

# Geometric Manifolds in Neural Circuits: Toroidal Dynamics, Hopf Fibrations, and Attention

## Ring and Torus Attractors in Spatial Navigation Circuits

**Head-Direction Cells – A 1D Ring Manifold:** Rodent head-direction (HD) cells provide a canonical example of a one-dimensional continuous attractor. Each HD neuron fires maximally when the animal's head faces a specific direction, and collectively the population maintains a persistent representation of heading even without visual cues. Theoretical models long hypothesized that HD networks form a ring attractor – neurons arranged in a loop where activity settles into a “bump” that can rotate around the circle as the animal turns [1](#) [2](#). Empirical evidence confirms this ring topology. **Ila Fiete** and colleagues showed that the space of joint activity of thalamic HD cells is confined to a continuous **one-dimensional ring**, i.e. the population states lie on a circle [3](#). Position along this ring directly corresponds to the animal's heading angle [3](#). In other words, the network's activity vector moves around a circular manifold as the animal's head rotates, providing a durable compass-like signal.

**Grid Cells – A 2D Toroidal Manifold:** Grid cells in the medial entorhinal cortex encode the animal's position in physical space via a periodic firing grid. Each grid cell fires at multiple locations that form a hexagonal lattice covering an environment. Early models posited that a **two-dimensional continuous attractor** network could produce this repeating pattern, effectively by “gluing” the planar sheet of neuronal positions into a torus so that activity patterns repeat seamlessly across space [4](#) [5](#). This predicts that the collective activity of a grid cell module should reside on a toroidal manifold (topologically equivalent to a donut). Recent large-scale recordings have spectacularly confirmed this. By simultaneously recording hundreds of grid cells and applying nonlinear dimensionality reduction and topological analysis, **Gardner et al. (2022)** demonstrated that the **population activity indeed lies on a torus** [6](#). When plotted in the discovered low-dimensional space, the neural activity forms a hollow doughnut shape [7](#). Positions on this torus correspond to the animal's location in the 2D environment [6](#). Intuitively, one ring of the torus represents the encoded position along the environment's x-axis and the other ring represents the y-axis; because each cell's firing is spatially periodic, the network naturally wraps these variables into a torus [8](#). This toroidal code was stable across different environments and even during sleep, implying it is an intrinsic property of the grid network's recurrent connectivity [9](#) [10](#). These results visualize the continuous attractor (CAN) dynamics long theorized for grid cells, providing “the first population-level visualization” of a neural torus attractor [11](#).

**Continuous Attractor Network Theory:** The ring and torus manifolds observed in HD and grid cells are hallmarks of continuous attractor networks. In such networks, recurrent synaptic connectivity is arranged so that activity states form a low-dimensional continuous manifold of possible steady states [2](#). A classic model is the “bump attractor,” where neurons with similar tuning (e.g. nearby preferred directions or positions) excite each other, supporting a localized bump of activity, while distant neurons inhibit each other [5](#). In HD networks this yields a circular bump (one preferred direction per neuron around a ring) [5](#), and in grid networks a bump on a toroidal sheet [5](#). The bump's location can move smoothly when driven by external motion cues (vestibular input, self-motion) or persist in one location without sensory input –

thereby storing the current value of the encoded variable (direction or position)<sup>12</sup>. Early computational papers laid the groundwork for this idea. For example, *Zhang (1996)* and *Redish et al. (1996)* modeled the rodent head-direction system as a ring attractor with symmetric connectivity<sup>13</sup>. Similarly, *Fuhs & Touretzky (2006)* proposed a 2D attractor (“spin glass” model) for grid cells that required a toroidal topology to account for the periodic firing fields<sup>14</sup>. The experimental demonstrations of ring and torus manifolds in neural data<sup>15</sup><sup>6</sup> have vindicated these predictions, confirming that the brain can indeed instantiate the continuous attractor geometries theorists envisioned.

## Neural Population Manifolds and High-Dimensional Geometry

The ring and torus are relatively “simple” manifolds, reflecting the encoding of one or two periodic variables. More complex behaviors and brain regions may exhibit higher-dimensional or less regular manifolds. For instance, **hippocampal populations** involved in memory-guided navigation can form a low-dimensional but non-intuitive manifold. In a virtual navigation task with alternating decision epochs, **Nieh et al. (2021)** found hippocampal neural activity was confined to an approximately four-dimensional curved surface<sup>16</sup><sup>17</sup>. The geometry of this manifold was not a clean torus or sphere, yet movement along different axes of the manifold corresponded to different task-relevant variables (the animal’s spatial position, evidence accumulation, past choices, etc.)<sup>18</sup><sup>19</sup>. This demonstrates that even without a neat geometric shape, a constrained low-dimensional population manifold can embed multiple cognitive variables. Such findings underscore that continuous attractor dynamics generalize beyond simple spatial maps – they may underlie internal cognitive spaces, albeit with higher complexity.

**Toroidal vs. Complex Manifolds:** The elegant torus of grid cells appears to be a special case of a highly ordered neural map. In more complex or high-dimensional cognitive representations, the manifolds might lack obvious geometric analogues. For example, the hippocampal 4D manifold did not lend itself to a straightforward shape like a torus<sup>17</sup>. Topological analyses in these cases might still detect abstract features (numbers of holes, connected components), but a clear visualization (like a torus) is harder to obtain<sup>17</sup><sup>20</sup>. Researchers speculate that higher-dimensional manifolds might be composed of multiple lower-dimensional components – e.g. “**conjoined tori**” or other modular structures<sup>21</sup><sup>22</sup>. Supporting this, adding a task variable in the Tank/Brody navigation experiment increased the manifold’s dimensionality by one, hinting that each new dimension might stack onto the existing structure in a modular way<sup>23</sup>. This raises the intriguing possibility that even complex neural manifolds could be understood as combinations of simpler geometric “building blocks.”

**3D and Hopf-Fibration Structures:** An open question is how the brain represents *three-dimensional* variables, which have more complicated topology. Consider an animal that can pitch and roll as well as yaw – its head orientation spans the full 3D rotation group (essentially requiring a sphere or 3-torus representation). One mathematical construct for parametrizing 3D orientations is the **Hopf fibration**, in which a 3-sphere ( $S^3$ ) is mapped onto a 2-sphere ( $S^2$ ) with circles ( $S^1$ ) as fibers. In principle, a neural attractor for 3D head direction could take the form of an  $S^2$  or  $S^3$  manifold (with, say, one circle of activity for yaw and another for pitch/roll). Real neural systems seem to approximate this in pieces: in bats, for example, cells in the presubiculum transition from classic 2D head-direction tuning to mixed 3D tuning along a gradient<sup>24</sup>. And entorhinal “**3D grid cells**” in flying bats were found to maintain only *local* lattice order without a global 3D grid structure<sup>25</sup>, suggesting the brain may not form a single elegant 3D attractor akin to the 2D torus. It remains an active area of research whether the brain can realize exotic topologies like  $S^3$ ; if it does, it might employ a Hopf bundle-like organization (multiple circular dimensions) to map our higher-dimensional movements or orientations. Notably, even eye movement control obeys

geometric constraints related to quaternions/Hopf maps (Listing's law)<sup>26</sup>, hinting that neural circuitry can respect these advanced geometric structures in practice.

## Bridging Physics and Neuroscience: Holography and Spin Networks

The discovery of toroidal manifolds and other geometric structures in neural activity has inspired analogies to theoretical physics. One compelling metaphor is drawn from the **holographic principle** (the idea that a higher-dimensional “bulk” system can be encoded on a lower-dimensional boundary). In the brain, one might imagine that a high-dimensional cognitive process (a “bulk” of neural states) is represented or constrained by lower-dimensional structures (a “boundary,” such as a cortical sheet or attractor manifold). Some theoretical work on consciousness has even invoked **holographic duality** explicitly, proposing that mental states might relate via a dual representation in a physically inspired lower-dimensional space<sup>27</sup>. While highly speculative, such boundary-bulk thinking provides a novel perspective: for example, the entorhinal grid network (a 2D sheet of neurons) could be seen as a “boundary” encoding the animal’s position in 2D space (the bulk), analogous to a hologram encoding volumetric information on a surface.

Another cross-disciplinary parallel is the concept of **spin networks** from loop quantum gravity (LQG). Spin networks, introduced by Penrose, are graphs whose nodes and links carry quantum numbers (“spins”) that define a discrete geometry of space<sup>28</sup>. They effectively quantize space into units (each link or node corresponds to a chunk of volume or area)<sup>28</sup>. In a fanciful analogy, one could view a neural network as a kind of “cognitive spin network” – each neuron (or ensemble of neurons) might represent a basic unit of a mental map, and synapses (connections) define adjacencies or relationships, somewhat like links in a spin network defining adjacency of space quanta. Just as spin networks produce a combinatorial skeleton of space itself<sup>29</sup>, neural networks produce a discrete scaffold that underlies our internal representations of continuous variables. Of course, neurons are far more complex than Planck-scale spins, and brain networks are not literally quantum gravity models. The value of this analogy is mainly conceptual: it highlights how *structured networks* can give rise to an emergent geometry. In neuroscience, this emergent geometry is the manifold of neural activity (like the torus for grid cells)<sup>6</sup>, whereas in LQG the emergent entity is physical space. Both domains suggest that **connectivity constrains geometry** – whether it’s the fabric of spacetime or the layout of a cognitive map.

These physics analogies are a *bridging perspective* rather than established science. They are not central to daily empirical research, but they stimulate interdisciplinary dialogue. The idea that a brain region could act as a “holographic screen” for higher cognitive variables, or that synaptic networks form something akin to a discretized space, can inspire new ways of thinking about neural coding. For instance, one might ask if there are “bulk” variables (like abstract goals or context) that are represented in a lower-dimensional subspace of activity (perhaps on the cortex’s surface) – echoing a holographic mapping. Or whether the brain employs combinatorial connectivity motifs that mirror topological invariants (like how spin-network nodes define holes or loops). While such comparisons are speculative, they underscore an exciting convergence: **the brain may be understood using tools of geometry and topology**, much as modern physics seeks deep geometric descriptions of nature.

## Attention on Neural Manifolds: Gain, Phase, and Dynamic Selection

Given that neural representations often live on manifolds (rings, tori, etc.), how might **attention** operate on these structures? Attention – the brain's mechanism for selectively enhancing certain signals or features – could modulate the underlying attractor manifold in several ways:

- **Gain Modulation and Bump Shape:** One effect of attention is to change the gain (excitability) of neurons, which in an attractor network alters the profile of the activity bump. Computational models of visual attention using continuous attractors show that a stronger recurrent gain or more sharply peaked neural response can **narrow the bump of activity**, focusing resources on a smaller region of the manifold <sup>30</sup>. For example, a model of divided visual attention represented multiple target locations as two “bubbles” of activity on a feature ring; increasing the output nonlinearity (steeper gain function) made each bubble more discrete and less spread out <sup>30</sup>. This corresponds to attention tightening the focus (higher precision at attended locations) at the expense of between-target activity. Conversely, a flatter gain (or more diffusive lateral interactions) lets the bump spread, corresponding to a broad or divided attentional focus <sup>31</sup>. Thus, by tuning neuronal gain, attention could **reshape the attractor landscape** – creating either a sharp, high peak for a single attended item or multiple smaller peaks for split attention.
- **Stabilizing Desired States:** Neuromodulators associated with attention (like acetylcholine and norepinephrine) are thought to adjust the stability of attractor states. ACh, for instance, can increase the recurrent drive in cortical networks and is linked to enhanced signal-to-noise during attention. Theoretical work suggests this promotes **stable attractor configurations** (e.g. a stable representational state corresponding to the attended target) that are resistant to distractions <sup>32</sup>. In an attractor framework, when attention is deployed, the network may settle more deeply into one basin of attraction (one spot on the ring/torus), so that competing inputs (distractors) cannot easily knock the activity bump away <sup>32</sup>. This aligns with observations that under attention, neurons tuned to the attended stimulus increase firing while others suppress firing <sup>33</sup> – effectively “choosing” one attractor bump to dominate. In contrast, inattention or diffuse neuromodulatory tone might leave the network in a more easily perturbed state where the bump can wander or split.
- **Phase and Oscillatory Gating:** Attention is also known to involve oscillatory dynamics – for example, aligning the phase of high-frequency oscillations (gamma) with task-relevant inputs, or modulating alpha/theta rhythms to gate information. On a neural manifold like the grid-cell torus, **oscillations can interact with the attractor state**. Recent analysis of grid cell data showed that the presence of theta-band oscillations is crucial for the **integrity of the toroidal manifold** <sup>34</sup> <sup>35</sup>. If spike timings were “jittered” to disrupt rhythmic timing, the torus structure in the population activity disappeared (even though individual cells still had hexagonal firing fields) <sup>36</sup>. This implies that coherent oscillatory modulation synchronizes the network's activity bump, knitting it into a topologically consistent torus. Attention could leverage this by resetting or aligning phases of oscillations to *selectively route* the bump movement. For instance, a top-down attention signal might phase-lock theta rhythms in a way that biases the grid attractor to a new position (as if internally “nudging” one's estimated location or focus). Likewise, inter-areal coherence (sometimes likened to communication through coherence) could allow a chosen portion of the manifold to be read out or updated preferentially. In short, attention might **steer the attractor** via oscillatory phase: much like a spotlight rotating around a stage, phase-aligned input can push the activity bump around the ring or torus to a desired location.

- **Selective Input Biasing:** Another straightforward mechanism is that attention provides a biased input to the network representing a guess or goal. In a head-direction ring, for example, a cue or internal desire to look a certain way could inject activity that pulls the bump toward that direction (like a weak force on the ring). In continuous attractor models, such “**endogenous**” inputs can re-center the bump at a new coordinate even without external movement <sup>37</sup> <sup>38</sup>. This is analogous to covert attention in space: one can mentally shift focus to a location without moving the eyes or body. Neurally, this might correspond to a bump of entorhinal/hippocampal activity shifting on the cognitive map of space purely by top-down influence. Indeed, during imagination or dream (REM sleep), grid cell ensembles sometimes replay trajectories – potentially reflecting the internal movement of the bump along the toroidal manifold without actual locomotion <sup>10</sup>. Attention could be the online, goal-directed version of this: a means to **dynamically reposition the active population state** along the manifold in accordance with task demands.

In summary, attention can be viewed as a control mechanism acting on neural manifolds. By modulating neural gain and coupling, it **reshapes the geometry** of population activity (sharpening or splitting bumps). By engaging neuromodulatory tone, it **stabilizes a particular attractor state** against perturbation, enforcing selective focus <sup>32</sup>. And through phase-aligned oscillations or biasing inputs, it can **move the network’s state** to highlight certain information (effectively moving the neural “cursor” on a ring or torus to the attended item). These operations illustrate how even abstract cognitive functions like attention may leverage the inherently geometric organization of neural circuits. The toroidal and other manifold representations are not static – they can be deformed and steered in real time, much as a pilot might adjust the heading of an aircraft on an internal compass (the HD ring) or a navigator might shift reference frames on a cognitive map (the grid torus). Understanding attention in this framework is an exciting frontier, requiring integration of neuroscience, dynamical systems, and even control theory to describe **how the brain selectively reads from and writes to its own geometric code**.

## Conclusion

Recent research highlights that neural population dynamics often inhabit **beautiful geometric manifolds** – from rings and tori in navigation circuits to more complex low-dimensional shapes in cognitive tasks. These structures validate decades of theoretical models (continuous attractor networks) and open new questions about brain organization. They also provide a natural language for cross-talk with physics and mathematics, inviting analogies to toroidal phase spaces, fiber bundles like the Hopf fibration, and even ideas from quantum gravity and holography. While such analogies are speculative, they underscore a unifying insight: **neural circuits instantiating a cognitive map are performing a kind of geometry**. The brain builds internal spaces (e.g. a torus for 2D position) and moves within them.

Crucially, the brain can *act* on these internal geometries through attention and neuromodulation – emphasizing that the manifolds are **functional, dynamic substrates** for thought and behavior, not merely epiphenomena. As experiments probe more complex behaviors (3D navigation, planning, abstract concept mapping), we may discover new manifold topologies and richer attentional control strategies operating on them. This interdisciplinary synthesis – rodents running on virtual tori, algebraic topology confirming neural holes, and analogies to holograms and spin networks – illustrates the depth of structure in neural population activity. It suggests that to truly understand higher brain function, we may need to chart both the “neural cartography” (the shapes of neural activity space) and the “neural geodesy” (how the brain flexibly traverses and warps those spaces through mechanisms like attention). Each new insight

strengthens the remarkable view of the brain as a **geometry engine**: one that creates and manipulates internal spaces to guide organisms through the external world. 6 7

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