## I-46. Traveling waves of the hippocampal theta rhythm encode rat position

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The theta rhythm is an ~8 Hz oscillation in the hippocampus that mirrors the timing and coordination of large groups of neurons. Its structure varies richly in both space and time. We seek to understand these variations in terms of the sequence of activity that unfolds as a rat runs along a linear track. Our data consists of multi-electrode recordings from layer CA1 of behaving rats. Exploratory analysis revealed that the theta rhythm exhibits a time-varying phase gradient along the axis defined by the apical dendrites of CA1 pyramidal cells. To identify putative sources responsible for this variation, we perform spatial ICA on the analytic (complex-valued) representation of the theta-band oscillation. This analysis reveals a population of sparse components, each with a characteristic spatial amplitude-phase relationship representing a traveling wave that propagates across the electrode array. We find that many of these components are activated in a place- and direction-selective manner; as a rat runs down the track, the components transiently activate in a specific sequence. Together, the set of 'place components' tiles the entire track. This observation is closely related to the known response properties of CA1 pyramidal cells, which also activate in a place-specific manner. However, unlike place cells, the sparse components in the theta band tile the track more uniformly, manifest across the entire electrode array, and are linked to unique cross-frequency dynamics, suggesting that they arise from a mechanistically distinct source. The LFP is commonly considered to be a relatively impoverished signal conveying only general information about behavioral state. In contrast, we find that the multi-electrode LFP can provide a rich behavioral readout. Our analysis approach may also be relevant for identifying the features encoded by other brain structures with prominent oscillations, such as the motor cortex and olfactory bulb.

## I-47. Are aperiodic 1D grid cell responses consistent with low-dimensional continuous attractor dynamics?

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Since the discovery of the striking activity of grid cells, the question of mechanism has received intense attention. One of two dominant models is based on 2D continuous attractor dynamics in recurrent networks. Briefly, lateral connections stabilize a state with a triangular lattice activity pattern in the population, and all its translations. This model is fully consistent with the rate dynamics of grid cells in 2D enclosures and has made many successful predictions. However, the response of cells along 1D tracks remains a confound and possible challenge. In 1D, grid cells fire at multiple locations, but the pattern is not periodic. Here we examine whether the 1D response patterns are consistent with continuous attractor dynamics, by analyzing multiple simultaneously recorded grid cells, with responses elicited in both 2D and 1D environments. First, we show that aperiodic responses are not

inconsistent with attractor dynamics: while attractor dynamics force cells to maintain fixed response relationships to each other, they do not dictate how network states are mapped to the external represented variable. This mapping may be continually varied or reset, e.g. by external landmarks. Second, we examine the stability of cell-cell relationships in 1D, even as individual cells exhibit drifts in the locations of fields over traversals of a track, showing that cell-cell response relationships are better preserved than the responses of individual cells. Third, we examine whether the 1D response is quasi-periodic, generated as a slice though a periodic 2D pattern, or whether resetting of fields by the environment is an important source of aperiodicity in the 1D response, and show evidence for the latter. Our results suggest that, independent of the spatial mapping between 1D and 2D, and despite the disparity in 1D and 2D-responses, the same low-dimensional dynamics observed in grid cells in 2D may underlie their 1D-responses.

## I-48. A single computational mechanism for both stability and flexibility in vocal error correction

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The brain uses sensory feedback to correct behavioral errors, and larger errors by definition require greater corrections. However, in several systems larger errors drive learning less effectively than smaller errors. Limiting motor changes in response to large sensory errors is reasonable, since sensory signals are inherently noisy. A successful control strategy must therefore use feedback to correct errors while disregarding aberrant sensory signals that would lead to maladaptive corrections. Our prior work has used online manipulations of auditory feedback to demonstrate that in adult songbirds, vocal error correction is inversely proportional to error size, with smaller errors corrected robustly but larger errors causing minimal vocal changes. These findings in adults, however, introduce an apparent paradox. If vocal learning is smaller in response to larger errors, and animals commit very large errors when initially learning to vocalize, then how does a young bird ever learn to sing? More generally, if error correction is an inverse function of error size, how can complex behaviors ever be acquired? Here, we propose a computational mechanism that can account for both the stability of adult behavior during large errors and the flexibility of behavior earlier in life. In adult songbirds, the extent of learning is well-predicted by the overlap between the prior distribution of sensory feedback and the distribution experienced during sensory perturbations. We therefore hypothesize that songbirds weight the probability of sensory feedback when computing how much to modify song during error correction. We test this hypothesis by quantifying error correction in younger birds, where vocal variability is greater than in older adults. We find that for the same error, learning is much greater in younger animals, but that this apparent difference can be explained by a single probabilistic weighting strategy. These findings suggest that throughout life, the statistics of prior experience constrain learning.

## I-49. Optimal foraging and multiscale representation by hippocampal place cells

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The size of place fields of hippocampal place cells varies systematically along the dorsoventral axis, dorsal place cells having smaller fields than ventral (Kjelstrup et. al. 2008). Moreover, the phase of the theta oscillation varies coherently along the dorsoventral axis (Lubenov and Siapas, 2009), so that place cells representing different spatial scales may potentially coordinate their activity temporally. It is not clear of what benefit is this multiscale