

Burak Y, Fiete I (2006) Do we understand the emergent dynamics of grid cell activity? *J Neurosci* 26:9352-9354.

Fuhs M, Touretzky D (2006) A spin glass model of path integration in rat medial entorhinal cortex. *J Neurosci* 26:4266-4276.

Dear Journal of Neuroscience,

Accurate path integration in 2D is a tricky business, and Burak and Fiete (2006) are correct that the simple weight matrices used in our simulations do not produce flawless results. However, previous work in one and two dimensional systems (e.g., Hahnloser, 2003; Conklin and Eliasmith, 2005) has demonstrated that excellent integration performance can be achieved in neural substrates using offset connectivity matrices similar to what we used. The main contribution of our model is to demonstrate how previously-studied neural integration architectures (offset connections, velocity modulation, and so on) could co-exist with periodic symmetry constraints that result in the observed properties of dMEC grid cells. Our prediction that some grid cells must be modulated by the animal's speed and direction of travel has already been confirmed (Sargolini et al., 2006).

In formulating the model, one of the unresolved questions we considered was how well the rat's path integration system actually does work, and hence, how well we need to "engineer" our simulations to work. Contrary to Burak and Fiete's assumption of accurate integration over 200 m trajectories without sensory cues, drift has been observed in both head direction (Goodridge et al., 1998) and place cell (Knierim et al., 1995) firing when animals forage in a cylinder for several minutes, either in the dark or after landmark devaluation through disorientation training. Moreover, when both visual landmarks and olfactory cues are removed, Save et al. (2000) report that hippocampal place fields recorded in a cylindrical arena were unstable and showed angular drift across 8 min recording sessions, even in the light. These results suggest similar behavior should be seen in grid cells, calling into question the precision of the rat's neural path integrator in the absence of any sensory information. The Save et al. (2000) study suggests that the stability of grid cell fields recorded for 10 min in darkness by Hafting et al. (2005) was likely aided by wall location and olfactory cue associations constructed during the prior 10 min.

The two footnotes in Burak and Fiete's commentary turn out to be intimately related. We agree that aperiodic boundaries seem more biologically plausible, but we did discuss an alternative hypothesis of a 2D sheet shaped as a diamond (60° and 120° angles) with toroidal boundary conditions. Such a model has been proposed by McNaughton et al. (2006). Shifting an activity bump over this torus also produces p6m wallpaper symmetry in the resulting firing fields. However, in at least one example from Hafting et al. (2005), a cell appears to have seven firing fields surrounding a central field instead of the usual six—but only in one of the two environments in which it was recorded. How such an effect could be achieved in a toroidal network is unclear. A spin glass model such as ours can account for these irregularities, and depending on the specific recurrent connectivity

used, they can be made to occur with some frequency. That these irregularities are locally stable—until they slide off the edge of the neural sheet—suggests an energy landscape with multiple families of local minima, each a separate 2D manifold.

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