

# Environmental Boundaries as an Error Correction Mechanism for Grid Cells

## Highlights

- Grid cells accumulate error relative to time and distance traveled
- Error in the grid code is corrected by encounters with environmental boundaries
- Grid error reflects systematic drift and is corrected in a direction-dependent manner
- Border cells can provide a neural substrate for error correction

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## In Brief

Medial entorhinal grid cells exhibit spatially periodic firing patterns and are proposed to support path integration. Hardcastle et al. found that grid cells accumulate error when animals are far from environmental boundaries and provide evidence for boundary-driven error correction.



# Environmental Boundaries as an Error Correction Mechanism for Grid Cells

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## SUMMARY

Medial entorhinal grid cells fire in periodic, hexagonally patterned locations and are proposed to support path-integration-based navigation. The recursive nature of path integration results in accumulating error and, without a corrective mechanism, a breakdown in the calculation of location. The observed long-term stability of grid patterns necessitates that the system either performs highly precise internal path integration or implements an external landmark-based error correction mechanism. To distinguish these possibilities, we examined grid cells in behaving rodents as they made long trajectories across an open arena. We found that error accumulates relative to time and distance traveled since the animal last encountered a boundary. This error reflects coherent drift in the grid pattern. Further, interactions with boundaries yield direction-dependent error correction, suggesting that border cells serve as a neural substrate for error correction. These observations, combined with simulations of an attractor network grid cell model, demonstrate that landmarks are crucial to grid stability.

## INTRODUCTION

Since first postulated by Darwin, diverse species have been shown to use an inertia-based navigation system, commonly referred to as path integration (Bartels, 1929; Darwin, 1873; Mittelstaedt and Mittelstaedt, 1980; Wehner and Srinivasan, 1981). Path integration utilizes self-motion information, such as optic flow and proprioceptive cues, to continuously track an animal's location within its internal representation of space. For example, the cumulative integration of direction and distance traveled from a starting point can allow an animal to calculate a direct path back rather than retracing its circuitous outbound trajectory (Mittelstaedt and Mittelstaedt, 1980). The additive nature of path integration, however, inevitably results in an accumulation of error; thus, over time, the calculation of location becomes

unreliable. One strategy for accomplishing accurate navigation in the presence of path-integration-based error is landmark-based navigation, whereby animals pilot based on their location relative to familiar landmarks (Etienne, 1992). While animals can simultaneously use path integration and landmark-based navigational strategies to differing degrees, how neural circuits integrate these two modalities to support accurate navigation remains unresolved (Buzsáki and Moser, 2013; Gothard et al., 1996b; Knierim et al., 1998).

Neurons in the medial entorhinal cortex (MEC) provide many of the building blocks for creating an internal representation of self-location (Hafting et al., 2005; Sargolini et al., 2006; Solstad et al., 2008). MEC grid cells fire in periodic, hexagonally patterned locations, potentially providing a neural metric for distance traveled and a neural substrate for path integration (Fyhn et al., 2004; Hafting et al., 2005). Grid cells retain their general periodic structure across different environmental contexts and for short periods of time in darkness, suggesting that they perform online integration of self-motion cues to continuously update their estimate of location (Hafting et al., 2005). This continuous integration of self-motion cues results in a cumulative grid code, in which any error in the current estimate of position gets added to the next integrative step. The stochastic nature of neural responses, along with heterogeneous synaptic weights and a finite number of neurons, introduces sources of error that can cause an eventual breakdown in the grid code (Burak and Fiete, 2009). In simulations of attractor-based network grid cell models, grid responses break down in a few to tens of minutes, depending on the nature of the assumed noise and the size of the grid population (Burak and Fiete, 2009). If grid cells accumulate error as predicted, then a mechanism for correcting error must exist, as experimentally recorded grid patterns appear relatively stable over minutes, hours, and days (Hafting et al., 2005).

Despite computational predictions regarding grid error, accumulation of error in the grid code has never been experimentally quantified, and the potential substrates for correcting this error remain unknown. Theoretical and computational work have proposed that sensory cues regarding environmental landmarks could correct accumulated grid error, with boundaries in the environment acting as possible landmarks capable of providing an error correction signal (Burak and Fiete, 2009; Burgess, 2008; Fuhs and Touretzky, 2006; Hasselmo, 2008; McNaughton et al., 1991, 1996; Moser et al., 2008; O'Keefe and Burgess, 2005;

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