On Conformal Isometry of Grid Cells: Learning Distance-Preserving Position Embedding

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Introduction

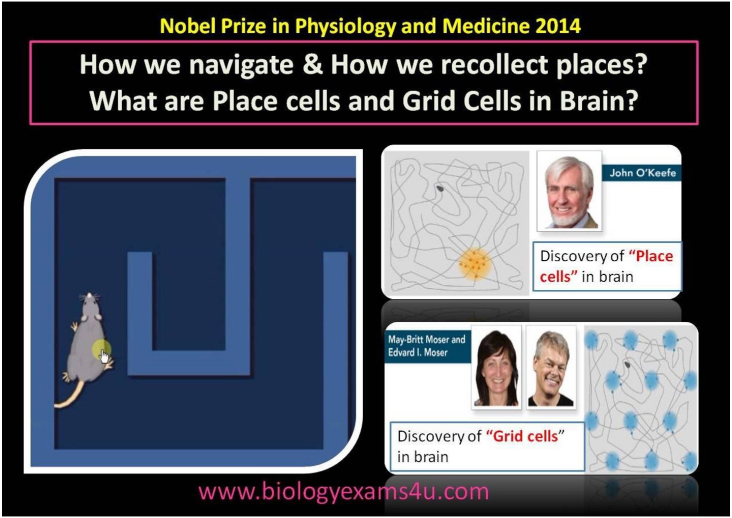

Figure: Place cells and grid cells

Introduction

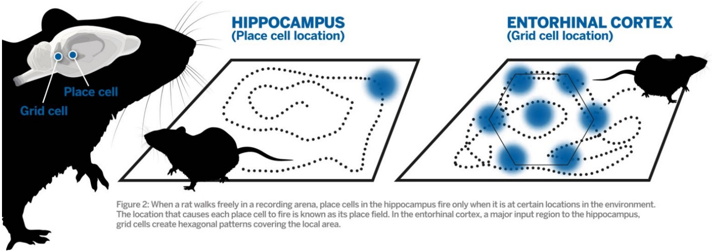

Figure: Place cells and grid cells

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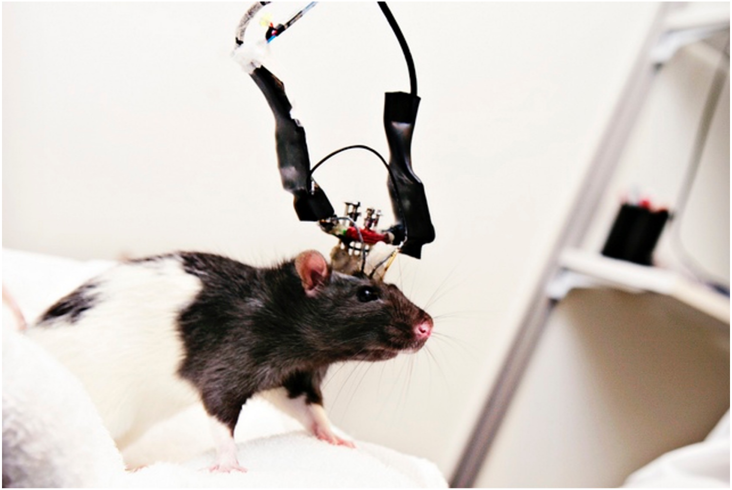

Figure: Neuron recording

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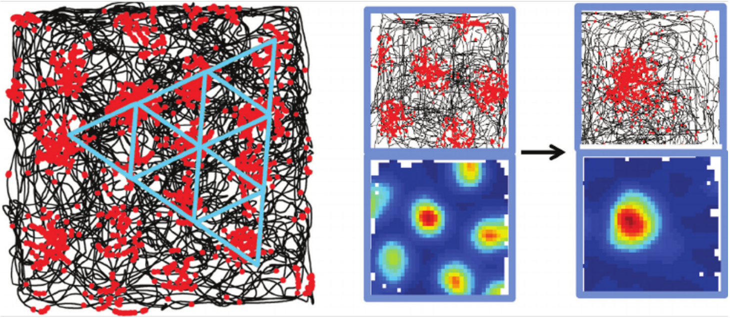

Figure: Firing of grid cells and place cells

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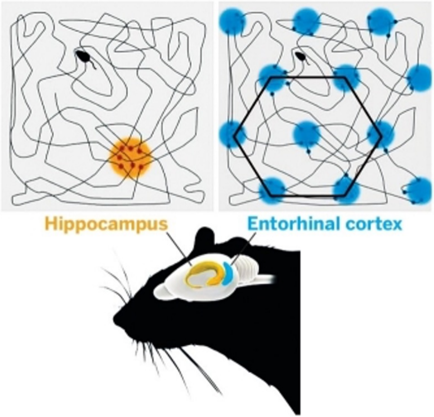

Figure: Place cells and grid cells

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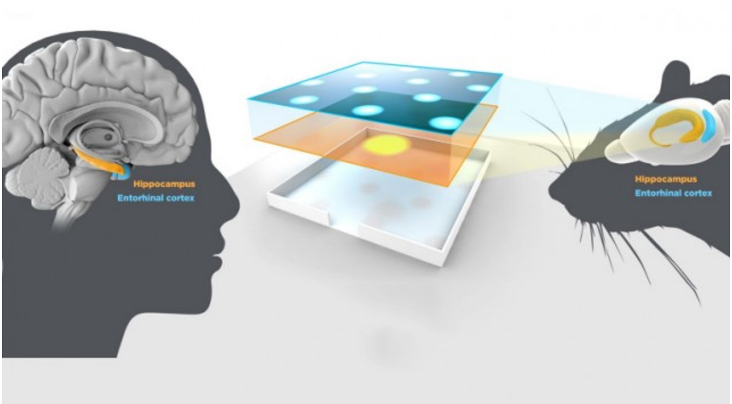

Figure: Place cells and grid cells

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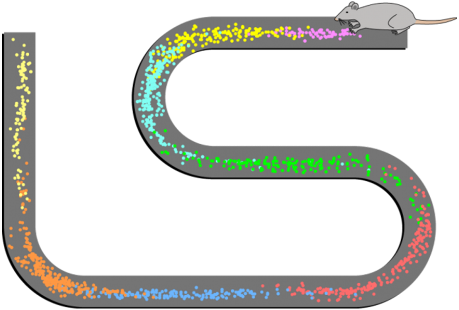

Figure: Different place cells fire at different places

Introduction

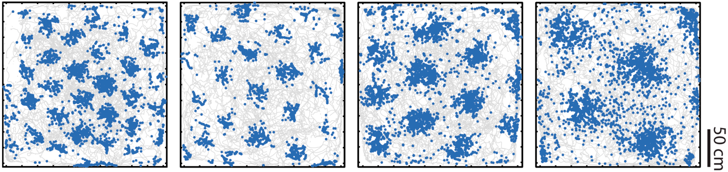

Figure: Response maps of different grid cells

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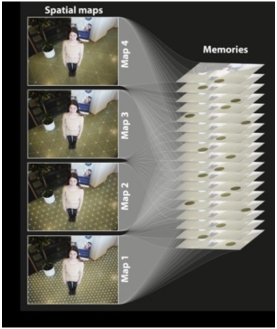

Figure: An internal GPS system

Introduction

- These cells are crucial for:
  - Path integration
  - Navigation
  - Spatial memory
- Key question: Why **hexagonal** patterns?
- Our work: Investigating the **conformal isometry hypothesis** as a mathematical explanation

Existing Models and Hypotheses

Several computational models have been proposed:

- Continuous attractor neural networks (CANN)
- RNN-based models for path integration
- Basis expansion models with non-negative constraints

However, the **mathematical principles** behind hexagonal patterns remain elusive.

Population Code

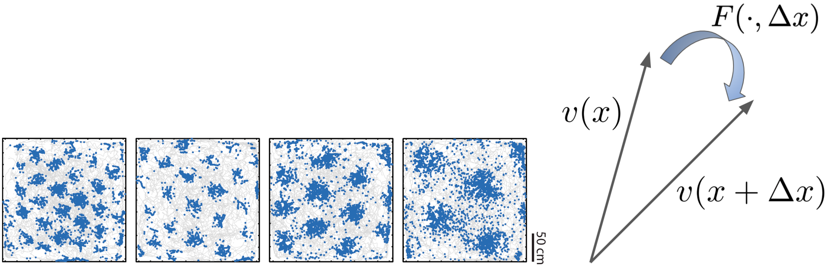

Figure: Left: $v_i(\mathbf{x})$ for different i. Right: $\mathbf{v}(\mathbf{x}) = (v_i(\mathbf{x}), i = 1, ..., d$ as a vector representation of $\mathbf{x} \in \mathbb{R}^2$, or position embedding of $\mathbf{x}$.

- The whole population forms a vector for representing position
- Each cell i is an element of the vector, with a response map $v_i(\mathbf{x})$
- But **do not think about a single cell at a time**
- Position embedding

Position Representation and Self-Motion

Self-position representation:

- Agent at position $\mathbf{x} = (x_1, x_2)$
- Grid cells form vector $\mathbf{v}(\mathbf{x})$
- $\mathbf{v}(\mathbf{x})$ is a position embedding

Self-motion representation:

- Agent moves by $\Delta\mathbf{x}$
- Vector transforms: $\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) = F(\mathbf{v}(\mathbf{x}), \Delta\mathbf{x})$
- F can be implemented by RNN

$$
\begin{tikzcd}
v(x) \arrow[r, "F(\cdot, \Delta x)"] & v(x + \Delta x) \\
x \arrow[u] \arrow[r, "+\Delta x"] & x + \Delta x \arrow[u]
\end{tikzcd}
$$

Figure: Transformation by self-motion

The Conformal Isometry Hypothesis

Key idea: Neural manifold is a conformal isometric embedding of 2D physical space
Mathematically:

$$\|\mathbf{v}(\mathbf{x}+\Delta\mathbf{x})-\mathbf{v}(\mathbf{x})\| = s\|\Delta\mathbf{x}\|+o(\|\Delta\mathbf{x}\|) \quad (1)$$

Where:

- s is scaling factor (metric unit)
- Distance in physical space is preserved in neural space

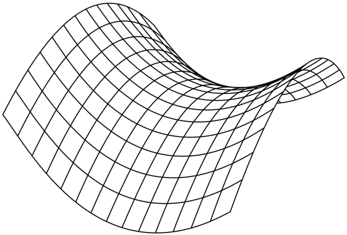

Figure: 2D manifold in neural space

Our Approach: Minimalistic Setting

We study grid cells with minimal assumptions:

1. **Conformal isometry:** $\|\mathbf{v}(\mathbf{x}+\Delta\mathbf{x}) - \mathbf{v}(\mathbf{x})\| = s\|\Delta\mathbf{x}\| + o(\|\Delta\mathbf{x}\|)$
2. **Transformation:** $\mathbf{v}(\mathbf{x}+\Delta\mathbf{x}) = F(\mathbf{v}(\mathbf{x}), \Delta\mathbf{x})$
3. **Normalization:** $\|\mathbf{v}(\mathbf{x})\| = 1$ for each $\mathbf{x}$
4. **Non-negativity:** $v_i(\mathbf{x}) \geq 0$ for each i and $\mathbf{x}$

Key advantages:

- No assumptions about place cells
- Agnostic to specific form of F
- Explicit metric s

Transformation Models

We studied multiple transformation models:

1. **Linear model:**

$$\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) = \mathbf{v}(\mathbf{x}) + \mathbf{B}(\theta)\mathbf{v}(\mathbf{x})\Delta r \tag{2}$$

2. **Nonlinear model 1:**

$$\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) = R(\mathbf{A}\mathbf{v}(\mathbf{x}) + \mathbf{B}(\theta)\mathbf{v}(\mathbf{x})\Delta r + \mathbf{b}) \tag{3}$$

3. **Nonlinear model 2:**

$$\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) = R(\mathbf{A}\mathbf{v}(\mathbf{x}) + \mathbf{B}(\theta)\Delta r + \mathbf{b}) \tag{4}$$

Where:

- $\Delta r = \|\Delta\mathbf{x}\|$ is displacement
- θ is heading direction
- R is elementwise nonlinearity

Learning Method

Loss function consists of:

$$L_1 = \mathbb{E}_{\mathbf{x},\Delta\mathbf{x}}[(\|\mathbf{v}(\mathbf{x}+\Delta\mathbf{x}) - \mathbf{v}(\mathbf{x})\| - s\|\Delta\mathbf{x}\|)^2] \tag{5}$$

$$L_2 = \mathbb{E}_{\mathbf{x},\Delta\mathbf{x}}[\|\mathbf{v}(\mathbf{x}+\Delta\mathbf{x}) - F(\mathbf{v}(\mathbf{x}), \Delta\mathbf{x})\|^2] \tag{6}$$

- L_1 enforces conformal isometry
- L_2 ensures accurate transformation
- For $\Delta\mathbf{x}$ in L_1: $s\|\Delta\mathbf{x}\| \leq 1.25$
- For $\Delta\mathbf{x}$ in L_2: $\|\Delta\mathbf{x}\| \leq 0.075$

We minimize $L = L_1 + \lambda L_2$ using stochastic gradient descent.

Maximally Distance-Preserving Embedding

- L_1 has a non-zero minimum due to the non-infinitesimal range
- Conformal isometry is nearly exact for $s\|\Delta\mathbf{x}\| \leq 0.8$
- Beyond that point, deviation increases due to extrinsic curvature
- Minimizing L_1 finds the maximally distance-preserving embedding

Key insight: The hexagon torus structure emerges as the optimal solution for preserving distances in all directions.

Numerical Experiments: Setup

- 1m $\times$ 1m environment with 40 $\times$ 40 regular lattice
- Learn $\mathbf{v}(\mathbf{x})$ on lattice points
- Bilinear interpolation for off-lattice points
- Linear model and nonlinear model 1: 24 grid cells
- Nonlinear model 2: 1000 grid cells
- Constrained $s\|\Delta \mathbf{x}\| \leq 1.25$ for L_1
- Constrained $\|\Delta \mathbf{x}\| \leq 0.075$ for L_2

Hexagonal Patterns in Linear Models

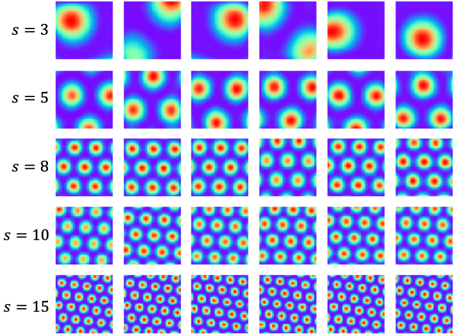

Figure: Learned grid cells with different scaling factors

- Hexagonal patterns emerge across different scaling factors
- Consistent scale and orientation within each module
- Variations in phases (spatial shifts)

Toroidal Analysis

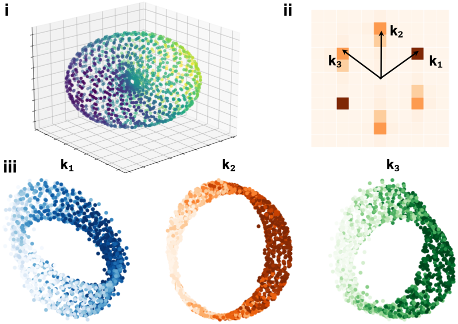

Figure: Toroidal structure spectral analysis

- Spectral embedding shows grid cell states fall on a toroidal manifold
- 2D Fourier transforms reveal hexagonal distribution along 3 principal directions
- 3 rings indicate 2D twisted torus topology

Nonlinear Models and Ablation Studies

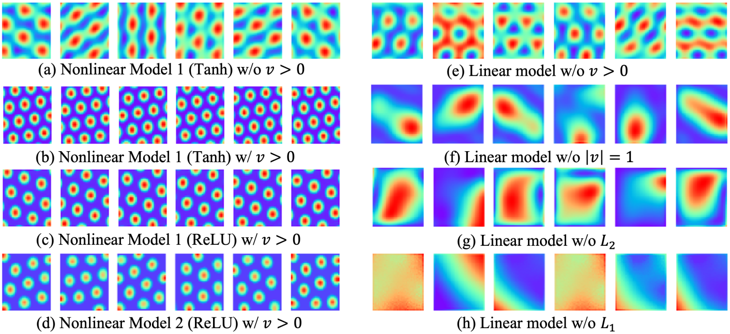

Figure: Left: Nonlinear models with different activations. Right: Ablation studies

- Hexagonal patterns emerge with various activation functions
- Without conformal isometry: non-hexagon patterns emerge
- Non-negativity constraint: not essential but improves stability
- Transformation and normalization: necessary for hexagonal patterns

Quantitative Evaluation

Model	Gridness(↑)	Valid rate(↑)
Banino2018	0.18	25.2%
Sorscher2023	0.48	56.1%
Gao2021	0.90	73.1%
Our Linear	1.70	100.0%
Our Nonlinear	1.17	100.0%

Table: Gridness scores and validity rates

- Our models achieve higher gridness scores
- 100% valid grid cells in both linear and nonlinear models
- Scale of patterns inversely proportional to scaling factor s

Scaling Factor and Grid Scale

Scaling factor	Estimated scale
$s = 5$	0.82
$s = 10$	0.41
$s = 15$	0.27

Table: Relationship between scaling factor and grid scale

The estimated scale of grid patterns is inversely proportional to the scaling factor s:

- Larger s: smaller grid spacing (higher resolution)
- Smaller s: larger grid spacing (lower resolution)

Evidence for Local Conformal Isometry

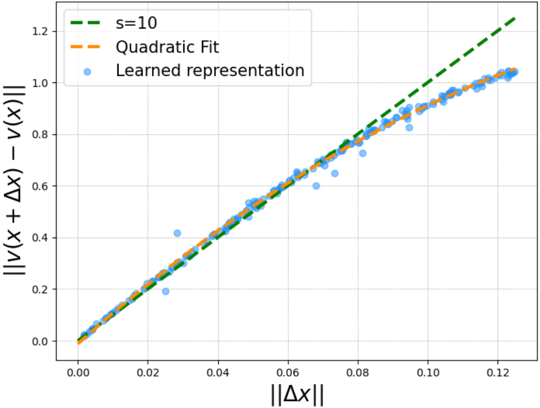

Figure: Relationship between $\|\mathbf{v}(\mathbf{x}+\Delta\mathbf{x})-\mathbf{v}(\mathbf{x})\|$ and $\|\Delta\mathbf{x}\|$

- Linear relationship for small $\|\Delta\mathbf{x}\|$ (blue line)
- Quadratic deviation for larger $\|\Delta\mathbf{x}\|$ (orange curve)
- Deviation due to extrinsic curvature of manifold $\mathbb{M}$

Neuroscience Evidence

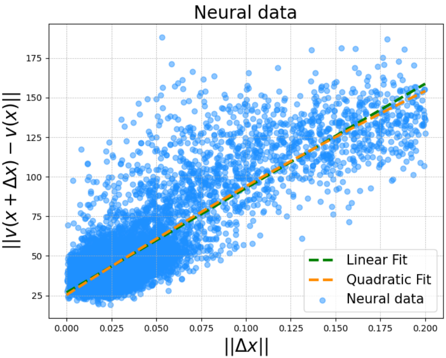

Figure: Analysis of real neural recording data (Gardner et al., 2021)

- Clear linear relationship between $\|\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) - \mathbf{v}(\mathbf{x})\|$ and $\|\Delta\mathbf{x}\|$
- Minimal deviation from linearity for local $\|\Delta\mathbf{x}\|$
- Distribution of $\|\mathbf{v}(\mathbf{x})\|$ approximately constant

Results consistent with conformal isometry hypothesis in real grid cells.

Theoretical Understanding: Torus Topology

Proposition

The transformations $(F(\cdot, \Delta\mathbf{x}), \forall \Delta\mathbf{x})$ *form a group acting on the manifold* $\mathbb{M} = (\mathbf{v}(\mathbf{x}), \forall \mathbf{x})$, *and the 2D manifold* $\mathbb{M}$ *has a torus topology.*

- Group $(F(\cdot, \Delta\mathbf{x}), \forall \Delta\mathbf{x})$ represents the 2D additive Euclidean group
- It's an abelian Lie group, compact and connected
- According to Lie group theory, such a group has torus topology
- Torus topology makes $\mathbf{v}(\mathbf{x})$ a 2D periodic function of $\mathbf{x}$

Analyzing Deviation from Local Flatness

For small displacements, conformal isometry holds:

$$\|\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) - \mathbf{v}(\mathbf{x})\|^2 = \|\Delta\mathbf{x}\|^2 + o(\|\Delta\mathbf{x}\|^2) \tag{7}$$

For larger displacements, we analyze higher-order deviations:

$$\|\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) - \mathbf{v}(\mathbf{x})\|^2 - \|\Delta\mathbf{x}\|^2 = -\frac{1}{12}D(\Delta\mathbf{x}) + o(\|\Delta\mathbf{x}\|^4) \tag{8}$$

Where $D(\Delta\mathbf{x})$ involves inner products of 4th-order derivatives and $\mathbf{v}$.

Hexagonal Isotropy

Theorem

If the torus $\mathbb{M} = (\mathbf{v}(\mathbf{x}), \forall \mathbf{x})$ *is a hexagon flat torus, then* $D(\Delta \mathbf{x}) = c\|\Delta \mathbf{x}\|^4$ *for a constant coefficient* c*, i.e.,* $D(\Delta \mathbf{x})$ *is isotropic.*

- Hexagon torus has 6-fold rotational symmetry (60-degree rotations)
- This symmetry leads to isotropic deviation from flatness
- $D(\Delta \mathbf{x}) = c(\Delta x_1^2 + \Delta x_2^2)^2 = c\|\Delta \mathbf{x}\|^4$
- Other flat tori (square, rectangle) lack this isotropy

Why Hexagons are Optimal

Theorem

For any fixed average extrinsic curvature, the overall deviation from local flatness:

$$L(\Delta r) = \int (\|\mathbf{v}(\mathbf{x} + \Delta\mathbf{x}) - \mathbf{v}(\mathbf{x})\|^2 - \|\Delta\mathbf{x}\|^2)^2 d\theta \tag{9}$$

is minimized if $D(\Delta\mathbf{x})$ is constant over all directions θ.

- Hexagon torus distributes extrinsic curvature evenly in all directions
- This minimizes the variance of $D(\Delta\mathbf{x})$ across directions
- Result holds for all displacement magnitudes Δr
- Therefore, hexagon torus forms maximally distance-preserving embedding

Multiple Modules of Grid Cells

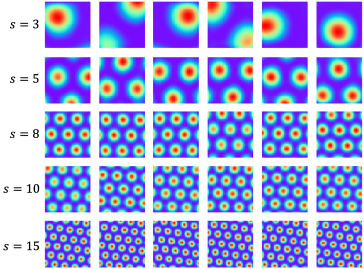

Figure: Multi-module patterns example

- Grid cells form multiple modules with different scales
- Each module satisfies conformal isometry with its own scaling factor s
- Trade-off: Small $s \rightarrow$ large range but low resolution
- Large $s \rightarrow$ small range but high resolution

Functional Benefits for Navigation

Conformal isometry provides crucial benefits for navigation:

- Preserves geometry of local environment
- Facilitates straight-path planning via steepest descent
- Supports planning at different spatial scales

Functional Necessity for Navigation

More plainly, grid cell embeddings serve as a coordinate system:

- We only have $\mathbf{v}$ and $F(\mathbf{v}, \Delta\mathbf{x})$ in the brain, not $\mathbf{x}$
- We overlay $(\mathbf{v})$ onto the 2D physical domain
- It has to be conformal to correctly calculate distance and direction
- Indispensable for path planning, shortest path requires correct distance and direction
- Multiple scales (resolutions, precisions, metrics)

Functional Benefits for Representation

Why high dimensional $\mathbf{v}(\mathbf{x})$ for 2D $\mathbf{x}$?

- $\mathbf{v}(\mathbf{x})$ serves as linear basis functions (similar to Fourier basis)
- Multi-scale isotropic basis for representing any $\mathbf{h}(\mathbf{x}) = \mathbf{W}\mathbf{v}(\mathbf{x})$
- $\mathbf{W}$ only needs to pick up scale and deviation from isotropy
- Enables fast learning of cognitive map

Comparison to Prior Work

Our approach differs from previous work:

- Prior RNN models: Don't consistently produce hexagonal patterns
- Non-negativity hypothesis: Relies on Difference-of-Gaussian assumption
- Previous conformal isometry work: Required place cells, specific transformations

Our contributions:

- Scientific reductionism: Isolated grid cell system of a single module
- No assumptions about place cells or their interactions
- Agnostic to transformation model
- Explicit scaling factor s

Conclusion

- Conformal isometry provides a fundamental explanation for hexagonal grid patterns
- Hexagon patterns emerge from maximally distance-preserving position embeddings
- Our theory is supported by:
  - Numerical experiments across various models
  - Analysis of real neural recordings
  - Mathematical proof of hexagon torus optimality
- This hypothesis serves as a foundation for further development of normative models

Project page:

`https://github.com/DehongXu/grid-cell-conformal-isometry`

Thank You!

Questions?

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