

# Coordinated Computations for Naturalistic Memory Encoding and Retrieval in Hippocampal subspaces

**Dasom Kwon<sup>1,2</sup> (dasom.kwon@g.skku.edu)**  
**Jungwoo Kim<sup>1,2,3</sup> (didch1789@g.skku.edu)**  
**Seng Bum Michael Yoo<sup>1,2,3,4,†</sup> (sbyoo@g.skku.edu)**  
**Won Mok Shim<sup>1,2,3,†</sup> (wonmokshim@skku.edu)**

<sup>1</sup>Department of Intelligent Precision Healthcare Convergence,  
Sungkyunkwan University, Suwon, Republic of Korea

<sup>2</sup>Center for Neuroscience Imaging Research,  
Institute for Basic Science, Suwon, Republic of Korea

<sup>3</sup>Department of Biomedical Engineering,  
Sungkyunkwan University, Suwon, Republic of Korea

<sup>4</sup>Department of Neurosurgery,  
Baylor College of Medicine, Houston, Texas 77030

†: co-senior author

## Abstract:

Our naturalistic experiences are organized into memories through multiple processes, including novelty encoding, memory formation, and retrieval. However, the neural mechanisms coordinating these processes remain unclear. Using fMRI data obtained during movie-viewing and subsequent narrative recall, we examined hippocampal neural subspaces associated with distinct memory processes and characterized their relationships. Within the hippocampus, novelty subspaces encoding different novelty types demonstrated partial overlap and these overlapping novelty subspaces aligned with the subspace involved in memorability. Following event boundaries, hippocampal states within these subspaces aligned inversely along a shared coding axis, predicting subsequent recall performance. However, this alignment was observed only during encoding, not retrieval. Additionally, we found that these hippocampal subspaces were organized along the hippocampal longitudinal axis. Our results offer mechanistic insights into how the hippocampus dynamically coordinates computations underlying memory encoding and retrieval at a population level.

**Keywords:** Hippocampus; subspace analysis; memory; novelty processing; naturalistic stimuli

## Introduction

The hippocampal memory processes involve three fundamental cognitive functions: novelty encoding (Knight, 1996), memory formation (Izquierdo & Medina, 1997), and retrieval (Frankland, Josselyn, & Köhler, 2019). While previous studies have linked distinct subregions of the medial temporal lobe to each individual memory process, how these processes are coordinated within the hippocampus remained poorly understood. To explore the computational mechanisms for coordinating memory processes, we leverage a narrative movie stimulus and the analytic methods extracting neural subspaces. To identify neural subspaces associated with memory processes of interest, we applied Targeted Dimensionality Reduction (Aoi, Mante, & Pillow, 2020; Mante et al., 2013) to fMRI data acquired as participants watched a movie and then verbally recalled its narrative. We focus on neural dynamics occurring around event boundaries where discontinuities in perceptual and semantic experiences trigger processing of preceding events and subsequent memory formation (Baldassano et al., 2017; Radvansky & Zacks, 2017) and around recall initiations where the memory retrieval process operates (Gelbard-Sagiv et al., 2008).

Upon extracting the hippocampal neural subspaces associated with memory processes, we propose three hypotheses: 1) Neural subspaces involved in encoding

novelty across distinct attributes in the movie are either aligned or orthogonal, 2) the axes of novelty subspaces are linked to the memorability subspace, which reflects a memory formation process, and 3) the memory retrieval subspace remains aligned with the memorability subspace.

## Methods

### Tasks and Measurements

During fMRI scans, twenty-four participants watched the movie and verbally recounted its narrative later. Trained annotators provided detailed annotation of the movie, such as character co-occurrences and emotional valence of character relationships. We quantified co-occurrence and valence novelty, and memorability for each movie event. Novelty was defined as  $1 - \text{Pearson correlation between co-occurrence and valence information from prior events and the current event}$ . Memorability was quantified as the ratio of the number of correctly retrieved words in the participants' recall to the total number of annotated words in each event.

### Subspace analysis

Within the hippocampus, we delineated a canonical space and three distinct subspaces related to novelty encoding, memory formation, and retrieval. We aggregated and averaged neural data collected during movie watching to establish the canonical subspace, applying Principal Component Analysis (PCA; Shine et al., 2019). For novelty and memory formation subspaces, we categorized events by novelty or memorability levels, applying Finite Impulse Response (FIR) modeling, linear regression, and PCA. To identify the memory retrieval subspace, we applied the same method to neural data collected during recall. Using these PC-based state spaces, we calculated encoding performance of hippocampal states for each memory process and computed the alignment scores between the subspaces to investigate the dynamics of coordinated computations (**Figure 1a**).

## Results

Irrespective of the novelty type, events with low novelty received significantly higher memorability scores compared to those with high novelty, indicating that memory formation was influenced by novelty of information.

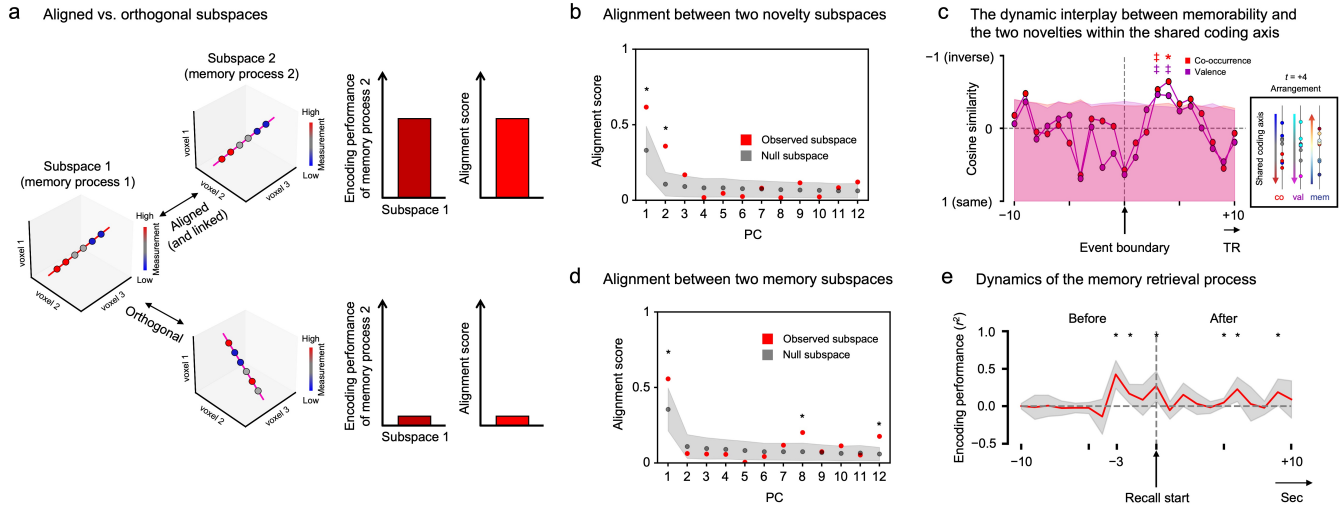


Figure 1. **a)** Hypothetical relationships between two memory processes. If the two memory processes share computations, their subspaces are aligned. **b)** The alignment scores between the co-occurrence and valence novelty subspaces were assessed by calculating the cosine similarity between each PC. **c)** Before event boundaries, neural states corresponding to novelty and memorability were disarranged, but following event boundaries, these states became inversely aligned along the shared coding axis. **d)** The alignment scores between the memory formation and retrieval subspaces. **e)** Hippocampal states within the memory retrieval subspace were arranged in order along the memory coding axis immediately before the onset of recall. \*  $p < .05$ , †  $ps < .072$ .

We found that two subspaces, each associated with distinct types of novelty, partially overlapped, with their major axes being non-orthogonal (**Figure 1b**). This novelty coding axis also aligned with the memorability subspace, suggesting a shared coding axis for coordinated computations between novelty encoding and memory formation. Notably, the neural states corresponding to novelty and memorability levels became inversely aligned along this shared coding axis following event boundaries, indicating a dynamic rearrangement of hippocampal states that is predictive of subsequent recall performance (**Figure 1c**).

The hippocampal states within the retrieval subspace reflected participants' recall performance, exhibiting an alignment with the memorability subspace immediately before the onset of recalling each event (**Figure 1d, 1e**). This result indicates coordination between memory encoding and retrieval processes. Furthermore, the alignment between the novelty and memorability subspaces was specific to memory formation during movie viewing and did not extend to retrieval during narrative recall, indicating a distinction between the processes of novelty encoding and retrieval.

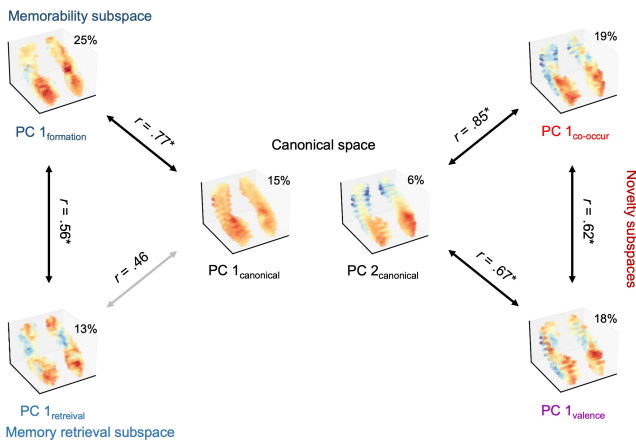


Figure 2. Overview of hippocampal subspaces for novelty encoding and memory processes. The ratio of explained variance for the corresponding PC is shown beside each spatial gradient map. \*  $p < .05$

Additionally, the functionally relevant subspaces identified in this study were organized along the hippocampal longitudinal axis, providing insights into the functional organization of the hippocampus (**Figure 2**).

## Discussion

Our findings offer novel insights into how event boundaries prompt the alignment of hippocampal states involved in both novelty encoding and memory formation processes along a shared coding axis. Furthermore, the alignment of memory encoding and retrieval subspaces suggests a potential mechanism for reinstating previous experiences. The extended application of neural subspace analysis tailored for fMRI data used in this study reveals the dynamic interplay and computational principles of coordinated memory processes within the hippocampus.

## Acknowledgements

This work was supported by IBS-R015-D1 (W.M.S. and S.B.M.Y.), RS-2023-00211018 (S.B.M.Y.), NRF-2019R1A2C1085566 (W.M.S.), 24-BR-03-04 (W.M.S.) and the Fourth Stage of Brain Korea 21 Project in Department of Intelligent Precision Healthcare, Sungkyunkwan University (W.M.S.).

## References

- Aoi, M. C., Mante, V., & Pillow, J. W. (2020). Prefrontal cortex exhibits multidimensional dynamic encoding during decision-making. *Nature neuroscience*, *23*(11), 1410-1420.
- Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering Event Structure in Continuous Narrative Perception and Memory. *Neuron*, *95*(3), 709–721.
- Frankland, P. W., Josselyn, S. A., & Köhler, S. (2019). The neurobiological foundation of memory retrieval. *Nature Neuroscience*, *22*(10), 1576–1585.
- Gelbard-Sagiv, H., Mukamel, R., Harel, M., Malach, R., & Fried, I. (2008). Internally generated reactivation of single neurons in human hippocampus during free recall. *Science*, *322*(5898), 96–101.
- Izquierdo, I., & Medina, J. H. (1997). Memory formation: the sequence of biochemical events in the hippocampus and its connection to activity in other brain structures. *Neurobiology of learning and memory*, *68*(3), 285-316.
- Knight, R. T. (1996). Contribution of human hippocampal region to novelty detection. *Nature*, *383*(6597), 256-259.
- Mante, V., Sussillo, D., Shenoy, K. V., & Newsome, W. T. (2013). Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature*, *503*(7474), 78–84.
- Radvansky, G. A., & Zacks, J. M. (2017). Event Boundaries in Memory and Cognition. *Current Opinion in Behavioral Sciences*, *17*, 133–140.
- Shine, J. M., Breakspear, M., Bell, P. T., Ehgoetz Martens, K. A., Shine, R., Koyejo, O., ... & Poldrack, R. A. (2019). Human cognition involves the dynamic integration of neural activity and neuromodulatory systems. *Nature neuroscience*, *22*(2), 289-296.