An Entorhinal-hippocampal Systems Model for Spatial Navigation and Memory

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Abstract

Simultaneously localizing one's position and constructing a map of the surrounding environment are fundamental processes underpinning model-based navigation, reasoning, and decision-making. The brain achieves this ability through two complementary strategies: inferring one's states in the environment from sensory inputs and updating previous states through path integration. However, how these two sources of information interact remains largely unknown. Here, we introduce EHSLAM, a mechanistic computational framework of the entorhinal-hippocampal system. By integrating sensory inputs and path-integrative signals, EHSLAM learns localized representations of space as place cells in the hippocampus, by updating synaptic connections in the network after encountering a novel environment. These phenomena are interrelated and mutually reinforce during spatial updates in this framework. Furthermore, EHSLAM captures key findings from empirical data, including place cell remapping and grid cell realignment across distinct environments, as well as making testable predictions. This computational framework provides a mechanistic understanding of the neural dynamics involved in spatial navigation and memory.

Keywords: grid cells; place cells; head direction cells; landmark vector cells; simultaneous localization and mapping; global remapping; grid cell realignment

The computational model

Inputs to EHSLAM consist of two components: self-motion-based information and landmark-based sensory information. Self-motion information includes the animal's linear and angular velocities, which are used to update the animal's position and head direction through linear and angular path integration. Specifically, the angular velocity signal activates head direction cells, which combines speed information to activate grid cells in MEC (Figure 1A).

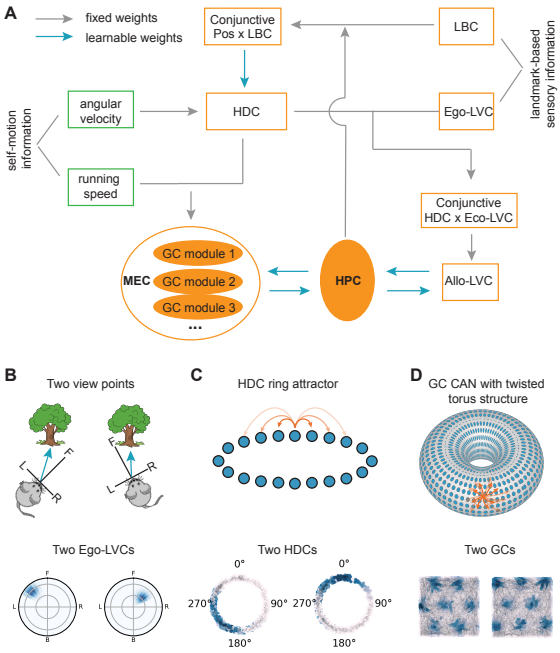

Figure 1: The mechanistic computational framework. **A**, the entorhinal-hippocampal systems model. Multiple grid modules in MEC receive self-motion input including both angular information (via head direction cells, HDCs) and speed information. The hippocampus receives landmark-based sensory information via allocentric landmark vector cells (Allo-LVCs) by combining input from egocentric landmark vector cells (Ego-LVCs) and allocentric directional information from HDCs. Apart from direct angular velocity input, HDCs also receive landmark-based sensory information from landmark bearing cells (LBCs) by combining position information from the hippocampus. Grey arrows represent fixed synaptic weights and blue arrows represents learnable weights. **B**, two example egocentric landmark vector cells (bottom) tuned to different distances and egocentric angles of a landmark in the field of view (top). **C**, the HDC ring attractor network (top) and two example HDCs (bottom). **D**, the grid cell continuous attractor network with a twisted torus structure (top) and two example GCs (bottom).

Emergence of place-cell tuning and a spatial map of the environment in the hippocampus

We first showed that EHSLAM can learn place-cell tuning in the hippocampus as the agent freely explores the environment. Before learning, hippocampal neurons do not show localized spatial preference since synaptic connections to the HPC and within the hippocampus have not yet been learned (Figure 2A). After synaptic updates while the agent navigates the environment, some neurons develop localized spatial tuning as place cells (Figure 2A). Among the simulated 2000 HPC neurons, nearly 40% develop clear place-cell-like tuning, as measured by the degree of localized firing of each cell (Figure 2B). This is similar to the proportion of place cells in CA1/CA3 pyramidal neurons reported in empirical data (approximately 30%-50%) Thompson & Best (1989). The reason only a fraction of HPC neurons develop as place cells is due to competitive Hebbian plasticity within the HPC. This mechanism allows EHSLAM to represent multiple spatial maps with different sets of neurons, as discussed later in the context of remapping.

The development of place-cell-like activity in the hippocam-

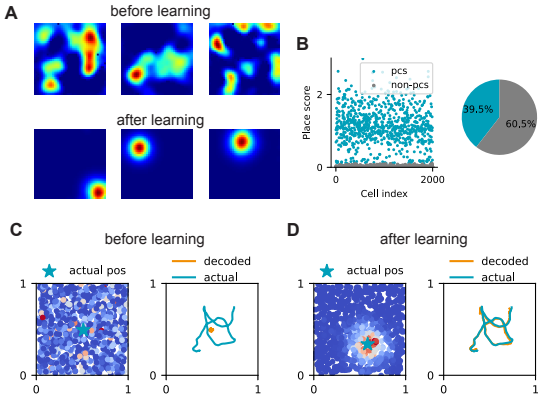

Figure 2: Emergence of place-cell tuning and a spatial map of the environment in the hippocampus.

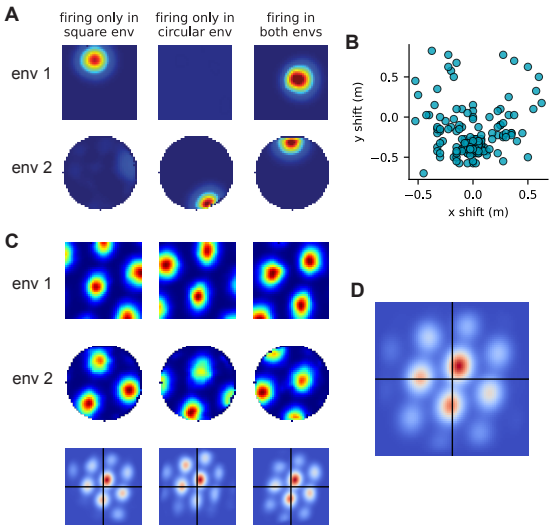

Figure 3: Global remapping in place cells and realignment in grid cells.

pus does not necessarily mean that it forms a spatial map of the environment. To form a spatial map, these cells need to encode an internal representation of the agent's actual position. To further demonstrate this, we sorted place cells that emerged after learning by their preferred firing location in the environment, and visualized the population activity. We found that before learning, the population activity does not reflect the actual position of the agent (Figure 2C, left), whereas after learning, place cells closely reflect the actual position with higher firing rate in cells coding for a space near the agent's actual position (Figure 2D, left). We further decoded the internal position from the population activity of place cells that emerged over a running period, and found that after learning, the decoded position closely aligns with the agent's actual position (Figure 2D, right), but not before learning (Figure 2C, right).

Global remapping in place cells and realignment in grid cells

It has been shown that when place cells are recorded in environments of different shapes (e.g., circular and square), some are active in one environment but silent in the other, while others are active in both but at different locations. This phenomenon, known as global remapping, allows the hippocampus to encode distinct spatial representations for different environments Muller & Kubie (1987); Bostock et al. (1991); Lever et al. (2002); Leutgeb et al. (2005); Wills et al. (2005). As expected, a subset of hippocampal neurons was recruited as place cells, forming a distinct spatial map for each environment (Figure 3A). Specifically, 459/2000 neurons were recruited as place cells for the square arena, while 469 out of 2000 were recruited as place cells for the circular arena. Among them, 191 neurons were active in both environments but at different firing locations. Importantly, the firing fields of these shared place cells did not exhibit coordinate shifts between the two environments (Figure 3B), suggesting that remapping occurred in a relatively random manner across the two learned environments.

In contrast, unlike global remapping in place cells, grid cells show realignment in response to different environments Fyhn et al. (2007). Specifically, the triangular firing fields of grid cells move in concert between the two environments, with grid spacing and grid orientation preserved. Based on the two environments we simulated (a square one and a circular one), we checked the tuning properties of grid cells in EHSLAM. First, grid cells display triangular grid-like firing patterns in both environments (Figure 3C). The cross-correlogram of the firing fields of individual grid cells also forms triangular grid-like patterns, suggesting that grid spacing, orientation, and spatial phase distribution were preserved between the two environments (Figure 3C). Importantly, peaks of the cross-correlograms are offset from the origin consistently across all grid cells (with the same distance and angle from the origin) (Figure 3D), suggesting that grid cell maps realigns with changes in the environment without losing its intrinsic spatial phase structure Fyhn et al. (2007).

Conclusion

In this study, we built a mechanistic computational framework for the entorhinal-hippocampal system with biologically plausible constraints. This model integrates both self-motion information and landmark-based sensory information from two complementary pathways via synaptic plasticity. Future work will extend this model to more complex navigational paradigms, such as the delayed matching-to-place task in a watermaze setup Foster et al. (2000), environments with barriers Widloski & Foster (2022), or tasks involving multiple fixed reward locations Boccara et al. (2019). Such extensions would allow testing the responses of various cell types and network dynamics, including replay, and provide mechanistic explanations for a broader range of empirical observations.

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