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A Minimalistic Representation Model for Head Direction System

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Abstract

We propose a minimalistic representational model for the head direction (HD) system, a crucial component of spatial navigation in mammals. Our model leverages the symmetry of the rotation group $U(1)$ and the inherent circular geometry of the head direction. We develop fully connected and convolutional versions of the model, both aiming to learn a high-dimensional representation of head direction that captures essential properties of HD cells. Our learning method results in representations that form a perfect 2D circle when projected onto their principal components, reflecting the underlying geometry of the problem. We also demonstrate that individual dimensions of our learned representation exhibit Gaussian-like tuning profiles akin to biological HD cells. Our model achieves accurate multi-step path integration, effectively updating its internal heading estimate over time. These results demonstrate that simple symmetry-based constraints can yield biologically realistic HD representations, offering new insights into the computational principles underlying spatial navigation in mammals.

Introduction

Spatial navigation is a fundamental cognitive function shared across many species, from insects to humans. A critical component of this navigational system is the perception of direction, which allows animals to maintain a consistent representation of their orientation in the environment. In mammals, this perception of direction is primarily mediated by the head direction (HD) system, a network of neurons that collectively encode the animal's current head orientation relative to its environment (Taube et al., 1990a).

HD cells, discovered in the rat's dorsal presubiculum (Rank, 1984; Taube et al., 1990b), exhibit a remarkable property: they fire maximally when the animal's head faces a specific direction in the horizontal plane, regardless of location or ongoing behavior. Each cell has a preferred direction, with firing rates decreasing as the head turns away, typically following a Gaussian-like tuning curve (Blair et al., 1997). Distributed across interconnected brain regions (Taube, 2007), these cells form a neural "compass" maintaining consistent directional representation (Cullen, 2019). Intriguingly, the HD system maintains direction representation even without external sensory cues – a phenomenon known as path integration (McNaughton et al., 2006). This suggests that the HD system functions as a neural integrator updating based on self-motion cues. Theoretical and computational models have proposed that the HD system functions as a continuous attractor network, where the collective activity of HD cells forms a stable "bump" of activity that can smoothly move to

represent different head directions (Zhang, 1996; Skaggs et al., 1994). These models often represent the head direction on a ring, reflecting the circular nature of directional space.

Despite significant progress in understanding the HD system, many questions remain about how its properties emerge from underlying neural circuits and how it interfaces with other components of the brain's spatial navigation system, such as place cells and grid cells (Moser et al., 2008). In this paper, we propose a minimalistic representation model for the HD system that captures its essential features while maintaining computational efficiency and biological plausibility. Our approach is motivated by recent advancements in direction representation learning in high-dimensional spaces (Cueva et al., 2019; Mante et al., 2013; Yang et al., 2019; Maheswaranathan et al., 2019). We leverage the fact that head direction transformations form a representation of the rotation group $U(1)$, acting on a ring of possible head direction representations. We present two versions of the model: a fully connected version and a convolutional version. Both models aim to learn a high-dimensional representation of head direction that exhibits key properties observed in biological HD systems. We demonstrate that our model can learn Gaussian-like tuning profiles for individual cells and produce a representation that exhibits a clear circle geometry when visualized with principal component analysis (PCA). The learned model is capable of accurate path integration. These emergent properties closely match the characteristics of biological HD systems, providing insights into the computational principles that may underlie their function.

By explicitly incorporating the symmetry of the rotation group and the circular geometry of head direction, our model offers a framework for understanding how these fundamental principles may shape the neural representations in the HD system. This approach not only captures key features of biological HD systems but also provides insights into the role of symmetry and geometry in neural computations for spatial navigation.

Model and Learning

General Framework

We represent head direction $x \in [0, 2\pi)$ in a continuous d -dimensional vector $v(x) \in \mathbb{R}^d$, which is regarded as responses of putative HD cells and subjects to three constraints:

(1) Nonnegativity constraint: $v(x) \geq 0$, reflecting neurons'

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nonnegative firing rates.

(2) Unit norm constraint: $|v(x)|^2 = \sum_{i=1}^d v_i(x)^2 = 1$ corresponds to a constant total activity of neurons regardless of direction x (to be one without loss of generality). This implies the direction x is only represented by spatial patterns of neuronal responses rather than summed responses, which has been widely used in neural coding (Pouget et al., 2003; Dayan & Abbott, 2005).

(3) Transformation rule: $v(x+dx) = F(v(x), dx)$, where F is a function describing changes in the representation $v(x)$ from a change dx in direction. The set of transformations $\{F(\cdot, dx), \forall dx\}$ and the set of representations $\{v(x), \forall x \in [0, 2\pi)\}$ together form a representation of the rotation symmetry group $U(1)$, so that $F(v(x), 0) = v(x)$, and $F(v(x), dx_1 + dx_2) = F(F(v(x), dx_1), dx_2)$. Here the addition in $x+dx$ is mod 2π . The transformation rule defines a recurrent neural network $v_t = F(v_{t-1}, dx_t)$ that enables path integration.

Model for local motion

For local motion dx , the first order Taylor expansion gives us

$$\begin{aligned} v(x+dx) &= F(v(x), dx) \\ &= F(v(x), 0) + F'(v(x), 0)dx \\ &= v(x) + f(v(x))dx, \end{aligned} \quad (1)$$

where $f(v(x)) = F'(v(x), 0)$ is the derivative of $F(v(x), dx)$ with respect to dx evaluated at $dx = 0$. This first-order Taylor expansion corresponds to the Lie algebra of the Lie group formed by the transformations $(F(v(x), dx), \forall dx)$. For larger motion dx , we can also use second-order Taylor expansion.

To parameterize $f(v(x))$, here we propose two models, which are the fully connected version and the topographical convolutional version. Our goal is to demonstrate that Gaussian-like head direction tuning profiles emerge regardless of the specific form of $f(v(x))$. Also, we keep both versions of the model as simple as possible, which presents the minimalistic setting.

Fully Connected Version In the fully connected version, we model local changes in direction as:

$$v(x+dx) = v(x) + Bv(x)dx, \quad (2)$$

where $B \in \mathbb{R}^{d \times d}$ is a learnable matrix, and $dx \in [-b, b]$ for a small $b > 0$. Here the matrix B enables every dimension of the representation to interact with every other dimension. This flexibility can capture complex, long-range dependencies in the neural code, but it does not impose any specific spatial structure on the arrangement of neurons.

Topographical Convolutional Version The topographical convolutional version of our model explicitly leverages the inherent circular structure of head direction by arranging neurons v_i on a ring. The local update is given by:

$$v(x+dx) = v(x) + B * v(x)dx, \quad (3)$$

where B is a learnable convolutional operator, and the symbol $*$ denotes a one-dimensional convolution operation with periodic boundary condition, and $dx \in [-b, b]$ for a small $b > 0$. The convolutional nature of B is expressed as:

$$(B * v(x))_i = \sum_{j=-k}^k B_j v_{(i+j) \bmod d}(x), \quad (4)$$

where B_j are learnable weights of the convolutional kernel, and k is the kernel size. For each neuron i , the output is computed as a weighted sum of the activities of neurons in its local neighborhood – specifically, the neurons at positions $i-k$ through $i+k$. The modulo operation $\bmod d$ ensures that the indexing wraps around when $i+j$ falls outside the range $[0, d-1]$, thereby preserving the circular structure of the representation. This local, circular convolution effectively captures the topological organization of head direction cells, where each neuron’s activity is influenced predominantly by its immediate neighbors.

Learning Method

Our model learns two sets of parameters:

(1) V : the representations $v(x)$ for all $x \in \{k \frac{2\pi}{n}, k = 0, \dots, n-1\}$, where n is the number of grid points. We denote these $v(x)$ collectively as V . For a general continuous x , we express $v(x)$ as a linear interpolation between the two nearest grid points.

(2) B : the update matrix or convolution kernel B .

We define a loss function to train B and v by minimizing the prediction error of local changes:

$$\mathcal{L}(V, B) = \mathbb{E}_{x, dx} [|v(x+dx) - F(v(x), dx)|^2] \quad (5)$$

This loss function comes from Equation 1 and focuses on the accuracy of single-step updates. This one-step loss function can eliminate the need for backpropagation through time, which significantly simplifies the learning process and reduces computational complexity.

The above loss function can be minimized by projected gradient descent, i.e., after a gradient descent step or a step of Adam optimizer (Kingma & Ba, 2014), we set all negative elements in each $v(x)$ to 0, and then normalize each $v(x)$ to have norm 1. Expectation $\mathbb{E}_{x, dx}$ can be approximated by uniformly sampling x from $[0, 2\pi)$ and dx from interval $[-b, b]$.

Model training

We use Adam optimizer (Kingma & Ba, 2014) to minimize the loss function. The algorithm proceeds as in Algorithm 1.

To achieve a continuous representation, we define $v(x)$ at discrete points $x_k = k \frac{2\pi}{n}$ for $k = 0, 1, \dots, n-1$, and use linear interpolation for intermediate values:

$$v(x) = (1-w)v(x_{\lfloor k \rfloor}) + wv(x_{\lceil k \rceil}), \quad (6)$$

where $k = \frac{n}{2\pi}x$, $w = k - \lfloor k \rfloor$, and $\lfloor \cdot \rfloor$, $\lceil \cdot \rceil$ denote floor and ceiling functions respectively.

Algorithm 1 Learning Head Direction Representation

Input: Number of directions n , dimension d , learning rate η , number of iterations T

Output: Learned representations $v(x_k)$ and transition function F

Initialize $v(x_k)$ for $x_k = k\frac{2\pi}{n}, k = 0, 1, \dots, n-1$

Initialize B (matrix or convolutional kernel)

```

1: for  $t \leftarrow 1$  to  $T$  do
2:   Sample a batch of  $(x, dx)$  pairs
3:   Compute the loss  $\mathcal{L}$  for the batch
4:   Update  $v(x_k)$  and  $B$  using gradients of  $\mathcal{L}$  and learning rate  $\eta$ 
5:   for  $k \leftarrow 0$  to  $n-1$  do
6:      $v(x_k) \leftarrow \max(v(x_k), 0)$   $\triangleright$  Enforce non-negativity
7:      $v(x_k) \leftarrow \text{project}(v(x_k))$   $\triangleright$  Project onto unit sphere
8:   end for
9: end for
10: return  $v(x)$  and  $B$ 

```

For larger local motion range b (specifically, $b = 20\frac{2\pi}{n}$ in our experiments), we employ a second-order model to capture higher-order dynamics:

$$v(x+dx) = v(x) + B_1 v(x)dx + B_2 v(x)dx^2, \quad (7)$$

where $C \in \mathbb{R}^{d \times d}$ is another learnable matrix. This second-order term allows the model to better account for changes over larger directional steps.

More specifically in our training process, we use $n = 100$ discrete directions. The model was trained for 200,000 epochs with a batch size of 256, using an Adam optimizer (Kingma & Ba, 2014) with an initial learning rate of $4e-5$. A learning rate scheduler (ReduceLROnPlateau) is employed with a factor of 0.8 and patience of 5000 epochs to adapt the learning rate during training. For the convolutional model, we use a kernel size of 3. An example training loss curve can be found in Figure 1, which shows a stable training process. The model can be trained on a single NVIDIA A6000 GPU in around 5 minutes.

Experiments and Results

We conduct a series of experiments to evaluate the performance and properties of our model across various configurations. We explore dimensions $d \in \{10, 20, 50, 100\}$ and local range $b \in \{m\frac{2\pi}{n}, m = 2, 5, 10, 20\}$ for both the fully connected and convolutional versions of the model. Here we fix $n = 100$ in all experiments.

Ring Structure in PCA Plot

We apply Principal Component Analysis (PCA) to the learned representations $v(x)$ across all directions as in Figure 2. The PCA plot of the first two principal components reveal a clear ring structure. This emergent property demonstrates that our model has learned a continuous, circular representation of

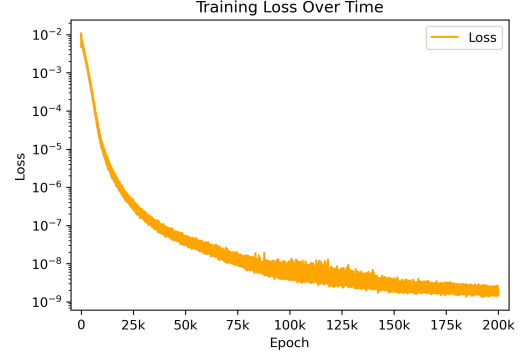


Figure 1: **Training loss** of an example fully-connected model with dimension $d = 20$. We train the model for 200,000 epochs where it converges.

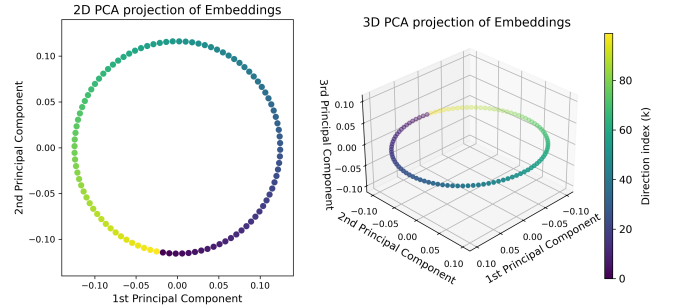


Figure 2: **2D and 3D PCA visualization** of learned head direction representations. Colors represent the discrete head direction indices from 0 to n , corresponding to angles from 0° to 360° . Both PCA plots reveal a clear ring structure, indicating that our model has learned a continuous, circular representation of head direction

head direction, mirroring both the topology of the actual direction space and the attractor dynamics observed in biological HD systems. The ring in our PCA plots confirms that even in a high-dimensional firing-rate space, the dominant latent structure reflects a one-dimensional continuum. In other words, small changes in head orientation correspond to smooth movement around the circular manifold, consistent with the view that the HD system operates as a rotationally invariant attractor (Zhang, 1996).

Moreover, this ring-like organization is consistent across both model versions, tested dimensions, and local ranges. This result underscores that our high-dimensional representation effectively captures the underlying one-dimensional nature of head direction while providing computational advantages, validating our model’s ability to capture essential features of biological head direction systems despite its minimalist design.

Gaussian-like Tuning Profiles

A defining feature of biological head direction (HD) cells is their unimodal tuning to a specific orientation, resulting in

bell-shaped firing curves around a preferred angle (Taube et al., 1990b; Taube, 1995; Blair & Sharp, 1996; McNaughton et al., 2006). In our trained model, we observe a strikingly similar phenomenon: each dimension (or “cell”) in the learned representation $v(x)$ shows a maximal response at a particular head direction and exhibits a smooth, approximately Gaussian drop-off for orientations deviating from that preferred angle.

This emergence of Gaussian-like tuning is critical for a stable and unambiguous directional code. First, it ensures that each cell encodes a unique portion of directional space, distributing orientations across the population (Blair & Sharp, 1996; Taube, 2007). Second, Gaussian tuning curves support stable attractor dynamics: small deviations in the system’s activity are naturally pulled back toward the peak direction, mirroring the continuous attractor models that have been proposed to underlie HD cell ensembles (Skaggs et al., 1994; Zhang, 1996). Third, the unimodal shape of these tuning curves facilitates robust decoding; a small set of maximally responding cells can reliably indicate the current heading, even under noisy or partial input conditions (McNaughton et al., 2006).

Figure 3 highlights four example neurons from our convolutional model with $d = 20$, each displaying a clear Gaussian-like profile centered on a different preferred direction. To confirm that this behavior holds consistently across the entire network, we further provide the tuning curves of all 100 neurons in our model with $d = 100$ in Figure 4. Every dimension in this high-dimensional representation preserves the same unimodal structure, indicating that fundamental symmetry and geometric constraints in the learning process produce stable, biologically realistic firing patterns. These findings closely align with experimental observations of unimodal HD cell tuning in rodents and other mammals.

Path integration

Path integration is a core function of biological head direction (HD) systems, enabling animals to track their heading in the absence of salient external cues by internally summing small changes in orientation (Etienne & Jeffery, 2004; Valerio & Taube, 2012; McNaughton et al., 2006). In neural terms, it can be seen as sequentially updating an internal representation of direction so that each incremental movement is reflected in the collective firing of HD cells. From a computational standpoint, this corresponds to repeatedly applying a learned update function to a latent state encoding the current heading (Gao et al., 2021; Xu et al., 2023a,b, 2025).

To evaluate our model’s ability to perform path integration, we begin by assigning an initial head direction $x_0 \in [0, 2\pi)$ and obtaining its latent representation $v_0 = v(x_0)$. We then apply a sequence of directional shifts $(dx_1, dx_2, \dots, dx_n)$. Given our direction representation function $v(x) \in \mathbb{R}^d$ and the update function $F(v, dx)$, we track the changes in the direction representation by updating the representation for each step t

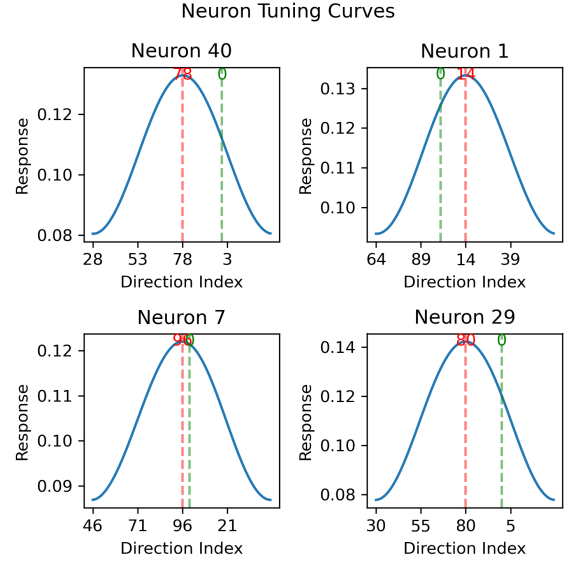


Figure 3: **Tuning curves of a sample of neurons** from our convolutional model with $d = 20$. This figure, presented as a complement to Figure 4, displays a random selection of neurons to highlight their Gaussian-like tuning profiles. The x-axis spans the full 360° range of head directions, with each curve centered on its neuron’s preferred direction (indicated by the red dotted line) to illustrate the circular nature of the representation. The green dotted line marks the direction index 0.

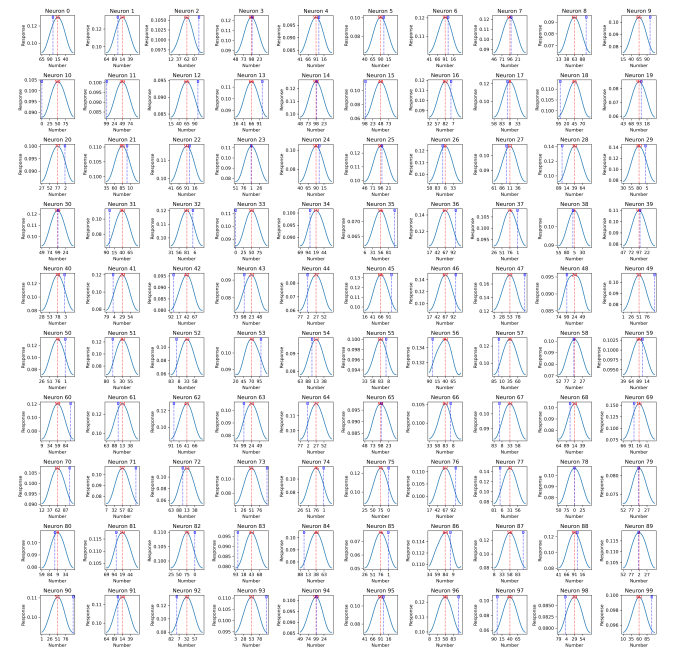


Figure 4: **Full tuning curves with $d = 100$.** We present all 100 head direction cells, and all tuning curves have Gaussian-like tuning profiles.

according to

$$v_t = F(v_{t-1}, dx_t), t = 1, \dots, n \quad (8)$$

This procedure ensures that v_t accumulates the integrated effects of all prior increments, thus approximating the final heading after $\sum_{i=1}^t dx_i$. After obtaining the final representation v_n , we decode the corresponding direction x_n by maximizing the inner product between v_n and $v(x)$ over all possible direction x :

$$x_n = \arg \max_{x \in [0, 2\pi)} \langle v_n, v(x) \rangle. \quad (9)$$

In the decoding phase, we leverage the property that v_n has the highest similarity with $v(x)$ at the true final direction. Such a simple yet effective decoding strategy reflects a population-vector-like scheme often used in neural coding research (Georgopoulos et al., 1986).

To systematically assess performance, path integration is evaluated using two local range scenarios: $b = \frac{2\pi}{n}$ radians, and $b = m \frac{2\pi}{n}$ radians, where m represents the multiple of the basic angular step size used during training. In both cases, the motion of each step dx_t is sampled uniformly from the range $[-b, b]$, thus varying the magnitude of each incremental rotation. We compare performance both with and without a re-encoding step:

1. Without re-encoding: the model simply applies $v_t = F(v_{t-1}, dx_t)$ over multiple steps, causing any representational errors to accumulate.
2. With re-encoding: we append an extra decode-then-re-encode procedure at each step. After each step, we first decode $v \rightarrow \hat{x}$ to the 1D head direction angle via $\hat{x} = \arg \max_{x' \in [0, 2\pi)} \langle v, v(x') \rangle$, and then encode $v_t \leftarrow v(\hat{x})$ back to the neuron space intermittently. Since our model is trained in a 1-step manner, this approach aids in rectifying the errors accumulated in the neural space throughout the transformation by resetting the state to a “clean” representation.

Table 1 presents the average angular difference (in radians) between the true and estimated directions after multiple steps of path integration. Results are shown for various dimensions d and multiples m , and are separated into the two local range conditions. The columns labeled “local range = $\frac{2\pi}{n}$ error” report accuracy when each step is sampled from the unit angular step range $\frac{2\pi}{n}$, whereas those labeled “local range = $m \frac{2\pi}{n}$ error” show results when each increment is sampled from the range as large as what was used during training. The model maintains low error under both conditions and, importantly, exhibits robust performance at larger step sizes $m \frac{2\pi}{n}$. Notably, despite being trained with a one-step predictive loss function, our model demonstrates remarkable accuracy in multi-step path integration tasks.

Figure 5 further shows the effectiveness of re-encoding by comparing the accumulated error over 20 steps in both conditions. The curve without re-encoding shows a gradual increase in error, whereas the error with re-encoding remains

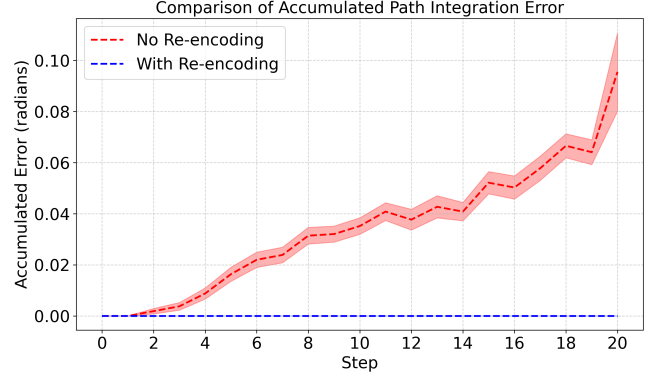


Figure 5: **Accumulated path integration error** over trajectories of 20 steps with and without re-encoding. We take the model with $d = 50$, $m = 5$ as an example, i.e., each step dx is sampled from $[-5 \frac{2\pi}{n}, 5 \frac{2\pi}{n}]$. Shaded regions indicate standard error across 100 trials. When re-encoding is disabled, we notice an accumulation of path integration error, whereas the re-encoded path remains error-free.

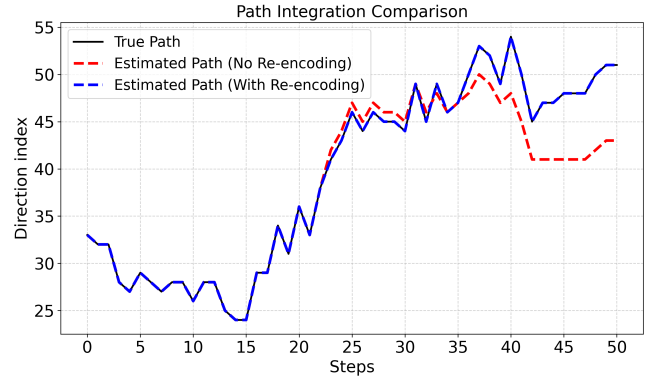


Figure 6: **Trajectory comparison** over an extended trajectory of 50 steps. We take the model with $d = 50$, $m = 5$ as an example. The true path (solid black) is overlaid with two estimated paths: one with re-encoding (blue dashed) and one without (red dashed). The re-encoded trajectory aligns perfectly with the true path, while the non-re-encoded estimate gradually deviates.

low, highlighting the benefit of intermittently snapping the network state back to a “clean” representation. Figure 6 provides an additional view of a 50-step trajectory, in which the re-encoded estimate (blue dashed line) remains essentially indistinguishable from the true path (black solid line), while the non-re-encoded estimate (red dashed line) slowly diverges as cumulative errors accumulate. These results indicate that our minimalistic representation model not only learns smooth, local transformations but also preserves directional accuracy over many updates, generalizing effectively from local updates to global navigation.

Table 1: **Path integration results.** m represents the multiple of the unit angular step size ($\frac{2\pi}{n}$) used for training and evaluation in the larger range scenario. Errors are reported as the average angular difference in radians over all steps in a sequence of length 20. Results are shown for two local motion range scenarios, $b = \frac{2\pi}{n}$ and $b = m\frac{2\pi}{n}$. In both settings, location motions dx are uniformly sampled from the range $[-b, b]$. We train models with $m = 2, 5, 10$ using the first-order transformation as in Equation 2 and Equation 3 and models with $m = 20$ using second-order formulations as in Equation 7.

Architecture	d	m	local range = $\frac{2\pi}{n}$ error (radians)		local range = $m\frac{2\pi}{n}$ error (radians)	
			without re-encoding	with re-encoding	without re-encoding	with re-encoding
Fully-connected	100	2	0.000	0.000	0.069	0.000
	100	5	0.007	0.000	0.765	0.010
	100	10	0.044	0.000	1.069	0.232
	100	20	0.356	0.000	1.362	0.179
	50	2	0.000	0.000	0.028	0.000
	50	5	0.000	0.000	0.036	0.000
	50	10	0.008	0.000	0.872	0.167
	50	20	0.363	0.000	0.149	0.182
	20	2	0.000	0.000	0.008	0.000
	20	5	0.001	0.000	0.024	0.009
	20	10	0.079	0.000	0.188	0.153
	20	20	0.385	0.000	0.186	0.154
	10	2	0.196	0.000	0.044	0.000
	10	5	0.000	0.000	0.047	0.014
	10	10	0.000	0.000	1.287	0.563
	10	20	0.000	0.000	0.897	0.338
Convolutional	100	2	0.000	0.000	0.110	0.000
	100	5	0.002	0.000	0.832	0.000
	100	10	0.056	0.000	1.252	0.184
	100	20	0.035	0.000	1.322	0.107
	50	2	0.000	0.000	0.070	0.000
	50	5	0.001	0.000	0.293	0.000
	50	10	0.008	0.000	0.866	0.167
	50	20	0.360	0.000	1.239	0.180
	20	2	0.000	0.000	0.088	0.000
	20	5	0.000	0.000	0.239	0.000
	20	10	0.105	0.000	0.883	0.287
	20	20	0.035	0.000	0.144	0.180
	10	2	0.000	0.000	0.065	0.000
	10	5	0.002	0.000	0.125	0.014
	10	10	0.005	0.000	0.323	0.028
	10	20	0.003	0.000	0.225	0.096

Discussion

The experimental results demonstrate that our minimalistic model captures key properties of biological HD systems. The emergence of Gaussian-like tuning profiles for individual dimensions of our representation closely resembles the behavior of biological HD cells, suggesting that such tuning properties may arise naturally from fundamental computational principles. The clear ring structure in the PCA plot indicates that our model has learned a continuous attractor representation of head direction, consistent with theoretical models of the HD system.

While head direction is inherently one-dimensional, our model learns a high-dimensional representation, potentially providing computational advantages such as increased robustness to noise and easier integration with other neural systems. Both versions of our model use local update rules that could be implemented by neural circuits, with the convolutional version bearing a particularly close resemblance to the anatomical organization of HD cells. The success of both versions suggests that capturing HD system properties depends more on the overall computational framework than specific architectural details, though the convolutional version may

offer advantages in parameter efficiency and biological interpretation.

Our model bridges the gap between detailed biophysical models and more abstract computational approaches. By explicitly incorporating the rotational symmetry of $U(1)$ and the circular geometry of head direction, our approach offers valuable insights into how these fundamental principles shape neural representations for spatial navigation. In doing so, we aim to contribute to a deeper understanding of the neural basis of spatial navigation and potentially inspire new approaches in both neuroscience and artificial intelligence.

Conclusion

We present a minimalistic representation model for the head direction system that captures essential features of biological HD systems while maintaining computational efficiency. Our model demonstrates that key properties of HD cells, such as Gaussian-like tuning and a ring structure, can emerge from a simple learning framework based on representing and updating directions in a high-dimensional space.

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