

Spatial rate/phase correlations in theta cells can stabilize randomly drifting path integrators

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Summary

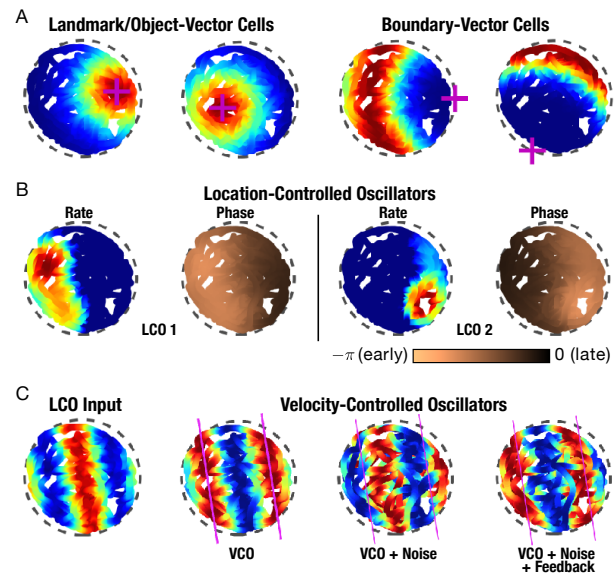
The spatial firing of place cells and grid cells is thought to reflect the association of environmental features, such as external sensory cues and local boundaries, with the path integration of idiosyncratic cues, such as movement direction and speed. Models of path integration as temporal phase interference among neural oscillators, supported by evidence of theta cells with directionally tuned burst frequency (Welday et al., 2011), must address the critical problem that interference patterns randomly drift in space in the presence of intrinsic phase noise (Monaco et al., 2011; Blair et al., 2014). Here, we present a synchronization theory in which a hypothetical population of theta-rhythmic (6–10 Hz) “location-controlled” oscillators (LCOs) mediates the ability of environmental features to stabilize path integration in a downstream layer of velocity-controlled oscillators (VCOs). We suppose that representations of objects/landmarks or boundaries are weakly theta-modulated and combine to form spatially modulated inputs to the LCOs that are fixed to the environment. This environmental drive combines with ongoing theta oscillations to create a robust correlation between higher firing rates and earlier theta phases of bursting. We show that this rate/phase correlation in LCOs is sufficient to selectively entrain VCOs to prevent drifting with noise. This entrainment requires associative learning during early theta phases at LCO-to-VCO synapses to construct spatially antiphase inputs that drive the environmental feedback to VCOs. We provide a mathematical derivation, an abstract rate–phase model, and an implementation of this sensory feedback mechanism in a spiking network model of phasic bursting neurons. Notably, we present preliminary recording data from subcortical regions in rats, including lateral septum, showing theta cells that qualitatively match the spatial rate/phase correlations of our hypothesized LCOs. These results support a hybrid “place-to-grid” framework where temporal and attractor mechanisms may be complementary without depending on the fine tuning of phase or connectivity.

Environmental features drive rate-to-phase conversion for stable path integration

Two primary theories of path integration underlying the hippocampal spatial map have been heavily studied since the discovery of grid cells: that continuous attractor networks create stable activity bumps on two-dimensional manifolds, or that theta-rhythmic neural oscillators create temporal interference patterns that map onto space. In both cases, the activity patterns must integrate over noisy signals for movement direction and velocity, whether in the connectivity of the attractor network or in the relative theta phases of the oscillators. There is supporting evidence for both accounts (e.g., Yoon et al., 2013; Welday et al., 2011). However, continuous attractor models require fine tuning of asymmetric interactions between grid cells and conjunctive grid-by-direction cells (Sargolini et al., 2006), temporal models have been challenged by inconsistent cross-species theta (Yartsev et al., 2011), and both require resetting to counteract cumulative integration errors.

The theory that we present here extends our previous modeling study (Monaco et al., 2011) that was originally presented at Cosyne (Monaco et al., 2010). While our earlier work assumed a generalized phase-code feedback mechanism, this theory provides a cellular and network level mechanism for how such phase-coded path integration can be achieved. The theory derives from recent data on object/landmark representations in lateral entorhinal cortex (Deshmukh & Knierim, 2011) and boundary representations in subiculum and medial entorhinal cortex (Lever et al., 2009; Solstad et al., 2008). We combine these environmental inputs with a robust neuronal rate-to-phase mechanism (Mehta et al., 2002) to generate a trajectory- and history-independent phase code tied to environmental features. In this framework, attractor dynamics among grid cells could maintain the structure of the population activity bump but would not be required for path integration.

Our rate–phase model has landmark/object and boundary inputs (panel *A*) that drive LCOs to have high firing rate and early theta phase at certain locations (panel *B*). We show that learning weights during early theta phases constructs spatially antiphase LCO input to each VCO, which then entrains the path integrators to earlier ($\sim \pi$) phase in the firing troughs between 2D stripes (panel *C*). This entrainment prevents drift relative to the landmarks and boundaries of the environment. Grid cells constructed directly from these calibrated VCOs have somewhat distorted grid structure due to the push/pull of noise and feedback, but the locations of activity peaks remain stable. We demonstrate that a spiking network of LCOs (based on Izhikevich (2003) bursters) can both implement the rate-to-phase conversion and drive the environmental feedback to VCOs. The spiking model delineates bursting characteristics and puts constraints on learning rules for producing the predicted type-II phase response (Monaco et al., 2011). We will describe preliminary long-duration recording data from foraging rats that reveals a population of theta cells in lateral septum, hypothalamus, and other subcortical areas with spatially modulated phases and rate/phase correlations that match our LCOs. We discuss implications for the anatomy of a place-to-grid theta feedback loop (Monaco et al., 2011) and how history-independence solves the cumulative error problem for temporal path-integration models.



Rate–phase model of LCO feedback. *A*, Environmental features are represented as landmark/object or boundary cells. *B*, LCOs create rate/phase correlations across space. *C*, Learned antiphase input from LCOs (left) drives feedback that stabilizes the 2D-stripe VCO activity pattern in space (right three panels).

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