

# Entorhinal Grid Cell Responses as Basis Functions for Spatial RL

Nicholas J. Gustafson<sup>1</sup> and Nathaniel D. Daw<sup>1,2</sup>

<sup>1</sup>Center for Neural Science, <sup>2</sup>Department of Psychology, New York University

Reinforcement learning (RL) has provided a popular framework for characterizing the neural and behavioral mechanisms of trial-and-error learned decision-making in simple tasks. Probably the most crucial open problem for extending this understanding to more complex, real-world behaviors is how tasks involving many relevant, structured features (or “states”) can be represented in a way that enables them to be learned efficiently. A promising domain for studying how the brain tackles this problem is spatial navigation tasks, such as mazes, since the structure of states can be complex but is transparently understood and manipulated. To that end, we hypothesize a novel, additional role for “grid cells” of the entorhinal cortex in such representation: specifically, we propose that their spatial response fields serve as basis functions for the learning of RL value functions in spatial tasks.

In foraging rats, entorhinal grid cells have response fields that tile space with a repeating, triangular lattice at varying scales, orientations, and phases. Prior modeling work in this system has largely focused on how these responses arise or on how they can be used as inputs to produce localized place fields in hippocampus. Meanwhile, models of spatial RL have generally assumed that systems such as striatum learn to map the latter, hippocampal, representation of position to a “value function” over space, which measures proximity to reward and can be used to guide locomotion toward it. Since hippocampal place cells each fire in a particular location, this would give rise to a redundant, “tabular” representation of the value function, which treats the values of nearby locations independently. However, because the value function typically changes gradually over space, we argue that it can actually be represented more efficiently using basis functions, like entorhinal firing fields, with more widely extended spatial support. Our simulations of RL in spatial navigation tasks demonstrate that basis functions patterned after the entorhinal code allow for much faster learning than does a tabular representation. We propose that plasticity in the corticostriatal projections from entorhinal neurons could subserves such a mapping.

Besides suggesting new mechanisms for spatial RL, our work suggests a richer perspective on the entorhinal code. The multiscale, oscillating lattices are viewed as playing a role analogous to a Fourier basis for representing arbitrary functions over 2D space; prior modeling work using them as input to produce hippocampal place fields (i.e., impulse functions) uses a special case of this capability. Further, we note similarities, and some differences, between the entorhinal code and bases constructed using recent RL methods that perform spectral analysis of the task transition graph (here, the connectivity of adjacent spatial locations). The key insight of these methods is that a useful basis should *not* generalize over space “as the crow flies,” but should respect obstacles such as walls. This motivates generalizing according to geodesic (i.e., along-path) rather than Euclidean distance. These two metrics coincide in the standard task of grid-cell physiology, random foraging in an open field, but are distinct in tasks with walls. We therefore use a version of the Isomap algorithm to predict how the open-field grid cell basis would adjust to the presence of walls if it were based on geodesic distance. The model makes the novel prediction that, when animals can navigate around obstacles, grid cells will show specific discontinuities and geometric distortions in their vicinity. Such experiments might distinguish our model from others that stress a role for the system in Euclidean path integration. Also, analogous changes in the entorhinal code should arise even without walls if animals tend to follow stereotyped, indirect paths. There is some indirect evidence for this effect, in that its downstream consequences would explain why the hippocampal place code remaps when rats switch between tasks involving different patterns of spatial behavior.