Figures and figure supplements

Probable nature of higher-dimensional symmetries underlying mammalian grid-cell activity patterns

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Figure 1. Grid cells and modules. (A) Construction of a grid cell: Given a tuning shape $\Omega$ and a lattice $\mathcal{L}$, here a square lattice generated by $v_1$ and $v_2$ with $\phi = \pi/2$, one periodifies $\Omega$ with respect to $\mathcal{L}$. One defines the value of $\Omega^\mathcal{L}(x)$ in the fundamental domain $L$ as the value of $\Omega(\cdot)$ applied to the distance from zero and then repeats this map over $\mathbb{R}^2$ like $\mathcal{L}$ tiles the space. This construction can be used for lattices $\mathcal{L}$ of arbitrary dimensions (Equation 7). (B) Grid module: The firing rates of three grid cells (orange, green, and blue) are indicated by color intensity. The cells’ tuning is identical ($\Omega$ and $\mathcal{L}$ are the same), yet they differ in their spatial phases $c_i$. Together, such identically tuned cells with different spatial phases define a grid module.

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Figure 2. Periodified grid-cell tuning curve $\Omega^\mathcal{L}$ for two planar lattices, (A) the hexagonal (equilateral triangle) lattice $\mathcal{H}$ and (B) the square lattice $\mathcal{Q}$, together with the basis vectors $v_1$ and $v_2$. These are $\pi/3$ apart for the hexagonal lattice and $\pi/2$ for the square lattice. The fundamental domain, that is, the Voronoi cell around $0$, is shown in gray. A few other domains that have been generated according to the lattice symmetries are marked by dashed lines. The blue disk shows the disk with maximal radius $R$ that can be inscribed in the two fundamental domains. For equal and unitary node-to-node distances, that is, $|v_1| = |v_2| = 1$, the maximal radius equals $1/2$ for both lattices. The packing ratio $\Delta$ is $\Delta(\mathcal{H}) = \pi/\sqrt{12}$ for the hexagonal and $\Delta(\mathcal{Q}) = \pi/4$ for the square lattice; the hexagonal lattice is approximately 15.5% denser than the square lattice.

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Figure 3. Fisher information for modules of two-dimensional grid cells. (A) Top: Periodified bump-function $\Omega$ and square lattice $L$, for various parameter combinations $\theta_1$ and $\theta_2$. Here, $\theta_1$ modulates the decay and $\theta_2$ the support. Middle: Average trace $\text{tr} J_L$ of the Fisher information (FI) for uniformly distributed grid cells $\Omega_L$. Hexagonal (H) and square (Q) lattices are considered for different $\theta_1$ and $\theta_2$ values. The FI of the hexagonal grid cells outperforms the quadratic grid when support is fully within the fundamental domain ($\theta_2 < 0.5$, see main text). Bottom: Ratio $\text{tr} J_H/\text{tr} J_Q$ as a function of the tuning parameter $\theta_2$. For $\theta_2 < 0.5$, the hexagonal population offers 3/2 times the resolution of the square population, as predicted by the respective packing ratios. (B) Average $\text{tr} J_L$ for grid cells distributed uniformly in lattices generated by basis vectors separated by an angle $\phi$ (basis depicted above graph). $\text{tr} J_L$ behaves like $1/\sin(\phi)$ and has its maximum at $\pi/3$. (C) Distribution of 5000 realizations of $\text{tr} J_L^M/M$ at 0 for a population of $M = 200$ randomly distributed neurons. For both the hexagonal and square lattice, parameters are $\theta_1 = 1/4$ and $\theta_2 = 0.4$. The means closely match the average values in (A). However, due to the finite neuron number the FI varies strongly for different realizations, and in about 20% of the cases a square lattice module outperforms a hexagonal lattice.

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Figure 3—figure supplement 1. The firing rate and Fisher information of the bump tuning shape. Upper left panel: Tuning shape $\Omega(r)$ with parameters $\theta_2 = 0.5$ and varying $\theta_1$. Lower left panel: Corresponding Fisher information (FI) integrand $\mathcal{F}(r)$. Upper right panel: Tuning shape $\Omega(r)$ with parameters $\theta_1 = 0.25$ and varying $\theta_2$. Lower right panel: Corresponding FI integrand $\mathcal{F}(r)$.
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Figure 4. Fisher information for modules of 3D grid cells. (A) The three lattices considered: face-centered cubic (FCC), body-centered cubic (BCC), and cubic (C). (B) $\text{tr} J_L$ for the periodified bump-function $\Omega$ for the three lattices and various parameter combinations $\theta_1$ and $\theta_2$. The Fisher information (FI) of the FCC grid cells outperforms the other lattices when the support is fully within the fundamental domain ($\theta_2 < 0.5$, see main text). For larger $\theta_2$ the best lattice depends on the relation between the Voronoi cell’s boundary and the tuning curve. (C) Ratio $\text{tr} J_C / \text{tr} J_L$ as a function of $\theta_2$ for $L \in \{ \text{FCC, BCC, C} \}$. For $\theta_2 < 0.5$, the hexagonal population has 3/2 times the resolution of the square population, as predicted by the packing ratios. (D) Average $\text{tr} J_{L_{\varphi,\psi}}$ for uniformly distributed grid cells within a lattice $L_{\varphi,\psi}$ generated by basis vectors separated by angles $\varphi$ and $\psi$ (as shown above; $\theta_1 = \theta_2 = 1/4$). $\text{tr} J_{L_{\varphi,\psi}}$ behaves like $1/(\sin \varphi \cdot \sin \psi)$ and has its maximum for the lattice with the smallest volume. (E) Distribution of 5000 realizations of $\text{tr} J^M_L / M$ at 0 for a population of $M = 200$ randomly distributed neurons. Parameters: $\theta_1 = 1/4$, $\theta_2 = 0.4$. The means closely match the averages in (B). Due to the finite neuron number, the FI varies strongly for different realizations.

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Figure 5. Lattice and non-lattice solutions in 3D. (A) Stacking of spheres as in an FCC lattice. In this densest lattice in 3D, each sphere touches 12 other spheres and there are four different planar hexagonal lattices through each node. (B) Over a layer of hexagonally arranged spheres centered at $\gamma_0$ (in black) one can put another hexagonal layer by starting from one of six locations, two of which are highlighted, $\gamma_1$ and $\gamma_2$. (C) If one arranges the hexagonal layers according to the sequence ($\ldots, \gamma_1, \gamma_0, \gamma_2, \ldots$) one obtains the FCC. Note that spheres in layer I are not aligned with those in layer III. (D) Arranging the hexagonal layers following the sequence ($\ldots, \gamma_0, \gamma_1, \gamma_0, \ldots$) leads to the hexagonal close packing HCP. Again, each sphere touches 12 other spheres. However, there is only one plane through each node for which the arrangement of the centers of the spheres is a regular hexagonal lattice. This packing has the same packing ratio as the FCC, but is not a lattice. (E) $\text{tr}J_L$ for bump-function $\Omega$ with $L = \text{FCC}$ and $\text{HCP}$ for various parameter combinations $\theta_1$ and $\theta_2$. $\theta_1$ modulates the decay and $\theta_2$ the support. The two packings have the same packing ratio and for this tuning curve also provide identical spatial resolution. FI: Fisher information. DOI: 10.7554/eLife.05979.009