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THE STRUCTURE OF NETWORKS THAT PRODUCE THE TRANSFORMATION FROM GRID CELLS TO PLACE CELLS

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Abstract—Since grid cells were discovered in the medial entorhinal cortex, several models have been proposed for the transformation from periodic grids to the punctate place fields of hippocampal place cells. These prior studies have each focused primarily on a particular model structure. By contrast, the goal of this study is to understand the general nature of the solutions that generate the grids-to-places transformation, and to exploit this insight to solve problems that were previously unsolved. First, we derive a family of feedforward networks that generate the grids-to-places transformations. These networks have in common an inverse relationship between the synaptic weights and a grid property that we call the normalized offset. Second, we analyze the solutions of prior models in terms of this novel measure and found to our surprise that almost all prior models yield solutions that can be described by this family of networks. The one exception is a model that is unrealistically sensitive to noise. Third, with this insight into the structure of the solutions, we then construct explicitly solutions for the grids-to-places transformation with multiple spatial maps, that is, with place fields in arbitrary locations either within the same (multiple place fields) or in different (global remapping) enclosures. These multiple maps are possible because the weights are learned or assigned in such a way that a group of weights contributes to spatial specificity in one context but remains spatially unstructured in another context. Fourth, we find parameters such that global remapping solutions can be found by synaptic learning in spiking neurons, despite previous suggestions that this might not be possible. In conclusion, our results demonstrate the power of understanding the structure of the solutions and suggest that we may have identified the structure that is common to all robust solutions of the grids-to-places transformation. © 2011 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: medial entorhinal cortex, hippocampus, global remapping, unsupervised learning.

Four decades ago, O'Keefe and Dostrovsky discovered place cells, neurons in the hippocampus that are selectively active in one or more restricted regions of space, called place fields (O'Keefe and Dostrovsky, 1971; O'Keefe and Nadel, 1978). Since their discovery, many models have attempted to explain how this spatial selectivity arises within the hippocampus (Samsonovich and McNaughton, 1997; Káli and Dayan, 2000; Hartley et al., 2000; Barry and Burgess, 2007). With the discovery of grid cells in the medial entorhinal cortex (MEC), the input structure to the hippocampus (Hafting et al., 2005), the problem of explaining the neural representation of space has shifted to focus on two separate questions: first, how does the periodic firing of hexagonal grid cells in the MEC emerge (Fuhs and Touretzky, 2006; McNaughton et al., 2006; Giocomo et al., 2007; Burgess et al., 2007; Burgess, 2008; Hasselmo and Brandon, 2008; Kropff and Treves, 2008; Burak and Fiete, 2009; Mhatre et al., in press)? and second, how are the periodic grids in the MEC transformed into punctate place fields in the hippocampus (Fuhs and Touretzky, 2006; Solstad et al., 2006; Rolls et al., 2006; Franzius et al., 2007; Blair et al., 2007; Gorchetchnikov and Grossberg, 2007; Molter and Yamaguchi, 2008; Si and Treves, 2009; de Almeida et al., 2009; Savelli and Knierim, 2010)? In this article, we focus on the latter question. We note, however, that there are alternatives to this simple view of how spatial representations arise in the hippocampus. We return to this issue in the Discussion.

The earliest model of the grids-to-places transformation viewed grid cells as the basis functions of a Fourier transformation and synaptic weights from MEC to hippocampus as the coefficients (Solstad et al., 2006). Other models are based on competition in the hippocampal layer: the summed input to a hippocampal cell from grid cells is only weakly spatially selective, but competition allows only the hippocampal cells with the strongest excitation at any given location to become active, thus increasing the spatial selectivity (Fuhs and Touretzky, 2006; Rolls et al., 2006; Gorchetchnikov and Grossberg, 2007; Molter and Yamaguchi, 2008; Si and Treves, 2009; de Almeida et al., 2009; Monaco and Abbott, 2011). Franzius et al. (2007) suggest that maximizing sparseness in periodic grid inputs leads to punctate place fields in the output of independent components analysis. Recently, Savelli and Knierim (2010) studied a Hebbian learning rule that could learn the weights in a feedforward network to generate the grids-to-places transformation. A few studies have also examined the network structure that produces the transformation (Solstad et al., 2006; Gorchetchnikov and Grossberg, 2007), but these solutions appear to be similar to each other, and

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Abbreviations: DG, dentate gyrus; ICA, independent components analysis; LEC, lateral entorhinal cortex; MEC, medial entorhinal cortex.
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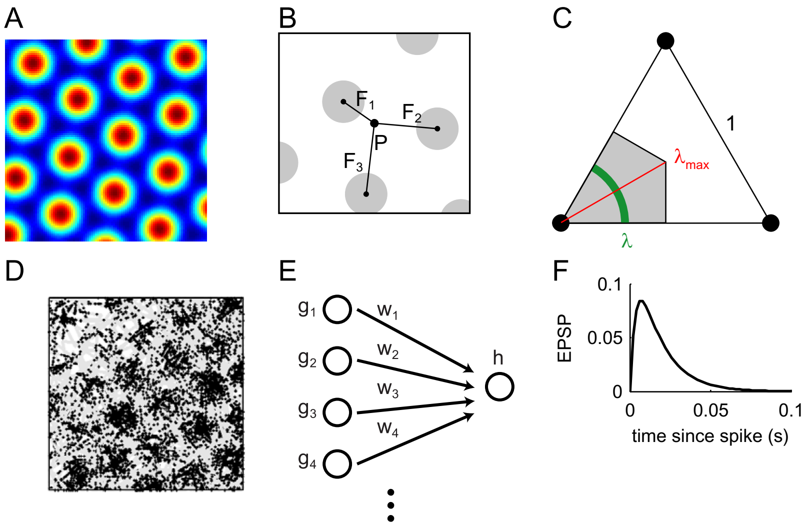

Fig. 1. Definition of models and normalized offset. (A) Schematic of grid cell firing rate map. As in all firing rate and activation maps in this article, red indicates maximum, while blue denotes zero. (B) The normalized offset is defined as the shortest distance between the reference point P and the locations of the firing field peaks F_k, divided by the grid spacing. Gray disks mark regions of elevated firing rate. (C) Schematic of key properties of normalized offset. For any point P within the equilateral triangle, those located within the gray-shaded area are closest to the vertex on the left. The normalized offsets with respect to all points in the green-shaded section are the same λ. The red line shows the maximum normalized offset that can occur in 2-d $\lambda_{\max}=1/\sqrt{3}$. (D) Example of grid cell spiking. Shown is a 10-min session of random exploration. The simulated trajectory of the virtual animal is shown in gray. Each spike is marked by a black dot at the animal's location when the spike occurred. (E) Feedforward network architecture used in this study. The hippocampal cell receives the weighted sum of grid cell inputs. (F) Time course of evoked post-synaptic potential.

it is not clear how they are related to the solutions of other models.

Here we derive a solution for the grids-to-places transformation that was previously unknown, at least in its general and explicit form. We then study the solutions of other models in ways that the original authors of those models had not. We find that all examined models, but one (Blair et al., 2007), yield solutions with very similar structures despite their apparent differences. We then present solutions for multiple place fields in one environment and distinct place fields across different environments (Muller and Kubie, 1987; Leutgeb et al., 2005; Fyhn et al., 2007). While other authors before us have hypothesized mechanisms to account for these two phenomena (Solstad et al., 2006; Rolls et al., 2006; Fyhn et al., 2007; de Almeida et al., 2009; Savelli and Knierim, 2010) no prior study has explicitly demonstrated a working solution where they could control the number and locations of place fields. We also find that multiple spatial maps can be learned by a local synaptic learning in a spiking network, something that Savelli and Knierim (2010) hypothesized to not be possible: "Any feed-forward model that implicates plasticity in the formation of place fields from only grid-cell inputs [. . .] is unlikely to account spontaneously for the memory of many place field maps [. . .]".

EXPERIMENTAL PROCEDURES

This article focuses on understanding the structure of the solutions for the grids-to-places transformation and exploiting that insight to construct and learn specific solutions. A major goal of this article is to study the solutions of prior models that are still not very well understood. In this section, we briefly describe these prior models as well as some of our novel analysis methods.

Grid cell firing maps

The rate map of grid cells over space ($\vec{x}$) can be described by a sum of three 2-d sinusoids (see Solstad et al., 2006; Blair et al., 2007):

$$g_j(\vec{x})=\frac{1}{4.5}\left(\sum_{\gamma=1}^{3}\cos 2\pi\vec{u}_j^{\gamma}\cdot\frac{\vec{x}-\vec{\xi}_j}{a_j}+1.5\right) \tag{1}$$

where ξ_j is the spatial phase or offset, and a_j is the grid spacing. The $\vec{u}_j^{\gamma}$ are direction vectors that are orthogonal to the main axes of the grid:

$$\vec{u}_j^{1}=\frac{2}{\sqrt{3}}\begin{pmatrix}\cos(\phi_j+30°)\\ \sin(\phi_j+30°)\end{pmatrix},\quad \vec{u}_j^{2}=\frac{2}{\sqrt{3}}\begin{pmatrix}\cos(\phi_j+90°)\\ \sin(\phi_j+90°)\end{pmatrix},\ \text{and}\quad \vec{u}_j^{3}=\frac{2}{\sqrt{3}}\begin{pmatrix}\cos(\phi_j+150°)\\ \sin(\phi_j+150°)\end{pmatrix} \tag{2}$$

where ϕ_j represents the orientation of the grid. An example of a grid cell firing map is shown in Fig. 1A. Since the sum of cosines in Eq. 1 yields values between $-3/2$ and 3, the linear transformation ensures that the rates of grid cells are always positive. Using other gain functions does not seem to affect the grids-to-places transformation (Blair et al., 2007). We used different numbers of grid cells (N) as indicated throughout this paper. As observed experimentally (Hafting et al., 2005), co-localized cells in our simulations ($n = 10$) share the same grid spacing a_j, and orientation ϕ_j, but each grid cell has its own independent spatial phase ζ_j. Grid spacings were drawn from a uniform distribution between 30 cm and 70 cm, orientations were uniformly distributed between 0° and 360°. Both grid spacings and orientations were independent between groups of grid cell with different spacings, except in one simulation, in which we studied the effect of aligning all grids at the same orientation as suggested by preliminary results (Stensland et al., 2010).