RETROSPECTIVE

Howard Eichenbaum (1947–2017)

A neuroscientist who was fascinated by the nature and mechanisms of memory

By **Michael Hasselmo** *and* **Chantal Stern**

Remembering Howard Eichenbaum's career prompts the recall of many vivid memories, which is appropriate given Howard's influential research on declarative memory function. His work elucidated the neural basis of memory organization in the brain. As director of the Center for Memory and Brain and the Laboratory of Cognitive Neurobiology and as Warren Professor in the Department of Psychological and Brain Sciences, all at Boston University, Massachusetts, Howard performed research on the intricacies of memory processing in the hippocampus, a brain structure essential for the memory of episodes. As editor-in-chief of the journal *Hippocampus* until his passing on 21 July at the age of 69, Howard remained a vital leader in elucidating the role of the hippocampus in cognition and behavior.

We remember Howard debating important scientific questions about the nature of memory, peppering his conversation with witty asides and sharp observations. His students and postdocs will recall the start of many discussions: a tough and insightful question from Howard, then a very short pause, followed by Howard quickly raising his eyebrows twice, as if to signal the start of game, the clock ticking as it does in a competitive chess match. He engaged in an ongoing scientific debate about the primacy of spatial coding for hippocampal function. With his lab, he demonstrated that the hippocampus in rodents also codes numerous nonspatial features relevant to memory function, including odors and the sequential order of events.

We have fond memories of Howard thinking, speaking, and writing at a faster speed than most others. With his insightful experiments, lucid articles, and fast-paced talks, Howard embodied an effective bridge between researchers working on human declarative memory and those working on the role of the hippocampus in animals.

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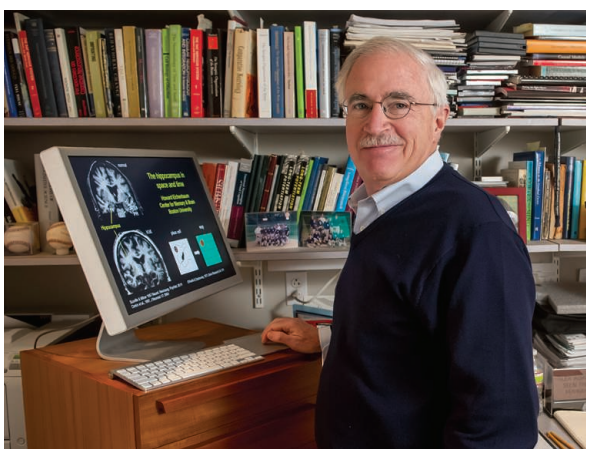
Howard Eichenbaum was born in Chicago, Illinois, in 1947, completed his B.S. and Ph.D. degrees at the University of Michigan, and a postdoctoral fellowship at the Massachusetts Institute of Technology (MIT) investigating neurochemical, electrophysiological, and structural aspects of memory across a range of species. He later worked with Suzanne Corkin at MIT studying olfaction in the human amnesic patient "H.M." During that time, Howard began a long-term friendship and collaboration with Neal Cohen. Together, they developed the influential theory of the role of the hippocampus in relational memory—that is, the binding into declarative memory of different elements of experience. Howard identified an essential role of the hippocampus in relational behaviors in rodents, using a range of different complex cognitive tasks. He demonstrated the role of the hippocampus in sequence disambiguation and memory for stimulus order, and showed that lesions of the hippocampus selectively impair mechanisms for recollection but not familiarity.



With his lab members at Boston University, Howard also showed how different events in the same location could be coded as different episodes in a spatial alternation task on a T-maze (which tests memory of a prior response). This seminal finding demonstrated that even if a rat runs in the same direction through the same location, individual neurons will respond selectively based on the future or past trajectory of the animal. By showing the effects of memory on the responses of hippocampal neurons, Howard helped resolve a paradox of hippocampal function. Brain lesion studies had shown that the hippocampus was important for memory of events occurring at different times in the same place, but numerous physiological recording studies identified neurons called place cells with similar firing during repeated visits to the same place. Howard's data addressed this conundrum by showing the important role of memory for behavioral context in determining the pattern of hippocampal neural activity in a given location.

In recent work, Howard coined the term "time cells" to describe neurons that respond at specific time intervals within a range of behavioral tasks. He proposed that these neurons could code the time of events in memory. Neurons traditionally seen as coding spatial location, such as place cells in hippocampus and grid cells in the medial entorhinal cortex, can also fire selectively at specific time intervals during behavior, indicating that the same cells could participate in coding both time and place for an episode in memory.

Howard received many honors, including selection as a fellow of the American Association for the Advancement of Science, the American Academy of Arts and Sciences, and the Association for Psychological Science. He also was a member of the Council of the Society for Neuroscience and the U.S. National Institute of Mental Health's National Advisory Mental Health Council.

With his door always open, Howard Eichenbaum was a generous mentor to an ever-growing population of students, postdoctoral fellows, and faculty (including ourselves), helping many researchers at crucial stages in their careers, and guiding them to successful funding and publications. He was devoted to education, founding both the Undergraduate Program for Neuroscience and what is now the Graduate Program for Neuroscience at Boston University. We all will remember his contributions to our individual development and to advancing our understanding of the mechanisms of remembering. His work will have a lasting influence as we integrate our knowledge about memory and time—the past, the present, and the future. ■

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