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## Intrinsic current generated, omnidirectional phase precession and grid field scaling in toroidal attractor model of medial entorhinal path integration

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Understanding of how hippocampal circuits accomplish path integration was advanced with the discovery of 'grid cells' in medial entorhinal cortex (MEC) [1]. Grid cells express a rhomboidal grid of high activity spots in any environment, indicating that they are part of a system that integrates velocity and direction of motion to track relative location. McNaughton et al. [2] suggested that grid cell path integration is based on a connectivity matrix originally proposed by Samsonovich and McNaughton [3]. Cells are connected as a function of relative grid phase, forming a torus-shaped continuous attractor. A 'bump' of activity stabilizes by a cooperative interaction among 'neighboring' (in the connectivity sense) cells and can move around the torus in a manner consistent with the rat's motion, causing each cell to reactivate periodically. This motion may be provided by cells observed in MEC layer III that are conjunctive for head direction, linear velocity, and grid location [4].

Grid cells also exhibit theta phase precession, firing at late phases of the theta rhythm when the animal enters a grid node and successively earlier phases as the animal traverses the node [5]. One model for phase precession [6,7] is based on asymmetry in the intrinsic connections, which causes the network to 'look-ahead' of the rat during each theta cycle and then reset at the 'actual' location of the animal at the beginning of the next theta cycle as a result of external input. This model, however, is inadequate to account for omnidirectional phase precession in

2-D environments or for precession during path integration without external cues to reset the activity each cycle.

We propose a more parsimonious system-level model in which the 'look-ahead' is determined by the rate of activity of the conjunctive cells, which drives the bump forward, and the reset is determined by an intrinsic after-depolarization current whose time constant induces the bump to form slightly ahead of its initial location on the previous cycle. A 1-D version of this model was implemented using the NEURON simulator. The model generates phase precession in both possible directions of travel, with no external reset mechanism. As predicted, changing the time constant of the after-depolarization, in a manner consistent with the observed variation along the dorsoventral axis of MEC [8] changes the grid scale accordingly.

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