



The hippocampus and declarative memory: cognitive mechanisms and neural codes

Howard Eichenbaum *

Department of Psychology, Boston University, Boston, MA02215, USA

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Abstract

It is widely accepted that the hippocampus and related brain areas mediate declarative (or explicit) memory in humans. However, little is known about the fundamental cognitive mechanisms of hippocampal dependent memory or about the nature of hippocampal neural representations that underlie properties of declarative memory. Here, it is proposed that the hippocampus plays a critical role, when distinct personal experiences must be encoded in relation to one another and linked within an organization that supports flexible, inferential memory expression. This set of fundamental cognitive mechanisms is consistent with key properties of declarative memory as observed in humans. Furthermore, emerging evidence from recordings of hippocampal neural activity shows that hippocampal networks encode episodic memories as sequences of events and the places, where they occur. In addition, hippocampal neuronal networks encode events and places that are common across related episodes. This combination of coding properties suggests that the hippocampus contributes to declarative memory by mediating the construction of a 'memory space' composed of a network of linked episodic representations. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

I am going to do nothing to dispel the widespread notion that the hippocampus plays a focal role in memory. Indeed, consistent with that view, my aim is to understand *how* the hippocampus plays such a role. On the other hand, I do have something to say that 'challenges the focal role of the hippocampus in memory', in three ways. First, I would vigorously challenge any narrow conception that implies the hippocampus is the 'pigeonhole' for memory, i.e., *the* brain module that accomplishes memory. It is abundantly clear that the role of the hippocampus within memory is quite limited in two ways. Specifically, its role is limited to a period between short-term memory and the permanent store and to a particular kind memory processing. Second, I would contest the implication that the hippocampus

mediates any particular form of memory all on its own. The hippocampus makes its contribution as one component of a large memory system composed of several interacting cortical areas [7].

Third, even while supporting the notion that the hippocampus plays a particular role within a particular phase and a particular kind of memory, a focal role in memory is not at all unique to the hippocampus. In a recent monograph, Neal Cohen and I explored in detail the concept of 'multiple memory systems', and concluded that all or nearly all functional systems of the brain contain mechanisms of plasticity by which their operation is modified by experience, and indeed there are several brain systems that subserve different forms of memory. Thus, it can reasonably be argued that nearly all brain structures play a focal role in some aspect of memory processing [8]. Indeed, we argued more grandly that memory should be viewed not as a segregated faculty, but rather as the result of plasticity within each of the brain's information processing systems. Such a view challenges whether 'Does the

* Corresponding author. Tel.: +1-617-353-1426; fax: +1-617-353-1414.

E-mail address: hbe@bu.edu (H. Eichenbaum).

hippocampus play a focal role in memory?’ is even the good question. Instead, our view begs the question, *what* role does the hippocampus (or any other brain area) play in information processing, and how does its plasticity contribute to the phenomenology of memory?

From that perspective, work in my laboratory does not focus on whether the hippocampus is involved in memory; we believe it is part of a brain system in which memory has clear behavioral consequences. Further, our efforts are not simply aimed at what ‘kind of memory’ the hippocampus mediates. Rather, our aims are to understand the fundamental information processing mechanisms of the hippocampus and to identify how the plasticity of these mechanisms contributes to memory. In other words, we seek to get beyond the asking whether the hippocampus is critical to a particular kind of memory (e.g., declarative, episodic, spatial), and instead aim to identify the underlying cognitive mechanisms and neural coding scheme that form the bases of its contribution to behavioral manifestations of memory.

2. Identification of critical role for the hippocampus in memory

The initial discovery of severe and selective amnesia in the patient H.M. provided the first major breakthroughs in understanding the mechanisms of memory in humans at the level of brain systems [24]. A second breakthrough came, when it was realized that even in severe cases of amnesia, there is also a domain of learning and memory capacity that is entirely spared [5]. This advance clarified the nature of amnesia associated with medial temporal damage in humans as a selective deficit in declarative memory, the ability to consciously recollect everyday facts and events and to use declarative memories to solve a variety of problems. Conversely, the collection of spared memory capacities in amnesia are typically characterized as intact acquisition of skills, habits, and dispositions that can be expressed unconsciously via other brain systems through alterations in biases and speed during performance of a large range of memory and non-memory tests [4]. While there are differences in the terminology used to describe these characteristics of impaired and spared memory in amnesia (declarative/procedural, explicit/implicit, etc.), there is a general consensus on the phenomenology of these domains of memory as applied to the findings on humans [23].

By contrast, little is known about the fundamental cognitive mechanisms, the basic psychological and representational elements and dimensions that underlie declarative memory. And perhaps even less is understood about the basic coding mechanisms that hippocampal networks use to mediate the capacity of

declarative memory. A major goal of research in my laboratory is to identify the role of the hippocampus and related structures in declarative memory in terms of the underlying cognitive mechanisms and dimensions, and in terms of information contained in the firing patterns of hippocampal neuronal networks. In the remainder of this paper, I will first provide a brief overview of some early conceptions of declarative memory, and then add to these some of the modern descriptions of basic properties of declarative memory that suggest a set of underlying cognitive mechanisms and dimensions. Then, I will describe experiments in animals that support these hypothetical mechanisms. Next, I will turn to the evidence from recording studies on the activity of hippocampal neurons in behaving animals, and review emerging evidence that hippocampal neuronal networks encode features of experience that would support the putative cognitive mechanisms of declarative memory.

3. A brief history of declarative memory

In his pioneering treatise *Principles of Psychology*, William James [13] distinguished in separate chapters the phenomena of *habit* and *memory*. James considered *habit* a very primitive mechanism that is common among biological systems, and due to plasticity of the organic materials. Within the nervous system, habits were viewed as nothing more than the ready discharge of a well-worn reflex path. But, James also attributed to habit great importance in the development of more complicated behavioral repertoires. He suggested that well practiced behaviors and skills, including walking, writing, fencing, and singing, are mediated by concatenated reflex paths, organized to generate the serial production of movements and unconscious sensations leading to other movements and sensations. He thought of habits as eliminating the need for conscious supervision once a behavior becomes routine and recommended early and frequent reinforcement of good habits as a key exercise in ethical and cognitive development.

James distinguished *memory* (today called declarative memory) as something altogether different from habit, albeit based on that mechanism, a very complicated phenomenon with many facets. He defined memory as ‘the knowledge of an event, or fact, of which meantime we have not been thinking, with the additional consciousness that we have thought or experienced it before.’ (p. 648). In addition to its personal and temporal aspects, the full characterization of memory was framed in terms of two other properties, its structure as an elaborate network of associations and its basis in habit mechanisms. Thus, James theorized a mechanistic basis for how habits could be elaborated for the formation of

multiple and linked associations to support the richness of memory. The underlying foundation of recall was a complex, yet systematic set of associations between any particular item and anything co-occurring in one's previous experiences with the item. He argued that, when we search for a memory, we navigate through the elaborate network of the associations, and if successful locate the sought memory among them. The goodness of memory, he believed, was as much dependent on the number of associations in the network as on the strength of those associations.

Research on memory following James' book in the early 20th century was dominated by the radical 'behaviorists', whose aim was to reduce memory to the elemental 'S-R' mechanisms of habits and, contrary to James' approach, eliminate consideration of elaborate memory networks. But this theme was not universal, and the protagonists of a more complex formulation of memory offered insightful elaborations on James' perspective. Edward Tolman [28] was perhaps the most successful in challenging radical behaviorism, because he developed operational definitions for mentalistic processes including 'purposive behavior' and 'expectancy', while maintaining the general approach of using behavior to understand cognitive mechanisms. Thus, Tolman's goal was to get behind the behavior, not by specifying particular elements of habits or their linkage, but by identifying the complex cognitive mechanisms, purposes, expectations, and insights that guided behavior. Tolman's basic premise was that learning involved the acquisition of *knowledge* about the world, and in particular about relationships among stimuli and between stimuli and their consequences, and that this knowledge led to expectancies, when the animal was put in testing situations. He argued that learning involved the creation of a 'cognitive map' that organized the relations among stimuli and consequences based on interconnections between groups of stimuli, and allowed animals to make generalizations and inferences from memory. While he never viewed the use of cognitive maps as dedicated only to spatial learning, he rigorously tested these ideas using the same species (rats) and maze learning paradigms that were a major focus of the prominent S-R behaviorists. In a series of studies, he showed that rats were capable of solving maze problems by taking novel detours or shortcuts, and they exhibited a capacity for 'latent learning', in which they acquired problem solutions in the absence of reinforcement, capabilities that could not have been mediated by S-R representations.

In the field of studies on human memory, the work of British psychologist Fredric Bartlett [1] starkly contrasted with the rigorous and reductionistic approach introduced by Ebbinghaus years before. Bartlett was primarily interested in the mental processes used to search out and reconstruct memories. He argued that

'real' memory is embedded in the full fabric of a lifetime of experience including prominently one's culture. Bartlett was not so much interested in the probability of recall of specific items (as was Ebbinghaus), but instead focused on the content and structure of the memory recalled. His main strategy was to have subjects read a short folk tale, whose syntax and prose were derived from a culture quite different from that of his British experimental subjects, and for which the contents of the story lacked explicit connections between some of the events and contained dramatic and supernatural events that would evoke vivid imagery. In the reproduction of these stories, Bartlett found that the syntax became more modern and taken from the subject's culture, and the story became more coherent and consequential. From these observations, Bartlett concluded that remembering was not simply a process of recovery or forgetting of items, but rather that memory seemed to evolve over time. Items were not lost or recovered at random. Rather, material that was more foreign to the subject, or lacked sequence, or was stated in unfamiliar terms, was more likely to be lost or changed substantially in both syntax and meaning, becoming more consistent with the subject's common experiences. To account for these observations, Bartlett developed his 'schema' theory. In this view, the simplest schemata were habit-like traces of items in sequential order of experience. But in more complicated situations, representations of related experiences built up en masse, such that particular past events are dated, or placed, in relation to other associated events in a dynamic organization from which one can reconstruct or infer both specific contents of memories and their logical order.

There were many advances over the ensuing years in the 'cognitive revolution', during which radical behaviorism was largely discarded in favor of efforts to understand underlying mental representations, at least in considerations of human memory [20]. This work contributed new concepts about different forms of memory (e.g. working memory, episodic and semantic memory, and more). At the same time, this work has also led to a rediscovery of notions about the rich organization of 'conscious' memory introduced by James, Tolman, and Bartlett. These concepts strongly influenced the interpretation of findings on the neural bases of memory to this day, as will become evident in my considerations below.

4. A working hypothesis about cognitive mechanisms that underlie declarative memory

The above historical summary provides ample convergence of ideas on the central features of declarative memory. This kind of memory involves a record of

everyday experiences woven together into the framework of our knowledge. It supports our capacity to consciously recollect previous events and facts as they can be reconstructed via active processing of the overall memory organization. Our approach to identifying the fundamental cognitive mechanisms of declarative memory is to combine this summary of properties of declarative memory with what is known about memory capacities dependent on the hippocampal region, and then use this information to develop a model for the basic cognitive mechanisms that might be mediated by the hippocampus in support of declarative memory. I will begin with the two most prominent characterizations of declarative memory, and attempt to analyze these characterizations in the light of the views introduced above.

One prominent characterization of declarative memory is that it can be decomposed into episodic and semantic memory, a key distinction from the cognitive revolution offered by Tulving in 1972 [29]. Episodic memory involves the capacity to remember specific personal experiences. These memories contain the detailed sequence of events that constitute an experience and the spatial and temporal context in which the experience occurred. Semantic memory involves the acquisition of world knowledge, an organization of information about the physical features of the world, about the content and meaning of language, social structure, geography, and a myriad of other domains of knowledge. The ability to retain and recall episodic memories is highly dependent on the hippocampus in humans [30]. But the full scope of hippocampal involvement also extends to semantic memory, as demonstrated by the inability of amnesics to acquire and freely employ new word meanings or other specific information [26].

To the extent that the hippocampus plays a role in both episodic and semantic memory, it is worth asking how episodic and semantic memory are related. Here, I will adopt a common view about that relationship (albeit a view somewhat different from Tulving's). We acquire our declarative memories through everyday personal experiences. Thus, episodic memory may be considered the conscious 'gateway' to all memories. Many episodic memories are maintained as such, i.e., as context-specific sequences of events in which one participated. But many of our episodic memories will ultimately not be remembered as such, but rather contribute mainly to the elaboration and modification of the body of general knowledge about the world, semantic memory. According to this view, episodic and semantic memory are closely related—semantic memory is accrued from linking multiple experiences that share some of the same information. Ultimately, semantic memory is a complex network of links between some items that have lost unique episodic information, and links among maintained episodic memories.

The second prominent characterization of declarative memory is that this kind of memory is special in that the contents of these memories are accessible through various routes. Most commonly in humans declarative memory is accessed through conscious, effortful recollection. This means that one can recall and express declarative memories in the effort to solve novel problems by making generalizations or inferences from memory. Within this view, a broad range of memory networks can be created, with their central organizing principle the linkage of episodic memories by their common events and places, and a consequent capacity to move among related memories within the network.

A simple, three-stage, conceptual model emerges from this accounting of episodic and semantic memory, and the a capacity for inferences from memory [10]. First, it is proposed that the hippocampus mediates the recording of sequential and context-specific information about events that compose episodic memories. Second, it is proposed that the hippocampus has the capacity to identify common features between episodes that could link episodic representations together. Third, it is proposed that a full set of such linked episodic representations composes a 'memory space' that can support inferences from memory, i.e., generalizations based on links between information acquired between distinct experiences. The remainder of this paper considers evidence in support of this hypothesis.

5. Testing the memory space hypothesis

The model just described suggests the hippocampus plays a critical role in our ability to remember a set of distinct experiences, to link them together in a larger organization, and then to use this organization to infer solutions to new problems. A prototypical example of this set of demands is the transitive inference task. Transitive inference is a cognitive assessment that was pioneered by Piaget [22] in his efforts to characterize the cognitive development of young children. He initially presented subjects with multiple premises that shared overlapping elements, and then tested for the capacity to organize the premises into a larger organization that supports logical inferences among indirectly related items. From the perspective of testing of the memory space model of declarative memory, one can view the premises as a set of distinctive experiences that can be organized within a simple one-dimensional 'semantic' network that supports flexible expression in the form of a capacity for inference between indirectly related items.

Dusek and Eichenbaum [6] developed a transitive inference task for rats, exploiting rodents' superb learning and memory capacities in the olfactory modality and their natural foraging strategies to provide a means

of testing their expression of odor memories. The stimuli consisted of distinctive odorous spices added to clean playground sand through which the rats dug to obtain buried cereal rewards. Animals were first presented with a series of blocks of trials on four pair-wise odor discrimination problems. Each problem was composed of two adjacent items in an arbitrarily assigned hierarchical ordering of odors. Thus, subjects were initially rewarded for selecting the appropriate item in overlapping premise pairs, $A > B$, $B > C$, $C > D$, and $D > E$, where A–E are different odors and ‘>’ indicates ‘is selected over’. Then, in the transitive inference testing sessions, all the premise problems were presented in random order, along with occasional probe trials including the pair $B > D$ as the critical test of transitive inference.

Two types of control probes were also presented in this format. One probe involved the pair $A > E$. Like the transitive probe, this pairing is novel, but it can be solved without reference to the orderly relations among the items because, during training, item A was always rewarded and item E never rewarded. Thus, the animal could be expected to choose A over E without reference to knowledge about the items in between them in the series. In addition, because rats would rapidly have extinguished responding to non-rewarded probe trials, the expected choice was always rewarded on each of these tests (B on the BD trials, and A on the AE trials). To test whether consistencies in probe performance could have been due to learning the new pairings, additional tests involved new odor pairs intermingled among premise pair trials similar to the testing protocol on $B > D$.

Intact rats acquired each of the premise pairs rapidly and performed well on concurrent presentations of all the pairings during probe testing. Furthermore, normal rats made the appropriate transitive judgment between stimuli B and D about as accurately as their overall performance on the premise pairs. This finding indicates that rats have a robust capacity for transitive inference and therefore are capable of developing and flexibly expressing a relational organization of the odor items.

The effects of two different disconnections of the hippocampus were tested. In some subjects, the hippocampus was disconnected from its subcortical associations via a fornix transection. In other subjects, the hippocampus was disconnected from its cortical associations by removal of the perirhinal and entorhinal cortex. Both groups of animals with hippocampal disconnections acquired the premise pairs at the normal rate and performed them accurately in concurrent presentations of all the premise pairs. Indeed, all groups showed a characteristic ‘U’ shaped curve in which performance is better on the end-anchored pairs that include one of the consistently rewarded or non-re-

warded items (AB and DE). These observations indicate that the rats with hippocampal disconnections had somehow acquired appropriate responses to each repetitively stimulus pairing and their performance was sensitive to consistent reinforcement contingencies.

However, rats with either type of hippocampal disconnection showed no capacity for the transitive inference. They performed much worse than normal rats on the $B > D$ transitive judgement, and their performance was not better than that expected by chance. In the AE control probes, intact rats and rats with either type of hippocampal disconnection accurately selected A over E, which could be guided by biases about these individual stimuli. This finding indicates that the deficit in rats with hippocampal disconnections was not due merely to the novelty of the stimulus combination, when no transitive judgment was required. In the novel control probes, none of the groups learned the new pairs within the few intermixed trials in which they were presented. Finally, an additional and highly conservative measure was used to confirm the ability of rats to make the transitive inference—we compared the number of rats in each group that correctly chose B over D on the very first transitive probe trial, before any rewards were provided for choices on the probe. Eighty eight percent of normal animals made the correct transitive choice, whereas only 50% of rats with hippocampal disconnection made this choice.

A very simple conception of how the memory space hypothesis applies to the transitive inference problem is illustrated in Fig. 1. In this ‘movie-like’ model, which includes only part of the entire training regimen, schematic representations of two kinds of training episodes (BC and CD) are provided. Both representations appear as a series of codings, each of which contain information about salient stimuli, an animal’s actions, and the locations, where sequential events occur. In addition, some frames in these episodic representations contain common features of events that are encoded by the same representational elements. Note that the memory space that emerges from this set of linked episodic representations could support an inference from memory, in that one can simultaneously envision the ‘B is selected over C’ and ‘C is selected over D’ episodes, allowing the inference between indirectly related items B and D.

If the memory space model has a general applicability, it should extend to other forms of learning. In particular, because of the prevalent view that the hippocampus is dedicated to spatial learning and memory, I will provide here a similar characterization for the common observation of deficits in Morris water maze learning and memory following hippocampal damage. In this task, rats or mice learn to escape from submersion in a pool filled with cloudy water by swimming towards a hidden platform located just under-

neath the surface. Importantly, training in the conventional version of the task involves an intermixing of four different kinds of trial episodes that differ in the starting point of the swim. One can view these four kinds of trial episodes as parallel to the four types of trials presented in the transitive inference task just described. Thus, the AB, BC, CD, and DE trials in transitive inference had considerable common information, including some of the critical odor cues. But the use of individual cues was unique to each particular type of trial (e.g., the response to B was different in AB and BC trials). Similarly, in the Morris water maze task, trials from different starting points share considerable common information, including some of the same spatial cues. But the use of individual spatial cues is unique to each type of trial (e.g., the rat must swim to the left of a particular distal cue on some trials and to its right on swims from the opposite starting point). In the transitive inference task, the challenge was to reconcile the different meanings of the individual stimuli by constructing a fully organized representation, and the existence of this representation in normal animals was

demonstrated by the capacity for transitive inference. In the water maze, the challenge is to reconcile differences in the distinct views from different starting points by constructing a spatial organization. And this organization should support spatial inferences in the form of a capacity to navigate among the cues from any starting point.

In the water maze, the typical training condition involves the use of all four trial types concurrently presenting an especially strong demand on constructing the organized representation. Under this condition, animals with hippocampal damage typically fail to acquire the task [18]. However, animals are trained gradually on each trial type, animals with hippocampal damage can succeed [32]. In our own work, we eliminated the demand for synthesizing a solution from four different types of episodes by allowing the animal to repeatedly start from the same start position [9]. In this condition, animals with hippocampal damage acquired the task almost as readily as normal rats and used the same distant spatial cues in identifying the escape site. Nevertheless, even when rats with hippocampal damage were

A simple memory space

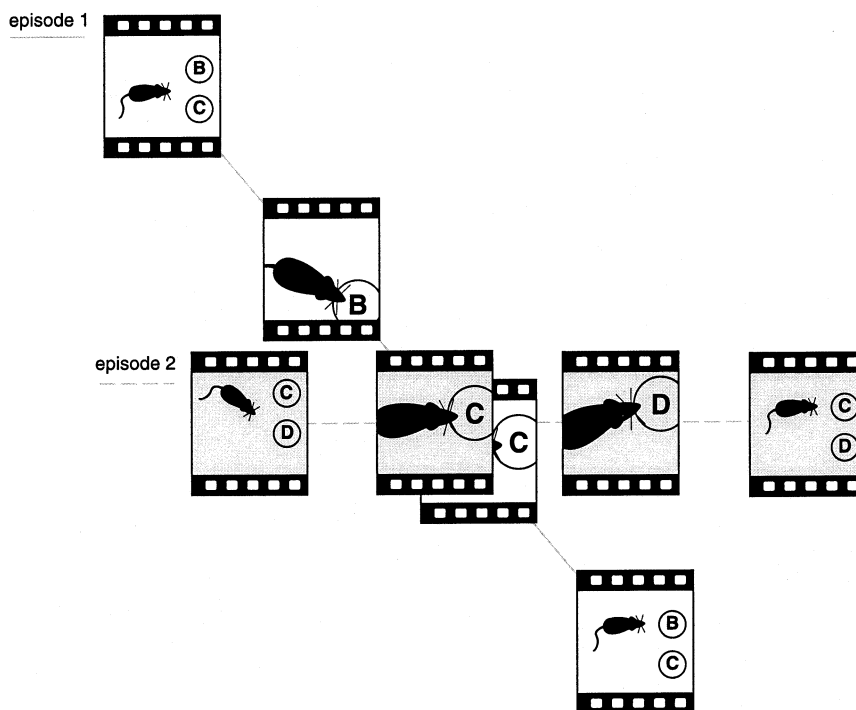


Fig. 1. A schematic illustration of a simple memory space, one that would support a transitive inference based on two episodic memories. The space is constructed of two episodic representations, each of which is composed of 'movie clip' sequence of event codings, each pictured as one 'frame' in the movie clip. In Episode 1, the rat is presented with two odors (B and C), then in sequential events (frames) samples odor B then odor C, and finally selects odor B. In this episode, the rat has learned to select B over C. In Episode 2, the rat is presented with the two odors C and D, then in sequential events samples odor C then odor D, and finally selects odor C. In this episode, the rat has learned to select C over D. Most of the event codings (frames) for each episode reflect combinations of stimuli, behavior, and place information that are unique to one of the episodes. But one event coding (the sampling of odor C) contains common information between the two episodes and could serve to link them. Note that this simple memory space could support an inference about the indirect relationship between items B, which appears only in Episode 1, and D, which appears only in Episode 2, via the common representation of item C. Thus, having learned to pick B over C, and C over D, the rat may make the inference to select B over D.

successful in learning to locate the escape platform from a single start position, they were unable to use this information for inferential memory expression. Thus, once trained to find the platform from a single start position, normal rats readily locate the platform from any of a set of novel start positions. But under these same conditions, rats with hippocampal damage fail to readily locate the platform, often swimming endlessly and unsuccessfully in the highly familiar environment.

The view that has emerged from these and many other studies is that the hippocampus plays a central role in the creation of a broad range of memory networks, with their central organizing principle the linkage of episodic memories by their common events and places, and a consequent capacity to move among related memories within the network. The scope of such network reaches to various domains relevant to the lives of animals, from knowledge about spatial relations among stimuli in an environment, to associations among and categorizations of foods, to learned organizations of odor or visual stimuli or social relationships. Progress is being made in investigating a variety of these domains [8].

6. Neural coding

How does the hippocampus encode information to support the capacity for remembering distinct experiences and linking them within a larger memory organization? My simple working hypothesis is that the model is more or less directly constituted by matching hippocampal neural elements to specific event codings, such as the elemental events depicted in Fig. 1. Thus, the information about each event pictured is encoded by a single hippocampal element. That is, individual cells encode a complex combination of a particular set of salient stimuli, the animal's own behavior, and the spatial-contextual background. A temporal sequence of such elements constitutes an episodic representation with the sequential events bound together via strengthening of associational connections during the course of an experience, as several have proposed [14,17,31]. Finally, while the elements so far described are seen as encoding a particular configuration of stimuli, actions, and place information that is unique to a particular experience, it is postulated that some cells will encode features that are common among episodes [10].

What is the evidence that hippocampal networks exhibit these coding properties? There is substantial evidence that hippocampal neurons exhibit firing properties that include the representation of entire experiences, and include both codings that are specific to distinct experiences and codings that reflect common features among distinct episodes [10]. First, virtually all experiments that have recorded the activity of

hippocampal neurons in behaving animals have reported that the hippocampal network is continuously active, with individual cells firing associated with each sequential event during behavior. Thus, there is overwhelming evidence that the hippocampus contains a continuous stream of information about ongoing episodes.

Second, there is a wealth of evidence that many hippocampal neurons respond to highly complex conjunctions of features, such as those that define spatial locations [21], stimulus configurations [11], and behavioral actions [2]. In virtually all situations, where the behavioral sequences can be identified, the activity of individual hippocampal neurons reflects both the ongoing behavior of the animal and the place where it occurs. A common example is the observation that, when rats perform the radial maze task, most hippocampal cells fire as the animal is moving through a particular place either outward as they traverse a maze arm to obtain a reward or inbound as the rat returns to the center of the maze [16,19]. This combination of firing properties is not dependent on the physical structure of the maze, but occurs even in situations, where there are no physical constraints on the animal's movements [15,33]. In addition, there is an emerging large body of evidence that hippocampal cells fire differentially associated with different kinds of experience within the same environment, such that largely different representations are constructed within the hippocampus, whenever the animal likely perceives two experiences within the environment as distinctive [3,12,15,25].

A particularly compelling example comes from a recent study by Wood et al. [35] in which we found strong evidence indicating that hippocampal networks represent distinct experiences even when spatial and behavioral features of performance are tightly controlled. In this experiment, rats performed a spatial alternation task in a T-maze. Each trial began with the rat at the base of the stem of the T and commenced, when the rat traversed the stem and then selected either the left- or the right-choice arm. Rewards were available at the end of each arm according to an alternation sequence, requiring the rat to distinguish between their left- and right-turn experiences and to use their memory for the most recent previous experience to guide the current choice. Individual hippocampal cells fired as the rats passed through a sequence of locations within the maze during each trial. The key observation in this experiment was that the firing patterns of many of the cells depended on whether the rat was in the midst of a left- or right-turn episode. Thus, these cells fired selectively on either a left- or a right-turn trial, even when the rat was in the same segment of the stem of the T and running similarly on both types of trials. Indeed, detailed analyses indicated that minor variations in the animal's speed, direction of movement, or position

within the relevant areas on the stem did not account for the different firing patterns on left- and right-turn trials. Some cells fired at least somewhat, when the rat was at the same point in the stem on either trial type, indicating a representation of the common spatial information between the two trial types. Thus, the hippocampus encoded both the left- and right-turn experiences using distinct representations, and included information that could link them by their common features.

Third, in each of these situations, whereas many cells encode the events and places that are distinct to a particular type of experience, some cells encode features of the situation that are common between the experiences. Thus, when an animal walks between two identical environments, some hippocampal cells fire similarly in both environments, whereas other simultaneously recorded cells fire quite differently [25]. Also, when a rat switches from foraging randomly to directed food retrievals in the same environment, some cells maintain the same firing patterns, whereas other simultaneously recorded cells alter their firing patterns [15]. Finally, as rats alternate between two versions of an environment, where some of the spatial cues are rotated relative to others, some cells maintain firing with respect to particular subsets of the cues and other simultaneously recorded cells change their firing patterns dramatically [27]. Each of these observations is consistent with the notion that some hippocampal cells encode distinct aspects of related tasks, and others encode the common features between related tasks.

A particularly striking example of the coding common features among distinct types of trials within a task comes from a study by Wood et al. [34]. In this experiment, hippocampal cells were recorded as rats performed an odor recognition task at several different locations on a tabletop. The memory cues were nine cups each filled with different kind of scented sand. On each trial, a cup was placed in any of nine locations, and contained a reward if the odor was a non-match with cup odor on the previous trial regardless of its the place on the table. Because the location of the discriminative stimuli was varied randomly, cellular activity related to the stimuli and behaviors could be dissociated from that related to the animal's location per se. As in many previous studies, individual hippocampal cells were active during each event of task performance, consistent with the representation of entire trial episodes. Also, some cells fired associated with highly specific combinations of stimuli, behavior, and location, consistent with the coding of events unique to particular types of trial experiences. In addition, other cells encoded features of the task that were common between distinct types of trials. For example, some cells fired at a particular phase during the approach to any stimulus cup regardless of its location. Other cells fired

as the rat sampled a particular odor, regardless of its location or match status. Yet others distinguished the match and non-match relationship between successive stimuli, independently of the odor or its location. And some cells fired only when the rat performed the task at a particular place, independent of the odor or its match/non-match status. The combination of these observations indicates that hippocampal networks encode both configurations of stimuli, actions, and places that are unique to distinct experiences and features that are common among them. The codings that involve shared features could serve to link the related episodes. For example, a cell that fires associated with sampling a particular odor regardless of its place could link representations of all trials in which that odor had appeared. Similarly, a cell that fires associated with sampling at a particular place regardless of the odor could link representations of all trials that occurred at that location. Together the coding of distinct experiences as sequences of events and places, plus the codings of common features that connect related episodes, would constitute the framework for a memory network that could support inferential memory expression.

7. Whither goeth the memory space model

A major attraction of the memory space model is that it captures the central properties of declarative memory and offers a framework of cognitive and neural mechanisms by which it could be instantiated. Surely though, there is more to explain than this overview of a simplistic model holds. For example, the model needs to be expanded to incorporate the important interactions between the hippocampus and the cerebral cortex. Most likely the hippocampal representations outlined above reflect 'pointers' to numerous cortical representations that contain details of the information that is contained in the coding of events. How the hippocampal and cortical interactions mediate memory consolidation is another area that requires further elaboration.

Another attractive feature of the memory space model is that it offers a set of dimensions that could mediate both the properties of spatial memory contained in the cognitive mapping theory and the properties of other types of memory organization. Thus, as an alternative to the view that cognitive maps are stored in Cartesian co-ordinates, the memory space model suggests the relevant dimensions of space begin as the sequence of place representations experienced as one takes different paths through an environment. Links between path-specific representations would be expected to form where the paths cross-over one another. So, according to this model, a representation of space is built from a highly interconnected set of paths. The

overall representation of the environment is constrained by its spatial features, not because distances and angles are encoded directly, but instead, because the relations between sequences of events and places in paths are constrained by the physical layout of the environment. This model of physical space is attractive, because it offers a realistic alternative to the conventional view of a ‘map-like’ representation of space in the hippocampus. Hippocampal spatial representations change depending on one’s direction of movement [19], on the ongoing behavior or task demands [15], and on the locus of specific relevant cues in a fixed environment [12]. These and other recent findings have made it clear that hippocampal spatial representations are unlike real maps. On the other hand, a spatial code based on representations of a network of episodes in space would be expected involve all of these features. So the memory space model offers a reconciliation of the controversy between spatial and declarative memory conceptions of hippocampal function, a conception that can move us towards consensus on the focal role of the hippocampus.

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