

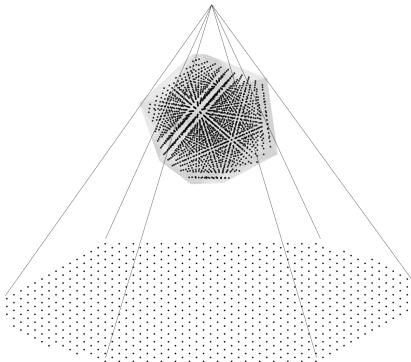
ABELIAN PHASE CODING: A LINEAR PROJECTION MODEL LINKING PREFRONTAL PHASE CODES TO ENTORHINAL GRIDS

ABSTRACT. We propose a linear projection model that maps high-dimensional task-phase information from the prefrontal cortex onto the entorhinal grid code. In our model, a key subset of working memory buffers from the medial prefrontal cortex is represented as an abelian group - specifically, a $\mathbb{Z}[\omega]$ module - reflecting a hexagonal structure in phase space. A linear projection maps the prefrontal phase code onto the entorhinal grid code, thereby linking the prefrontal and entorhinal representations through a shared algebraic structure. Our model makes specific predictions about entorhinal-prefrontal coding, explains observed features of the grid code such as shifts, scaling, coherence, and novelty-based rescaling, and predicts the presence of representations with hexagonal phase-tuning in additional regions.

INTRODUCTION & MOTIVATION

In order to act flexibly and creatively, intelligent agents must build rich internal models of their environments—both for spatial navigation and for more abstract task representations. Rodent studies have revealed lattice-based coding in hippocampal place cells and entorhinal grid cells, while in humans (and bats) analogous “grid-like” representations appear in multiple brain regions [Doeller *et al.*, 2010]. Meanwhile, recent findings indicate that the prefrontal cortex (PFC) maintains working memory buffers that track progress through abstract tasks [El-Gaby *et al.*, 2024], potentially interfacing with the entorhinal grid system [Whittington *et al.*, 2024]. Our aim is to formally connect these spatial and abstract representations, demonstrating that they share a common, lattice-based organisational principle.

Using the theory of theta functions [Riemann 1857; Weil 1964; Mumford, 1980], we show that the prefrontal cyclic buffer system can be understood as a high-dimensional phase space—a complex torus that is mathematically equivalent to a lattice—and that the entorhinal grid code can be seen as a localised, 2D projection of this space:



In the simplest terms, we show:

- Section 1: Prefrontal working memory can be modelled as a high-dimensional phase space.
- Section 2: When this space is organised with a hexagonal symmetry, it can be linearly projected onto a 2D lattice that mirrors the entorhinal grid code.
- Section 3: The Riemann theta function shows us how the entorhinal grid code localises position within the prefrontal phase space.
- Section 4: Imperfect projections from a lattice to a 2D subspace produce distortions that closely resemble those of actual grid cells, supporting our model.

1. PREFRONTAL PHASE SPACE AS AN ABELIAN VARIETY

Experimental work shows that the prefrontal cortex (PFC) maintains several cyclic (or ring) buffers [El-Gaby et al. 2024]. We can model each as tracking a phase variable $z_j \in \mathbb{C}$. Combining g such buffers yields a high-dimensional phase space \mathbb{C}^g , where interactions among these modes are captured by a lattice Λ generated from a period matrix Ω . Formally,

$$(1) \quad \Omega = \begin{bmatrix} \omega_{11} & \omega_{12} & \cdots & \omega_{1g} \\ \omega_{21} & \omega_{22} & \cdots & \omega_{2g} \\ \vdots & \vdots & \ddots & \vdots \\ \omega_{g1} & \omega_{g2} & \cdots & \omega_{gg} \end{bmatrix}, \quad \Lambda = \mathbb{Z}^g + \Omega \mathbb{Z}^g.$$

The way to read this is to think of how tasks and goals, and the dynamics of the world more generally, are inter-related. We don't focus on tasks in the world one at a time: as I write a paper, I also get closer to conference goals, funding goals, closer to bedtime, etc. The period matrix Ω captures the algebraic structure of the phase space that the PFC buffers track.

Identifying points in \mathbb{C}^g modulo this lattice Λ yields a g -dimensional *complex torus*, as illustrated in Figure 1. If Ω satisfies Riemann's bilinear relations, then \mathbb{C}^g/Λ becomes an *abelian variety*, endowing the PFC phase space with a rich algebraic-geometric structure.

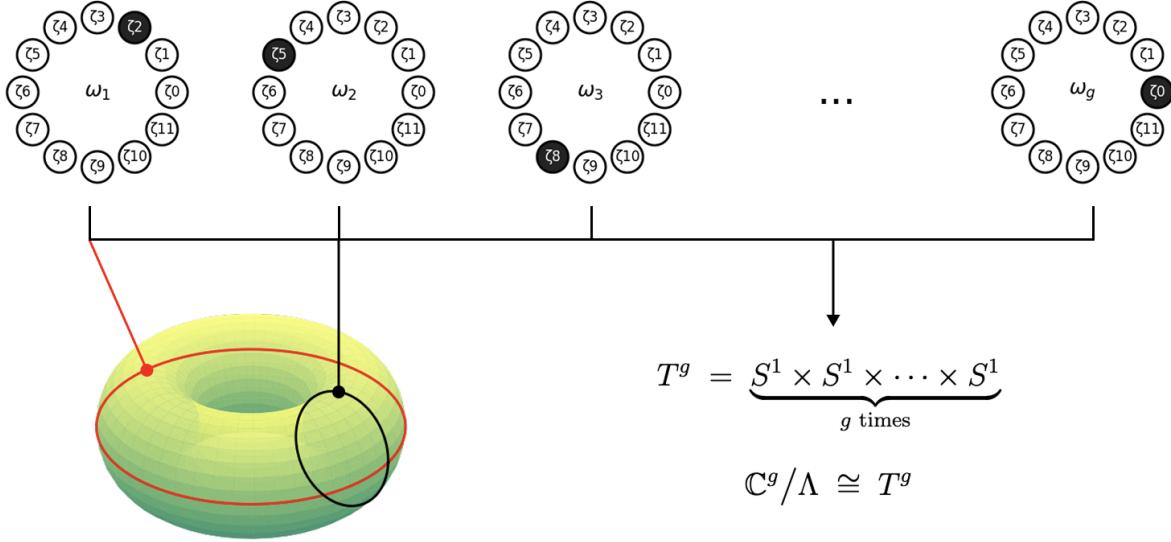


FIGURE 1. The Cartesian product of g circles (each representing a prefrontal cyclic buffer) forms a g -dimensional complex torus T^g , which is isomorphic to \mathbb{C}^g/Λ for some g -dimensional lattice Λ . By definition, if the period matrix Ω satisfies Riemann's bilinear relations, this complex torus is an abelian variety.

Interpretation for PFC. Each z_j represents a phase in one working memory buffer. Coupling among buffers is recorded in Ω . Viewed this way, prefrontal working memory becomes a torus-like structure: large-scale recurrent loops track multiple phases. Ensuring that Ω meets abelian variety criteria ($\Omega = \Omega^T$; $\Im(\Omega) > 0$) is not just formal: it lets us exploit well-studied tools (e.g. theta functions) to show how such a *phase space* might project onto hexagonal grid codes. Defining it as an abelian variety opens up the full power of modern mathematics, and helps us understand what the grid code encodes in Fourier-specific terms.

2. $\mathbb{Z}[\omega]$ -STRUCTURE AND THE LINEAR PROJECTION MODEL

Although an abelian variety has many possible lattices, not all will project neatly into a 2D hexagonal grid. To achieve the 60° symmetry observed in entorhinal cells, we impose a *ring* structure on the subset of cyclic buffers in PFC phase space that we expect to project most directly to MEC (i.e. vmPFC [Doeller *et al.*, 2010]) via the Eisenstein integers, $\mathbb{Z}[\omega]$, where

$$\omega = e^{2\pi i/3} \quad (\text{analogous to how } i = e^{\pi i/2} \text{ defines a } 90^\circ\text{-rotation}).$$

This enforces a 60° rotational symmetry in each coordinate, effectively “wiring in” a hexagonal (triangular) lattice constraint. *Resonances with MEC* may naturally lead to this hexagonal phase-space structure, as a stable attractor forms in relation to the 2D lattice projection.

Linear Projection onto a 2D Grid. In the ideal case, we define a linear map

$$(2) \quad \phi : \mathbb{C}^g \longrightarrow \mathbb{C}, \quad \phi(z_1, \dots, z_g) = \sum_{j=1}^g \alpha_j z_j, \quad \alpha_j \in \mathbb{Z}[\omega].$$

The coefficients α_j each carry the same 60° (hexagonal) symmetry. Consequently, as the PFC high-dimensional phase code (z_1, \dots, z_g) evolves, ϕ projects it down to a 2D plane while *preserving* the hexagonal geometry (Figure 2). In neural terms, one can imagine ϕ as a feed-forward layer that sums input phases with weights in $\mathbb{Z}[\omega]$.

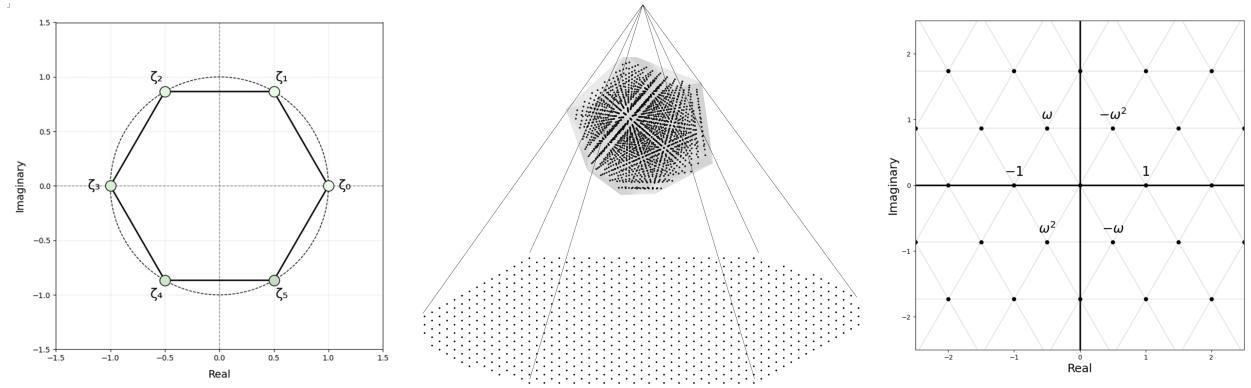


FIGURE 2. Sketch: If PFC cyclic buffers have a hexagonal structure in phase space (left) then a projection from the high-dimensional lattice can linearly map onto a 2D hexagonal lattice (center), which is isomorphic to $\mathbb{Z}[\omega]$ (right).

Prediction 1: PFC buffers most coupled with MEC exhibit 60° phase offsets. If certain PFC buffers strictly follow $\mathbb{Z}[\omega]$ -symmetry, then pairwise phase differences should cluster around multiples of 60° (e.g. $0^\circ, 60^\circ, 120^\circ, \dots$). *This reflects a hexagonal structure in phase space.* We expect these PFC buffers to show the most robust coupling to entorhinal grid cells. Disrupting such buffers (e.g. via optogenetics) should degrade grid regularity.

Prediction 2: Other regions with hexadirectional modulation. Beyond MEC-PFC, studies such as Doeller *et al.* (2010) have reported hexadirectional firing in retrosplenial cortex (RSC), parahippocampal cortex (PHC), posterior parietal cortex (PPC), and lateral temporal cortex (LTC). Our model predicts that these regions either:

- also adopt a $\mathbb{Z}[\omega]$ -tuned structure in their phase codes (potentially new mechanisms), or
- receive strong $\mathbb{Z}[\omega]$ -based input (via MEC/PFC) that confers the 60° modulation pattern.

In summary, $\mathbb{Z}[\omega]$ imposes the crucial hexagonal constraint needed for a 2D grid code via linear projection. The projection ϕ maps high-dimensional PFC phases into an MEC-like grid, linking both spatial and abstract coding under a shared algebraic principle.

3. LOCALISING POSITION IN PHASE SPACE VIA THE RIEMANN THETA FUNCTION

Having established a $\mathbb{Z}[\omega]$ -structured abelian variety for the PFC phase space, we next consider how the *entorhinal grid code* identifies positions within it. A powerful tool is the **Riemann theta function**, often defined as:

$$(3) \quad \Theta(z, \Omega) = \sum_{n \in \mathbb{Z}^g} \exp\left(\pi i n^T \Omega n + 2\pi i n^T z\right),$$

where $z \in \mathbb{C}^g$ is a local phase coordinate and Ω is the period matrix. Although an integral version [Weil 1964] highlights topological aspects better, the classical approach suffices here.

Shifts, Harmonic Modes, and Grid Localisation. Each vector $n \in \mathbb{Z}^g$ acts like a “shift” or coset in phase space. Grouping terms by $n^T \Omega n$ yields discrete “energy levels,” akin to harmonic modes in a multi-scale grid. As z varies, $\exp(2\pi i n^T z)$ constructively interferes at specific lattice points, creating the *localised peaks* observed in grid cells.

- **Shifts:** Global translations $z \mapsto z + \lambda$ (with $\lambda \in \Lambda$) change phases predictably, merging local information into a global structure by integrating over coset shifts [Weil 1964].
- **Discrete Harmonic Decomposition:** The quadratic form $n^T \Omega n$ defines an “energy.” Reorganising Θ by these energies produces distinct harmonic modes with discrete scale ratios (e.g. $3/2, 4/3, 5/4, \dots$) (see a matching theoretical justification in [Fiete *et al.*, 2023]).

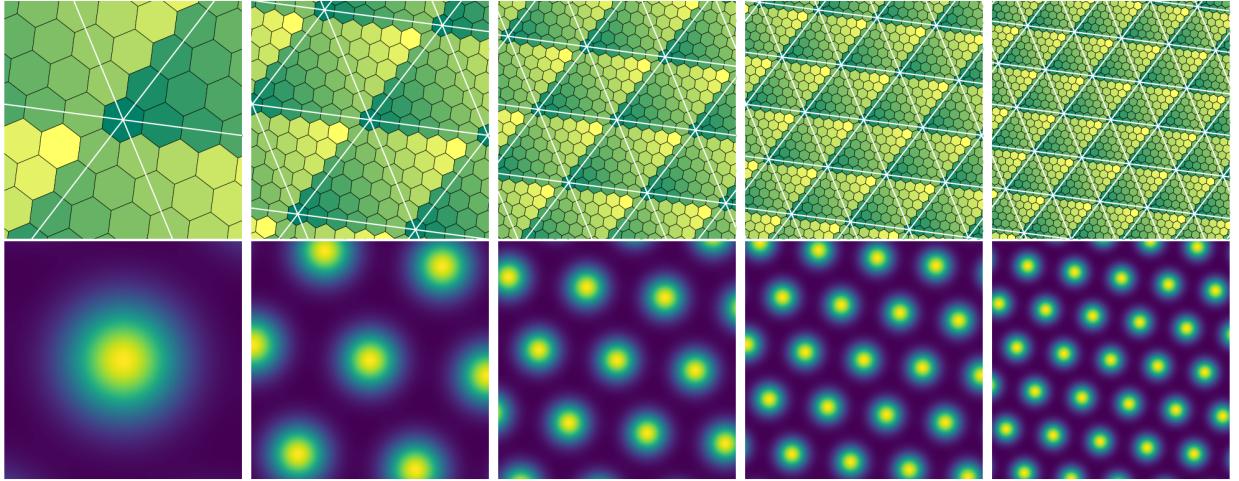


FIGURE 3. Ideal grid code from a theta function with shifts and harmonic scaling. Each cell represents a distinct coset; scaling ($\alpha \Omega$) transitions from integrating over local details to more global structures. Data suggest low-frequency (low-theta) coherence integrates global PFC structure, while high-theta primarily refines local HPC detail (see [Hasselmo *et al.*, 2002] and more).

Prediction 3: Artificially shifting z (e.g. changing the active phase in a prefrontal buffer via optogenetics) should yield *quantised jumps* in the entorhinal grid code - probably also causing an artificial phase precession. Tim Behrens and co. are certainly already doing this.

Prediction 4: PFC buffers should exhibit the same multi-scale structure as MEC grid modules. If known grid modules show ratios $3/2, 4/3, \dots$, we expect parallel ratios in PFC phases. Consistently measuring these discrete scales in PFC would substantiate the model.

Rescaling: From Local to Global Integration. Empirically, grid spacing expands under uncertainty or novelty [Barry *et al.*, 2012], implying a shift toward *coarser* or more global coding. In $\Theta(z, \Omega)$, rescaling $\Omega \mapsto \alpha \Omega$ changes which frequencies (modes) dominate. Larger

α “stretches” the lattice, coalescing multiple peaks into broader fields, whereas smaller α sharpens local structure. This aligns with evidence that MEC can switch between local HPC alignments and more global PFC strategies. In humanistic terms, when your environment suddenly changes and you have no idea what’s going on, you switch from thinking about local details to bigger picture patterns such as “what the fuck just happened and where am I”, then over time as you figure this out, you can meaningfully focus on local details again.

Conclusion. In short, the Riemann theta function provides a compact mathematical lens through which a high-dimensional lattice code can relate to a localised 2D hexagonal grid. Rescaling Ω toggles local vs. global representation, and shifts in z produce quantised updates—tying the abelian variety model directly to observable grid patterns in MEC.

4. COHERENCE AND PARTIAL ALIGNMENT

All of our preceding equations assume a perfect $\mathbb{Z}[\omega]$ -linear projection (§2). In reality, neural systems operate with noise and partial alignments between the PFC, MEC, and HPC. We introduce a *coherence* measure that quantifies how closely the entorhinal grid code adheres to the ideal hexagonal pattern. Concretely, we replace the perfect projection $\phi(z)$ by

$$(4) \quad \tilde{\phi}(z) = \phi(z) + \eta \quad \text{with} \quad \eta \sim \mathcal{N}(0, \sigma^2),$$

which progressively blurs or distorts the 60° structure. Figures 4 and 5 illustrate how increasing σ reduces grid regularity, mirroring the degraded patterns observed under novelty or high uncertainty in experimental data [Barry *et al.*, 2012; Garder *et al.* 2022 (Figure 5)].

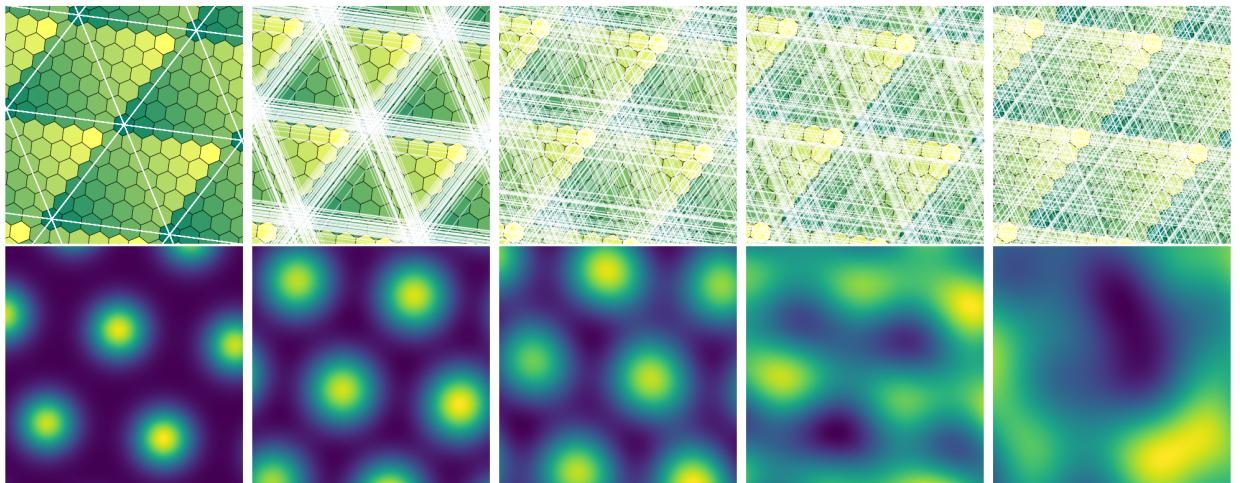


FIGURE 4. Decreasing grid coherence (left to right) in the linear projection model. Each panel increases the noise level σ in Eq. (4), blurring the perfect hexagonal structure. The white lines show where the lattice basis vectors fall.

Interpretation for PFC–MEC–HPC Interactions. Biologically, a perfect coherence would require the PFC’s high-dimensional phase code to align exactly with the entorhinal lattice. In practice, partial or inconsistent input from the HPC (representing local detail) or from other cortical areas (representing alternative tasks) lowers coherence:

- **Disconnect with HPC:** If the hippocampus signals a local map that conflicts with the PFC’s global expectation, the MEC grid code can slip from a neat attractor, showing the partial or full loss of hexagonal precision.
- **Noisy PFC Input:** The PFC might only approximate a $\mathbb{Z}[\omega]$ -module. We see a continuum from nearly perfect grid alignment ($\sigma \approx 0$) to highly irregular patterns (σ large).

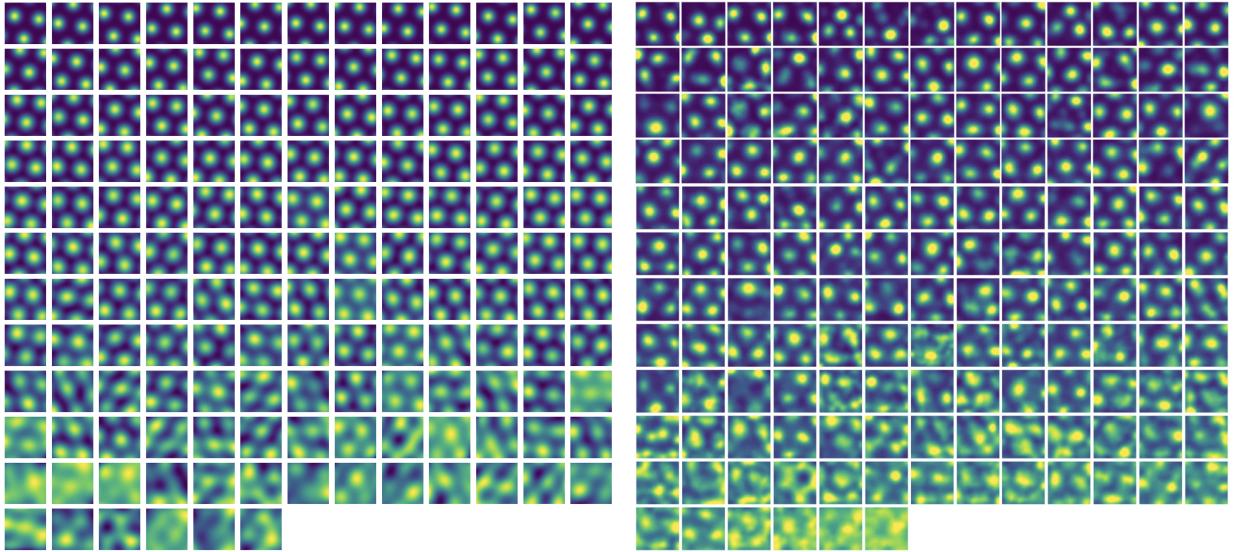


FIGURE 5. A comparison of decreasing grid coherence in our model (left) vs. experimental recordings (right) from Moser *et al.* (2022). The progressive loss of regular grid structure is qualitatively captured by increasing noise in Eq. (4). This already looks pretty convincing, but I still need to order my cells by spatial information as the Mosers did, and capture the non-linearities.

SUMMARY AND NEXT STEPS

Summary. We have shown how entorhinal and prefrontal representations may share an underlying, lattice-based coding principle. Imposing a hexagonal ($\mathbb{Z}[\omega]$) module structure on the high-dimensional PFC phase code yields, under a linear projection, the 2D grid patterns observed in MEC. Imperfections in this projection naturally mirror real-world distortions from novelty-driven rescaling and reduced coherence. The approach unifies spatial and abstract cognition under a single algebraic framework, offering precise predictions about phase offsets, regional coupling, harmonic scaling, and suggestions of where to look next:

- (1) **Computational Model Integration:** Incorporate these phase-buffer dynamics into the hybrid continuous attractor and oscillatory interference model of grid firing [Bush and Burgess, 2014] replacing VCOs with PFC buffers and linking them to MEC grids and *possibly* place cells. This will allow us to simulate how partial noise or mismatched inputs affect grid regularity in a biologically plausible circuit.
- (2) **Further Mathematical Formalisation:** Collaborate with MPI MiS mathematicians to refine the abelian variety structure (including $\mathbb{Z}[\omega]$ -linearity) and expand the Θ -function predictions. The aim is to generate additional, more precise, testable predictions and to see if other advanced theorems can guide experiments.
- (3) **Extending to Hyperbolic Spaces:** The current framework uses a Euclidean metric (hexagonal codes), but under higher cognitive load—or when tasks branch hierarchically—hyperbolic geometry might better capture the resulting expansions in phase space. When theta-gamma resonances need to accommodate numerous parallel modes, a hyperbolic embedding may offer a natural explanation for observed flexibility in capacity limits (e.g. 7 ± 2 [Lisman and idiair 1995; Lisman and Jensen 2013]). Note: 7 cycles relates to a full rotation in hexagonal phase space: one gamma unit per hexagonal vertex, with the base point included twice for topological closure. Under hyperbolic metrics, we can have stable resonance patterns that allow deviations from ideal 7 unit cycles, although the hexagon remains the baseline attractor.

REFERENCES

- [1] [Barry *et al.*, 2012] Barry, C., Ginzberg, L. L., O'Keefe, J., & Burgess, N. (2012). *Grid cell firing patterns signal environmental novelty by expansion*. *Nature Neuroscience*, 15(6), 763–771. <https://doi.org/10.1038/nn.3061>
- [2] [Bush & Burgess, 2014] Bush, D., & Burgess, N. (2014). *A hybrid oscillatory interference/continuous attractor network model of grid cell firing*. *Journal of Neuroscience*, 34(14), 5065–5079. <https://doi.org/10.1523/JNEUROSCI.4017-13.2014>
- [3] [Doeller *et al.*, 2010] Doeller, C. F., Barry, C., & Burgess, N. (2010). *Evidence for grid cells in a human memory network*. *Nature*, 463, 657–661. <https://doi.org/10.1038/nature08704>
- [4] [El-Gaby *et al.*, 2024] El-Gaby, M., Harris, A. L., Whittington, J. C. R., Dorrell, W., Bhomick, A., Walton, M. E., Akam, T., & Behrens, T. E. J. (2024, November 6). *A cellular basis for mapping behavioural structure*. *Nature*, 636, 671–680.
- [5] [Fiete *et al.*, 2023] Fiete, I., Khona, M., & Chandra, S. (2023, July 7). *Emergence of robust global modules from local interactions and smooth gradients*. Research Square Preprint. <https://doi.org/10.21203/rs.3.rs-2929056/v1>
- [6] [Gardner *et al.*, 2022] Gardner, R. J., Hermansen, E., Pachitariu, M., Burak, Y., Baas, N. A., Dunn, B. A., Moser, M.-B., & Moser, E. I. (2022). *Toroidal topology of population activity in grid cells*. *Nature*, 601(7893), 347–353. <https://doi.org/10.1038/s41586-021-04268-7>
- [7] [Hasselmo *et al.*, 2002] Hasselmo, M. E., Bodelon, C., & Wyble, B. P. (2002). *A proposed function for hippocampal theta rhythm: separate phases of encoding and retrieval enhance reversal of prior learning*. *Neural Computation*, 14(4), 793–817. <https://doi.org/10.1162/089976602317318965>
- [8] [Lisman & Idiart, 1995] Lisman, J. E., & Idiart, M. A. (1995). *Storage of 7 ± 2 short-term memories in oscillatory subcycles*. *Science*, 267(5203), 1512–1515. <https://doi.org/10.1126/science.7878473>
- [9] [Lisman & Jensen, 2013] Lisman, J. E., & Jensen, O. (2013). *The theta-gamma neural code*. *Neuron*, 77(6), 1002–1016. <https://doi.org/10.1016/j.neuron.2013.03.007>
- [10] [Mumford, 1980/1983] Mumford, D. (1983). *Tata Lectures on Theta I*. Progress in Mathematics, Vol. 28. Birkhäuser.
- [11] [O'Keefe & Dostrovsky, 1971] O'Keefe, J., & Dostrovsky, J. (1971). *The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat*. *Brain Research*, 34(1), 171–175. [https://doi.org/10.1016/0006-8993\(71\)90358-1](https://doi.org/10.1016/0006-8993(71)90358-1)
- [12] [Riemann, 1857] Riemann, B. (1857). *Theorie der Abelschen Functionen*. *Journal für die reine und angewandte Mathematik*, 54, 115–155.
- [13] [Weil, 1964] Weil, A. (1964). *Sur certains groupes d'opérateurs unitaires*. *Acta Mathematica*, 111, 143–211. <https://doi.org/10.1007/BF02391012>
- [14] [Whittington *et al.*, 2024] Whittington, J. C. R., Dorrell, W., Behrens, T. E. J., Ganguli, S., & El-Gaby, M. (2025, January 22). *A tale of two algorithms: Structured slots explain prefrontal sequence memory and are unified with hippocampal cognitive maps*. *Neuron*, 113(2), 321–333.e6. [https://doi.org/10.1016/https://www.cell.com/neuron/fulltext/S0896-6273\(24\)00765-7](https://doi.org/10.1016/https://www.cell.com/neuron/fulltext/S0896-6273(24)00765-7)