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Editorial overview: Bound together through space and time: reminiscences of Howard Eichenbaum

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There is a saying: "*When you meet a true friend, you will be bound together through space and time for 500 years.*" I became bound together with Howard Eichenbaum a little more than 36 years ago. In the preface of our first book [1], we wrote that our association grew out of "the housing situation that got us together one day in Boston", and we suggested that it was a story for another book, or at least another time. Now is definitely that time.

Let's go back in time to January 1981; the place, the greater Boston area, Massachusetts. My wife and I had just moved there from a very warm San Diego to record cold weather in Boston, only to discover that the house we had arranged sight-unseen to rent was basically uninhabitable, at least in those sub-zero temperatures. Suzanne Corkin, in whose laboratory at MIT I was about to start a postdoctoral stint, invited us to stay at her home for a few days, until we arranged a new rental. Karen Shedlack, then working in Suzanne's lab, happened to tell her friend Howard, who was then an Assistant Professor at Wellesley College, about this "poor new postdoc who had just moved to town and unexpectedly had no place to live". Howard asked who this poor postdoc was, and upon hearing my name, but without having ever met me, said to Karen "Neal Cohen? I just read his Science paper! Tell him he can live with me." What?! A truly uncommon act of generosity on Howard's part that led to an equally uncommon career-long friendship and collaboration.

That collaboration was described in the preface to our book, as follows: "We embarked [on] a systematic program of collaborative work on the idea of corresponding memory mechanisms in humans and rodents . . . What was required in order to really work simultaneously on humans and rodents was an articulation of the functional role of the hippocampal system in memory, and of the nature of the memory impairment in amnesia, that would permit experimental predictions for studies performed on any species and that would permit us to make contact with and contribute to work ranging from cognitive processes to neural mechanisms."

The theory we articulated was about *declarative* (or *relational*) memory and was framed at the level of the memory representations uniquely supported by the hippocampal system, the behavioral performances that were afforded by such representations, and the neural mechanisms that enabled those representations. We argued, based on converging lines of evidence, that hippocampal representations of experience are fundamentally relational. They capture the spatial, temporal, and other contextual relations among the constituent elements of experience, forming a multidimensional *memory*

space. And so it came to pass that Howard and I were bound together in pursuit of understanding how space and time, and the details of the events of our lives, are bound together in declarative (relational) memory.

The early stages of writing the 1993 book — for the initial articulation of our theory — occurred during the last extended period of time when we were able to physically work together. Subsequently, we had to take advantage of moments when we were together at conferences, workshops, invited talks, review meetings, etc., and of moments together we purposely created by writing joint grants, jointly organizing symposia, serving on the quals or thesis committee of the other's students (my favorite was being on the undergrad honors thesis committee for Howard's son Alex), and each of us trying (unsuccessfully, alas) to recruit the other to a faculty position at our respective university. Those moments were essential for us to discuss whatever new findings appeared in the animal and human memory literatures since our last time together so that we could continue to critically evaluate, extend, and improve our conceptualization of relational memory.

Mostly, we each went off in search of further empirical findings that could illuminate the nature of, and the brain systems and mechanisms underlying, the binding together of spatial, temporal, and other event information in relational representations. Howard had the harder challenge in garnering evidence for this in studies of rodent hippocampus. In the field at that time, findings from electrophysiological recordings of the activity of hippocampal neurons in behaving animals pointed to exclusively spatial accounts of hippocampal function, due to the discovery by John O'Keefe of *place cells*, whereby different single hippocampal neurons fired preferentially at different locations within a spatial environment, permitting the entire spatial environment to be coded by the population of individually selective place cells. So, although Howard and I had already argued in a 1988 review paper [2] that hippocampal neurons should more properly be called *relational cells*, "representing various relationships among multiple stimuli and contingencies or responses," this was clearly a minority opinion at the time, and it seemed very difficult indeed to reconcile the literatures.

But Howard was undeterred, and the findings he obtained and the insights he provided throughout the rest of his career were immensely important to the field. His laboratory conducted a remarkable series of elegant and original studies recording from single neurons and neuronal ensembles while rodents performed tasks that tested memory for various items, relations, and contexts, for multiple types of information, taking particular advantage of their superb olfactory abilities. This work provided powerful evidence that hippocampal neuronal activity is not limited to place or spatial information. Hippocampal activity also codes for sensory or object information, the conjunction of sensory or object information with spatial location or spatial context, and the conjunction of such information with different learned behaviors. *Relational cells*, indeed. Saving the best for last, Howard's discovery and characterization of "time cells" revealed temporal coding mechanisms in hippocampus, permitting the entire time period of some event (e.g., the task trial) to be coded across a population of individually tuned time cells, just as an entire spatial environment can be coded by a population of individually selective place cells. Accordingly, the hippocampus represents events not just within their spatial context but also within their temporal context. In his most recent writings, Howard offered insights into how this resulting temporal-spatial contextual coding could provide (the means for) the fundamental organization of experience in memory, in animals and humans alike.

Events unfold in space and time. Howard's work greatly advanced our understanding of how the brain captures a record of those events, and provides new insights in particular to the aspect of time. He showed the role of the hippocampal system in capturing in memory the relations among the people, objects, places, actions, etc. that populate events as they unfold in their particular temporal-spatial context, and, further, the relations among successive events as they unfold over the course of an extended episode. A life, too, unfolds through space and time, and Howard's work also addressed the hippocampal contribution to memory for relations among multiple episodes extended across time. Howard's own life unfolded with extraordinary richness and consequence, and, to many observers, his best science was still ahead of him. His untimely passing was a terrible loss. But, Howard did have time enough to create a remarkable legacy of accomplishment and impact in our field, and to see his mother's 100th birthday celebrated this year with their extended family. There was also time enough to create and tend to at least one friendship that, to my great good fortune, may indeed keep us bound together through space and time for 500 years.

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