cooper LA, Schacter DL, Ballesteros S, Moore C. J Exp Psychol Learn Mem Cognit 1992; 18: 43-57.
29 Watkins MJ, Peynircioglu ZF. J Verb Learn Verb Behav 1983; 22: 385-394.
30 Smith MC. J Exp Psychol Learn Mem Cognit 1991; 17: 234-244.
31 Hyde TS, Jenkins JJ. J Exp Psychol 1969; 82: 275-292.
32 Craik FIM, Tulving E. J Exp Psychol Gen 1975; 104: 268-294.
33 Jacoby LL, Dallas M. J Exp Psychol Gen 1981; 110: 306-340.
34 Graf P, Mandler G. J Verb Learn Verb Behav 1984; 25: 553-568.
35 Challis BH, Sidhu R. J Exp Psychol Learn Mem Cognit 1993; 19:115-127.
36 Bowers JS, Schacter DL. J Exp Psychol Learn Mem Cognit 1990;16: 404-416.
37 Gardiner JM. Br J Psychol 1989; 80: 163-168.
38 Madigan S, McDowd J, Murphy D. Bull Psychon Soc 1991; 29: 189-191.
39 Jacoby LL, Witherspoon D. Can J Psychol 1982; 32: 300-324.
40 Gardiner JM, Dawson AJ, Sutton EA. Am J Psychol 1989; 102:295-305.
41 Sloman SA, Hayman CAG, Ohta N, Law J, Tulving E, J Exp Psychol Learn Mem Cognit 1987; 14: 223-239.
42 Tulving E, Hayman CAG, Macdonald CA. J Exp Psychol Learn Mem Cognit 1991; 17: 595-617.
43 Craik FIM, Jennings JM. In: Craik FIM, Salthouse TA, eds. Handbook of aging and cognition. Hillsdale, NJ: Erlbaum, in press.
44 Light LL, Singh A, Capps JL. J Clin Exp Neuropsychol 1986; 8: 62-74.
45 Mitchell DB. J Exp Psychol Learn Mem Cognit 1989; 15: 31-49.
46 Naito M. J Exp Child Psychol 1990; 50: 462-484.
47 Parkin AJ, Streete S. Br J Psychol 1988; 79: 361-369.
48 Danion J-M, Zimmermann M-A, Willard-Schroeder D, et al. Psychopharmacology 1989; 99: 238-243.
49 Ghoneim MM, Mewaldt SP. Anesthesiology 1990; 72: 926-938.

50 Brown MW, Brown J, Bowes JB. Q J Exp Psychol 1989; 41A:599-617.
51 Graf P, Squire LR, Mandler G. J Exp Psychol Learn Mem Cognit 1984; 10: 164-178.
52 Shimamura AP. Q J Exp Psychol 1986; 38A: 619-644.
53 Warrington EK, Weiskrantz L. Nature 1970; 228: 628-630.
54 Paller KA. J Exp Psychol Learn Mem Cognit 1990; 16: 1021-1032.
55 Rugg M. In: Gazzaniga MS, ed. The Cognitive Neuroscience. Cambridge, MA: MIT Press, in press.
56 Petersen SE, Fox PT, Posner MI, et al. Nature 1988; 331: 585-589.
57 Warrington EK, Taylor AM. Perception 1978; 7: 695-705.
58 James W. Principles of psychology. New York: Holt, 1890.
59 Tulving E. Episodic and semantic memory. In E.Tulving & W. Donaldson (Eds.), Organization of memory, (pp. 381-403). New York: Academic Press, 1972.
60 Corkin S. Semin Neurol 1984; 4: 249-259.
61 Hayman CAG, Macdonald CA, Tulving E. J Cognit Neurosci; in press.
62 Tulving E, Schacter DL, McLachlan DR, Moscovitch M. Brain Cognit 1988; 8: 3-20.
63 Markowitsch HJ, Calabrese P, Haupts M, et al. J Clin Exp Neuropsychol in press.
65 Cermak LS, O'Connor M. Neuropsychologia 1983; 21: 213-234.
66 Squire LR. J Cognit Neurosci 1992; 4: 232-243.
67 Schacter DL. Psychobiology 1987; 15: 21-36.
68 Milner B, Petrides M, Smith ML. Human Neurobiol 1985; 4: 137-142.
69 Janowsky JS, Shimamura AP, Squire LR. Neuropsychologia 1989; 27: 1043-1056.
70 Fuster JM. The Prefrontal Cortex. New York: Raven, 1980.
71 Sherry DF, Schacter DL. Psychol Rev 1987; 94: 439-454.
72 Johnson MK. In J.L. McGaugh, N.M. Weinberger, & G. Lynch (Eds.), Brain organization and memory: Cells, systems, and circuits, (pp. 106-134). New York: Oxford University Press, 1990.
64 Kapur N, Ellison D, Smith MP, et al. Brain 1992; 115: 73-85.
73 Moscovitch M. J Cognit Neurosci 1992; 4: 257-267.
74 Lynch G, Granger R. J Cognit Neurosci 1992; 4: 189-199.