

# Septal GABAergic Timing in Entorhinal-Hippocampal Retrieval

Gil Raites

## 1 Motivation and Gap

Memory updating in the hippocampal-entorhinal system preserves prior traces while changing retrieval access. Distinct engram populations can persist and compete, with accessibility shaped by context, inhibitory tone, and network state [100, 10, 2]. The central question is how one learned context-value association gains behavioral control during retrieval while another association remains accessible but unused.

The medial septum is positioned to regulate this selection process because septal GABAergic neurons organize hippocampal and entorhinal rhythmic state. Septal output supports theta-promoting circuit dynamics, state transitions between active processing and replay, and long-range timing control within the hippocampal formation [103]. Related work on hippocampal-entorhinal information-sharing networks shows that ensemble structure can reconfigure across temporal windows, providing a network-level substrate for switching between active computational states [80].

The unresolved transformation is how septal GABAergic timing input becomes a medial entorhinal output-timing signal that reorganizes downstream CA1 ensemble selection. The medial septum-to-medial entorhinal cortex pathway is implicated in oscillatory control, arousal-sensitive coordination, and behavioral switching, but a retrieval model needs the intermediate timing step. A circuit explanation must specify how medial entorhinal inhibitory microcircuits alter output timing and how that timing shift changes the CA1 ensemble state expressed during retrieval.

The primary circuit study motivates this gap by showing that inhibition of MS GABAergic terminals in MEC reverses updated behavior and shifts CA1 population activity back toward the pre-update pattern. The gap sits at timing-based retrieval selection after sequential learning in the same context. Memory enhancement, arousal, and locomotor facilitation become control alternatives rather than the core mechanism.

## 2 Background

The hippocampal-entorhinal circuit supports memory retrieval through sparse coding, inhibitory competition, and temporal coordination. In the dentate gyrus and CA3, inhibitory control contributes to pattern separation and winner-take-all dynamics, allowing similar inputs to activate distinct population states [45, 41]. In computational models, context-dependent gating and sparse hippocampal memory architectures reduce interference while preserving prior representations [2, 97].

At the CA1 output stage, firing rate is one readout of the active memory state, while temporal organization provides the selection-sensitive readout. Several retrieved references treat CA1 as a temporal and predictive structure in which spike timing, co-firing relationships, replay, and phase organization carry sequence and transition information [33, 50, 101]. If retrieval selection depends on which context-value association controls CA1 temporal ensemble structure, then disruption of the mechanism should be visible in timing relationships and

cross-correlated activity in addition to mean rate changes.

The medial entorhinal cortex provides a major route through which spatial and contextual information reaches CA1. The temporoammonic pathway supplies direct entorhinal input to distal CA1 dendrites, where local inhibition can regulate gain, delay sensitivity, and synchrony [24, 25]. Models of the entorhinal-hippocampal loop describe CA1 as a comparison and readout layer that balances internal hippocampal sequences with current entorhinal context [59, 50].

Medial entorhinal inhibitory populations form the transformation layer between septal input and CA1 output. Medial entorhinal cortex influences CA1 through direct temporoammonic input and indirect pathways via CA3, giving inhibitory timing multiple routes into CA1 ensemble structure. Parvalbumin-expressing interneurons and related inhibitory motifs constrain spike timing, support phase locking, and shape response distributions in recurrent circuits [51, 56, 57]. Septal GABAergic projections can therefore be treated as an upstream timing source, medial entorhinal inhibitory microcircuits as the local timing transformation, and CA1 temporal ensemble organization as the retrieval readout that drives behavior.

## 3 Research Goal and Hypothesis

The research goal is to explain how medial septum GABAergic input to medial entorhinal cortex alters CA1 temporal ensemble structure during retrieval after sequential learning in the same context. The analysis targets retrieval selection among preserved context-value associations. The behavioral problem is the expression of the later learned association when prior and updated associations remain expressible under different retrieval conditions.

The primary circuit study anchors the hypothesis by showing that inhibition of MS GABAergic terminals in MEC reverses updated behavior and shifts CA1 population activity back toward the pre-update pattern.

The central hypothesis is that medial septum GABAergic projections regulate retrieval by changing inhibitory microcircuit timing in medial entorhinal cortex. This local timing change is expected to alter the phase and precision of entorhinal output arriving in CA1. The resulting shift in input timing should reorganize CA1 ensemble structure so that the later learned context value is expressed during retrieval.

The hypothesis links three mechanisms in sequence. Hippocampal updating preserves competing traces, creating a retrieval-selection problem [100, 29, 97]. Inhibitory circuits regulate trace accessibility by adjusting thresholds, synchrony, and ensemble competition [41, 95, 86]. CA1 expresses the selected trace through temporal ensemble organization, with temporal predictive coding, successor-representation models, and phase-native coding supporting a readout based on structured timing as well as rate [101, 50, 1].

The falsifiability criterion is the linked timing chain: septal GABAergic control of medial entorhinal timing, medial

entorhinal inhibitory control of output precision, and CA1 temporal reorganization during the retrieval decision. Missing evidence at any link localizes the selection mechanism outside the proposed pathway.

## 4 Proposed Approach

The proposed analysis tests a timing chain from MS GABAergic output to MEC inhibitory timing to CA1 temporal ensemble structure. The first level treats medial septum GABAergic output as the upstream timing source. Work on theta-promoting septal circuits, optogenetic control, and sleep-wake state transitions establishes that septal activity can regulate hippocampal-entorhinal rhythmic state at the temporal scale needed for information routing [103, 75, 104].

The second level treats medial entorhinal inhibitory microcircuits as the transformation layer. Septal GABAergic input should change the timing of local inhibitory populations that regulate entorhinal output. Parvalbumin-related and recurrent inhibitory motifs can narrow spike windows, normalize response distributions, and accelerate adaptation to changing input statistics [51, 56, 57]. Support at this level requires timing-specific changes in entorhinal output precision.

The third level treats CA1 ensemble dynamics as the retrieval readout. CA1 should be evaluated through phase relationships, cross-correlations, replay-like sequence organization, and ensemble composition. A compact readout for this comparison is

$$S_{CA1}(a, b) = \text{corr}(C_a, C_b),$$

where  $C_a$  and  $C_b$  are pairwise CA1 cross-correlation matrices from two retrieval conditions. Temporal coding, predictive coding, and calcium-imaging-based ensemble decoding provide complementary readouts for testing whether altered entorhinal timing changes which CA1 temporal ensemble structure is expressed [33, 101, 17].

Behavioral controls separate retrieval-specific selection from state effects. Septal manipulation can influence locomotion, arousal, and anxiety-related state, so movement and state variables should be measured alongside retrieval behavior [26, 58]. Support for the mechanism requires convergence across the pathway: septal control alters MEC timing, MEC inhibitory control reshapes output precision, and CA1 shows retrieval-specific temporal reorganization. A dissociation at any level localizes the selection signal outside the proposed transformation layer.

## 5 Outcomes and Significance

The proposed mechanism is supported when perturbing MS GABAergic input to MEC shifts both retrieval behavior and CA1 temporal ensemble organization under conditions that require selection between sequentially learned context-value associations.

The core support pattern is timing-selection convergence. Septal perturbation should alter MEC timing, MEC inhibitory control should reshape output precision, CA1 should shift its temporal ensemble structure, and behavior should follow the selected association [26, 75, 80, 33, 17]. Behavioral controls should track locomotion, arousal, and anxiety-related state so

retrieval-selection effects can be separated from state changes. Alternative outcomes localize the mechanism. A firing-rate change with weak temporal reorganization supports a gain-control account. Behavioral switching with preserved CA1 temporal organization points toward downstream output circuits or direct CA1 inhibition. MEC timing changes without behavioral switching indicate an upstream timing effect that fails to control retrieval [93, 56, 19].

The storage-rule alternative is also testable. Prior and updated context-value associations should remain expressible under different retrieval conditions while inhibitory timing determines which association becomes behaviorally expressed. This pattern supports retrieval selection among preserved traces [100, 95, 86].

The significance is that memory updating can be modeled as a timing-based retrieval-selection problem at the level of inhibitory control. The hippocampal-entorhinal system can preserve multiple learned associations while regulating which association dominates CA1 temporal ensemble structure during retrieval. Positive and negative outcomes both constrain where the selection signal enters the MS-MEC-CA1 pathway.

## References

- [1] *A Unified Phase-native Computational Principle Governs Hippocampal Spike Timing and Neural Coding*. 2026. arXiv: 2603.19690. URL: <https://arxiv.org/abs/2603.19690>.
- [2] *Context-modulation of hippocampal dynamics and deep convolutional networks*. 2017. arXiv: 1711.09876. URL: <https://arxiv.org/abs/1711.09876>.
- [3] *Discretization of continuous input spaces in the hippocampal autoencoder*. 2024. arXiv: 2405.14600. URL: <https://arxiv.org/abs/2405.14600>.
- [4] “Linking In-context Learning in Transformers to Human Episodic Memory”. In: *Advances in Neural Information Processing Systems 37*. 2024. DOI: 10.52202/079017-0200.
- [5] *Automatic Neuron Detection in Calcium Imaging Data Using Convolutional Networks*. 2016. arXiv: 1606.07372. URL: <https://arxiv.org/abs/1606.07372>.
- [6] “Feedforward architectures driven by inhibitory interactions”. In: *Journal of Computational Neuroscience* (2018). DOI: 10.1007/s10827-017-0669-1.
- [7] *Cross-Frequency Coupling Increases Memory Capacity in Oscillatory Neural Networks*. 2022. arXiv: 2204.07163. URL: <https://arxiv.org/abs/2204.07163>.
- [8] “Spike-based computational models of bio-inspired memories in the hippocampal CA3 region on SpiNNaker”. In: *2022 International Joint Conference on Neural Networks (IJCNN)*. 2022. DOI: 10.1109/ijcnn55064.2022.9892606.
- [9] “Bio-inspired computational memory model of the Hippocampus: An approach to a neuromorphic spike-based Content-Addressable Memory”. In: *Neural Networks* (2024). DOI: 10.1016/j.neunet.2024.106474.
- [10] “A Bio-Inspired Implementation of a Sparse-Learning Spike-Based Hippocampus Memory Model”. In: *IEEE Transactions on Emerging Topics in Computing* (2025). DOI: 10.1109/tetc.2024.3387026.
- [11] “Statistical mechanics of learning via reverberation in bidirectional associative memories”. In: *Physica A: Statistical Mechanics and its Applications* (2024). DOI: 10.1016/j.physa.2024.129512.
- [12] *Transformers Remember First, Forget Last: Dual-Process Interference in LLMs*. 2026. arXiv: 2603.00270. URL: <https://arxiv.org/abs/2603.00270>.
- [13] “Recurrent auto-encoder with multi-resolution ensemble and predictive coding for multivariate time-series anomaly detection”. In: *Applied Intelligence* (2023). DOI: 10.1007/s10489-023-04764-5.
- [14] *Neurogenesis and multiple plasticity mechanisms enhance associative memory retrieval in a spiking network model of the hippocampus*. 2017. arXiv: 1704.07526. URL: <https://arxiv.org/abs/1704.07526>.
- [15] *Cortical microcircuits as gated-recurrent neural networks*. 2017. arXiv: 1711.02448. URL: <https://arxiv.org/abs/1711.02448>.
- [16] *Recurrent neural network models for working memory of continuous variables: activity manifolds, connectivity patterns, and dynamic codes*. 2021. arXiv: 2111.01275. URL: <https://arxiv.org/abs/2111.01275>.
- [17] *Decoding Neuronal Ensembles from Spatially-Referenced Calcium Traces: A Bayesian Semiparametric Approach*. 2025. arXiv: 2508.09576. URL: <https://arxiv.org/abs/2508.09576>.
- [18] *Grid cells show field-to-field variability and this explains the aperiodic response of inhibitory interneurons*. 2017. arXiv: 1701.04893. URL: <https://arxiv.org/abs/1701.04893>.
- [19] *Adaptive whitening in neural populations with gain-modulating interneurons*. 2023. arXiv: 2301.11955. URL: <https://arxiv.org/abs/2301.11955>.
- [20] *Temporary changes in large-scale memory neural networks after fear learning and extinction in healthy adults*. 2020. arXiv: 2011.00257. URL: <https://arxiv.org/abs/2011.00257>.
- [21] “Outan: An On-Head System for Driving  $\mu$ LED Arrays Implanted in Freely Moving Mice”. In: *IEEE Transactions on Biomedical Circuits and Systems* (2021). DOI: 10.1109/tbcas.2021.3068556.
- [22] “Neural correlates of episodic memory in the Memento cohort”. In: *Alzheimer’s & Dementia: Translational Research & Clinical Interventions* (2018). DOI: 10.1016/j.trci.2018.03.010.
- [23] *Pattern Separation in a Spiking Neural Network of Hippocampus Robust to Imbalanced Excitation/Inhibition*. 2018. arXiv: 1808.00367. URL: <https://arxiv.org/abs/1808.00367>.
- [24] “Effects of synapse location, delay and background stochastic activity on synchronising hippocampal CA1 neurons”. In: *Chaos, Solitons & Fractals: X* (2024). DOI: 10.1016/j.csfx.2024.100122.
- [25] “Hippocampal synchronization in a realistic CA1 neuron model”. In: *Physical Review E* (2024). DOI: 10.1103/physreve.110.044406.
- [26] “State-Dependent Modulation of Locomotion by GABAergic Spinal Sensory Neurons”. In: *Current Biology* (2015). DOI: 10.1016/j.cub.2015.09.070.
- [27] *Human-inspired Episodic Memory for Infinite Context LLMs*. 2024. arXiv: 2407.09450. URL: <https://arxiv.org/abs/2407.09450>.
- [28] “Robust computation with rhythmic spike patterns”. In: *Proceedings of the National Academy of Sciences* (2019). DOI: 10.1073/pnas.1902653116.
- [29] “Key-value memory in the brain”. In: *Neuron* (2025). DOI: 10.1016/j.neuron.2025.02.029.
- [30] “Palimpsest memories stored in memristive synapses”. In: *Science Advances* (2022). DOI: 10.1126/sciadv.abn7920.
- [31] *Optimal rate-variance coding due to firing threshold adaptation near criticality*. 2025. arXiv: 2509.04106. URL: <https://arxiv.org/abs/2509.04106>.
- [32] *Neuromodulation-inspired gated associative memory networks: extended memory retrieval and emergent multistability*. 2025. arXiv: 2512.13859. URL: <https://arxiv.org/abs/2512.13859>.
- [33] *An uncertainty principle for neural coding: Conjugate representations of position and velocity are mapped onto firing rates and co-firing rates of neural spike trains*. 2019. arXiv: 1912.11126. URL: <https://arxiv.org/abs/1912.11126>.
- [34] “HippoRAG: Neurobiologically Inspired Long-Term Memory for Large Language Models”. In: *Advances in Neural Information Processing Systems 37*. 2024. DOI: 10.52202/079017-1902.
- [35] *Extended temporal association memory by inhibitory Hebbian learning*. 2018. arXiv: 1809.05254. URL: <https://arxiv.org/abs/1809.05254>.

- [36] “Efficient Neural Network Approximation of Robust PCA for Automated Analysis of Calcium Imaging Data”. In: *Lecture Notes in Computer Science*. 2021. DOI: 10.1007/978-3-030-87234-2\_56.
- [37] “Local inhibitory plasticity tunes macroscopic brain dynamics and allows the emergence of functional brain networks”. In: *NeuroImage* (2016). DOI: 10.1016/j.neuroimage.2015.08.069.
- [38] “Robust Retrieval of Dynamic Sequences through Interaction Modulation”. In: *PRX Life* (2023). DOI: 10.1103/prxlife.1.023012.
- [39] “SynapticRAG: Enhancing Temporal Memory Retrieval in Large Language Models through Synaptic Mechanisms”. In: *Findings of the Association for Computational Linguistics: ACL 2025*. 2025. DOI: 10.18653/v1/2025.findings-acl.1048.
- [40] *PhiNets: Brain-inspired Non-contrastive Learning Based on Temporal Prediction Hypothesis*. 2024. arXiv: 2405.14650. URL: <https://arxiv.org/abs/2405.14650>.
- [41] “Feedback Inhibition Shapes Emergent Computational Properties of Cortical Microcircuit Motifs”. In: *The Journal of Neuroscience* (2017). DOI: 10.1523/jneurosci.2078-16.2017.
- [42] *Hippocampal representations emerge when training recurrent neural networks on a memory dependent maze navigation task*. 2020. arXiv: 2012.01328. URL: <https://arxiv.org/abs/2012.01328>.
- [43] “Coupled neural associative memories”. In: *2013 IEEE Information Theory Workshop (ITW)*. 2013. DOI: 10.1109/itw.2013.6691267.
- [44] “Noise Facilitation in Associative Memories of Exponential Capacity”. In: *Neural Computation* (2014). DOI: 10.1162/neco\_a\_00655.
- [45] *Dynamical Origin for Winner-Take-All Competition in A Biological Network of The Hippocampal Dentate Gyrus*. 2021. arXiv: 2105.06057. URL: <https://arxiv.org/abs/2105.06057>.
- [46] “Effect of adult-born immature granule cells on pattern separation in the hippocampal dentate gyrus”. In: *Cognitive Neurodynamics* (2024). DOI: 10.1007/s11571-023-09985-5.
- [47] *Structural Correlates Of Spatial Navigation And Memory Formation*. 2022. arXiv: 2203.13434. URL: <https://arxiv.org/abs/2203.13434>.
- [48] “Neuronal mechanisms for sequential activation of memory items: Dynamics and reliability”. In: *PLOS ONE* (2020). DOI: 10.1371/journal.pone.0231165.
- [49] “Binding in hippocampal-entorhinal circuits enables compositionality in cognitive maps”. In: *Advances in Neural Information Processing Systems 37*. 2024. DOI: 10.52202/079017-1235.
- [50] “Toward the biological model of the hippocampus as the successor representation agent”. In: *Biosystems* (2022). DOI: 10.1016/j.biosystems.2022.104612.
- [51] “A Computational Analysis of the Function of Three Inhibitory Cell Types in Contextual Visual Processing”. In: *Frontiers in Computational Neuroscience* (2017). DOI: 10.3389/fncom.2017.00028.
- [52] *Hippocampal Spatial Mapping As Fast Graph Learning*. 2021. arXiv: 2107.00567. URL: <https://arxiv.org/abs/2107.00567>.
- [53] “Memory-Dependent Computation and Learning in Spiking Neural Networks Through Hebbian Plasticity”. In: *IEEE Transactions on Neural Networks and Learning Systems* (2025). DOI: 10.1109/tnnls.2023.3341446.
- [54] *Emergence of Spatial Representation in an Actor-Critic Agent with Hippocampus-Inspired Sequence Generator*. 2025. arXiv: 2510.09951. URL: <https://arxiv.org/abs/2510.09951>.
- [55] *HippoMM: Hippocampal-inspired Multimodal Memory for Long Audiovisual Event Understanding*. 2025. arXiv: 2504.10739. URL: <https://arxiv.org/abs/2504.10739>.
- [56] *Interneurons accelerate learning dynamics in recurrent neural networks for statistical adaptation*. 2022. arXiv: 2209.10634. URL: <https://arxiv.org/abs/2209.10634>.
- [57] “Shaping the distribution of neural responses with interneurons in a recurrent circuit model”. In: *Advances in Neural Information Processing Systems 37*. 2024. DOI: 10.52202/079017-1078.
- [58] “A System-on-Chip for Closed-loop Optogenetic Sleep Modulation”. In: *2021 43rd Annual International Conference of the IEEE Engineering in Medicine & Biology Society (EMBC)*. 2021. DOI: 10.1109/embc46164.2021.9629745.
- [59] *GATE: Adaptive Learning with Working Memory by Information Gating in Multi-lamellar Hippocampal Formation*. 2025. arXiv: 2501.12615. URL: <https://arxiv.org/abs/2501.12615>.
- [60] “A hierarchical active inference model of spatial alternation tasks and the hippocampal-prefrontal circuit”. In: *Nature Communications* (2024). DOI: 10.1038/s41467-024-54257-3.
- [61] “Mechanisms underlying the response of mouse cortical networks to optogenetic manipulation”. In: *eLife* (2020). DOI: 10.7554/eLife.49967.
- [62] “Bifurcation of spiking oscillations from a center in resonate-and-fire neurons”. In: *Biological Cybernetics* (2026). DOI: 10.1007/s00422-026-01035-7.
- [63] “Alleviating catastrophic forgetting using context-dependent gating and synaptic stabilization”. In: *Proceedings of the National Academy of Sciences* (2018). DOI: 10.1073/pnas.1803839115.
- [64] *A Hippocampus Model for Online One-Shot Storage of Pattern Sequences*. 2019. arXiv: 1905.12937. URL: <https://arxiv.org/abs/1905.12937>.
- [65] *Grid-like structure is optimal for path integration*. 2016. arXiv: 1606.01239. URL: <https://arxiv.org/abs/1606.01239>.
- [66] “Effect of Neuromodulation of Short-term Plasticity on Information Processing in Hippocampal Interneuron Synapses”. In: *The Journal of Mathematical Neuroscience* (2018). DOI: 10.1186/s13408-018-0062-z.
- [67] “Crosstalk and transitions between multiple spatial maps in an attractor neural network model of the hippocampus: Phase diagram”. In: *Physical Review E* (2013). DOI: 10.1103/physreve.87.062813.
- [68] “Hippocampal Spike-Timing Correlations Lead to Hexagonal Grid Fields”. In: *Physical Review Letters* (2017). DOI: 10.1103/physrevlett.119.038101.
- [69] “An efficient coding theory for a dynamic trajectory predicts non-uniform allocation of entorhinal grid cells to modules”. In: *PLOS Computational Biology* (2017). DOI: 10.1371/journal.pcbi.1005597.

- [70] *Stable Memory Allocation in the Hippocampus: Fundamental Limits and Neural Realization*. 2016. arXiv: 1612.04659. URL: <https://arxiv.org/abs/1612.04659>.
- [71] *A Coupled Neural Field Model for the Standard Consolidation Theory*. 2024. arXiv: 2404.02938. URL: <https://arxiv.org/abs/2404.02938>.
- [72] *CREIMBO: Cross-Regional Ensemble Interactions in Multi-view Brain Observations*. 2024. arXiv: 2405.17395. URL: <https://arxiv.org/abs/2405.17395>.
- [73] *Spatial and Temporal Correlates of Vesicular Release at Hippocampal Synapses*. 2010. arXiv: 1004.2009. URL: <https://arxiv.org/abs/1004.2009>.
- [74] “High fidelity optogenetic control of individual prefrontal cortical pyramidal neurons in vivo”. In: *F1000Research* (2012). DOI: 10.12688/f1000research.1-7.v1.
- [75] “Bidirectional Optogenetic Control of Inhibitory Neurons in Freely-Moving Mice”. In: *IEEE Transactions on Biomedical Engineering* (2021). DOI: 10.1109/tbme.2020.3001242.
- [76] *Multisensory learning recruits visual neurons into an olfactory memory engram*. 2026. arXiv: 2604.28007. URL: <https://arxiv.org/abs/2604.28007>.
- [77] *Modulation of metastable ensemble dynamics explains the inverted-U relationship between tone discriminability and arousal in auditory cortex*. 2024. arXiv: 2404.03902. URL: <https://arxiv.org/abs/2404.03902>.
- [78] *The cross-frequency mediation mechanism of intracortical information transactions*. 2017. arXiv: 1703.07654. URL: <https://arxiv.org/abs/1703.07654>.
- [79] “Algebraic approach to spike-time neural codes in the hippocampus”. In: *Physical Review E* (2023). DOI: 10.1103/physreve.108.054404.
- [80] “Dynamic core-periphery structure of information sharing networks in entorhinal cortex and hippocampus”. In: *Network Neuroscience* (2020). DOI: 10.1162/netn\_a\_00142.
- [81] “Forgetting Leads to Chaos in Attractor Networks”. In: *Physical Review X* (2023). DOI: 10.1103/physrevx.13.011009.
- [82] “Querying hippocampal replay with subcortical inputs”. In: *Current Opinion in Neurobiology* (2022). DOI: 10.1016/j.conb.2022.102645.
- [83] “A neurally constrained computational model of context-dependent fear extinction recall and relapse”. In: *Communications Biology* (2025). DOI: 10.1038/s42003-025-08107-7.
- [84] *A Cognitive Architecture for Machine Consciousness and Artificial Superintelligence: Thought Is Structured by the Iterative Updating of Working Memory*. 2022. arXiv: 2203.17255. URL: <https://arxiv.org/abs/2203.17255>.
- [85] “Memory recall and spike-frequency adaptation”. In: *Physical Review E* (2016). DOI: 10.1103/physreve.93.052307.
- [86] “Dis-inhibitory neuronal circuits can control the sign of synaptic plasticity”. In: *Advances in Neural Information Processing Systems 36*. 2023. DOI: 10.52202/075280-2799.
- [87] “Deep Episodic Memory: Encoding, Recalling, and Predicting Episodic Experiences for Robot Action Execution”. In: *IEEE Robotics and Automation Letters* (2018). DOI: 10.1109/lra.2018.2860057.
- [88] “A Balanced Memory Network”. In: *PLoS Computational Biology* (2007). DOI: 10.1371/journal.pcbi.0030141.
- [89] *A Neural Network Model of Continual Learning with Cognitive Control*. 2022. arXiv: 2202.04773. URL: <https://arxiv.org/abs/2202.04773>.
- [90] “Competition Through Selective Inhibitory Synchrony”. In: *Neural Computation* (2012). DOI: 10.1162/neco\_a\_00304.
- [91] *Associative Memories via Predictive Coding*. 2021. arXiv: 2109.08063. URL: <https://arxiv.org/abs/2109.08063>.
- [92] “The role of oscillations in grid cells’ toroidal topology”. In: *PLOS Computational Biology* (2025). DOI: 10.1371/journal.pcbi.1012776.
- [93] “On the Organization of Grid and Place Cells: Neural Denoising via Subspace Learning”. In: *Neural Computation* (2019). DOI: 10.1162/neco\_a\_01208.
- [94] *Dynamical Mechanisms for Coordinating Long-term Working Memory Based on the Precision of Spike-timing in Cortical Neurons*. 2025. arXiv: 2512.15891. URL: <https://arxiv.org/abs/2512.15891>.
- [95] *Unsupervised learning by a nonlinear network with Hebbian excitatory and anti-Hebbian inhibitory neurons*. 2018. arXiv: 1812.11581. URL: <https://arxiv.org/abs/1812.11581>.
- [96] *AI-native Memory: A Pathway from LLMs Towards AGI*. 2024. arXiv: 2406.18312. URL: <https://arxiv.org/abs/2406.18312>.
- [97] *Content Addressable Memory Without Catastrophic Forgetting by Heteroassociation with a Fixed Scaffold*. 2022. arXiv: 2202.00159. URL: <https://arxiv.org/abs/2202.00159>.
- [98] *Theta, alpha and gamma traveling waves in a multi-item working memory model*. 2021. arXiv: 2103.15266. URL: <https://arxiv.org/abs/2103.15266>.
- [99] *Fast amortized inference of neural activity from calcium imaging data with variational autoencoders*. 2017. arXiv: 1711.01846. URL: <https://arxiv.org/abs/1711.01846>.
- [100] *Engram Memory Encoding and Retrieval: A Neurocomputational Perspective*. 2025. arXiv: 2506.01659. URL: <https://arxiv.org/abs/2506.01659>.
- [101] “Sequential Memory with Temporal Predictive Coding”. In: *Advances in Neural Information Processing Systems 36*. 2023. DOI: 10.52202/075280-1919.
- [102] *Artificial Neuronal Ensembles with Learned Context Dependent Gating*. 2023. arXiv: 2301.07187. URL: <https://arxiv.org/abs/2301.07187>.
- [103] *SWS promoting Mhb-IPN-MRN circuit opposes the theta promoting circuit, active wake and REM sleep*. 2015. arXiv: 1510.01100. URL: <https://arxiv.org/abs/1510.01100>.
- [104] *Mechanisms for anesthesia, unawareness, respiratory depression, memory replay and sleep: Mhb > IPN > PAG + DRN + MRN > claustrum > cortical slow waves*. 2025. arXiv: 2509.04454. URL: <https://arxiv.org/abs/2509.04454>.
- [105] “Neuronal response impedance mechanism implementing cooperative networks with low firing rates and  $\hat{I}$ ’s precision”. In: *Frontiers in Neural Circuits* (2015). DOI: 10.3389/fncir.2015.00029.
- [106] “Ripple oscillations in the left temporal neocortex are associated with impaired verbal episodic memory encoding”. In: *Epilepsy & Behavior* (2018). DOI: 10.1016/j.yebeh.2018.08.018.
- [107] “Anti-retroactive Interference for Lifelong Learning”. In: *Lecture Notes in Computer Science*. 2022. DOI: 10.1007/978-3-031-20053-3\_10.

- [108] *GAM-RAG: Gain-Adaptive Memory for Evolving Retrieval in Retrieval-Augmented Generation*. 2026. arXiv: 2603.01783. URL: <https://arxiv.org/abs/2603.01783>.
- [109] *Time Makes Space: Emergence of Place Fields in Networks Encoding Temporally Continuous Sensory Experiences*. 2024. arXiv: 2408.05798. URL: <https://arxiv.org/abs/2408.05798>.
- [110] *REMI: Reconstructing Episodic Memory During Internally Driven Path Planning*. 2025. arXiv: 2507.02064. URL: <https://arxiv.org/abs/2507.02064>.
- [111] “A robotic model of hippocampal reverse replay for reinforcement learning”. In: *Bioinspiration & Biomimetics* (2023). DOI: 10.1088/1748-3190/ac9ffc.
- [112] *Generalisation of structural knowledge in the hippocampal-entorhinal system*. 2018. arXiv: 1805.09042. URL: <https://arxiv.org/abs/1805.09042>.
- [113] “BayesPCN: A Continually Learnable Predictive Coding Associative Memory”. In: *Advances in Neural Information Processing Systems 35*. 2022. DOI: 10.52202/068431-2168.
- [114] “Mapping the Genetic-Imaging-Clinical Pathway with Applications to Alzheimer’s Disease”. In: *Journal of the American Statistical Association* (2022). DOI: 10.1080/01621459.2022.2087658.
- [115] *Learning Sparse Spatial Codes for Cognitive Mapping Inspired by Entorhinal-Hippocampal Neurocircuit*. 2019. arXiv: 1910.04590. URL: <https://arxiv.org/abs/1910.04590>.
- [116] “Theories of synaptic memory consolidation and intelligent plasticity for continual learning”. In: *Learning and Memory: A Comprehensive Reference*. 2025. DOI: 10.1016/b978-0-443-15754-7.00070-5.
- [117] “Episodic memory governs choices: An RNN-based reinforcement learning model for decision-making task”. In: *Neural Networks* (2021). DOI: 10.1016/j.neunet.2020.11.003.
- [118] “Efficient and accurate extraction of in vivo calcium signals from microendoscopic video data”. In: *eLife* (2018). DOI: 10.7554/eLife.28728.