THE ENTORHINAL GRID CODE ENCODES LOCATION IN PREFRONTAL TASK SPACE

Abstract. Intelligent agents build rich internal models of their environment for spatial navigation and to perform more abstract tasks. These 'cognitive maps' rely on a network of brain regions including medial prefrontal cortex (mPFC), hippocampus (HPC), and medial entorhinal cortex (MEC). Neurons in mPFC are arranged into cyclic 'memory buffers' that encode progress towards specific behavioural goals. Meanwhile, MEC 'grid cells' exhibit a periodic array of spatial firing fields that cover all environments. Importantly, recent studies have shown that grid firing patterns can also map abstract task dimensions. However, the relationship between grid cells and memory buffers, and how they interact to support flexible behaviour, is not yet clear.

Here, we propose that mPFC representations form a high-dimensional torus $\mathbb{C}^g/\Lambda$, where Λ is a lattice defined by the period matrix Ω that encodes interactions between different cyclic buffers. Behavioural states are points z on this torus, with location in the prefrontal phase space defined by the Riemann theta function $\Theta(z, \Omega)$. This high-dimensional representation projects onto MEC, generating a scalar wave field that closely resembles grid firing patterns. Importantly, this bilinear form integrates global task information from mPFC with local spatial features from HPC. The resulting MEC grid code enables vector navigation in prefrontal task space while respecting local environmental structure. This model accounts for several known properties of grid cells, including why grids do not form perfect hexagonal lattices, and how spatial distortions in the grid-cde reflect local environmental geometry In this model, we propose that the brain uses a unified computational framework to accomplish both physical navigation and abstract reasoning.

Introduction & Motivation

These notes to cover how I envision each section in the poster, and give extra information:

(1) Introduction
(2) Prefrontal Phase Space in Fourier Theoeretic Terms
(3) The Riemann Theta Function
(4) The τ-function as a naturalistic model of the Grid Code
(5) Using Mapper to decode Task structure From Prefrontal Phase Space
(6) Next steps: Formally linking mPFC phase space with the MEC grid code - ($\sim$*1 year*)
(7) Ending: Sketches of three extra sections for a paper but not the poster.

1. Introduction

While it has long been known that HPC/MEC encodes spatial structure [O'Keefe and Dostrovsky, 1971; Hafting *et al.*, 2005], it has recently been shown that the prefrontal cortex, and mPFC more specifically, encodes more abstract task structures [El-Gaby *et al.*, 2024]. We think it's very likely that these two sets of represions are connected, and they work together to form a cognitive map [Behrens *et al.*, 2018] that allows mammals and other intelligent agents to egnage in flexible behaviour in a complex world. Recent computational models have started to show how the mPFC task code and hippocampal place code may relate ("A Tale of Two Algorithms" [Whittington *et al.*, 2024]). In this poster, we make the claim that the MEC has a central role in how the mPFC task phase code relates to the hippocampal place code. This allows the MEC to perform vector navigation in prefrontal task space; a structured navigation between two states: $\phi : \xi \to \xi'$.

2. Prefrontal Phase Space in Fourier Theoeretic Terms

We show how mPFC cyclic buffers [El-Gaby *et al.*, 2024] can be seen in Forier theoretic terms. We show that cyclces and tasks are interconnected; this leads to a representation of task space in terms of a complex set of interconnected loops. Formally, this system of interconnected task-loops can be modelled by a period matrix Ω. This forms a high-dimension torus that algebraciy represents mPFC task space. More formally, we might instead call this mPFC *phase* space, as we expect it is not just tasks being tracked, but the dynamics of the world. The full set of these dynamics forms a predictive model of the world; they tell you how you expect the world to change over time, and what actions can direct the future state of the world during intelligent behaviour.

Formally: The prefrontal cortex (PFC) maintains several cyclic (or ring) buffers [El-Gaby et al. 2024]. We can model each cyclic buffer as tracking a phase variable $z_j \in \mathbb{C}$ on a circle. 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,

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

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 (ω) 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 abstract phase space you navigate through life. The space of all tasks and cycles (ω) you track, and how they relate.

Identifying points in $\mathbb{C}^g$ modulo this lattice Λ yields a g-dimensional *complex torus*, (see Fig. 1 and Fig. 2). In simple terms, you are always at some vector (z - see Fig. 2 or §3) in the phase space $\mathbb{C}^g/\Lambda$, as identified by the set of active phase cells across all mPFC buffers.

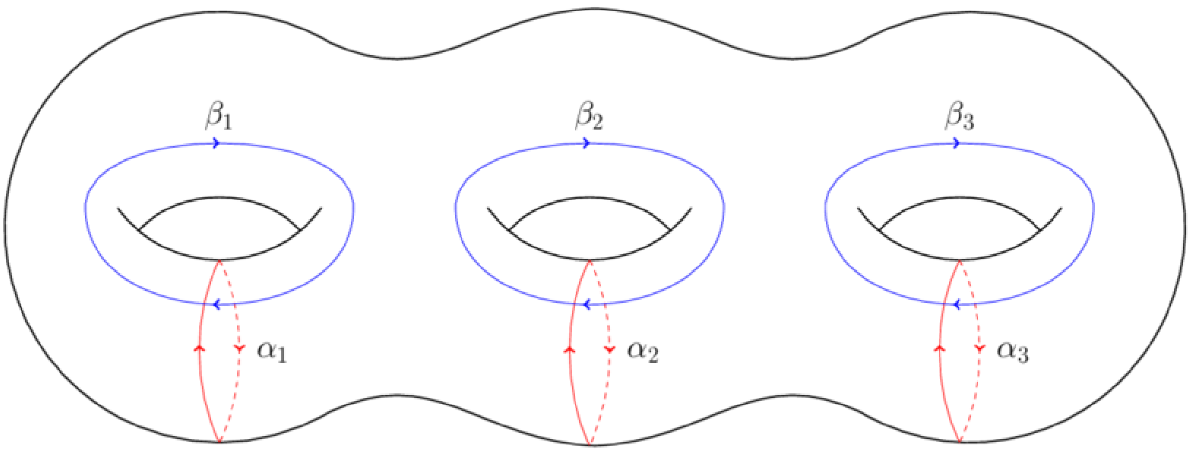

Figure 1. Formally, this big set of loops (when modelled on the complex plane) forms a *Riemann Surface*. One way you can understand it is a 2d sheet with g holes. the number of holes in the Riemann Surface we call the *genus (g)*. This is how mathematicians draw this g-dimensional torus that we have introduced as a model for the set of internconnected loops that form the mPFC phase space. Don't worry, it gets easier from here, this is the formality.

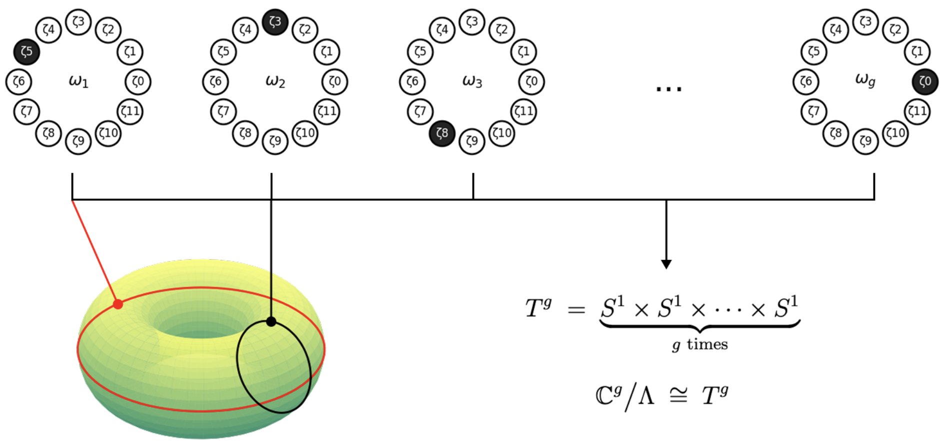

FIGURE 2. The Cartesian product of g circles (each representing an mPFC cyclic buffer) forms a g-dimensional complex torus T^g, which is isomorphic to $\mathbb{C}^g/\Lambda$ for some g-dimensional lattice (Λ). A torus is probably an idealisation of the actual biological reality, but you get the idea of a big inter-connected space of loops defined by the period matrix (Ω). Different mPFC buffers relate to each other structurally in time (e.g. they are not linearly-independent), and their differential forms define a smooth Riemann surface (see Fig. 1).

Projection from mPFC to MEC. While this remains semi-informal at this stage (the full details need real maths to be doe justice). The central thrust of this poster is that a high-dimensional structre in mPFC is projected down to a set of lower dimensional representations in MEC. This mirrors dimensionality reductions ideas from previous papers [Dorderk *et al.*, 2016; Stachenfeld *et al.*, 2017]. However, in our case, we identify mPFC as the source of the high-dimensional representation; of course, the high-dimensional representation likely exists in a distributed form across all of PFC-MEC-HPC. To quote Alan Turing: “This model will be a simplification and an idealization, and consequently a falsification.” [Turing, 1952].

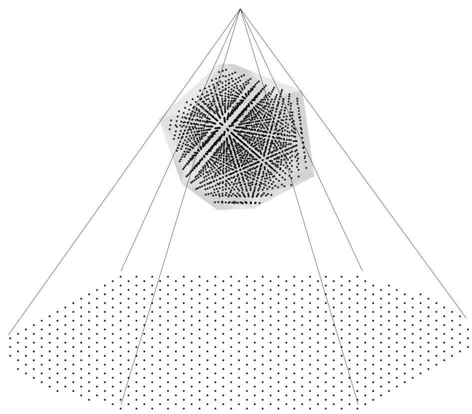

FIGURE 3. Sketch: mPFC cyclic buffers form a topological structure defined by a high-dimensional lattice (Λ) in prefrontal phase space. A projection maps mPFC onto a lower-dimension lattice in MEC. thes projections blends task-space information from mPFC with the geomery of the local spatial environment from HPC. [see Fig. 5]. The MEC mediates between HPC and PFC. This is our extension of ”A Tale of Two Algorithms” [Whttington *et al.*, 2024].

3. The Riemann Theta Function

Location in this high-dimension mPFC phase space can naturally be localised by the Riemann theta function $\Theta(z|\Omega)$. We keep the maths here light, but we note the centrality of the Riemann theta function in modern mathematics. In essence, the Riemann theta function $\Theta(z|\Omega)$ allows us to localise position (z) in the prefrontal phase space structured by (Ω). The period matrix Ω defines a big space of loops (a high-dimensional torus), and it is the *topology* of this space of loops that we will ultimately use to connect MEC to PFC in terms that allow us to make experimental predictions and falsify this theory. The end goal is to show how the structured system (Ω) allows you to use the MEC to vector navigate in the mPFC phase space. MEC tracks where you are *locally* in the big space of mPFC loops in a way that the respects the physical geometry of your local environment from HPC: (see: §4).

Formally linking the cognitive map to the Riemann theta function would be a *highly* significant step in linking modern neuroscience with modern pure mathematcs. If true: *it is hard to over-state how big this could be.* It opens up a wide range of possible collaborations between the two fields, and could be very exciting direction in modern mathematics/science.

4. The τ-function as a naturalistic model of the Grid Code

While the the Riemann theta function itself is highly-structured, it is formally related to the τ-function, which takes the structred period matrix (Ω) and includes the non-linearities that we naturally expect in a representation of the world. The τ-function provides a direct solution to shallow water waves; using this fact, we can easily model where grid cells form in complex environments: just fill the room with water! We discuss coherence effects [Fig. 5; Fig. 6] and provide 3d Renders of the grid code: (https://webgpu.aufbau.io/experience/gridcode/) - which provides a model of the grid code using the τ-function. Lots of nice 3D graphics...

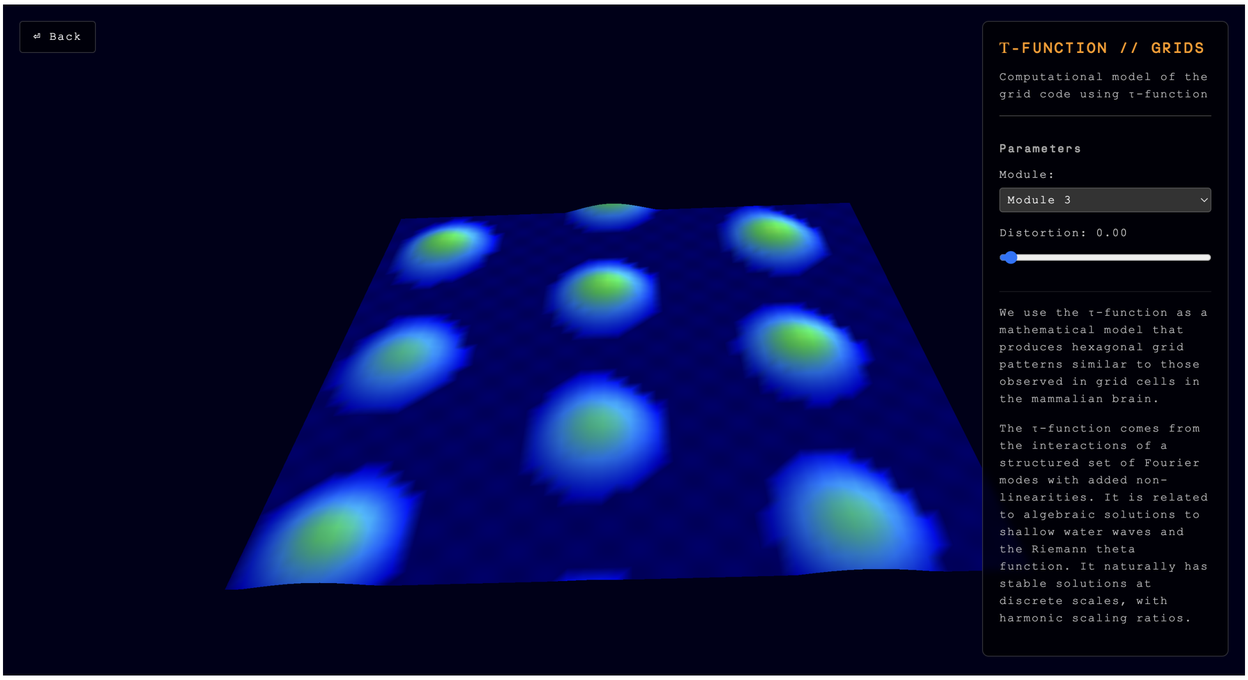

Figure 4. I only finished the tool late last night before writing this, check it out for yourself. I think it can generate a lot of neat 3D graphics. While it still needs some tweaking, it nicely captures quite organic looking grid cells?

The τ-function forms the basis of linking tht topological phase-spaace information in mPFC with the local representations in MEC. Working out what exactly is happening here is non-trivial (see §6), but we expect individual grid cells to be encoding local aspects of the mPFC topology, such that the full grid code can be used to navigate the mPFC phase space in a way that respects the geometry of your local environment: **Prefrontal Vector Navigation**.

Below are a couple figures (we can maybe remove them) that explore related aspects. [Fig. 5] captures an idea of how we can use shallow water waves (and thus the τ-function) to model how the grid code fills complex environments. [Fig. 6] shows how adding an incoherence metric (adding noise in the wave equation) captures actual experimental data fairly well.

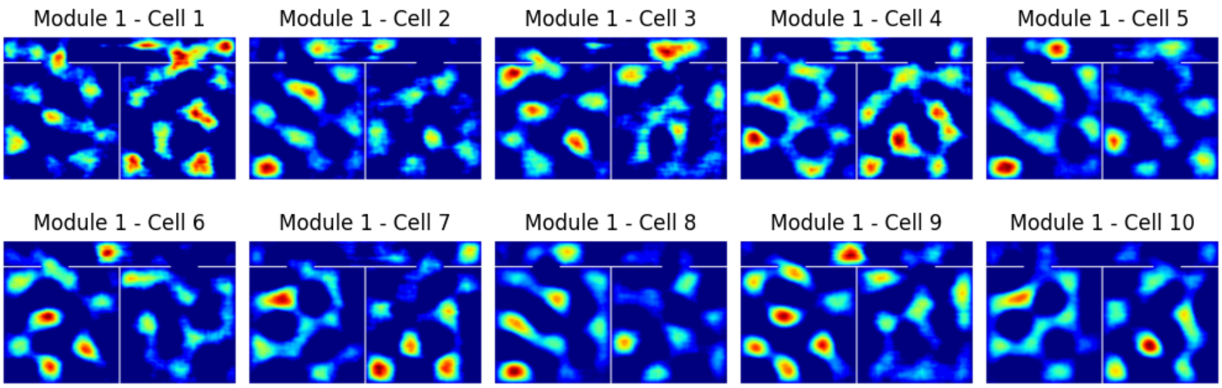

FIGURE 5. While I need to improve the rendering here (eg. this is not hexagonal or structured enough as the ones above), the τ-function produces a scalar wave field that naturally mirrors how grid cells tile complex environments. Crucially, it does so in a way that produces phase offset grids, which other current methods [Dordek *et al.*, 2016; Stachenfekd *et al.*, 2017] do not. It is still *Laplacians* under the hood, but the Fourier wave system add a fluid/dynamic edge that tiles the space and more *heuristically* matches the MEC grid code.

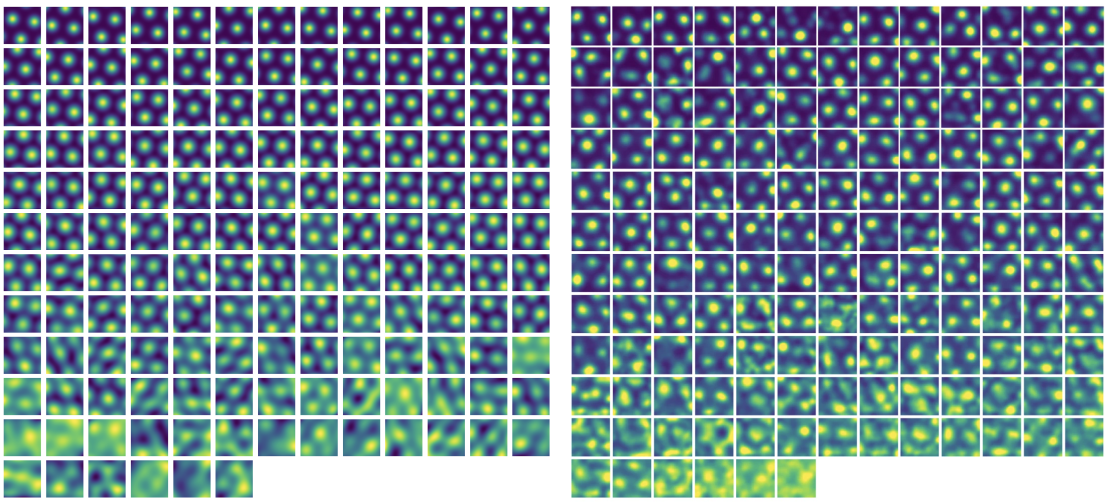

FIGURE 6. A comparison of decreasing grid coherence in our model (left) vs. experimental recordings (right) from Gardner *et al.* (2022). It already looks good, but I still need to order my cells by spatial information as the Mosers did, and capture the non-linearities a little better. Maybe we can ditch this figure, it tells a story that confuses 'Prefrontal Vector Navigation'? It is a nice figure of a *noisy/incoherent* projection from PFC to MEC in any case.

5. Using Mapper to decode Task structure From Prefrontal Phase Space

There is a growing branch of applied mathematics (starting somewhere in the early 2000s) called 'Topological Data Analysis' (TDA). TDA is behind recent papers such as the Toroidal grid cell paper [Gardner *et al.*, 2022]. We use an algorithm from TDA (Mapper [Singh *et al.*, 2007]) that allows us to decode a graph of prefrontal task-space structure from neural data. Mapper looks for cycles, and builds a graph (a *Reeb graph*) that captures the set of loops in the data. The Reeb graph encodes the topology of the dataset that Mapper was given. We ran Mapper on the data from El-Gaby *et al.* (2024) and found some very simple cyclical topology. This was somewhat expected, as the animals were given very simple cyclic tasks.

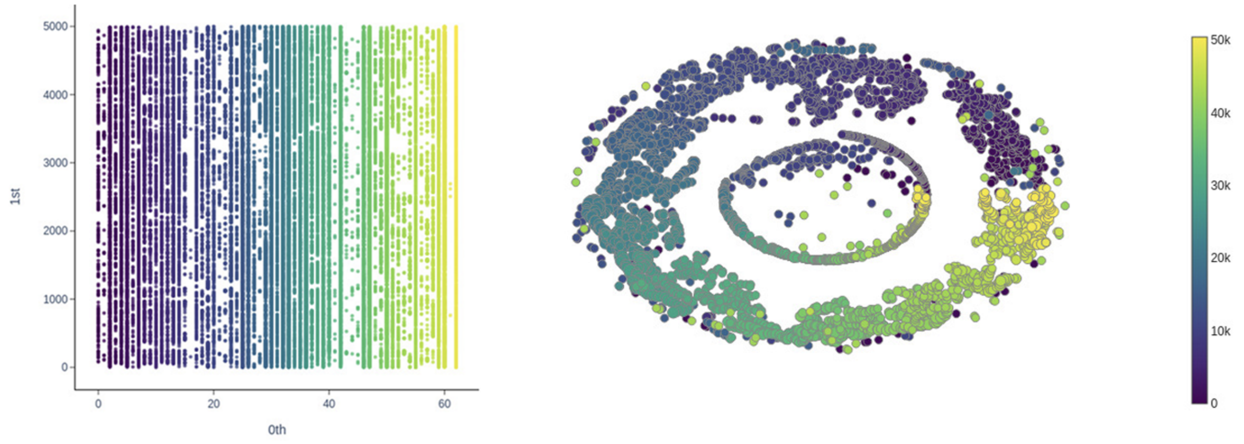

Figure 7. On the left we have spikes from the actual mPFC data in EL-Gaby *et al.* (2024) We ran Mapper on this data and found two cycles. This is natural, as the mice had two cyclical tasks to do. I left Miguel to do this by himself, so he only did some rough preliminary analysis. Once working out the experimental data from myself a bit better, I expect we can produce something cooler. Especially looking at the global structure of mPFC space.

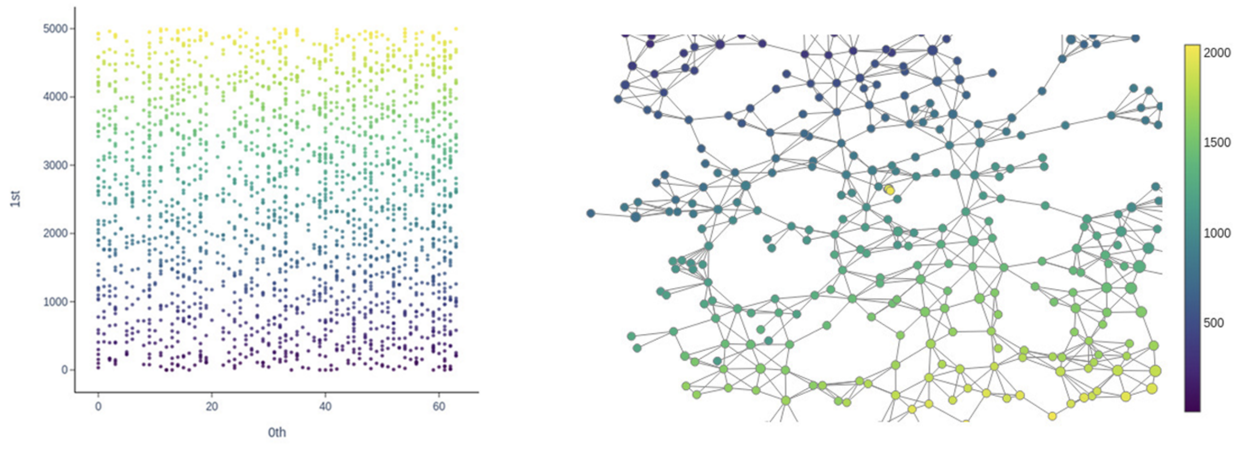

Figure 8. We then generated data from a (*made-up*) more abstract task space. Running mapper on this data allowed us to deconstruct the topology of this task space. Given a suitable experimental setup, this should allow us to decode task-space/phase-space strucre from future mPFC experiments with more complex task structures. This forms an experimental basis for decoding topological information from mPFC. These methods give experimentalists tools for getting data about the topology of the task-spaces stored in mPFC.

6. Next steps: Formally linking mPFC phase space with the MEC grid code

This is the crux of the paper and it ultimately comes down to 'do we publish this now to get feedback', or 'do we wait until we have a more complete model'. The local representations in MEC (from the τ-function) derive from the Rieman Theta Function $\Theta(z|\Omega)$ that localises positon in a big space of loops structured by the period matrix (Ω) in mPFC. We have described more of a theoretical bridge, based on MEC and PFC sharing the same topology - albeit a topology that is merged with local spatial data (HPC) to allow MEC vector navigation through mPFC task space that respects local environemntal structure. Our model complements "A Tale of Two Algorithms" [Whittington *et al.*, 2024], while aiming to extend this framework by showing the centrality of MEC in the link between PFC-HPC. The model presented here presents a novel view of the mathematics behind cognitive maps.

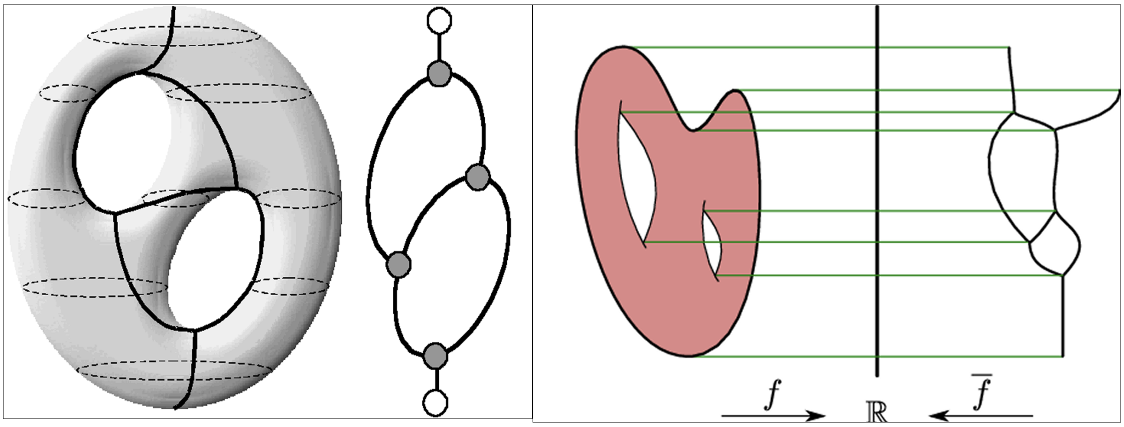

Figure 9. Sketch: The Reeb graphs of PFC phase space stucture generated by Mapper can be seen as compactifications of the Riemann surfaces that we suggest are behind the MEC representations. This is the shared algebraic structure that we suggests lies at the heart - or the mathematics - of cognitive maps. By MEC and PFC sharing this underlying algebraic structure, the entorhinal grid code can encode location in prefrontal task space, allowing vector navigation through abstract spaces while respecting local environments.

If representations in MEC/mPFC are actually related, we should be able to make experimental predictions, e.g. co-recording mPFC data and MEC data in less trivial spatial and environmental setups and comparing the topological information decoded from either set of representations. If the two systems are connected, there should be some decent form of overlap in the topological information decoded here. Acutually working out methods for doing this isn't that trivial, and is probably ~ 1 years worth of work. Luckily, the maths we are working with *excites* mathematicians at the MPIs in Leipzig/Dresden, so getting help on the more complex parts - and then making them 'simple' - should be fairly straightforward.

I think that getting feedback in the conference at this midpoint is useful. I think the chance of getting scooped is pretty low. But ultimately this is your choice and I trust your instinct. In this doc, I worrry I have too many angles, so it may be on you to help me narrow it down.

7. Grid Expansion under Uncertainty and Fourier Dual Represemtations

I have so far totally skipped the 'grid expansion under uncertainty' angle [Barry *et al.* 2012]. The Riemann theta function explains the funtional role of this expansion perfectly, but this angle should probably be ditched from the poster and just be kept for the paper; in brief:

There is a neat extension of the theta function [Weil 1964] that rephrases it 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 (HPC) and global phase information (PFC) at the same time. The MEC (or the theta function) acts as the bridge that formally links the two domains and localises position in the Fourier-dual phase space: the *cognitive map*. The theta function integrates local information with respect to global symmetries structured via a lattice. The scale of the lattice dictactes which domain you are integrating over: a finer lattice integrates local information in direct space, a coarser lattice integrates global information in the dual space.

[Informal]: While we expect grid expansion to relate to basic Hebbian mechanisms (i.e. when the MEC model fails to agree with HPC data, the grid coherence decreases and the grid code falls into a stable set of attractors with a coarser grid.). In a formal equivalance (e.g using Marr's levels, where different levels explain different aspects of neural computation), then during uncertainty, a coarser lattice means you integrate more over the global information stored in mPFC than the local information in HPC. I anticipate this would correlate with an increase in low-theta band phase coupling between MEC-PFC during these periods of uncertainty. It would be interesting to look at the data, I have no time, maybe a student?

In effect, during uncertainty you resort to big picture narratives (mPFC global model) to work out "what the hell is going on", then once you've figured this out, the grid code naturally becomes finer, and you start focussing on local details again (HPC local information).

8. Optimal Coding in the MEC Grid Code

Finally, I think a paper topic but certianly not a poster one. This mathematics (theta functions etc.) underlies modular coding systems, primes, and all the things you need to produce optimal compression mechanisms. If we want the MEC grid code to perform modular coding [Fiete *et al.*, 2008] and error-correcting coding [Fiete *et al.*, 2011] and all this jazz, it's the maths you would use if you were designing the perfect agent [Paley, 1802].

9. Final Note on this not being a mechanistic model

This is purely a formal model. I fear including too much mechanism would push it past a point of complexity that it is already pushing. mPFC cyclic buffers can happily play the role of VCOs, and we can suggest using a framework that fits this and CANs, so as not to ruffle any feathers [Bush and Burgess, 2014]. Neil also told me to check out his paper "Controlling Phase Noise in Oscillatory Interference Models of Grid Cell Firing" [Burgess and Burgess, 2013] but I don't know how much to think about mechanics. Ideally, we keep any mechanics as impartial as possible, so as not to ruffle feathers - or at least try our best.

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