COMMENTARY

Episodic and Declarative Memory: Role of the Hippocampus

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ABSTRACT: The fact that medial temporal lobe structures, including the hippocampus, are critical for declarative memory is firmly established by now. The understanding of the role that these structures play in declarative memory, however, despite great efforts spent in the quest, has eluded investigators so far. Given the existing scenario, novel ideas that hold the promise of clarifying matters should be eagerly sought. One such idea was recently proposed by Vargha-Khadem and her colleagues (Science 1997; 277:376–380) on the basis of their study of three young people suffering from anterograde amnesia caused by early-onset hippocampal pathology. The idea is that the hippocampus is necessary for remembering ongoing life's experiences (episodic memory), but not necessary for the acquisition of factual knowledge (semantic memory). We discuss the reasons why this novel proposal makes good sense and why it and its ramifications should be vigorously pursued. We review and compare declarative and episodic theories of amnesia, and argue that the findings reported by Vargha-Khadem and her colleagues fit well into an episodic theory that retains components already publicized, and adds new ones suggested by the Vargha-Khadem et al. study. Existing components of this theory include the idea that acquisition of factual knowledge can occur independently of episodic memory, and the idea that in anterograde amnesia it is quite possible for episodic memory to be more severely impaired than semantic memory. We suggest a realignment of organization of memory such that declarative memory is defined in terms of features and properties that are common to both episodic and semantic memory. The organization of memory thus modified gives greater precision to the Vargha-Khadem et al. neuroanatomical model in which declarative memory depends on perihippocampal cortical regions but not on the hippocampus, whereas episodic memory, which is separate from declarative memory, depends on the hippocampus. *Hippocampus 1998;8:198–204.* © 1998 Wiley-Liss, Inc.

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INTRODUCTION

Memory systems in all mammals are complex, and in humans they are especially so. Scientific study of such systems usually proceeds by tiny increments of knowledge and understanding of their properties and workings. Major breakthroughs are rare. Therefore, whenever a truly new discovery is made, it should be considered big news.

One such discovery was recently reported by Vargha-Khadem et al. (1997). These investigators (henceforth abbreviated as V.-K.) studied three young neurological patients of a kind that have not been studied before: patients with focal bilateral hippocampal pathology originating very early in life. The study showed three things. First, all three young people have great difficulty remembering ongoing daily events and experiences, and retaining information learned under the laboratory conditions. Thus, by accepted clinical criteria, all three can be classified as "anterograde amnesic." Second, all three young people have normal or near normal intelligence and have made near-normal progress through school, meaning that they have somehow managed to acquire a great deal of concrete and abstract knowledge about the world. Third, careful radiological examination revealed more-or-less severe bilateral hippocampal pathology, while other brain structures, including perihippocampal cortex, seemed to be normal.

Because of the novelty of the V.-K.'s findings, and their potentially important impact on the theory of memory and memory impairment, the findings deserve careful attention and analysis. The present multiple discussion of the V.-K. report organized by the Editor of *Hippocampus,* Howard Eichenbaum, will not only alert students of memory to the important work described by V.-K. but also serve to encourage their participation in what can be expected to become a spirited controversy. The discussion joins two previous commentaries on the V.-K. article (Eichenbaum, 1997b; Gaffan, 1997).

THE NOVEL FINDINGS

The overall picture that emerges from the V.-K. study is that of individuals with early-onset hippocampal

damage whose memory impairment manifests itself in the severe difficulty of remembering ongoing experiences. Because the radiologically detectable brain damage was limited to the bilateral hippocampus, whereas other brain regions, including temporal lobes, appeared to be normal, V.-K. attributed the behavioral impairment to hippocampal pathology. All this, of course, is as it should be, in excellent agreement with current textbook knowledge and understanding of memory and amnesia: hippocampal damage causes memory impairment.

The unexpected finding is the other half of the overall picture: the apparently normal or near-normal intellectual development of the three young people. They have mastered both spoken and written language, and amassed an impressive amount of factual information about the world. Their knowledge of the world allows them to perform satisfactorily on standard intelligence tests, and their ability to acquire such knowledge allows them to keep up with many of their age-mates at school. Thus, the three patients of V.-K. have accomplished something that for a long time has been thought to be impossible in anterograde amnesia: they have managed to learn and retain a lot of declarative information.

These findings are novel in three ways. First, no well-documented cases of early-onset amnesia have been previously reported for patients whose underlying brain pathology has been precisely delineated (cf. Wood et al., 1989; Ostergaard and Squire, 1990). Second, the anatomical model proposed by V.-K.—that the hippocampus is necessary for remembering past experiences and the remaining medial temporal lobe (MTL) regions are necessary for the learning of factual information—is unprecedented. Although many models of hippocampal memory have been described in the literature (e.g., Teyler and DiScenna, 1986; Alvarez and Squire, 1994; Eichenbaum, 1994; Horel, 1994; McClelland et al., 1995; Nadel, 1995; Bear and Abraham, 1996; Cowey and Green, 1996; Hampton and Shettleworth, 1996; Rolls, 1996; Izquierdo and Medina, 1997; Petersson et al., 1997; Redish and Toretzky, 1997), none has much similarity to V.-K.'s model. Third, V.-K.'s interpretation of their findings is important, because it goes to the very heart of a fundamental question concerning the organization of memory: How do we conceptualize declarative memory, and how is it related to amnesia?

V.-K.'s interpretation runs clearly counter to what we will refer to as the theory of (unitary) declarative memory, advocated by a number of theorists (e.g., Squire and Knowlton, 1995; Squire and Zola, 1996; Cohen et al., 1997) and further defended by Squire and Zola in this issue. It defines anterograde amnesia as an impairment of declarative memory in which the operations of episodic and semantic memory are equally affected. This impairment in remembering ongoing experiences and in learning of new facts results from damage to the MTL memory system, and is proportional to the extent of the damage. The following summary statement provides the essential flavor of the idea: "[The] pattern of results is also easily accommodated by a *single-function view* whereby declarative memory function depends on all the structures of the hippocampal system. More complete damage to the system produces more severe memory impairment" (Squire et al., 1994:496, emphasis added). Once this position is accepted, and granted, there are essentially only two ways of interpreting cases

such as those reported by V.-K.: 1) because their episodic and semantic memory show differential impairment, the patients are not typical of anterograde amnesia, or 2) because their syndrome is that of anterograde amnesia, these episodic and semantic memory must be equally impaired. Squire and Zola (this issue) have opted for the latter alternative. Their basic argument is that V.-K.'s patients may have *some* preserved episodic memory capability to enable them, slowly and laboriously, to acquire and retain factual knowledge.

A variation on the basic theme of the unitary declarative memory theory has been proposed by Eichenbaum and his colleagues (Eichenbaum et al., 1994, 1996; Eichenbaum, 1997a). This variation retains the idea that declarative memory comprises both learning of facts and remembering of events, but incorporates a division between two kinds of declarative memory, supported by different components of the MTL memory system. The hippocampus supports the processes involved in the creation and use of flexibly accessible relational representations, whereas the underlying cortical regions (entorhinal, perirhinal, and parahippocampal cortices, which collectively are referred to as "parahippocampal region" by Eichenbaum) support the less flexible learning of individual representations.

V.-K.'s findings fit neither version of the declarative theory. They are more compatible with what we will refer to as the "episodic" theory. In this essay we will try to explain how and why.

ISSUES AT STAKE

It is important that we be as clear as possible about where the conflict lies between declarative and episodic theories. There are three kinds of closely related issues involved. They have to do with: 1) organization of human memory, 2) the relation of this organization to memory impairment seen in amnesia, and 3) the cerebral systems that underlie the organizational structure and functions. We limit the coverage of these complex matters to those directly related to the V.-K. findings and their interpretation. Thus, under "organization" we consider only declarative, semantic, and episodic memory; under "impairment" we stay close to clinically defined amnesia; and under "cerebral systems" we discuss only the MTL region. We briefly summarize the conflicts first, and then discuss them at greater length.

Organization

Squire and Zola view the episodic memory and semantic memory as two parallel side-by-side subsystems of declarative memory that can be differentiated in terms of the kind of information they deal with, personal events vs. general facts. We have also thought of episodic and semantic memory as two subsystems of declarative memory, although not as parallel subsystems. We view episodic memory as a unique extension of semantic memory. The two systems share many features, but episodic memory has additional capabilities that semantic memory does not. The relation between the two subsystems of declarative
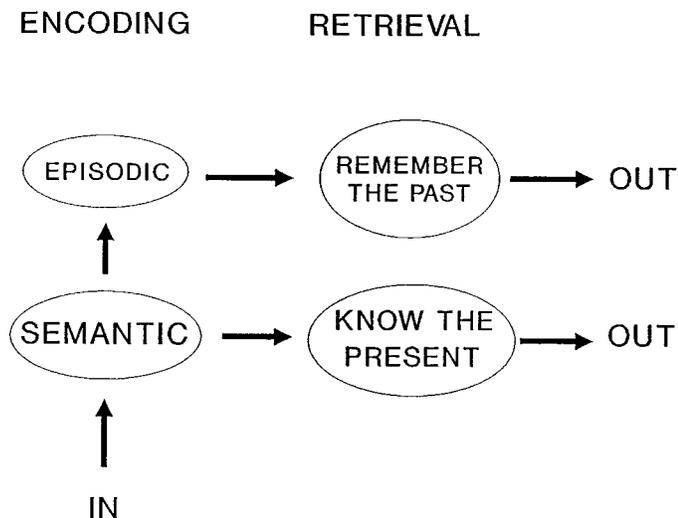
ENCODING   RETRIEVAL

FIGURE 1. **Sketch of the relations between semantic and episodic memory as envisaged by the SPI model. Information can be encoded into semantic memory independently of episodic memory, but must be encoded into episodic memory 'through' semantic memory. Encoded and stored information is potentially available for retrieval from one of the two systems, or from both of them.**

memory initially sketched in terms of the "embeddedness" hypothesis (Tulving, 1984:260) and later refined as the Serial Parallel Independent (SPI) model (Tulving, 1993a, 1995), is process-specific, that is, dependent on the processes. Encoding of information into the episodic system depends critically on the semantic system whereas encoding of information into the semantic system could not operate without it. In retrieval of stored information, on the other hand, the basic operations of the two systems are independent of each other: retrieval can be supported by either of the two systems, or both of them. Figure 1 presents a schematic outline of the basic propositions of the SPI model as applied to episodic and semantic memory. An important point that the model makes is that only single dissociations are possible in encoding, whereas both single and double associations are possible in retrieval (Tulving, 1995). Its structure can also be seen as isomorphic with the basic elements of V.-K.'s neuroanatomical model.

Amnesia

In the declarative theory, episodic and semantic memory are equally impaired in amnesia. Thus, there is only one kind of amnesic patients, and they have equal difficulties with "event memory" and with "fact memory." In the episodic theory, on the other hand, matters are again a bit more complex, as summarized by the SPI model (Tulving, 1995). With respect to anterograde amnesia, the episodic theory holds that an organism (i) can acquire factual information about the world regardless of how impaired its episodic system is, but (ii) its remembering of ongoing experiences depends on the degree of damage to either the semantic or the episodic system. Thus, there can be at least two kinds of anterograde amnesics: those who have similar difficulties with remembering of experiences and with learning of facts (Squire, 1987; Wilson et al., 1995) and those whose ability to

remember experiences is more impaired than their ability to learn new facts (Vargha-Khadem et al., 1997; Hayman et al., 1993). The episodic theory also rules out as impossible a form of anterograde amnesia in which semantic memory is impaired (or more impaired) while episodic memory is intact (or less impaired). With respect to retrograde amnesia, the episodic theory, like the declarative theory, is quite comfortable with equal impairment of the two systems. But unlike declarative memory that precludes any dissociation between episodic and semantic memory, the episodic theory allows both single and double dissociations. Thus, in retrograde amnesia episodic memory may be more impaired and semantic memory not impaired or less impaired (Hayman et al., 1993; Markowitsch et al., 1993b; Verfaellie and Cermak, 1994; Kihlstrom 1995), or semantic memory may be more impaired and episodic memory not impaired or less impaired (DeRenzi et al., 1987; Yasuda et al., 1997). According to the declarative theory such asymmetry of retrieval cannot occur.

Neuroanatomy

Until now, both episodic and semantic theories have held that declarative, semantic, and episodic forms of memory are all crucially dependent on the MTL memory system. There has also been good agreement on the additional role for the frontal lobes in episodic memory that it may not quite have in semantic memory. Until recently, episodic theory was quite vague on relevant neuroanatomical details, because of lack of appropriately relevant neuropsychological data. Therefore, no specific neuroanatomical models of episodic memory have been proposed. Squire and Zola, on the other hand, as we mentioned earlier, have postulated that the impairment of declarative memory is proportional to the extent of the damage of the hippocampal system.

We see then that V.-K.'s interpretation is closer to the episodic theory than the declarative theory. The episodic theory allows learning of factual information in the absence of episodic memory, whereas declarative theory does not. And the episodic theory, in addition to equal impairment of remembering of events and learning of facts, allows a situation to arise in which remembering of events is more severely impaired than is learning of facts. V.-K.'s patients nicely illustrate the reality of this possibility, adding to a number of other cases that have presented a similar clinical picture (Hayman et al., 1993; Verfaellie and Cermak, 1994; Kihlstrom, 1995; Van Der Linden et al., 1997; Markowitsch et al., 1993b).

The anatomical model proposed by V.-K.—that the hippocampus is necessary for episodic but not semantic memory—constitutes an important addition to the existing episodic theory. We now propose to reformulate the theory, and accept the V.-K.'s suggestion that the hippocampus is necessary for episodic memory but not declarative memory. In order to do so clearly, however, it is necessary that we realign the existing organization of declarative memory. The central proposal is to separate episodic memory from declarative memory.

Until now, episodic and semantic memory have been conceptualized as two subsystems of declarative memory (Tulving, 1983; Squire, 1987) and the disagreement has had to do with the issues we have just discussed. The new suggestion is that "declarative memory" be defined in terms of properties and features that are

common to semantic and episodic memory, and that "episodic memory" be defined in terms of features that "declarative" ("semantic") memory does not have. We point to the advantages of this realignment as we proceed with the debate.

DECLARATIVE MEMORY: OVERLAP BETWEEN EPISODIC AND SEMANTIC MEMORY

Episodic memory originally (Tulving, 1972) was defined as a memory system that had to do with learning and retention of material presented in a particular place at a particular time, such as in typical memory experiments in the laboratory. Many writers are still using episodic memory in this sense (Gaffan, 1997; Garrard et al., 1997; Maguire et al., 1997). The concept, however, has undergone considerable changes in its development, and today means something rather different from what it did a quarter century ago (Tulving, 1993b; Schacter and Tulving, 1994; Tulving, 1995; Wheeler et al., 1997). When we talk about episodic in what follows, we have in mind its current form.

Episodic (event) memory and semantic (fact) memory do have many features in common (Wheeler et al., 1997). Our proposal here is that the list of these common properties (Schacter and Tulving, 1994) be taken as a property list of declarative memory. That is, we suggest that declarative memory overlap between episodic and semantic memory. The common properties are the following:

1. Both episodic and semantic memory systems (Schacter and Tulving, 1994) are large, complex, highly structured, and both can hold practically unlimited amounts of information (Dudai, 1997).

2. Both can receive information for storage through different sensory modalities (Markowitsch et al., 1993a), as well as from internally generated sources (Johnson and Raye, 1981).

3. The processes involved in encoding of information "into" long-term storage are quite similar for both episodic and semantic memory. Frequently a single experience of an event, or a single exposure to a fact, is sufficient for such storage.

4. Stored information in both systems is "representational": the information is functionally isomorphic with what is, or could be, in the world.

5. Stored information in both systems is "propositional," in the sense that an intelligent observer can describe it, and its expression, symbolically.

6. Information in both systems has truth value (it either matches or does not match a state of affairs in some other system, such as the external world), unlike information supporting many other forms of learned behavior that have no such value.

7. Information in both systems is accessible flexibly, through a wide variety of retrieval queries and routes, and can be expressed flexibly, through a variety of signs and or behaviors.

8. Information in either system can be used as a basis of inferences (Tulving, 1984).

9. Processing (encoding, storing, retrieval) of information is highly sensitive to context. For example, both systems are governed by basic principles such as encoding specificity and transfer-appropriate processing (Tulving, 1983; Roediger et al., 1989).

10. Both systems are "cognitive" as distinguished from "behavioral": products of retrieval can be consciously (introspectively) contemplated or "thought about."

11. Behavioral (overt) expression of the products of retrieval in both systems is optional rather than obligatory. (It is one way in which cognitive systems differ from procedural memory in which retrieval is always expressed through overt behavior.) Retrieved information from either system can guide behavior although it need not to.

12. Both systems interact closely with other brain/behavior systems, such as language (in humans), emotion, affect, and reasoning.

Defining declarative memory in terms of these common properties, we can say that it is 1) large and complex, 2) multi-modal, and 3) characterized by similar, fast, encoding operations. Information in it 4) is representational, 5) propositionally describable, 6) has truth value, 7) is accessible and expressible flexibly, and 8) can serve as a basis of inferences. Its operations are 9) context sensitive, and 10) cognitive. Finally, 11) the products of be retrieval of declarative memory need not, although they can, be expressed in overt behavior, and 12) it interacts closely with other brain/behavior systems.

This property list of declarative memory corresponds closely to how the proponents of the declarative theory have written about it (Squire, 1987; Hamann and Squire, 1995; Knowlton and Squire, 1995; Squire and Zola, 1996; Cohen et al., 1997; Eichenbaum, 1997a). One of the advantages of the proposed description of declarative memory is that its definition holds equally well for humans and nonhuman animals. With the exception of a few minor details, and overlooking references to language, the listed properties can be reasonably attributed to declarative memory of all species capable of learning facts about their world. An important corollary of this fact is that declarative memory, as defined, satisfies one of the logical requirements for the foundation of usefulness of animal models of memory: declarative memory is reasonably homogeneous across the species. Therefore, as long as one works within the domain of the declarative memory as defined, data from animal experiments can be very useful, and animal models of human memory entirely reasonable.

Another advantage of the proposed characterization of declarative memory is that it allows us to reserve the category of semantic memory to language-related declarative memory operations, in keeping with its original definition (Tulving, 1972). Everybody knows that language can greatly facilitate the operations of most memory systems, including declarative and episodic, but because language is not necessary for declarative memory, the terminological distinction helps to clarify matters.

UNIQUENESS OF EPISODIC MEMORY

A crucial point about declarative memory as described is that it lacks certain properties that episodic memory has (Tulving,

1993b, 1995; Wheeler et al., 1997). Indeed, as no other memory system has these properties, episodic memory can be regarded as unique. We describe these properties and compare them with the properties of declarative memory as defined above.

1. Episodic and declarative memory differ with respect to their function. Episodic memory is concerned with remembering past experiences as such. This is the crux of episodic memory: it has to do with conscious recollection of previous *experiences* of events, happenings, and situations. The emphasis is on "experience," rather than "event" or "happening." Declarative memory, on the other hand, is concerned with facts and events of the physical world, that is, with the acquisition and use of the knowledge of what is what, or what could be in the world, and what is appropriate behavior in a given situation.

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

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

4. The relation between remembering and knowing is one of embeddedness: episodic remembering always implies semantic knowing, whereas knowing does not imply remembering (Tulving, 1984). If one remembers that on the last trip to London it rained for three days straight, one knows that English weather can be wet. But if one knows that summer days are hot in the Sahara desert, one need not remember having ever been there.

5. The relations between episodic and memory systems, as already mentioned (Tulving, 1995) and as shown in Figure 1, are "process-specific": serial (S) encoding, parallel (P) storage, and independent (I) retrieval. Note that information gets "into" episodic memory only "through" semantic memory, although common sense holds the contrary view: information gets "into" semantic memory "through" episodic memory.

6. Episodic lags behind declarative memory in human development. Young children acquire a great deal of knowledge about their world before they become capable of adult-like episodic remembering (Pillemer and White, 1989; Perner and Ruffman, 1995).

7. Episodic memory is more vulnerable than declarative memory to a number of pathological conditions of the brain (Evans et al., 1993; Duffy and O'Carroll, 1994; Greene et al., 1996), as well as to the normal process of aging (Herlitz and Forsell, 1996; Nilsson et al., 1997).

8. Episodic memory is, arguably, a more recent arrival on the evolutionary scene than declarative memory (Suddendorf and Corballis, 1997). Many animals other than humans, especially mammals and birds, possess well developed knowledge-of-the-world (declarative memory) systems, and are capable of acquiring vast amounts of flexibly expressible information. But there is no evidence that they have the ability to autonoetically remember past events in the way that humans do.

9. Finally, although both episodic and declarative memory depend on MTL and diencephalic structures, and may share other neural resources, it has been known for some time that episodic memory depends on the frontal lobes in a way that declarative memory does not (Schacter, 1987; Squire, 1987). The evidence that episodic and semantic memory processes are correlated with the activity in different cortical circuits has been growing steadily in recent years. For example, semantic retrieval hardly ever, but episodic retrieval very frequently, under conditions where language requirements are held constant, is associated with changes in regional cerebral blood flow in right prefrontal cortex, as shown by brain imaging studies (Fletcher et al., 1995; Nyberg et al., 1996). This episodic right-frontal retrieval activation has been identified with a special episodic retrieval mode, or episodic retrieval attempt, that is absent in semantic-memory retrieval (Fletcher et al., 1996; Maguire et al., 1997; Nyberg et al., 1997).

In summary, episodic memory can be said to be unique to the extent that it possesses features not possessed by any other memory system. Episodic memory is 1) a system that makes possible remembering of previous experiences, 2) the only form of memory oriented towards the past, and 3) associated with autonoetic conscious awareness. It 4) includes but goes beyond knowledge of the world, and 5) its relations to semantic memory are process-specific. Episodic memory 6) develops later than semantic memory in young children, 7) is impaired sooner than semantic memory in old age, 8) is probably unique to humans, and 9) is known associated with selective and unique cortical activity.

It is important to note that this property list of episodic memory holds only for humans. Although the absence of episodic memory in nonhuman animals cannot be empirically proven any more than any other universal negative can, there is no evidence that nonhuman animals do have any episodic-memory capabilities as defined above. The fact that no studies with nonhuman animals have yet demonstrated the difference between episodic memory and declarative memory, as defined, could be rationalized in terms of the animals' lack of the kinds of language abilities that humans need to provide evidence of their ability to remember past events. Such an explanation, however, is far-fetched, based purely on anthropomorphic reasoning that has no scientific value or validity. A more reasonable explanation of the failure to empirically demonstrate any distinction between remembering and

knowing in nonhuman animals is that the distinction does not exist, that animals do not have the same kind of episodic memory as humans do, that their declarative memory corresponds to semantic memory in humans (Murray, 1996), and that their episodic memory is just an analog of human episodic memory (Gaffan, 1992).

CONCLUSIONS

Vargha-Khadem and her collaborators' (1997) interpretation of their findings fits the scheme of memory organization in which episodic and declarative memory are distinct systems. It goes beyond the existing theory, however, in proposing a specific MTL-based neuroanatomical model of the two systems: the hippocampus is necessary for episodic but not declarative memory, whereas the surrounding cortical regions are necessary for declarative memory. This model fits reassuringly into already existing ideas about the organization of memory, and provides a welcome neuroanatomical addition to these ideas. By mapping the intact and impaired process-specific capabilities of the two kinds of memory, episodic and declarative, onto memory pathology specified in terms of a particular pattern of damaged and preserved neuroanatomical sites, the V.-K. model can account for the novel findings in a way that other theories cannot.

Note two points here. First, the crux of the matter lies in the juxtaposition of two propositions: (i) the hippocampus plays an important role, whose nature is still unknown, in enabling the operations of episodic memory, as defined, and (ii) the hippocampus is not necessary for the acquisition of new, normally organized, closely integrated, and flexibly usable declarative knowledge. Either statement alone, taken separately, could be embraced by most existing theories without requiring any unnatural contortions. Together they greatly constrain theoretical freedom, and thus contribute to the progress to our science.

Second, the V.-K. model of memory in the MTL can be tested, and rejected by the data. The simplest and strongest case against the model, one that would be sufficient for its rejection, would be made by patients with focal bilateral hippocampal pathology who have normal episodic memory but who cannot acquire new factual knowledge. Another finding that would be at variance with the episodic model more generally (that is, not just with respect to the VK findings) would be a close positive relation between remembering of recent events and learning of new facts, at the level of individual subjects. No such data have yet been reported.

Although a single study hardly ever provides final proof for any controversial idea, the V.-K. findings add important support to the accumulating evidence from a number of recently described focally brain-damaged patients with selective and specific retrograde amnesia for autobiographical experiences but largely intact semantic memories (Markowitsch, 1995). V.-K.'s neuroanatomical model represents a genuinely new twist in the apparently never-ending saga of the role of "the hippocampus" in memory. The idea that, in humans, the hippocampus plays a special role in episodic but not in declarative memory, whereas the other MTL structures are important for declarative memory, is refreshingly novel and intriguing. Experimenters and theorists should pay careful attention to the V.-K. study and its implications for the advanced understanding of the memory systems of the brain.

Acknowledgments

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