



# The hippocampal formation and action at a distance

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**The question of why our conceptions of space and time are intertwined with memory in the hippocampal formation is at the forefront of much current theorizing about this brain system. In this article I argue that animals bridge spatial and temporal gaps through the creation of internal models that allow them to act on the basis of things that exist in a distant place and/or existed at a different time. The hippocampal formation plays a critical role in these processes by stitching together spatiotemporally disparate entities and events. It does this by 1) constructing cognitive maps that represent extended spatial contexts, incorporating and linking aspects of an environment that may never have been experienced together; 2) creating neural trajectories that link the parts of an event, whether they occur in close temporal proximity or not, enabling the construction of event representations even when elements of that event were experienced at quite different times; and 3) using these maps and trajectories to simulate possible futures. As a function of these hippocampally driven processes, our subjective sense of both space and time are interwoven constructions of the mind, much as the philosopher Immanuel Kant postulated.**

hippocampus | memory | cognitive maps

**A**ction at a distance in physics involves the nonlocal interaction of objects separated in space and/or time. It has a long and checkered history and is frequently discussed in terms of quantum entanglement, which Einstein famously called “spooky.” Philosophers talk about action at a distance whenever there is a spatial or temporal gap (or both) between a cause and its effect. Controversy arises with regard to the notion of unmediated action at a distance, involving a gap between cause and effect with no obvious intermediaries filling the gap. There is little argument with examples of mediated action at a distance, where spatially and temporally continuous events stretch across time and space to fill an apparent gap.

Mediated action at a distance is central to much of what psychologists care about, given that behavior is frequently motivated by things that are at a spatial and/or temporal remove from the here and now. I will argue that mediating action at a distance is so important that a brain system, centered on the hippocampal formation, is largely devoted to carrying it out. Staresina and Davachi (1) pointed to a role for this brain region in “minding” the small spatial and temporal gaps they manipulated in their stimulus displays. Expanding on this idea, I will assert that animals, including humans, bridge large spatial and temporal gaps through the creation of internal models that allow them to act on the basis of things that exist in a distant place, and/or existed at a different time. But not only to act: Humans often think about, and plan for, the future. The hippocampal formation also plays a role in imagining places and times in the future (2). Memory, in this view, serves to bridge these extensive spatiotemporal gaps, providing the mechanistic basis for action at an apparent distance. In brief, the hippocampal formation accomplishes the goal of stitching together spatiotemporally disparate entities and events by 1) constructing cognitive maps that represent extended spatial contexts, incorporating and linking aspects of an environment that may never have been experienced together; 2) creating neural trajectories that link the parts of an event, whether they

occur in close temporal proximity or not, enabling the construction of event representations even when elements of that event were experienced at quite different times; and 3) using these maps and trajectories to simulate possible futures. As a function of these hippocampally driven processes, our subjective sense of both space and time are interwoven constructions of the mind, much as the philosopher Kant postulated.

The question of why our conceptions of space and time are intertwined with memory in the hippocampal formation is at the forefront of much current theorizing about this brain system (e.g., refs. 3–7). I will suggest that what distinguishes its involvement from that of most other brain systems engaged with space, time and memory is its role in mediating action at a distance. Without a hippocampal formation, I will argue, organisms are largely incapable of escaping the here and now—a state of being captured quite well in the title of Suzanne Corkin’s book (8) about the famous amnesic patient H.M.: “Permanent Present Tense.” This assertion leads to a number of implications, which I consider, albeit briefly, in the conclusion.

## Hippocampal Formation and Space

Animals live in and move about space. Much of the brain is concerned with how organisms relate to the space around them and the things it contains. Multiple brain systems engaged with space provide the organism with the information it needs to survive and thrive in an extended world.

The simplest of animals move in relatively unprogrammed ways, going where the winds or water currents take them, for good or for ill. Most animals, however, move in ways that reflect aspects of their external environment and their needs. At one end of the continuum, animals can find what they need by moving with respect to immediately detectable features of the environment, be they odors, sounds, sights, or more rarely, such things as magnetic, or electric, fields. In these cases, at a minimum, animals must come equipped with the capacity to sense these features, and probably to detect feature gradients so they can move up or down gradient. At the other end of the continuum, animals can have a more complicated set of spatial

### Significance

**This article proposes an overarching hypothesis about the function of the hippocampal formation, namely, that it enables organisms to bridge significant spatial and temporal gaps in experience and is thereby deeply involved in aspects of spatial cognition, event segmentation, and memory. This brain system enables organisms to go beyond the here and now, utilizing prior experience to plan current and future behavior.**

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requirements—they need to find food, avoid predators, seek out mates, identify their current location, and importantly, know how to return to a home base, particularly when these goals are at a distance and not within the range of current sensory inputs. Some highly specialized animals, e.g., desert ants, can manage highly complex spatial feats such as returning to their nest across a virtually featureless terrain with miniature brains (9). Other, nonspecialists, including most mammals, depend upon more flexible strategies to navigate the spatial world. It is with these kinds of animals, and their hippocampi, that this paper, and my lifelong scholarly endeavors, are largely concerned.

The idea that the hippocampal formation plays a role in aspects of spatial cognition emerged after the discovery of place cells by O'Keefe and Dostrovsky (10) 50 y ago. Defining that role was central to the development of cognitive map theory (11–13). A theme that emerged in 1978 in the chapters dealing with humans in ref. 12 was the notion that the hippocampus was critical for context coding and context-dependent memory—a theme broadened and taken up in more detail in subsequent publications over several decades (14–17).

Context is a notoriously difficult concept to define, as it has been used in many different settings (or, to prove the point, contexts). In behavioral settings we can be somewhat more specific—here, context typically refers to the spatial setting in which an organism finds itself. By extension, one can talk about temporal contexts, or event contexts, or social contexts. What is common across all these examples is the notion that the context can strongly determine which behaviors are appropriate, and which are not. When an organism shifts contexts, behavior often has to shift as well. One aspect of the hippocampal role in context coding is its contribution to determining where one context ends and another begins. The presence of “boundary” cells in the hippocampal formation lends support to this proposed function (18).

Empirical evidence supporting a hippocampal role in spatial context began to emerge in the 1990s (19–21) and this view is now widely accepted. Evidence has accumulated that it is the anterior hippocampus (in humans) and ventral hippocampus (in rodents) that are critical for global context representation (21–24), an issue that cannot be taken up in detail here, but which I hope to treat at length elsewhere. This role in representing spatial context is central to the ability of the hippocampal formation to mediate action at a distance.

One way the hippocampal formation carries out its action-at-a-distance role is in mediating behavioral choices when an animal's goal is not within the range of any of its sense modalities. Animals seeking food, water, safety, their home base, or other tangible goals located in distant places can only navigate to these places if they can accomplish a set of things: They have to know where they are at any given moment, they have to be oriented directionally, and they have to know where the goal is located relative to their position and direction. O'Keefe and Nadel (12) proposed that a hippocampally based cognitive map lets the animal know what context it is in, where within that context it is located, and its orientation at that location. This knowledge, paired with knowledge of the goal location, enables an animal to plot a path to the goal. There is strong consensus that the hippocampal formation contributes to each of these components—that it helps the animal determine its precise location within a context, that it contributes to determining an animal's orientation at that location, and that it also is essential in enabling an animal to flexibly navigate from where it is to a goal location. By doing so, the hippocampal formation makes it possible for animals to behave adaptively when action at a spatial distance is required.

### Hippocampal Formation and Time

While animals live and behave in the present moment, they are nevertheless strongly influenced by times past and times yet to

be. Prior and possible future experiences have a major impact on current behavior, where “prior” and “future” can be measured in terms of milliseconds, minutes, or many days, weeks, or months. Given this, it is no surprise that much of the brain is devoted to representing prior experiences, and enabling behavior that is influenced by one's memory for these experiences. Neurons have been discovered in the hippocampal formation whose activity reflects aspects of temporal experience (25, 26). While a role for the hippocampus in representing temporal duration remains up for debate (27, 28), there is little doubt that it is critical to representing events that play out over time, that is, temporal order and sequence (29).

An early indication that the hippocampal formation might play a role with respect to time came in studies using the operant task known as the differential reinforcement of low rates (DRL). In this task, rats are required to delay responding (typically the response is pressing a lever in a standard operant chamber, or Skinner box) for a fixed amount of time, say 20 s, after which a response is rewarded. Responses prior to 20 s reset the delay clock. Rats with hippocampal lesions perform quite poorly on this task (30), which led some to suggest that the hippocampus is critical for timing the delay interval. Rawlins et al. (31) explored a number of explanations for the deficit in DRL in rats with hippocampal formation damage, failing to support a simple loss of timing as the cause of the deficit. Instead their results supported the conclusion that in such rats “behavior is less easily controlled by events that are temporally distant than by events that are more temporally contiguous” (p. 870). In other words, without a functional hippocampal formation rats had trouble bridging temporal gaps.

A second source of data suggesting a hippocampal role in timing emerged in studies of trace conditioning (32). Here, animals are exposed to a conditional stimulus (CS), then a period of no stimulation (the trace interval), and only then the unconditional stimulus (US). This task requires that an animal connect events occurring across a temporal gap. Here too, animals with hippocampal lesions perform poorly, once again suggesting an inability to bridge such gaps. Some time ago Willner and I suggested that animals solve this task by using the spatial context, which remains constantly available through the trace interval, to help bridge the temporal gap (14). The deficit observed after hippocampal damage reflects, in our view, the inability of the lesioned animals to represent spatial context, and hence their inability to use context to bridge the gap. Bangasser et al. (33) explored the role of temporal contiguity in the deficit observed in trace conditioning in rats with hippocampal lesions. In a condition that included both a trace interval and a combined CS-US presentation, they showed that rats with hippocampal lesions can acquire trace conditioning. They concluded that “rats with hippocampal lesions can form a memory of a trace CS-US association when contiguity is restored” and that “the dependence of traditional trace paradigms on the hippocampus can be attributed to the absence of temporal contiguity” (p. 8702). These experimental findings support the view that the hippocampus helps animals bridge temporal gaps in their ongoing behavior by providing spatial (contextual) representations that allow them to overcome the absence of temporal contiguity.

Context representations capture what is stable over time in the environment. Things that are unstable in the environment, that come and go, comprise what are otherwise called “events.” It is now clear that the hippocampal formation plays a crucial role in memory for events unfolding over time. Events, like spatial contexts, begin and end, and again as with contexts, it is adaptive to know when one event ends and another begins. The hippocampal formation appears to be involved in this process of event segmentation (34, 35). In both the spatial and temporal cases, it helps the organism decide between two opposed outcomes, one that leads to linking spaces or events together,

and the other that leads to keeping them apart (36). The standard terminology for describing this invokes a dichotomy between pattern completion and pattern separation, a dichotomy that, though useful, is in our view too restrictive (17), failing to capture the dynamism of the underlying representation (37). It is preferable to think about the hippocampal role as one of pattern formation, as this more aptly captures its nuanced role in segmenting events, and in representing the spatiotemporal flow of experience. The hippocampus can settle into a variety of states, not just two. This is observed when animals modify an existing representation through what has been referred to as “rate remapping” (38). In this case an existing representation is not simply completed, or held separate, but is instead updated to reflect change in an otherwise familiar context.

### Hippocampal Formation and Memory

Though debates remain about the details, ever since the seminal work with the amnesic patient H.M. (39), there are few who doubt that the hippocampal formation plays a central role in episodic memory. Most current views assign it a special role in the acquisition of new information from the episodes of one’s daily life, a role that depends upon its representing contexts and event trajectories, and detecting when current experience does not match the expectations generated by these representations. These considerations point to the critical importance of novelty detection and exploration, to which we gave a central role when laying out cognitive map theory (12). The memory representations the hippocampal formation creates, that provide the basis for its role in action at a distance, depend on detecting and reacting appropriately to novel circumstances. Recent evidence shows that in familiar circumstances, marked by the absence of such novelty, the human hippocampus plays a relatively minimal role in guiding behavior. Cortical regions, prominently including the ventromedial prefrontal cortex, play the lead role instead (40). This brain region is widely thought to be critical for maintaining schematic representations of familiar experiences (41). In the face of novelty, however, the hippocampus inhibits prefrontal activity (42) and plays a significant role in determining whether or not to form a new and distinct event memory. The extent of the novelty (incongruity, or prediction error) determines whether a distinct memory is created (43) or whether an existing memory is updated with this new knowledge and reconsolidated [see Nadel and Sederberg (44) for further discussion of this issue]. In this latter case, by combining an existing memory representation with new information the brain stitches together elements of experience that were not coextensive in time and space (45). This enables an organism to connect, within the same memory representation, only those experiences judged to be part of the same event.

In addition to the role it plays during encoding, the hippocampal formation is engaged in events that transpire after encoding, in the so-called consolidation phase, during which newly acquired information both solidifies in its own right, and interacts with previously existing memories. One result is the creation and refinement of mental representations—schemas—that capture structure recurring from one episode to another. What is known as “systems consolidation” enables this critical function, by which an individual can benefit from prior experiences that share common elements. Much has been written about systems consolidation, but for present purposes it suffices to say that early views of this process (46) failed to include the transformations that occur during the consolidation phase, concentrating instead on the notion that a given memory remains largely unchanged over consolidation time, except for which brain regions are required to retrieve it. Later perspectives (e.g., multiple trace theory) (47, 48)

pay more heed to the ways in which memories can be transformed over the course of consolidation. The schemas that result from these transformations provide the basis for predictions about what is most likely to take place when one finds oneself in a situation that resembles experiences from the past.

To summarize, the hippocampus plays several roles in event memory: enabling the creation of new event memories, integrating new information into existing event memories, and facilitating interaction with cortical regions responsible for schematic memories. These related roles all contribute to the organism’s ability to act in the present on the basis of experiences distant in both space and time. Space limitations prevent me from doing anything other than pointing out that this capacity applies not only to experiences in the past, but also to imagining events that might unfold in the future (ref. 49 and see ref. 50, for a review of hippocampal contributions to future simulation).

### The Big Picture

This thought piece offers an organizing principle—the need to mediate action at a distance—for understanding the interwoven hippocampal roles in spatial cognition, temporal cognition, and memory. Others have discussed the role of the hippocampal formation in bridging temporal gaps (see Rawlins, ref. 51, for an early attempt), and I have referred to some of them in my comments above. With the exception of Staresina and Davachi (1) none, to my knowledge, have viewed this role in conjunction with a similar role in bridging spatial gaps, which elevates the concept to a general principle of hippocampal function. There are a number of implications of the broader view of this idea adopted here, only some of which can be taken up in concluding comments.

Many aspects of space, time and memory do not require hippocampal involvement. Animals, and people with hippocampal damage, can interact effectively with the spatial and temporal world and can bring a good deal of memory to bear on current behavior. What they generally cannot do is bridge spatial and temporal gaps. This results in their being unusually dependent upon the here and now, upon things that are spatially and temporally contiguous. Absent the hippocampal formation, organisms move about in space largely on the basis of stimuli that are detectable at the moment and their memories related to these stimuli. Instead of using stored knowledge about distant places, they use what they know about local landmarks to find their way. They are incapable of generating detours in what should be familiar environments when their typical pathways through those environments are no longer available.

More subtly, animals without a hippocampal formation seem to understand the world largely in terms of temporally contiguous events. This has important consequences. For much of the history of both philosophy and psychology, temporal contiguity was given primary, if not sole, agency in determining what organisms learn from experience. Thinkers as far back as Aristotle talked about influences on association that went beyond temporal contiguity, but these other influences were typically subsumed under it in the theories of learning, derived largely from British associationism, that came to dominate psychology in the 20th century. All this changed when Rescorla and Wagner (52) argued that contingency, not just temporal contiguity, governs what we learn from experience. Extracting contingent relations from experience requires evaluating events that stretch over extended time periods and that typically occur within the same context. Contingencies acquired in a specific context can affect behavior in a different context, though frequently with some fall-off in the strength of this behavior, often referred to as “generalization decrement” (53).

Four decades ago, Devenport and Holloway (54) reported that rats with hippocampal damage were slaves to temporal contiguity alone and were, in effect, highly “superstitious.” They suggested that “the hippocampus permits the control of behavior by contingency and that without the structure, operant behavior is guided by simple response-reinforcer contiguity” (p. 691). Some decades later, using more precise lesion methods, Corbit and Balleine (55) and Corbit et al. (56) showed that these effects resulted from interruption of a broader network incorporating the entorhinal cortex. Most recently, Yu et al. (57) have pointed to the lateral entorhinal cortex as critical for these processes. That the hippocampal–entorhinal cortex network is essential to appreciating contingency in the environment is a clear pointer to its role in bridging temporal gaps.

It is useful to consider, briefly, what this view means for understanding disorders that involve hippocampal dysfunction. Animals, and people, with such dysfunction will be atypically tied to the here and now. They will understand the world, and their experiences in it, from this unusual perspective. They will make inferences about what leads to what on the basis of a very narrow construction of reality. They will fail to make use of specific memories from the past. They will likewise fail to consider, and plan for, the future. In all these ways, they will lack the ability to stitch together aspects of their life that are disconnected in space and time. On a slightly different note, the current proposal has implications for cognitive development, as the hippocampal formation shows extensive postnatal development. Some components of the hippocampal network develop relatively early, enabling the extraction of statistical regularities in ongoing experience (58). By and large, the ability to represent contexts, and to benefit from these representations in the way discussed here, is absent in immature animals. I don’t have room here to explore this issue in detail—the broad implications of postnatal hippocampal maturation were taken up in a recent paper (59).

Nearly 45 y ago we proposed the “cognitive map” theory of hippocampal function (12). Spurred by the discovery by O’Keefe and Dostrovsky (10) of place cells in the hippocampus, this theory spelled out the ways in which this brain structure, and its neighbors, allowed organisms to move about and explore space and to store in memory specific experiences that played out over time. Much has been discovered about the hippocampus and its neural confederates since then, most of which is consistent with the broad outlines of cognitive map theory.

But one enigma remains: Why is it that the same neural system is so intimately involved in aspects of space and time and memory? Recently, Maurer and I (17) proposed that one can think about the hippocampus as constantly answering two critical questions for the organism: What context am I in, and is it the same context I was in a moment ago? This function gives to the hippocampus a critical role in stitching together an animal’s continuous experience in space. In this brief exposition I have tried to broaden this idea to incorporate the hippocampal role in allowing an animal to stitch together its experiences over time (60). Memory, in this view, is the keystone of these processes, linking through time and space those aspects of experience that belong together and separating those that do not. It is critical to note that Maurer and Nadel (17) did not view the hippocampus as a stimulus-response machine, linking events across space and time in a linear fashion. Rather, we suggested that highly nonlinear recurrent circuitries lay at the heart of this system, carrying out the pattern formation critical to its role in space, time and memory.

Much current research focuses on how the hippocampal formation carries out its role in such things as memory recall, retrieval, reconsolidation, and updating. These studies are probing the circumstances under which the brain decides if events separated in space and time belong together and should be conjoined. This work will ultimately uncover the mechanisms enabling the literal stitching together of disparate experiences. One thing we already know is that fundamental building blocks of these stitching functions are prewired in the hippocampus—prestructured spatial scaffolds and sequential neural trajectories are evident before relevant experience on the part of developing organisms (61–63).

Action at a distance is neither spooky nor something that lies beyond our understanding. We can make sense of it when we unpack the specific brain activities that mediate our ability to bridge spatial and temporal gaps. The hippocampal formation, it would seem, is a central contributor to our capacity to fill these gaps.

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