

**Coordinated learning of grid cell and place cell spatial and temporal properties:
Multiple scales, attention, and oscillations**

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How do grid cells and place cells arise through development and learning? Medial entorhinal grid cells and hippocampal place cells provide neural correlates of spatial representation in the brain. A place cell typically fires whenever an animal is present in one or more spatial regions, or places, of an environment. A grid cell typically fires in multiple spatial regions that form a regular hexagonal grid structure extending throughout the environment. Different grid and place cells prefer spatially offset regions, with their firing fields increasing in size along the dorsoventral axes of the medial entorhinal cortex and hippocampus. The spacing between neighboring fields for a grid cell also increases along the dorsoventral axis.

The GridPlaceMap neural model shows how grid cells and place cells may develop in a hierarchy of self-organizing maps. In this conception, grid cells and place cells are learned spatial categories in these maps. The model responds to realistic rat navigational trajectories by learning grid cells with hexagonal grid firing fields of multiple spatial scales, and place cells with one or more firing fields that match neurophysiological data about these cells and their development in juvenile rats. The place cells represent much larger spaces than the grid cells, which enable them to support navigational behaviors.

Homologous self-organizing map laws for grid cell and place cell learning. The grid cell and place cell self-organizing maps both obey the same laws, and both amplify and learn to categorize the most frequent and energetic co-occurrences of their inputs. The different receptive field properties emerge because they experience different input sources. The place cells learn from the developing grid cells of multiple scales that input to them. The grid cells learn from stripe cells of multiple scales that input to them, each with a different directional selectivity. The name “stripe cell” acknowledges that the spatial firing pattern of each such cell exhibits parallel stripes as the environment is navigated. Burgess and his colleagues introduced an analogous concept of “band cells”, but they are formed by the mechanism of oscillatory interference.

Grid and place cell learning occurs in models that are built up from either rate-based or spiking neurons. The results using spiking neurons build upon a previous rate-based model of grid and place cell learning, and thus illustrate a general method for converting rate-based adaptive neural models into models whose cells obey spiking dynamics. Remarkably, the spiking model continues to exhibit key analog properties of the data. New properties also arise in the spiking model, including the appearance of theta band modulation. The spiking model also opens a path for implementation in brain-emulating nanochips comprised of networks of noisy spiking neurons with multiple-level adaptive weights for controlling autonomous adaptive robots capable of spatial navigation.

Learning the dorsoventral gradient of receptive field sizes and oscillation frequencies. Both the spatial and temporal properties of grid cells vary along the dorsoventral axis of the medial entorhinal cortex. *In vitro* recordings of medial entorhinal layer II stellate cells have revealed subthreshold membrane potential oscillations (MPOs) whose temporal periods, and time constants of excitatory postsynaptic potentials (EPSPs), both increase along

this axis. Slower (faster) subthreshold MPOs and slower (faster) EPSPs correlate with larger (smaller) grid spacings and field widths. The self-organizing map model simulates how the anatomical gradient of grid spatial scales can be learned by cells that respond more slowly along the gradient to their inputs from stripe cells of multiple scales. The model cells also exhibit MPO frequencies that covary with their response rates, and exhibit some properties of modular organization of the different spatial scales. The gradient in intrinsic rhythmicity is thus not compelling evidence for oscillatory interference as a mechanism of grid cell firing.

Homologous spatial and temporal mechanisms: Neural relativity. This spatial gradient mechanism is homologous to a gradient mechanism for temporal learning in the lateral entorhinal cortex and its hippocampal projections that was proposed in the 1980s. Such adaptively timed learning has simulated data about the role of hippocampus in supporting learning that bridges temporal gaps, such as occurs during trace conditioning and delayed matching-to-sample. This type of "spectrally timed learning" has Weber Law properties that have been confirmed by recent experiments that have discovered "time cells" in the hippocampus. Spatial and temporal representations may hereby arise from homologous mechanisms, thereby embodying a mechanistic "neural relativity" that may clarify how episodic memories are learned.

Homologous processing of angular and linear velocity path integration inputs. The inputs that drive the initial development of grid cells and place cells are angular and linear velocity signals that are activated by an animal's navigational movements. The model proposes that both angular and linear velocity signals are processed by ring attractor neural circuits. Angular velocity signals are proposed to be processed by ring attractors that are composed of head direction cells, whereas linear velocity signals are proposed to be processed by ring attractors that are composed of stripe cells. The outputs of head direction cells modulate the linear velocity signals to multiple directionally-selective stripe cell ring attractor circuits. This modulation is sensitive to the cosine of the difference between the current heading direction of movement and the ring attractor's directional preference. Each stripe cell ring attractor is sensitive to a different direction and spatial scale. Stripe cells are the individual cells within each such ring attractor circuit and are activated at different spatial phases as the activity bump moves across their ring locations. They may be activated periodically as the activity bump moves around the ring attractor more than once in response to the navigational movements of the animal.

The model's assumption that both head direction cells and stripe cells are computed by ring attractors that drive grid and place cell development is consistent with data showing that adultlike head direction cells already exist in parahippocampal regions of rat pups when they actively move out of their nests for the first time at around two weeks of age.

Stable learning, attention, realignment, and remapping. Place cell selectivity can develop within seconds to minutes, and can remain stable for months. The hippocampus needs additional mechanisms to ensure this long-term stability. This combination of fast learning and stable memory is often called the *stability-plasticity dilemma*. Self-organizing maps are themselves insufficient to solve the stability-plasticity dilemma in environments whose input patterns are dense and are non-stationary through time, as occurs regularly during real-world navigation. However, self-organizing maps augmented by learned top-down expectations that focus attention upon expected combinations of features can do so.

Adaptive Resonance Theory, or ART, proposes how to dynamically stabilize the learned categorical memories of self-organizing maps. Experimental data about the hippocampus from several labs are compatible with the predicted role of top-down expectations and attentional matching in memory stabilization. These experiments clarify

how cognitive processes like attention may play a role in entorhinal-hippocampal spatial learning and memory stability. The proposed mechanism of top-down attentional matching may also help to clarify data about grid and place cell remapping and alignment of grid orientations.

Beta, gamma, and theta oscillations. Within ART, a sufficiently good match can trigger fast gamma oscillations that enable spike-timing dependent plasticity to occur, whereas a big enough mismatch can trigger slow beta oscillations that do not. Such beta oscillations occur in hippocampus during the learning of novel place cells, and have the properties expected when mismatches occur and receptive field refinements are learned. Beta oscillations also occur at the expected times in visual cortex and in the frontal eye fields during shifts in spatial attention. Thus, the match/mismatch dynamics leading to gamma/beta oscillations seem to occur in multiple brain systems.

The theta rhythm has been associated with properties of spatial navigation, as has firing of entorhinal grid cells. Recent experiments have reduced the theta rhythm by inactivating the medial septum (MS) and demonstrated a correlated reduction in the hexagonal spatial firing patterns of grid cells. These results, along with properties of intrinsic membrane potential oscillations in slice preparations of entorhinal cells, have been proposed to support an oscillatory interference model of grid cells. Our self-organizing map model of grid cells can explain these data without invoking oscillatory interference. In particular, the adverse effects of MS inactivation on grid cells can be understood from how the concomitant reduction in cholinergic inputs may increase conductances of leak potassium and slow and medium after-hyperpolarization channels.

Model parsimony. Our emerging neural theory of spatial and temporal processing in the entorhinal-hippocampal system exhibits a remarkable parsimony and unity in at least three ways: It proposes that similar ring attractor mechanisms compute the linear and angular path integration inputs that drive map learning; that the same self-organizing map mechanisms can learn grid cell and place cell receptive fields, despite their dramatically different appearances; and that the dorsoventral gradient of multiple scales and modules of spatial learning through the medial entorhinal cortex to hippocampus may use mechanisms that are homologous to mechanisms earlier proposed for temporal learning through the lateral entorhinal cortex to hippocampus ("neural relativity"), as reflected by data about trace conditioning, delayed matching-to-sample, and "time cells". This mechanistic homolog clarifies why both spatial and temporal processing occur in the entorhinal-hippocampal system and why episodic learning may be supported by this system. No less striking is the fact that both grid cells and place cells can develop by detecting, learning, and remembering the most frequent and energetic co-occurrences of their inputs, properly understood. This co-occurrence property is naturally computed in response to data, such as navigational signals, that take on contextual meaning through time.

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Modeling References (see <http://cns.bu.edu/~steve>)

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