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Self-organized formation of discrete grid cell modules from smooth gradients

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Modular structures in myriad forms — genetic, structural, functional — are ubiquitous in the brain. While modularization may be shaped by genetic instruction or extensive learning, the mechanisms of module emergence are poorly understood. Here, we explore complementary mechanisms in the form of bottom-up dynamics that push systems spontaneously toward modularization. As a paradigmatic example of modularity in the brain, we focus on the grid cell system. Grid cells of the mammalian medial entorhinal cortex (mEC) exhibit periodic lattice-like tuning curves in their encoding of space as animals navigate the world. Nearby grid cells have identical lattice periods, but at larger separations along the long axis of mEC the period jumps in discrete steps so that the full set of periods cluster into 5-7 discrete modules. These modules endow the grid code with many striking properties such as an exponential capacity to represent space and unprecedented robustness to noise. However, the formation of discrete modules is puzzling given that biophysical properties of mEC stellate cells (including inhibitory inputs from PV interneurons, time constants of EPSPs, intrinsic resonance frequency and differences in gene expression) vary smoothly in continuous topographic gradients along the mEC. How does discreteness in grid modules arise from continuous gradients? We propose a novel mechanism involving two simple types of lateral interaction that leads a continuous network to robustly decompose into discrete functional modules. We show analytically that this mechanism is a generic multi-scale linear instability that converts smooth gradients into discrete modules via a topological “peak selection” process. Further, this model generates detailed predictions about the sequence of adjacent period ratios, and explains existing grid cell data better than existing models. Thus, we contribute a robust new principle for bottom-up module formation in biology, and show that it might be leveraged by grid cells in the brain.

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