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Topology of the neural connectivity of grid cells

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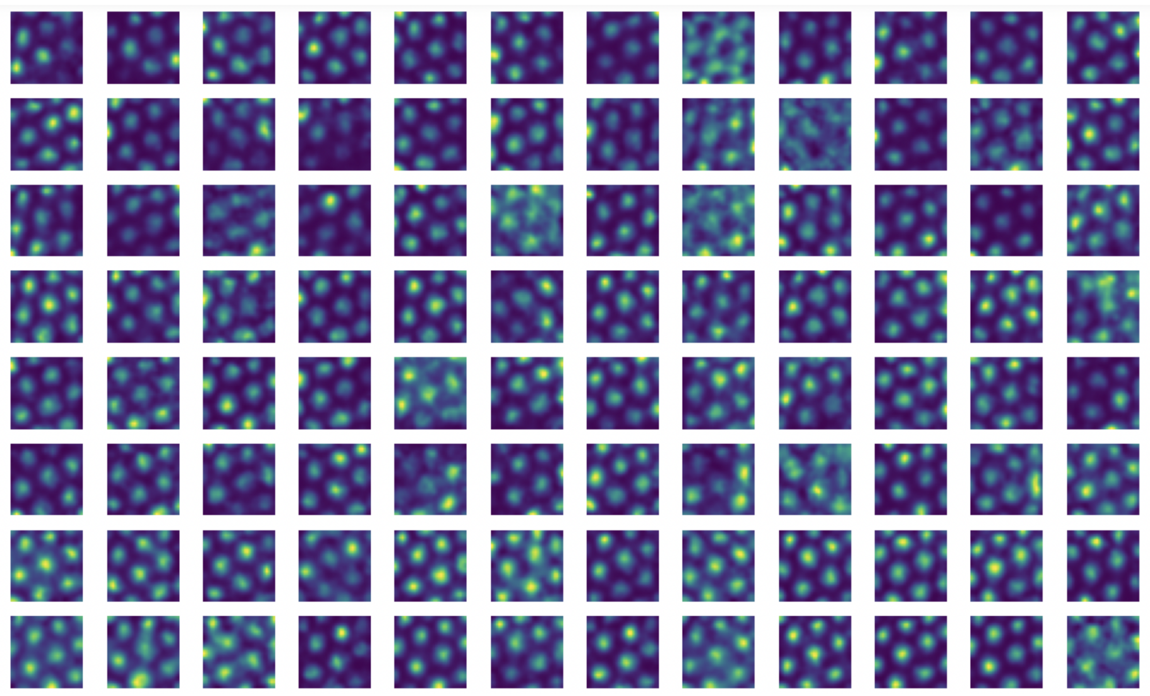
Abstract

Grid cells are a key component of the neural system for mapping the position of an individual within a physical environment. These entorhinal neurons fire in a characteristic **hexagonal pattern** of locations, and are organized in modules that collectively form a population code for the animal's allocentric position. Whereas the **population activity** of grid cells in the same module lies in a **toroidal manifold**, the **connectivity pattern** of grid cells in the brain is still unknown. It is conjectured that the neural network of grid cells has also a toroidal architecture, inherited by the geometry of the attractor. In this work [1], we give a **negative answer** to this question for modeled grid cells.

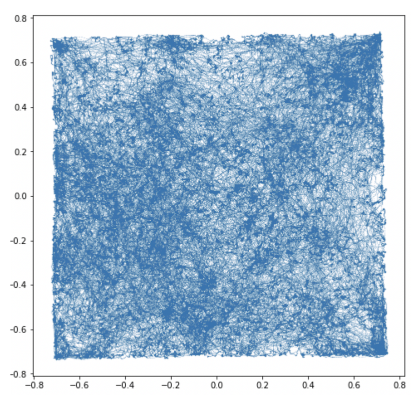
Keywords: Grid Cells, Manifold Learning, Persistent Homology, Neural Network Connectivity.

Population activity

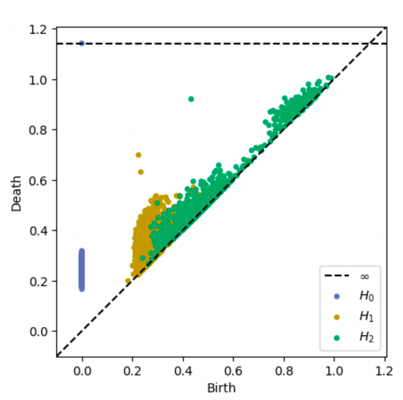
In [2], the authors recorded the activity of hundreds of grid cells for a rat in the open field and showed that the joint activity of grid cells from an individual module presents the homology of a **toroidal manifold**.



Firing rates of grid cells co-recorded from the same module and shown as a function of rat position in open field arena.



Path of the rat in the square track



Persistence diagram of pop. activity

Non-linear dim. reduction

References

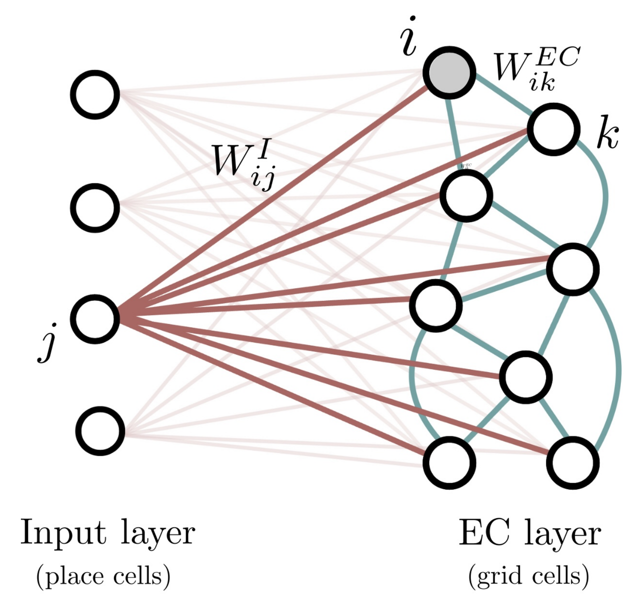
[1] S. Benas, X. Fernandez, and E. Kropff. Modeled grid cells aligned by a flexible attractor. *bioRxiv 2022.06.13.495956*, 2022.

[2] R.J. Gardner et al. Toroidal topology of population activity in grid cells. *Nature 602*, 123–128, 2022.

[3] E. Kropff and A. Treves. The emergence of grid cells: intelligent design or just adaptation? *Hippocampus 18 (12)*, 1256-1269, 2008.

The physical model

Feedforward network dynamics [3].



The **total field** $h_i(t)$ received by grid cell i at time t is

$$h_i(t) = \sum_{j=1}^{N_I} W^I_{ij} r^I_j(t) + \sum_{k=1}^{N_{EC}} W^{EC}_{ik} r^{EC}_k(t)$$

where

- the **synaptic weight** $W^{EC}_{i,k}(t)$ is fixed,
- the **feedforward synaptic weight** $W^I_{ij}(t)$ is updated according to the *Hebbian learning rule*

$$W^I_{ij}(t+1) = W^I_{ij}(t) + \epsilon\left(r^I_j(t) r^{EC}_i(t) - \overline{r^I_j}(t)\overline{r^{EC}_i}(t)\right)$$

  where ϵ is a learning parameter and $\overline{\bullet}(t)$ means the exponential moving average at time t,
- the **activity of grid cell** $r^{EC}_i(t)$ is updated as

$$r^{EC}_i(t+1) = G\frac{|h^{\text{act}}_i(t) - T|_{>0}}{(|h^{\text{act}}_\bullet(t) - T|_{>0})_{\text{avg}}}$$

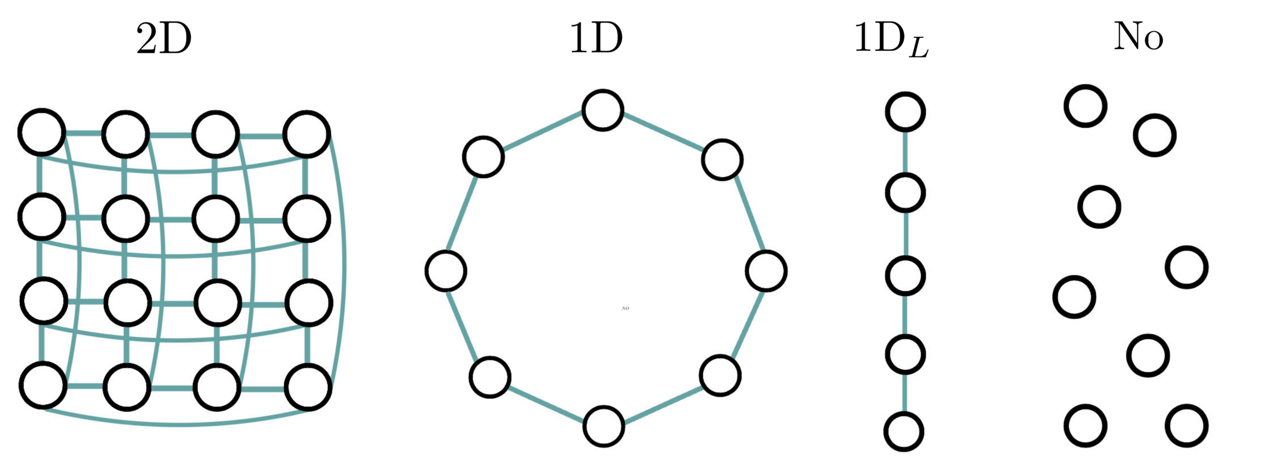
  for a gain parameter G, a threshold T representing *inhibition* and internal variables $h^{\text{act}}_i(t)$ and $h^{\text{inact}}_i(t)$ mimicking *adaptation* or *fatigue* within the neuron

$$h^{\text{act}}_i(t+1) = h_i(t) - h^{\text{inact}}_i(t),$$
$$h^{\text{inact}}_i(t+1) = h^{\text{inact}}_i + \beta h^{\text{act}}_i(t)$$

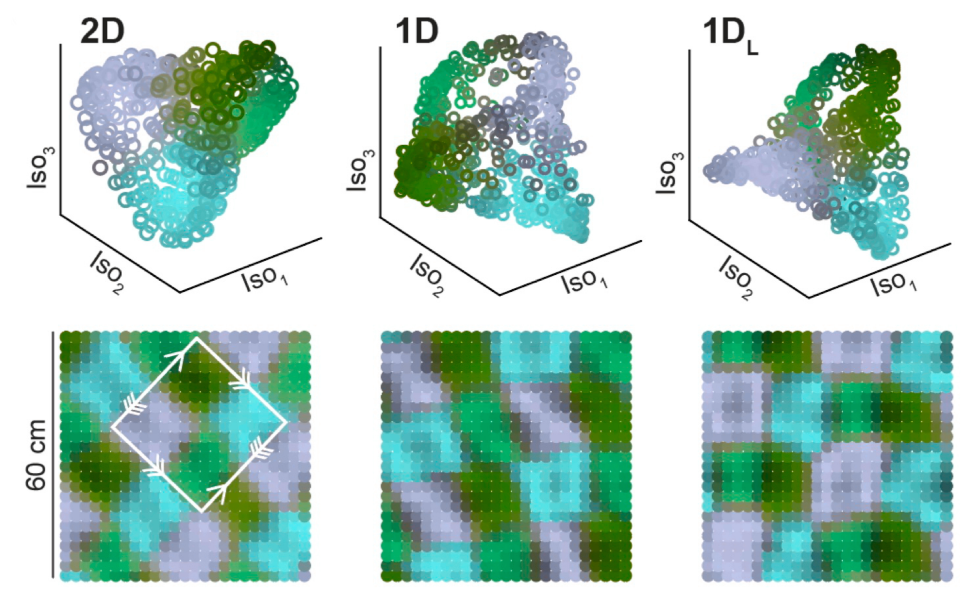
  for some parameter β.

Connectivity pattern of grid cells

Network architecture. We simulated the activity of $N_{EC} = 100$ grid cells with an input layer of $N_I = 225$ place cells. We tested different architectures for the connectivity network determined by the matrix W^{EC}: **toroidal architecture (2D)**, **cyclic architecture (1D)**, **linear architecture (1D$_L$)** and **no connectivity (No)**.

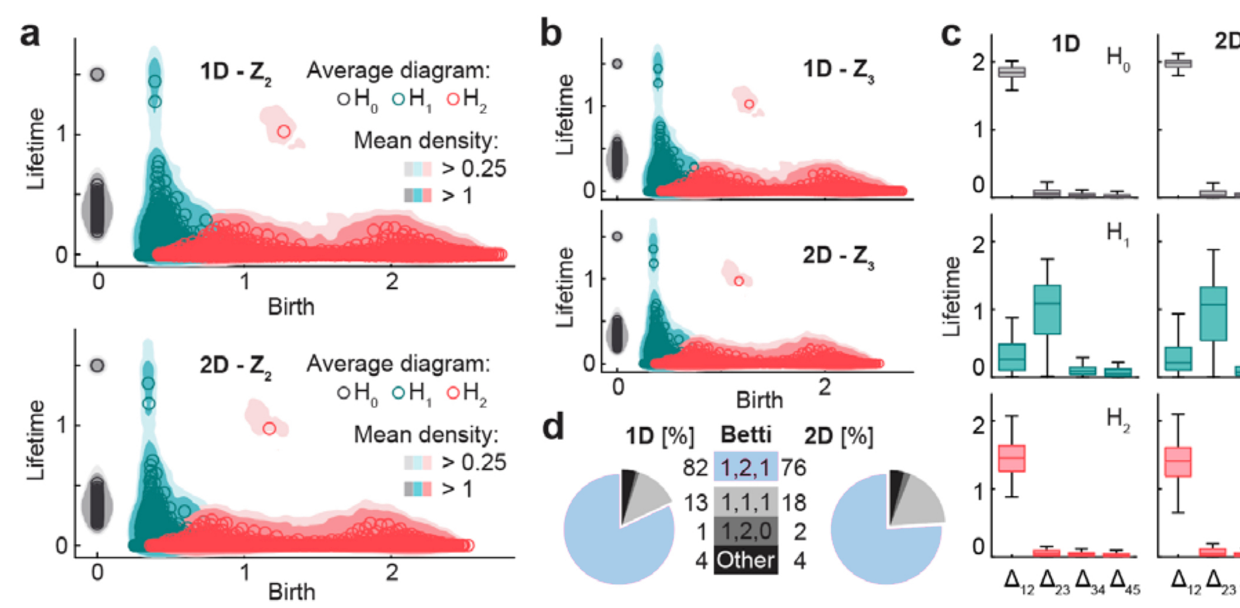


Twisted torus embedding. For every simulation, we obtained a point cloud of $N_{pix} = 625$ points describing the average activity of every neuron at every point in space, as result of the movement of a rat in a square track. The joint population activity is a quotient of the spacial input, determining a **twisted torus**.

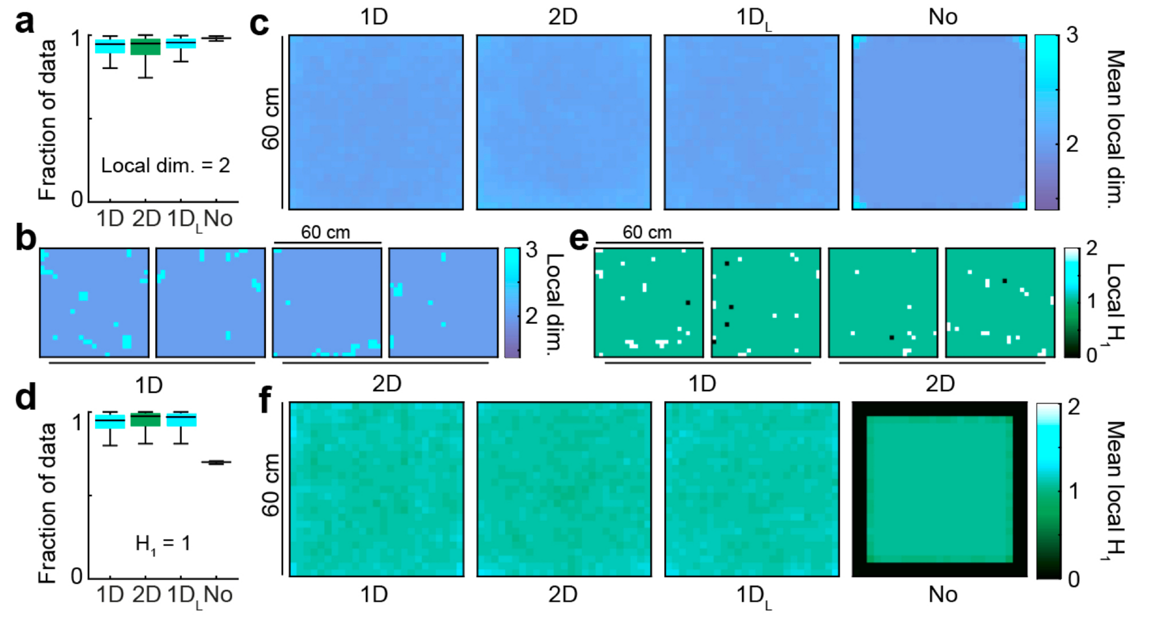


Homeomorphism type of the attractor

Classification of closed surfaces. In order to completely determine the homeomorphism type of the population activity of the module of grid cells for every connectivity type, we applied the **Theorem of classification of closed surfaces**. We proved that, for most of the simulations, the point cloud with either connectivity 1D, 1D$_L$ or 2D has (persistent) Betti numbers $\beta_0 = 1, \beta_1 = 2, \beta_2 = 1$ with coefficients in both $\mathbb{Z}_2$ and $\mathbb{Z}_3$. We also estimated a local dimension equal to 2 for most of local neighborhoods of the points, and determined that there were no singularities nor boundary. This implies that the population activity for either 1D, 1D$_L$ or 2D connectivities is a 2-dimensional closed orientable surface with the homology of a torus and, hence, homeomorphic to a torus. For the case of No connectivity, the population activity is just an embedding of the square track in $\mathbb{R}^{100}$.



a. Smoothed density and Frechet mean across simulations of persistence diagrams with coefficients in $\mathbb{Z}_2$, for 1D (top) and 2D (bottom) connectivity condition. **b.** As a. but with coefficients in $\mathbb{Z}_3$. **c.** Distribution of the difference between lifetime of consecutive generators for each simulation (ordered from longest to shortest lifetime) for 1D (left) and 2D (right) connectivity. **d.** Pie plot and table indicating the number of simulations (out of 100 in each condition) classified according to their Betti numbers.



a. Distribution of the fraction of the population data with local dimensionality equal to 2, for every connectivity condition. **b.** Distribution of local dimensionality across physical space in representative examples of 1D and 2D conditions. **c.** Average distribution of local dimensionality for all conditions (same color code as in b.) **d-f.** As a-c but exploring deviations of the local homology H_1 from a value equal to 1, the value expected away from boundary points and singularities.

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