

A Grid/Place Cell Model of Episodic Memory and Spatial Navigation in the Medial Temporal Lobe

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Abstract:

The precise spatial tuning of hippocampal place cells and entorhinal grid cells suggest that the medial temporal lobe (MTL) plays a primary role in spatial navigation. At the same time, neuropsychological studies find that the MTL supports the formation of episodic memories. Reconciling these results, we present a neural network model that produces grid cell and place cell representations from episodic memories in a high dimensional feature space. A representation of a new episode (i.e., a place cell) is created when the current situation (including location) is sufficiently novel. Online consolidation adjusts memory representations such that the current (perceived) state of the world is well-enclosed by surrounding memories. When simulating a rat in an arena devoid of landmarks, there are only three dimensions of variation during an episode of navigation: X/Y, which reflect border cells, and head direction. This results in a three-dimensional face-centered close packing of memories within the high dimensional space. Owing to strong hippocampal feedback, head direction cells in entorhinal cortex exhibit a widely spaced grid pattern while cells representing features ubiquitous in the navigation context (e.g., odor, surface texture, etc.) exhibit a tightly spaced grid, reflecting a 2D projection of the 3D memories.

Keywords: spatial cognition; episodic memory; artificial neural networks; memory consolidation

Spatial Cells in Rodents

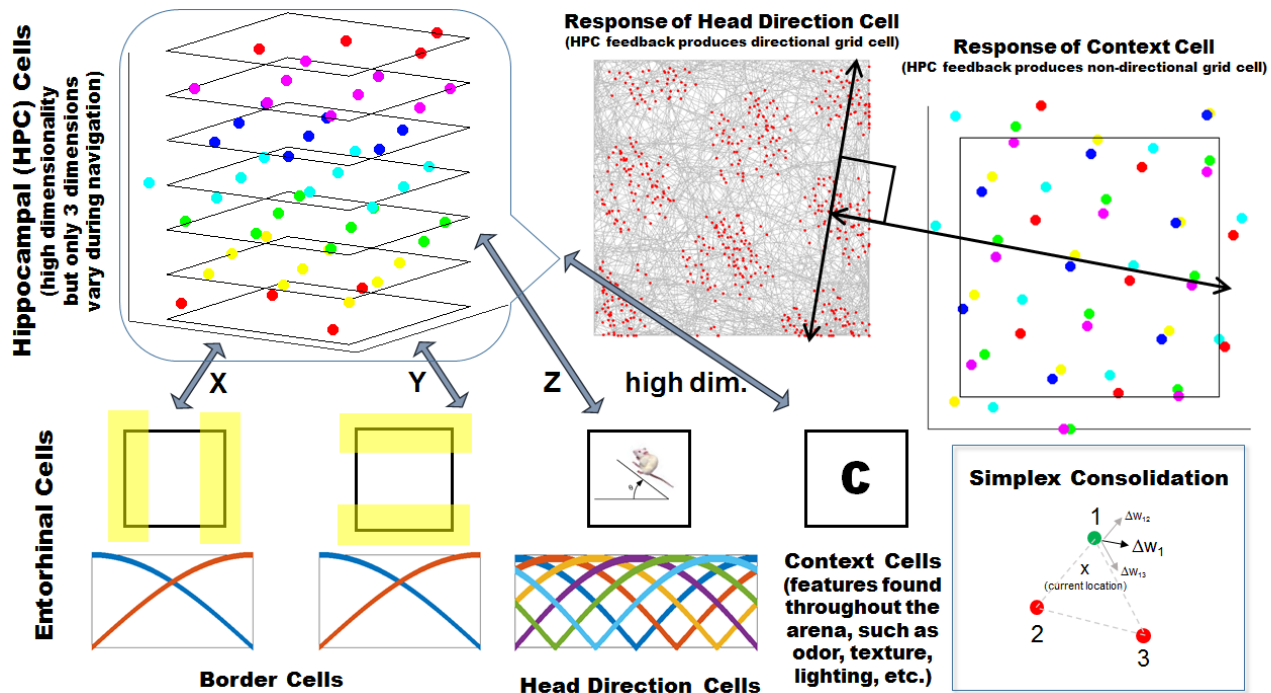
Place cells, which are found in the hippocampus, discharge whenever an animal visits a particular location within an arena (Okeefe, 1976). In contrast to this single receptive field, grid cells, which are found in the entorhinal cortex, respond to multiple locations that are arrayed in a precise hexagonal grid (Hafting, Fyhn, Molden, Moser, & Moser, 2005). Other cells in the entorhinal cortex exhibit different spatial responses: Border cells respond when the animal is close to a border of a particular orientation (Solstad, Boccara, Kropff, Moser, & Moser, 2008) while head direction cells respond when the animal's head is pointed in a particular direction relative to salient cues. Many grid cells are head direction conjunctive, such that they reveal a grid pattern only when the animal is navigating in a particular direction. Grid cells

have the same grid orientation and spacing as their anatomical neighbors, but different phases (i.e., a shift of the grid pattern). Furthermore, grid cells are discretely modular across the entorhinal cortex, with approximately four to ten modules differing in grid spacing and orientation (Stensola et al., 2012).

The spatial specificity of these cells found with rodent electrophysiology suggests that navigation is a primary function of the MTL. However, neuropsychological studies with humans suggest that the primary function of the MTL is the creation of new episodic memories (Scoville & Milner, 1957). We attempt to reconcile these conclusions with a memory model of the MTL that explains grid cells as reflecting the retrieval of very recent (e.g., minutes ago) experiences with the current arena as well as more remote memories of similar arenas. This account makes sense of recent results that are problematic for prior grid cell models, such as the finding that inactivation of the hippocampus eliminates the hexagonal firing patterns and converts some grid cells into head direction cells (Bonnievie et al., 2013). Thus, hippocampal feedback may be a crucial component of the entorhinal grid response.

A Grid/Place Cell Memory Model

Similar to other proposals, we assume that the hippocampus binds together different features to form a conjunctive representation. Prior to binding, these separate features reflect the feedforward response of entorhinal cortex cells. Thus, episodic memories are points in a high dimensional feature space, with the collection of features (e.g., time of day, location, ambient odor, landmarks, level of hunger, etc.) specifying a unique combination that is unlikely to be exactly the same over time. However, the combination of the current context and location can retrieve a similar hippocampal memory, re-activating the original entorhinal features owing to strong feedback from the hippocampus to the entorhinal cortex.



As seen in the figure, the model contains two X-dimension border cells, representing the distance to the West/East walls, two Y-dimension border cells (North/South), and six head direction cells. In addition, there are entorhinal cells capturing context features that are constant during navigation (e.g., floor texture, odor, etc.). Winner-take-all activation specifies that one hippocampal cell is activated if that cell is above the threshold of activation based on entorhinal input. When this occurs, the corresponding memory is retrieved, providing strong feedback to the entorhinal cortex. If no memory is retrieved, a new hippocampal cell is recruited and its weights are set equal to the activation values of the entorhinal cells (i.e., Hebbian learning). Hippocampal cells experience continual consolidation via small nudges to their weights using a novel simplex-based δ -rule learning algorithm (see figure insert). Thus, the weights of the most active hippocampal cell adjust to become equidistant (using the same activation threshold as Hebbian learning) from up to k neighbors, where k is the dimensionality of variation (3 in the simulation, although the insert shows a k of 2, in which case consolidation created equilateral triangles).

Because they have monotonic half-sine tuning functions, the border cells create a Euclidean metric in the X and Y directions whereas the non-monotonic circular head direction tuning functions create a city block metric in the Z direction, giving rise to a planar structure of place cell representations, after sufficient memory consolidation. Feedback from each plane of place cells causes the corresponding (entorhinal) head direction cell to behave as a head direction conjunctive grid cell (the figure shows the gray navigation path and spike locations as red dots), with different head direction cells having the same grid spacing and orientation, but different

phases. This explains the Bonnevie et al (2013) finding that some grid cells become head direction cells in the absence of hippocampal feedback. These planes tessellate together such that context cells exhibit a grid pattern that is more tightly spaced, and rotated by 90° (the figure plots the place cell projection, with color indicating head direction, revealing that each place field is a combination of two different head directions). Thus, based on a set of 3D varying memories, there are two different classes of grid cells (i.e., two modules) differing in grid spacing and orientation, and if the current context triggers memories for more than one similar arena, this explains the modularity found by Stensola et al. (2012).

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