

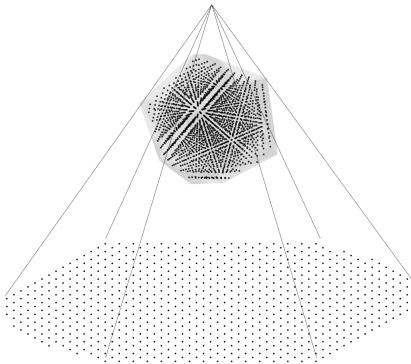
# ABELIAN PHASE CODING: A LINEAR PROJECTION FROM PREFRONTAL PHASE CODES TO THE ENTORHINAL GRID

**ABSTRACT.** We propose a linear projection model that maps high-dimensional task-phase information from the prefrontal cortex to 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 [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 the PFC buffers track.

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

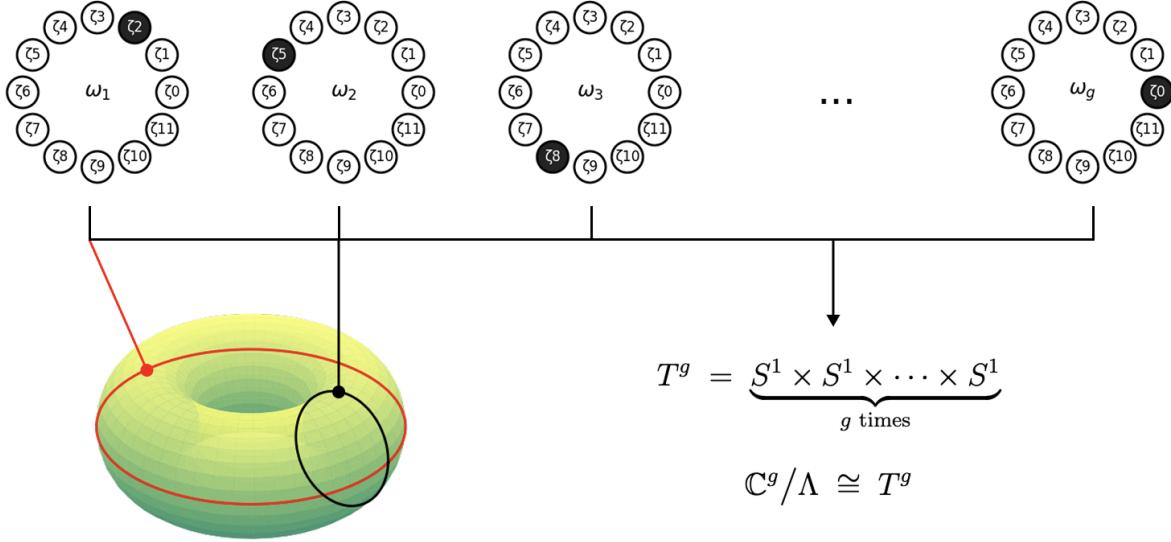


FIGURE 1. The Cartesian product of  $g$  circles (each representing a prefrontal cyclic buffer) forms a  $g$ -dimensional complex torus  $T^g$ , which is isomorphic to  $\mathbb{C}^g/\Lambda$  for some  $g$ -dimensional lattice  $\Lambda$ . By definition, if the period matrix  $\Omega$  satisfies Riemann's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

**Interpretation for PFC.** Each  $z_j$  represents a phase in one working memory buffer. Coupling among buffers is recorded in  $\Omega$ . Viewed this way, prefrontal working memory becomes a torus-like structure: large-scale recurrent loops track 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, 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. In fact, almost all will fail. For the PFC to be able to project (or linearly map in any way) to the entorhinal grid code it must have a certain degree of hexagonal structure built in within phase space. To achieve the  $60^\circ$  symmetry observed in entorhinal cells, we impose a *ring* structure on the subset of prefrontal cyclic buffers that project most directly to MEC (i.e. vmPFC [Doeller *et al.*, 2010]) via the Eisenstein integers,  $\mathbb{Z}[\omega]$ , where

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

In reality, this doesn't need to be "wired in", as recurrent relations with entorhinal grid mechanisms should create resonance patterns that help enforce the symmetry in phase space.

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

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

This projection maps the high-dimensional lattice from the PFC phase space to a 2d subspace, producing a hexagonal grid pattern. The hexagonal structure built into the phase space allows us to project to a hexagonal lattice. The projection  $\phi$  could be modelled a feed-forward layer in a neural network, but that is a simplification. I would prefer a mechanism based on [Bush and Burgess 2014], with the VCOs swapped out for prefrontal cyclic buffers.

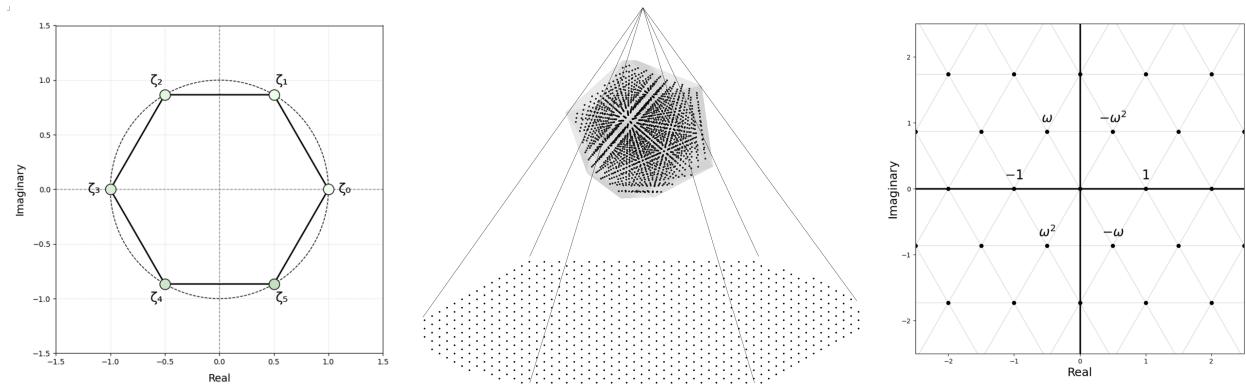


FIGURE 2. Sketch: If PFC cyclic buffers have a hexagonal structure in phase space (left) then a projection from the high-dimensional lattice can linearly map onto a 2D hexagonal lattice (center), which is isomorphic to  $\mathbb{Z}[\omega]$  (right).

**Prediction 1: PFC buffers most coupled with MEC exhibit  $60^\circ$  phase offsets.** If certain PFC buffers strictly follow  $\mathbb{Z}[\omega]$ -symmetry, then pairwise phase differences should cluster around multiples of  $60^\circ$  (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.** Alongside MEC and vmPFC [Doeller *et al.* 2010] reported hexadirectional firing in additional regions: 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  $60^\circ$  modulation pattern.

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.

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

I had a section on the theta function here but I removed it because it was a mess. I need help from Miguel and Elke. Instead I just speak informally.

Figure 3 shows a theta function with very suggestively chosen parameters. A theta function 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 was then a neat extension of theta functions [Weil 1964] that shows this in Fourier dual terms. In Weil's formulation, you implicitly have co-ordinates in a dual space. A direct space, and the 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) acts as the bridge that formally links to two domains, and localises position within phase space. The coup for us, will be to use MEC to bridge local HPC representations and global PFC representations in a manner that implicitly accounts for theta oscillations. This will need real modelling though, so can be skipped for the poster.

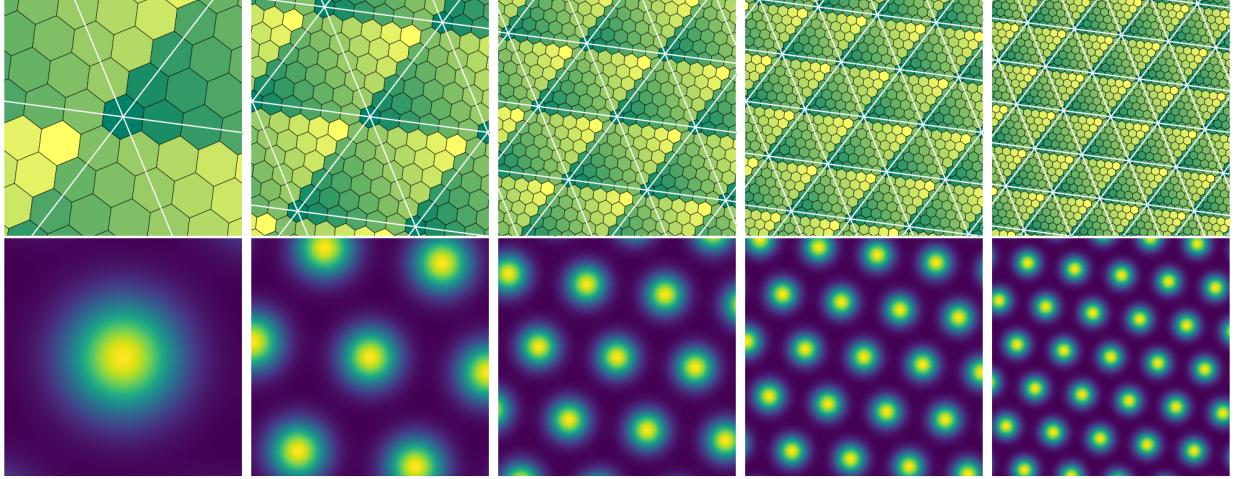


FIGURE 3. Ideal grid code from a theta function with shifts and harmonic scaling. Each cell represents a distinct coset. It is realistic to be able to get a properly justified construction of this by May. This bridges the high-level theory in the first sections with the realistic grid cells in the next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

**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.

#### 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  $60^\circ$  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; Gardner *et al.* 2022 (Figure 5)].

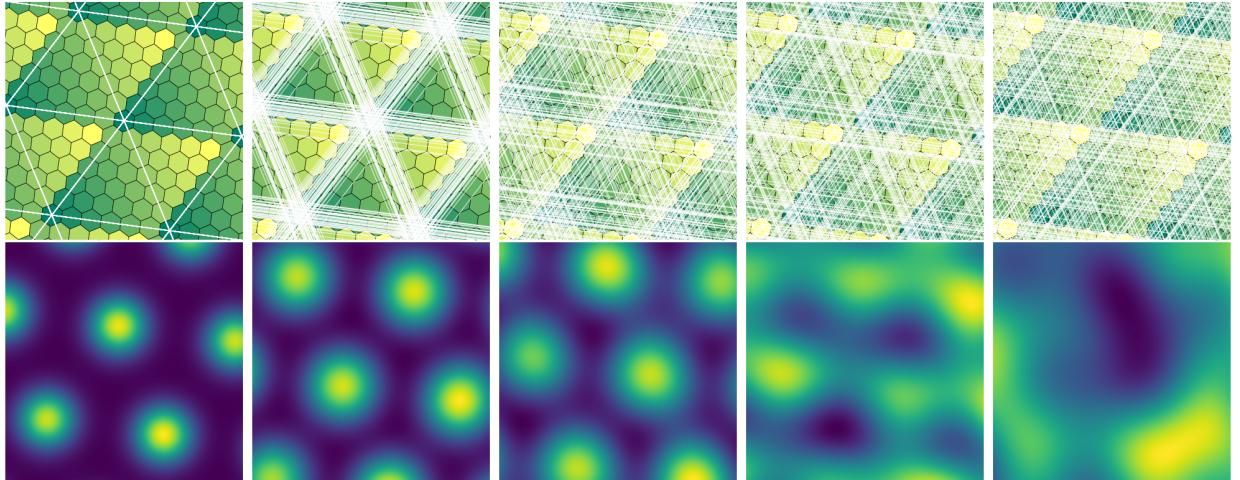


FIGURE 4. Decreasing grid coherence (left to right) in the linear projection model. Each panel increases the noise level  $\sigma$  in Eq. (4), blurring the perfect hexagonal structure. The white lines show where the lattice basis vectors fall.

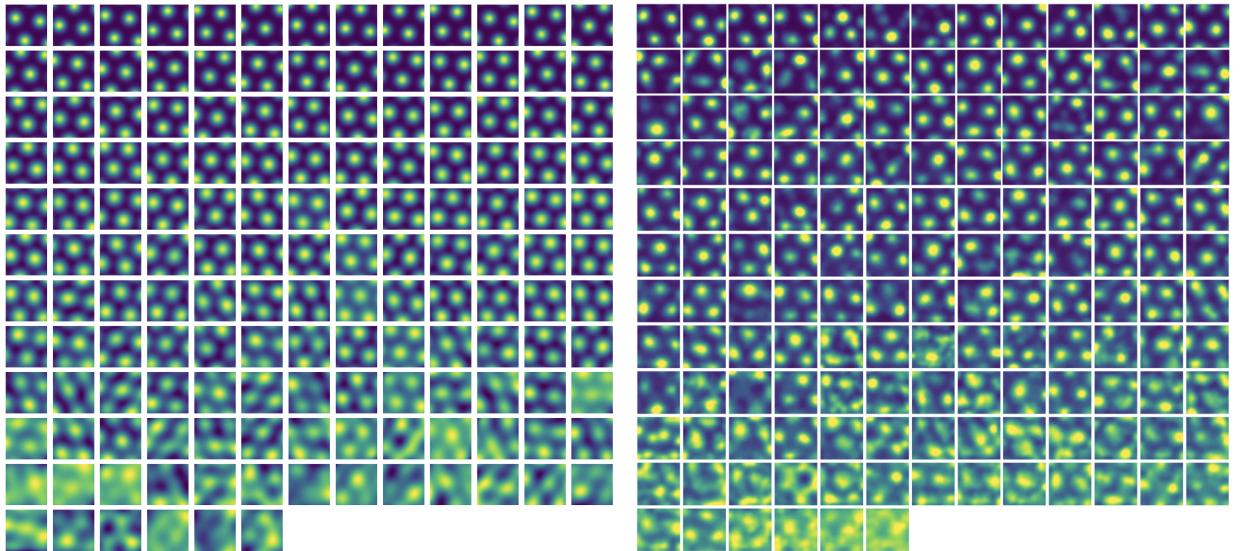


FIGURE 5. A comparison of decreasing grid coherence in our model (left) vs. experimental recordings (right) from Gardner *et al.* (2022). The progressive loss of regular grid structure is qualitatively captured by increasing noise in Eq. (4). This already looks pretty convincing, but I still need to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

**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:

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. incorrect signalling). This in turn would decrease local coherence, and the system would fall back into stable resonances at lower frequencies (coarser grids). Mathematically this reflects integrating over more global, PFC-based information. During this period you expect to see more MEC-PFC phase coupling in low-theta, and wider grid representations for a time. Then after time, as you learn the fine structure back, the grid will settle into a new set of stable attractors. This is a theoretical justification of the grid re-scaling under novelty effect [Barry *et al.*, 2012].

## SUMMARY AND NEXT STEPS

**Summary.** We have tried to show 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 allows us to go from abstract theory to an actual computational model.
- (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, or how we approach that) 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 will force MEC-PFC into these precise conditions naturally. Hexagonal grids are far from superfluous, but they are certainly inevitable. The aim is to generate additional, precise, testable predictions and to find more structure 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 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.

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