Spatial rate-phase coding in lateral septal 'phaser cells': single-unit data and theta-bursting models

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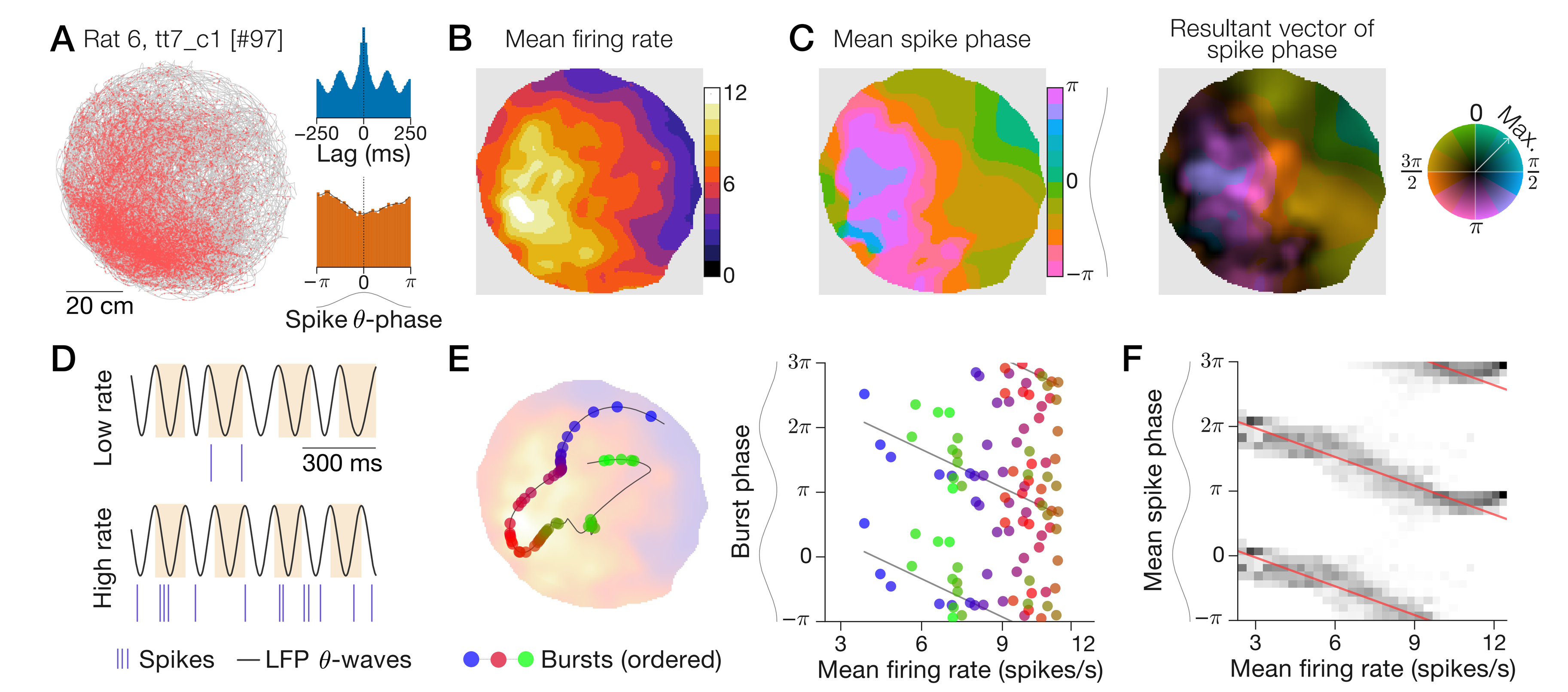
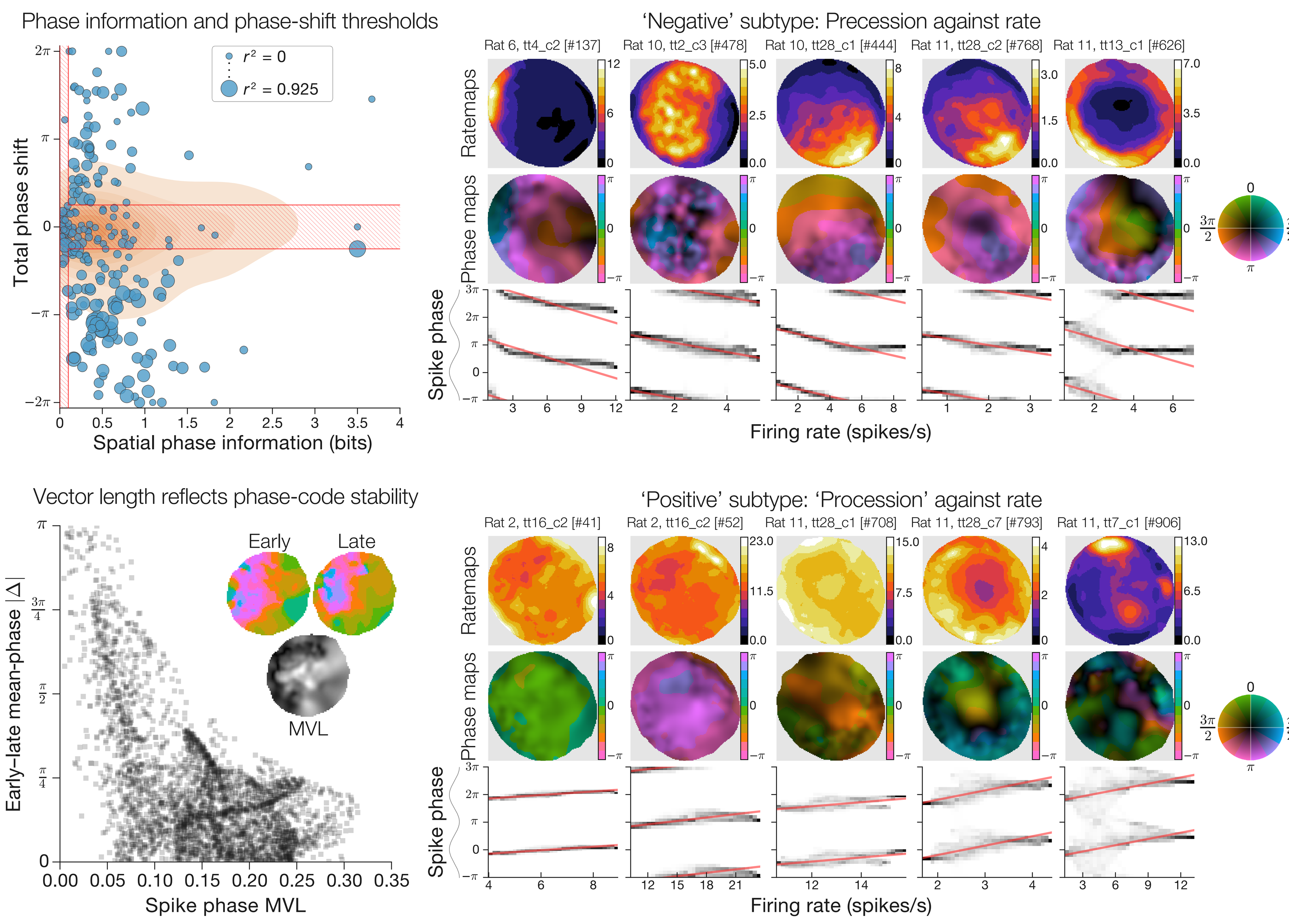
Abstract

During spatial navigation, the frequency and timing of spikes from spatial neurons including place cells in hippocampus and grid cells in medial entorhinal cortex are temporally organized by continuous theta oscillations (5–12 Hz). The theta rhythm is regulated by subcortical structures including the medial septum, but it is unclear how spatial information from place cells may reciprocally organize subcortical theta-rhythmic activity. Here we recorded single-unit spiking from a constellation of subcortical and hippocampal sites to study spatial modulation of rhythmic spike timing in rats freely exploring an open environment. Our analysis revealed a novel class of neurons that we termed 'phaser cells,' characterized by a symmetric coupling between firing rate and spike theta-phase. Phaser cells encoded space by assigning distinct phases to allocentric isocontour levels of each cell's spatial firing pattern. In our dataset, phaser cells were predominantly located in the lateral septum, but also the hippocampus, anteroventral thalamus, lateral hypothalamus, and nucleus accumbens. Unlike the unidirectional late-to-early phase precession of place cells, bidirectional phase modulation acted to return phaser cells to the same theta-phase along a given spatial isocontour, including cells that characteristically shifted to later phases at higher firing rates. Our dynamical models of intrinsic theta-bursting neurons demonstrated that experience-independent temporal coding mechanisms can qualitatively explain (1) the spatial rate-phase relationships of phaser cells and (2) the observed temporal segregation of phaser cells according to phase-shift direction. In open-field phaser cell simulations, competitive learning embedded phase-code entrainment maps into the weights of downstream targets, including path integration networks. Bayesian phase decoding revealed error correction capable of resetting path integration at subsecond timescales. Our findings suggest that phaser cells may instantiate a subcortical theta-rhythmic loop of spatial feedback. We outline a framework in which location-dependent synchrony reconciles internal idiothetic processes with the allothetic reference points of sensory experience.

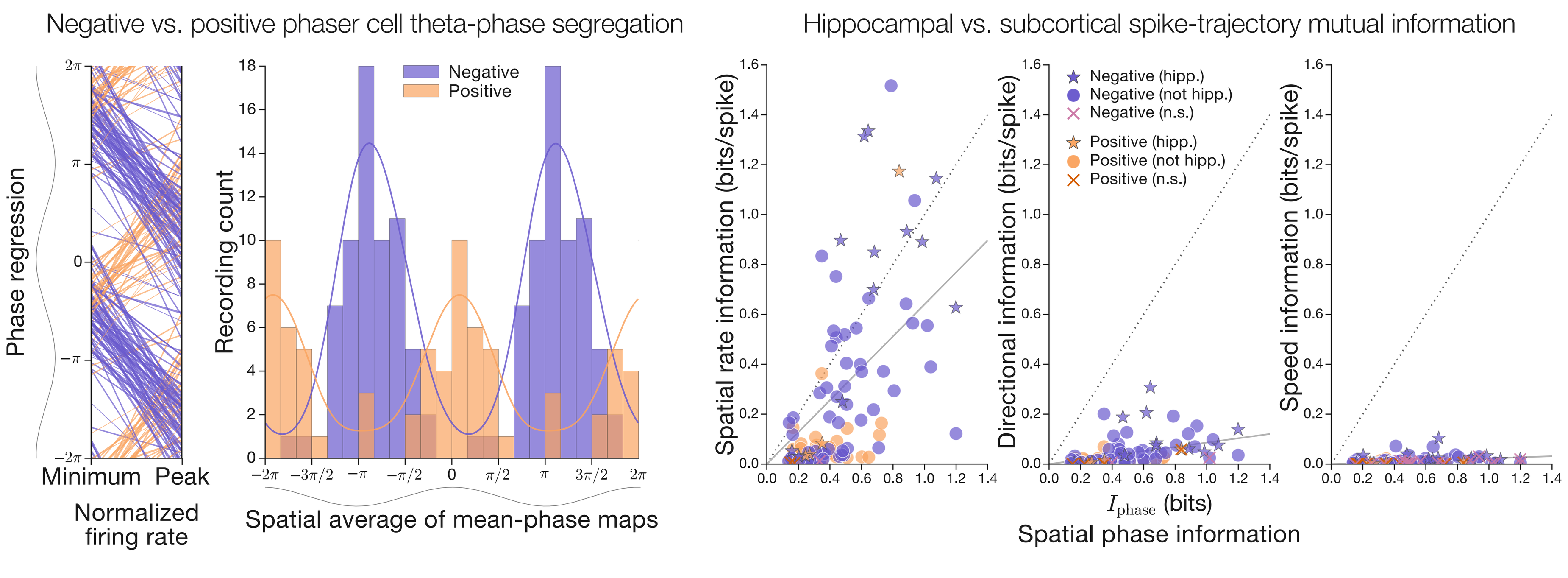
Example neuron from lateral septum with rate-phase code



Quantitative selection of 'phaser cell' recordings



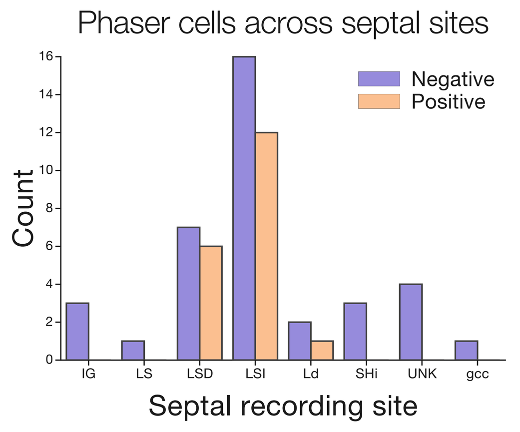
Temporal segregation, phase information, and brain location



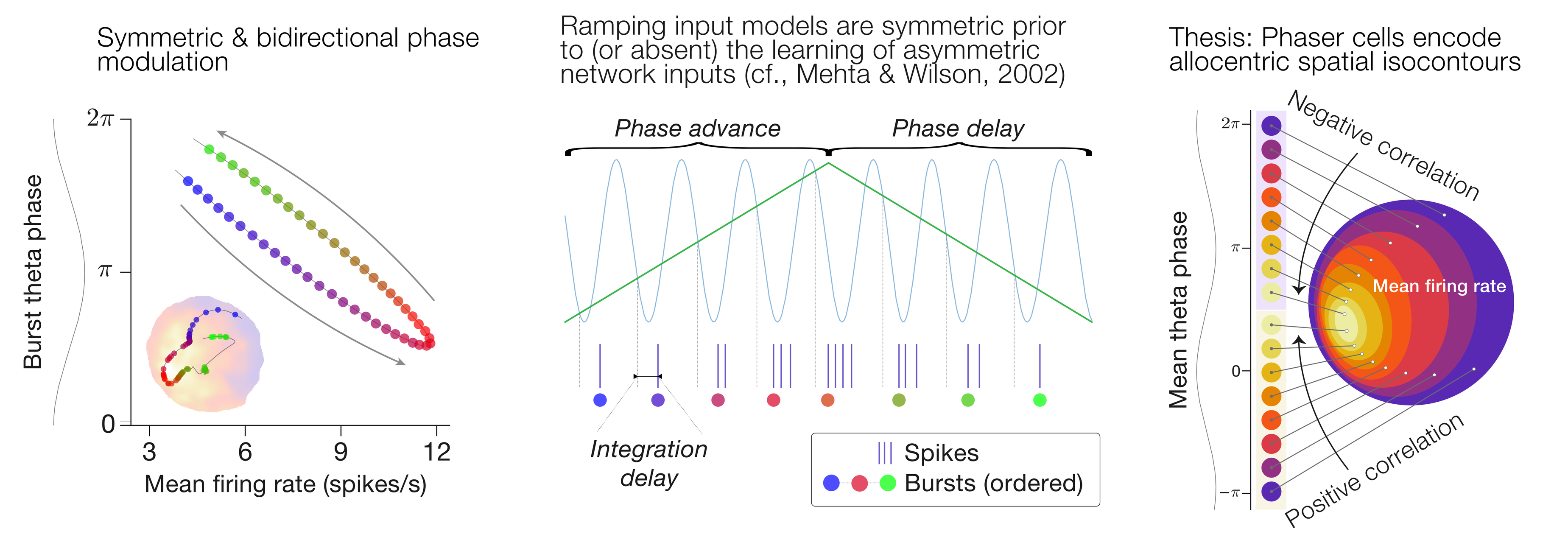
Phase-coding subtype across recording locations

Recording Area	Negative	Positive	Mixed	None	Total
Lateral septum	31 (9.7%)	17 (5.3%)	2 (0.6%)	287 (84.4%)	321
Medial septum	–	–	–	16 (100.0%)	16
Hippocampus	11 (12.4%)	4 (4.5%)	–	74 (83.1%)	89
Thalamus	1 (2.2%)	–	–	45 (97.8%)	46
Midbrain	1 (0.7%)	–	–	134 (99.3%)	135
Other	1 (1.6%)	–	1 (1.6%)	62 (96.8%)	64
Total	45 (6.7%)	21 (3.1%)	3 (0.4%)	602 (89.7%)	671

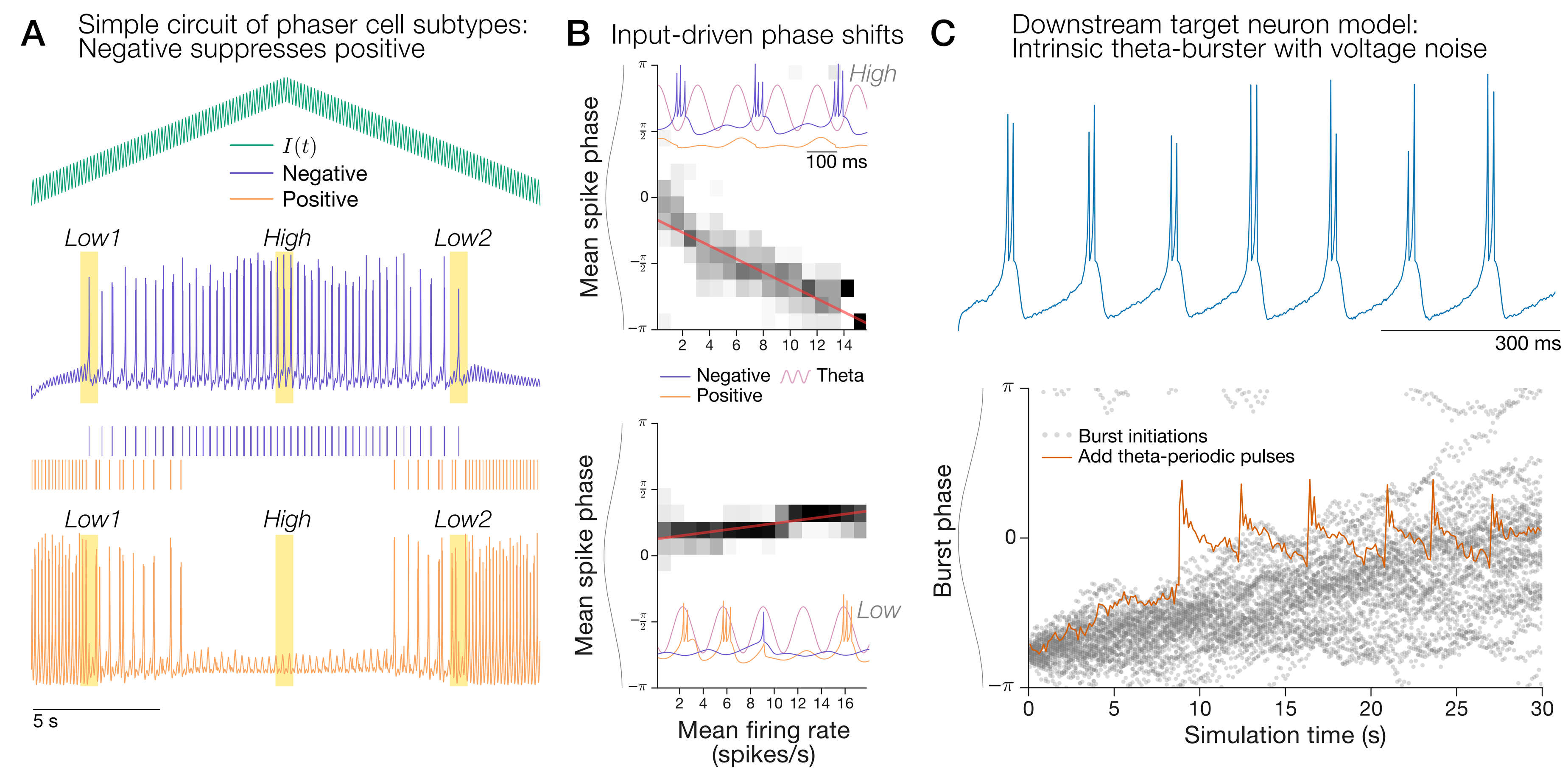
Columns: 'Negative'/'Positive', cells with at least one negative/positive phaser-classified recording and none of the other subtype; 'Mixed', cells with at least one negative and at least one positive phaser-classified recording; 'None', cells with no phaser-classified recordings.



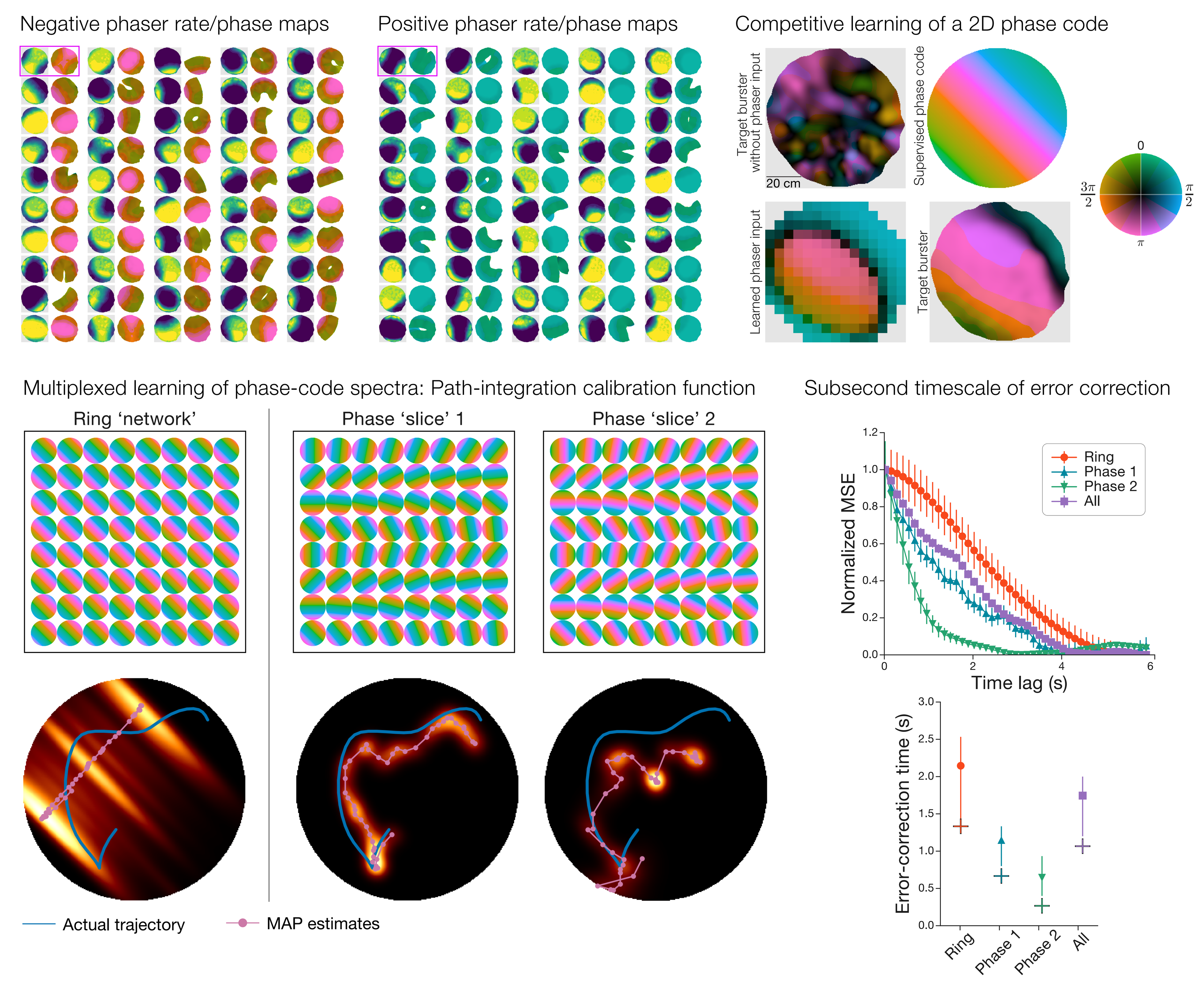
Symmetric phase codes represent 2D spatial isocontours



Single-neuron models of phaser cells & downstream targets



Position-coding by collectively entrained target networks



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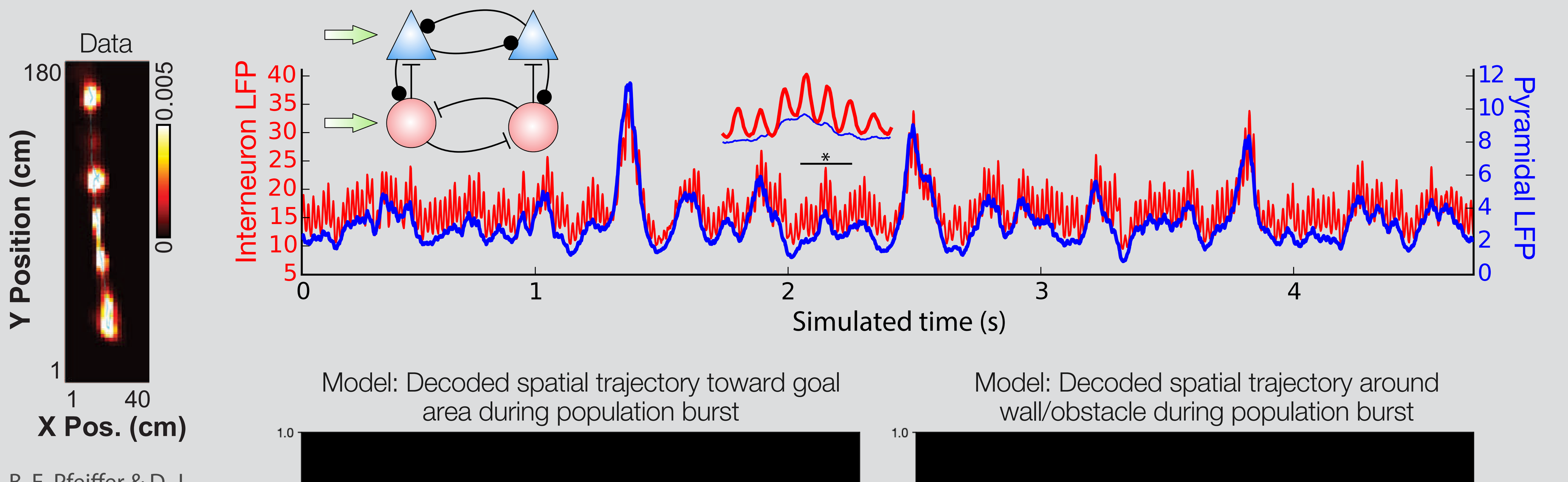
Future work: Sharp-wave sequences and gamma oscillations in spiking attractor-map networks

To study trajectory sequences that 'hover' at discrete location during peaks in the slow-gamma rhythm (Pfeiffer & Foster, 2015), we have developed a CA3-like recurrent excitatory/inhibitory network model of quadratic 'place cells' that produces sharp wave-like population bursts and gamma oscillations. The activity during the population bursts can be decoded into allowable spatial trajectories that find goals and avoid obstacles.



B. E. Pfeiffer & D. J. Foster (2015). Autoassociative dynamics in the generation of sequences of hippocampal place cells. Science, 349:180–3.