

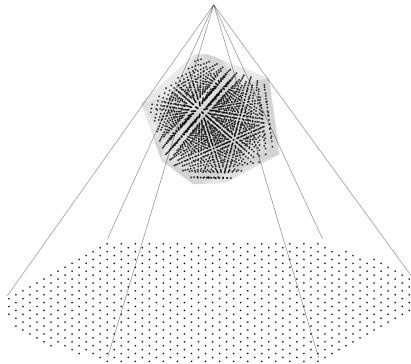
# ABELIAN PHASE CODING: A LINEAR PROJECTION FROM PREFRONTAL PHASE CODES TO THE ENTORHINAL GRID

**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 entorhinal grid cells [Hafting *et al.*, 2005], while in humans (and bats) analogous “grid-like” representations appear in multiple brain regions [e.g. 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  $\Lambda$  generated from a period matrix  $\Omega$ . 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  $\Omega$  captures the algebraic structure of the phase space that you navigate through life.

Identifying points in  $\mathbb{C}^g$  modulo this lattice  $\Lambda$  yields a  $g$ -dimensional *complex torus*, as ‘illustrated’ in Figure 1. In simple terms, you are always at some vector ( $z$  - see §3) in the phase space  $\mathbb{C}^g/\Lambda$ , as identified by the set of actice phase cells across all prefrontal buffers.

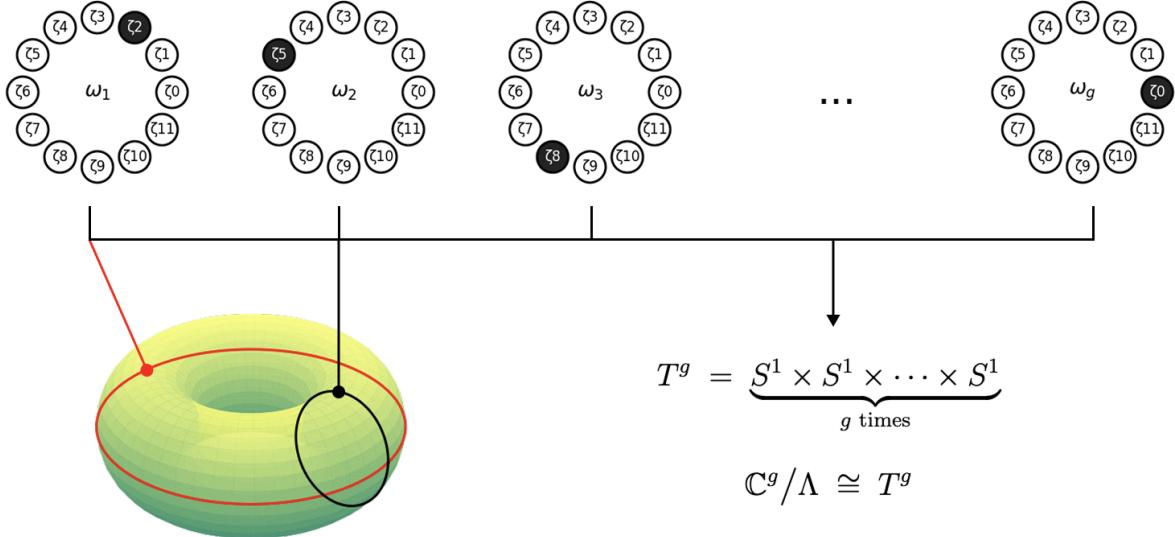


FIGURE 1. The Cartesian product of  $g$  circles (each representing a prefrontal cyclic buffer) forms a  $g$ -dimensional complex torus  $T^g$ , which is isomorphic to  $\mathbb{C}^g/\Lambda$  for some  $g$ -dimensional lattice  $\Lambda$ . (e.g., you can see how two prefrontal buffers identify a point on a 2-torus.) By definition, if the period matrix  $\Omega$  satisfies Riemann’s bilinear relations, this complex torus is an abelian variety.

**Interpretation for PFC.** Each  $z_j$  represents the current phase in a single prefrontal working memory buffer. Coupling among buffers is recorded in  $\Omega$ . Viewed this way, prefrontal working memory becomes a torus-like structure, with large-scale recurrent loops tracking multiple phases. Ensuring that  $\Omega$  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, gets mathematicians interested in collaborating, and helps us understand what the grid code may *actually* be doing in Fourier-specific terms.

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

Although an abelian variety supports many lattice structures, only a few project neatly onto a two-dimensional hexagonal grid. For the prefrontal phase space to align with entorhinal grid representations, its underlying geometry should exhibit a degree of hexagonal organization. One approach to achieve the observed  $60^\circ$  symmetry in grid cells is to endow a subset of prefrontal cyclic buffers—particularly those projecting strongly to the MEC (e.g., vmPFC as suggested by Doeller et al., 2010)—with a ring-like structure modeled on the Eisenstein integers,  $\mathbb{Z}[\omega]$ , where:

$$\omega = e^{2\pi i/3}.$$

This  $\mathbb{Z}[\omega]$ -like structure serves as an idealization that captures the required hexagonal symmetry. Importantly, we do not insist that this structure is hardwired in the neural substrate; rather, recurrent projections and dynamic interactions within the entorhinal-prefrontal network may naturally induce resonance patterns that approximate this hexagonal organization.

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

$$(2) \quad \phi : \mathbb{C}^g \longrightarrow \mathbb{C},$$

which projects the high-dimensional lattice of the PFC phase space onto a two-dimensional subspace, thereby producing a hexagonal grid pattern. The intrinsic hexagonal structure in the phase space is crucial, as it ensures that the projection yields a lattice consistent with the observed grid cell firing patterns. projection  $\phi$  could be modelled as a feed-forward layer in a neural network, but I think this is too simplistic. I would prefer a recurrent mechanism based on [Bush and Burgess 2014], with the VCOs swapped out for prefrontal cyclic buffers.

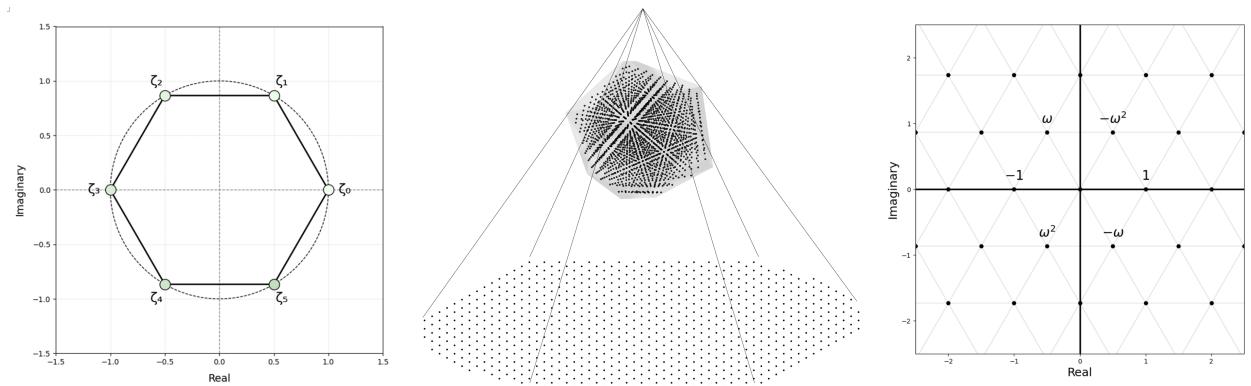


FIGURE 2. Sketch: If PFC cyclic buffers have a hexagonal structure in phase space (left) then a projection from the high-dimensional lattice can linearly map onto a 2D hexagonal lattice (center), which is isomorphic to  $\mathbb{Z}[\omega]$  (right).

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

**Prediction 2: Other regions with hexadirectional modulation.** Alongside MEC and vmPFC, Doeller et al. (2010) reported hexadirectional firing in additional DMN regions: retrosplenial cortex (RSC), parahippocampal cortex (PHC), posterior parietal cortex (PPC), and lateral temporal cortex (LTC). Our model predicts that these regions either:

- are themselves grid cells. To me, this seems unlikely, as true grid cells in the entorhinal cortex cells form a fairly large assembly, and have very specific functions and connections.
- also adopt a  $\mathbb{Z}[\omega]$ -tuned structure in their phase codes (potentially via new mechanisms). This seems to be the case vmPFC cells and their ring buffer structure; other regions may also follow the buffer structure, but possibly integrating information from other modalities.
- receive strong  $\mathbb{Z}[\omega]$ -based input (via MEC/PFC) that confers the  $60^\circ$  modulation pattern.

Tantalisingly, this may hint at a network of higher-cognitive areas all communicating via the same underlying coding scheme. Exploring their mechanistic relationships could unveil the deeper structure of DMN cognitive circuits, beyond just pinning everything on PFC. Currently we have been too quick to write this hexadirectional signal off as grid cells (see how people reference [Jacobs *et al.*, 2013], although in the paper itself he is fairly neutral.) Instead, you might be looking at a network of higher-cognitive areas that use a common coding scheme, even though they are integrating information from different source regions.

In summary,  $\mathbb{Z}[\omega]$  imposes the crucial hexagonal constraint needed for a 2D grid code via linear projection. The projection  $\phi$  maps high-dimensional PFC phase codes onto an MEC-like grid, linking spatial and abstract coding schemes through a shared algebraic principle. Exploring this further, in the regions implicated in Doeller *et al.* (2010), could be interesting.

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

The Riemann theta function [Riemann 1857] takes a period matrix  $\Omega$  (or the complex torus it defines) and indexes it through a variable  $z$ . It essentially gives you a way to track local position in a high-dimensional phase space, while respecting all the symmetries of the space:

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

There is a neat extension of the theta function [Weil 1964] that shows theta in Fourier dual terms. In Weil's formulation, you implicitly have co-ordinates in a dual space: a local direct space, and the global Fourier dual space. For us, that means you can simultaneously index local information (i.e. HPC) and global phase information (i.e. PFC) at the same time. The MEC (or the theta function) then acts as the bridge that formally links the two domains and localises position within the phase space. The theta function integrates local information with respect to global symmetries structured via a lattice. The scale of the lattice dictates which domain you are iterating over; a finer lattice is integration over local information in the direct space, a coarser lattice is integration over global information in the dual space. The coup for us, will be to use the theta function (as a model of MEC) to bridge local HPC representations with global PFC representations in a way that accounts for theta oscillations and phase coding. This will need real modelling though, so can be skipped for the poster.

**Prediction 3:** Artificially shifting  $z$  (e.g. changing the active phase cell in a prefrontal buffer via optogenetics) should yield *quantised jumps* in the entorhinal grid code - probably causing artificial phase precession. Tim Behrens and co. must surely already be 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. The precise scaling ratios, and the discrete harmonic scaling comes directly out of the theta function formalism. Fiete *et al.* (2023) has a justification of the same scaling ratios, so her model agrees with mine - but mine will capture the underlying maths better. Notably, these discrete, harmonic scaling ratios agree with our own grid cell data (personal communication).

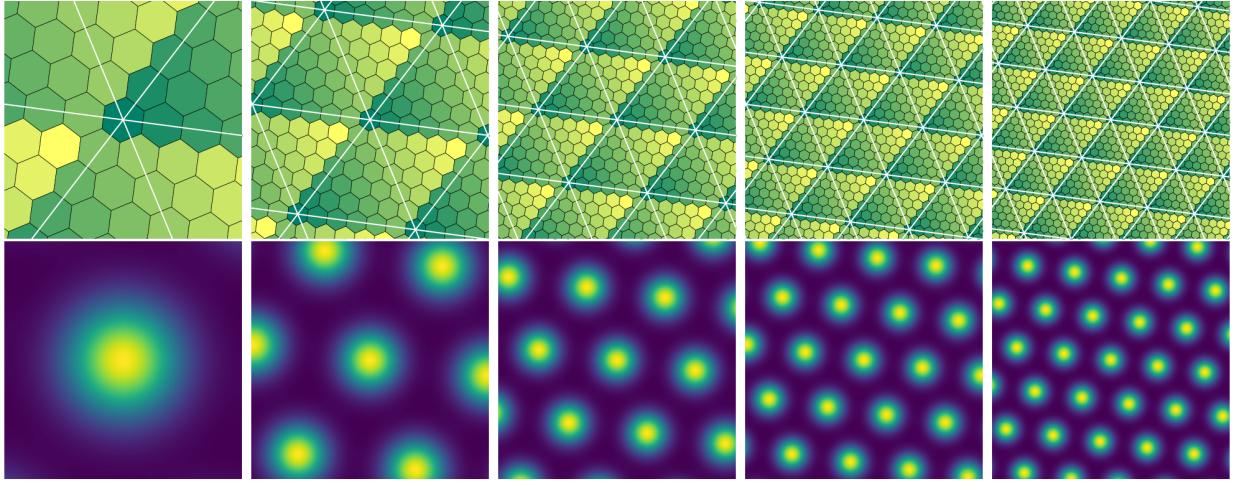


FIGURE 3. Ideal grid code from a theta function with shifts and harmonic scaling. Each cell represents a distinct lattice coset. It is realistic to be able to get a properly justified construction of this by May. This bridges the high-level theory in the first sections with the realistic grid cells in the next sections.

#### 4. COHERENCE AND PARTIAL ALIGNMENT

Our preceding sections assumed 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 shifts the lattices away from the perfect  $60^\circ$  structure. Figures 4 and 5 illustrate how increasing  $\sigma$  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)].

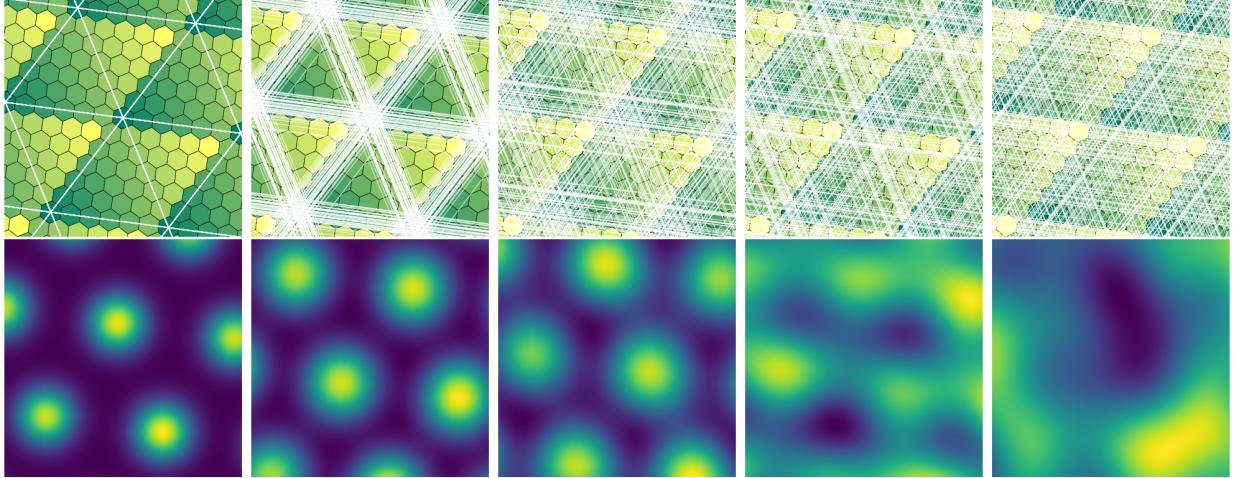


FIGURE 4. Decreasing grid coherence (left to right) in the linear projection model. Each panel increases the noise level  $\sigma$  in Eq. (4), blurring the perfect hexagonal structure. The white lines show where the lattice basis vectors fall.

**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

grid code. In practice, partial or inconsistent input from the HPC (representing local detail) or from PFC (global model) or other cortical areas (alternative schemae) lowers coherence.

If the hippocampus signals a local map that conflicts with the MEC-PFC expectations, the MEC grid code can be forced out of a stable attractor. This would manifest as a decrease in grid coherence, owing to a projection  $\phi$  with a greater degree of noise. This would break a lot of the fine scale structure in local MEC-HPC connections via Hebbian mechanisms (e.g. bad STDP signalling). This in turn would decrease local coherence, and the system would fall back into stable resonances at lower frequencies (coarser grids). Likewise, the formal explanation is that you integrate over global, model-based information during uncertainty; when your model fails to capture reality, you look at global patterns to work out what is happening. Importantly, the mathematical and biological explanations can both be true, they are just different pictures of what is happening. During uncertainty, you expect to see more MEC-PFC phase coupling in low-theta, and wider grid representations. Then, as you learn the fine structure back, the grids will settle into a new set of stable attractors. This is a theoretical justification for the grid re-scaling under novelty effect [Barry *et al.*, 2012].

Finally, I ran the noisy linear projection model against the data from the leading figure in the toroidal grid cells paper [Gardner *et al.* (2022)]. The results are in Figure 5. The coherence method is the same as in Figure 4. The results pretty convincing in my opinion:

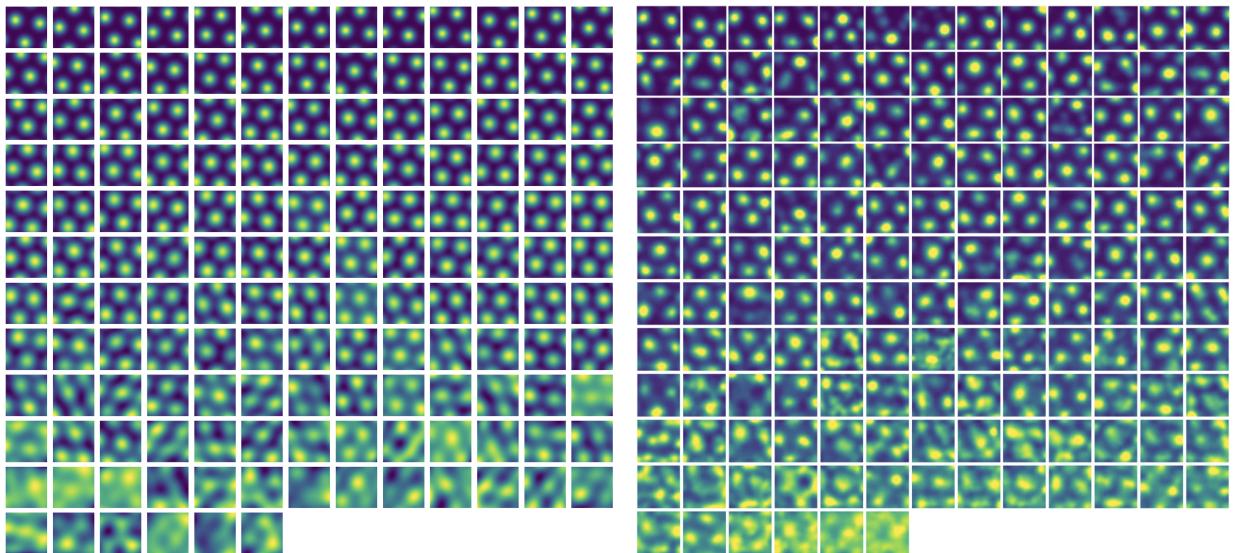


FIGURE 5. A comparison of decreasing grid coherence in our model (left) vs. experimental recordings (right) from Gardner *et al.* (2022). The progressive loss of regular grid structure is qualitatively captured by increasing noise in Eq. (4). It already looks good, but I still need to order my cells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

## 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 can formally relate spatial and abstract cognition under a common algebraic framework, offering predictions about phase offsets, regional coupling, harmonic scaling, and regions to record from next.

## Next Steps.

- (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 allows us to go from abstract theory to an actual computational model. Probably just MEC-PFC first, then maybe CA1-MEC-PFC.
- (2) **Further Mathematical Formalisation:** Collaborate with MPI MiS mathematicians to refine the abelian variety structure, including formally working out the  $\mathbb{Z}[\omega]$ -linearity parts, and properly building and connecting the  $\Theta$ -function. Using complex numbers in our model helps us a lot. Mathematics requires very precise conditions, but the resonances inherent in oscillating systems can force MEC-PFC into these precise conditions naturally. That is, hexagonal grids are inevitable, yet far from superfluous. The aim of this work is to generate additional, precise, falsifiable predictions, and for me to learn the mathematical structures better, to guide future modelling and experimental work. Once you have an abelian variety (which it very much looks like we do), it gets exponentially easier to get mathematicians interested.
- (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.  $7 \pm 2$  [Lisman and idiart 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. The maths here gets into the internal symmetries of hyperbolic phase spaces, which is just good, clean, fun, funky matheamtics. If the brain was optimally designed [Paley, 1802], this is the kind of maths it would use to store and transmit information.

## 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] **[Hafting *et al.*, 2005]**  
Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, 436(7052), 801–806. <https://doi.org/10.1038/nature03721>
- [8] **[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>
- [9] **[Lisman & Idiart, 1995]**  
Lisman, J. E., & Idiart, M. A. (1995). *Storage of  $7 \pm 2$  short-term memories in oscillatory subcycles*. *Science*, 267(5203), 1512–1515. <https://doi.org/10.1126/science.7878473>
- [10] **[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>
- [11] **[Mumford, 1980/1983]**  
Mumford, D. (1983). *Tata Lectures on Theta I*. Progress in Mathematics, Vol. 28. Birkhäuser.
- [12] **[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)
- [13] **[Paley, 1802]**  
Paley, W. (1802). *Natural Theology: or, Evidences of the Existence and Attributes of the Deity*. London: Printed for [publisher].
- [14] **[Riemann, 1857]**  
Riemann, B. (1857). *Theorie der Abelschen Functionen*. *Journal für die reine und angewandte Mathematik*, 54, 115–155.
- [15] **[Weil, 1964]**  
Weil, A. (1964). *Sur certains groupes d’opérateurs unitaires*. *Acta Mathematica*, 111, 143–211. <https://doi.org/10.1007/BF02391012>
- [16] **[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)