A model of episodic memory: Mental time travel along encoded trajectories using grid cells

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**Abstract**

The definition of episodic memory includes the concept of mental time travel: the ability to re-experience a previously experienced trajectory through continuous dimensions of space and time, and to recall specific events or stimuli along this trajectory. Lesions of the hippocampus and entorhinal cortex impair human episodic memory function and impair rat performance in tasks that could be solved by retrieval of trajectories. Recent physiological data suggests a novel model for encoding and retrieval of trajectories, and for associating specific stimuli with specific positions along the trajectory. During encoding in the model, external input drives the activity of head direction cells. Entorhinal grid cells integrate the head direction input to update an internal representation of location, and drive hippocampal place cells. Trajectories are encoded by Hebbian modification of excitatory synaptic connections between hippocampal place cells and head direction cells driven by external action. Associations are also formed between hippocampal cells and sensory stimuli. During retrieval, a sensory input cue activates hippocampal cells that drive head direction activity via previously modified synapses. Persistent spiking of head direction cells maintains the direction and speed of the action, updating the activity of entorhinal grid cells that thereby further update place cell activity. Additional cells, termed arc length cells, provide coding of trajectory segments based on the one-dimensional arc length from the context of prior actions or states, overcoming ambiguity where the overlap of trajectory segments causes multiple head directions to be associated with one place. These mechanisms allow retrieval of complex, self-crossing trajectories as continuous curves through space and time.

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1. Introduction

Episodic memory includes the capacity to internally re-experience the sequence of events that occurred at particular places and times, in what has been termed “mental time travel” (Eichenbaum & Cohen, 2001; Tulving, 2001, 2002). Episodic memory includes the capacity to mentally retrace trajectories through previously visited locations, including re-experiencing specific stimuli encountered on this trajectory, and the relative timing of events. For example, you can probably remember the route you followed when you left your home this morning, with a memory of the locations you visited and the time you spent in individual locations. You can use this memory to remember where you parked the car, who you saw on your trip, or where you left your car keys. This aspect of episodic memory requires some means by which neurons can code continuous trajectories through space with time intervals representing the original episode. This also requires some means for encoding the location and time of specific events or stimuli encountered along this trajectory.

Physiological data shows that hippocampal activity during REM sleep can replay the relative time intervals of spiking activity evoked by different spatial locations during waking (Louie & Wilson, 2001), indicating the capacity to replay spatiotemporal trajectories with the same time scale as actual behavior. Other experiments also show that spiking activity in the hippocampal formation can maintain information about the relative timing of events (Berger, Rinaldi, Weisz, & Thompson, 1983; Deadwyler & Hampson, 2006; Hoehler & Thompson, 1980).

Lesion data suggests that encoding and retrieval of previously experienced episodic trajectories involves the entorhinal cortex and hippocampus. In humans, lesions of these structures cause profound impairments of episodic memory, tested both qualitatively and with quantitative measures in verbal memory tasks (Corkin, 1984; Eichenbaum & Cohen, 2003; Graf, Squire, & Mandler, 1984; Rempel-Clower, Zola, Squire, & Amaral, 1996; Scoville & Milner, 1957). Impairments in formation of object-location associations occur with right hippocampal or parahippocampal lesions (Bohbot, Allen, & Nadel, 2000; Bohbot et al., 1998; Milner, Johnsrude, & Crane, 1997; Stepankova, Fenton, Pastalkova, Kalina, & Bohbot, 2004). In rats, hippocampal manipulations impair performance in tasks that can be solved using episodic retrieval...
of specific recent trajectories, including the 8-arm radial maze (Bunce, Sabolek, & Chrobak, 2004), delayed spatial alternation (Ennaceur, Neave, & Aggleton, 1996), the Morris water maze with new platform location on each day (Buresova, Bolhuis, & Bures, 1986; Steele & Morris, 1999) and a task testing a sequence of spatial locations (Lee, Jerman, & Kesner, 2005). Spatial memory is also impaired by lesions of the entorhinal cortex (Steffenach, Witter, Moser, & Moser, 2005) and postsubiculum (Taube, Kesslak, & Cotman, 1992). Learning of spatial trajectories may be a special case of a general capacity for learning sequences within the hippocampus (Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999), including the sequential order of sensory stimuli (Agster, Fortin, & Eichenbaum, 2002; Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua, 2002; Kesner & Novak, 1982).

Many previous models of hippocampal function focus on its role in spatial navigation to goals (Burgess, Donnett, Jeffery, & O'Keefe, et al., 2006) suggest a different approach (Hasselmo, 2008b) in Molden, Moser, & Moser, 2005; Moser & Moser, 2008; Sargolini et al., 2006) and postsubiculum (Taube, Kesslak, & Cotman, 1992). Learning of spatial trajectories may be a special case of a general capacity for learning sequences within the hippocampus (Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999), including the sequential order of sensory stimuli (Agster, Fortin, & Eichenbaum, 2002; Fortin, Agster, & Eichenbaum, 2002; Kesner, Gilbert, & Barua, 2002; Kesner & Novak, 1982).

The model presented here will consider encoding and retrieval of trajectories in a two-dimensional location of an animal at one time can be represented by the row vector \( \mathbf{x} = [x \ y] \). The trajectory through different locations over time can be represented by a sequence of vectors \( \mathbf{x}(t) \). This representation can be obtained by integration of the velocity row vector \( \mathbf{v}(t) = [dx/dt \ dy/dt] \). Integrating the velocity vector over time yields the current location vector \( \mathbf{x}(t) \) at time \( t \) relative to the starting location vector \( \mathbf{x}(0) \), as follows:
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