

## **Environmental boundaries as an error correction mechanism for grid cells**

Kiah Hardcastle, Surya Ganguli, Lisa M Giocomo

Accurate spatial navigation is critical for survival: it enables predator avoidance and piloting to remembered food locations. Navigational ability likely relies on internal neural maps of external space (Tolman 1948). Grid cells, found in medial entorhinal cortex (MEC), may serve this function, as they fire in periodic, hexagonally arranged locations reminiscent of a longitude and latitude coordinate system (Hafting et al., 2005).

Many have proposed that this firing pattern arises through path-integration, a landmark-independent calculation of position computed through integration of an inertia-based velocity signal. However, the additive nature of path-integration may lead to accumulating error and, without a corrective mechanism, inaccuracy in position estimates. We hypothesized that environmental boundaries could contribute to such a corrective mechanism. To test this, we examined grid cells in behaving rodents as they traveled across an open arena. First, we find that error in grid cell spiking accumulates at a rate of  $\sim 0.015$  cm/sec relative to time since the animal last encountered a boundary. Second, the spatial pattern of accumulating error spikes was consistent with coherent drift of grid-like neural activity patterns in attractor network models for grid cells (e.g. Burak & Fiete, 2009). Third, encounters with a boundary correct errors in grid cell spiking perpendicular, but not parallel, to the boundary, consistent with an error correction mechanism driven by border cells that fire along the entire boundary length.

Furthermore, we reproduced all of these experimental observations in an augmented attractor network model that combined grid cells and border cells. Connectivity between border cells and grid cells consistent with Hebbian plasticity was sufficient to account for all observations.

Our results propose a fundamental role for the use of landmarks in grid-cell driven spatial navigation, and suggest a specific neurobiological mechanism by which neurons that code for environmental boundaries support noise-robust representations of external space.