

Replay of factorized temporal journey

Xuanlong Zhu¹, Hongjie Jiang², Chenyang Li³, Kai Pan², Shaomin Zhang³, Sze Chai Kwok¹

¹Division of Natural and Applied Sciences, Duke Kunshan University, Kunshan, Jiangsu, 215316, China

²Department of Neurosurgery, The Second Affiliated Hospital, School of Medicine, Zhejiang University, Zhejiang, 310003, China

³Qiushi Academy for Advanced Studies, Zhejiang University, Zhejiang, 310014, China





Introduction

Time is a fundamental dimension of episodic memory, structuring the sequence of events that form our experiences. While replay of spatial paths and item sequences has been extensively studied in recent years, the role of temporal replay remains unclear. Here, we asked whether the brain replays time in a factorized manner. Our results revealed content-independent temporal trajectories that were replayed both during memory retrieval and postretrieval rest, with on-task replay supporting immediate recall and off-task replay contributing to the consolidation of weaker memories. Furthermore, the alignment between cortical replay and sharp wave ripples in the hippocampal reveals that hippocampal-cortical replay may serve as a unifying mechanism for organizing "where", "what", and "when" of episodic memory.

Method

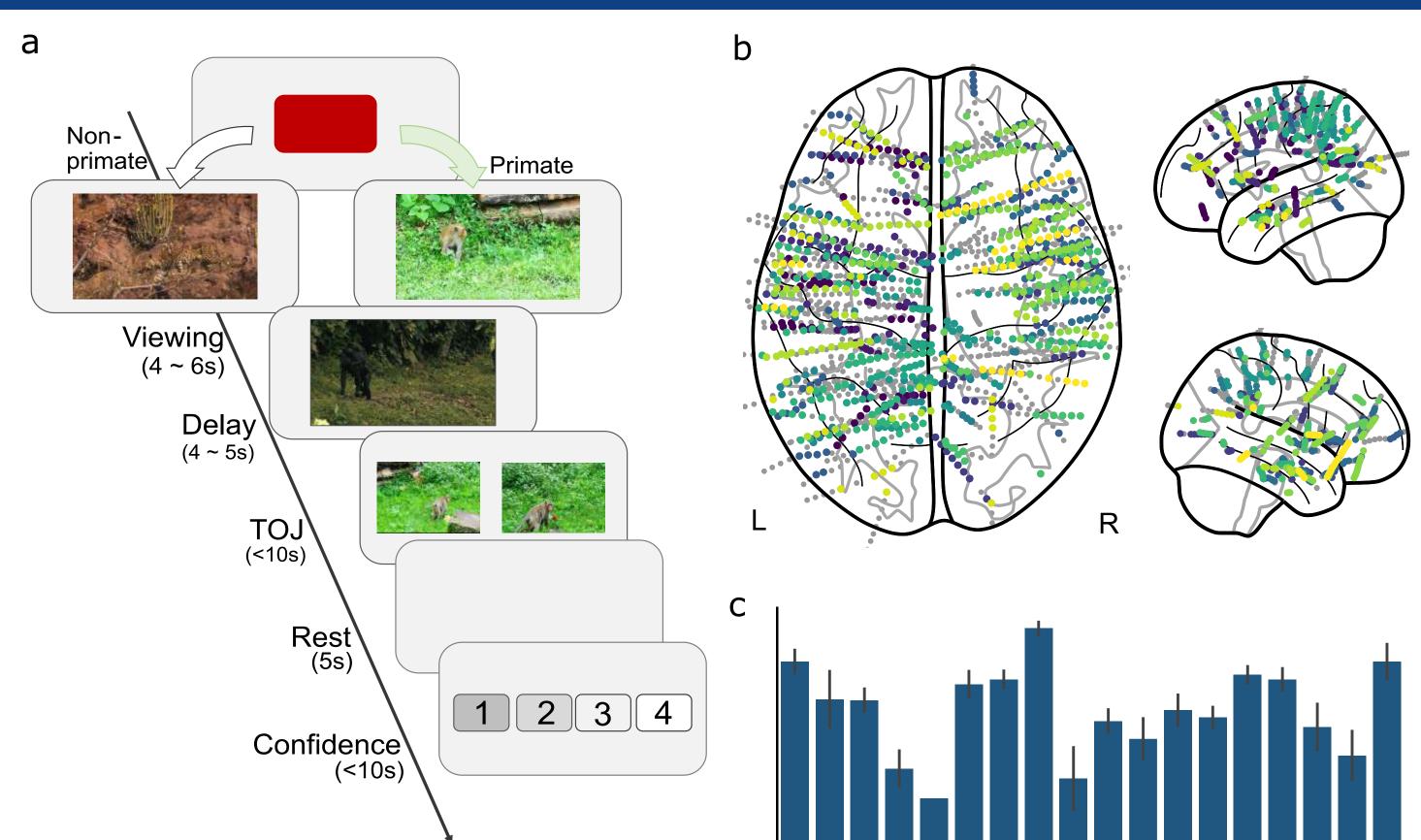


Fig 1. Experimental design, intracranial data acquisition and behavioral performance

- 1a. **Experimental paradigm**. Each trial began with a 4–6 s animal clip (primate or non-primate). Participants memorized the temporal order and later chose the earlier image in a temporal order judgment (TOJ) phase. A 5 s rest period followed each memory test, with no stimuli and instructions to relax.
- 1b. **Recording locations**. We recorded 2,492 channels from 18 participants. Anatomical locations of all implanted iEEG channels are shown in MNI space, with marker colors indicating participants.
- 1c. Behavioral performance. Error bars show the standard error of the mean (SEM) across sessions for each participant.

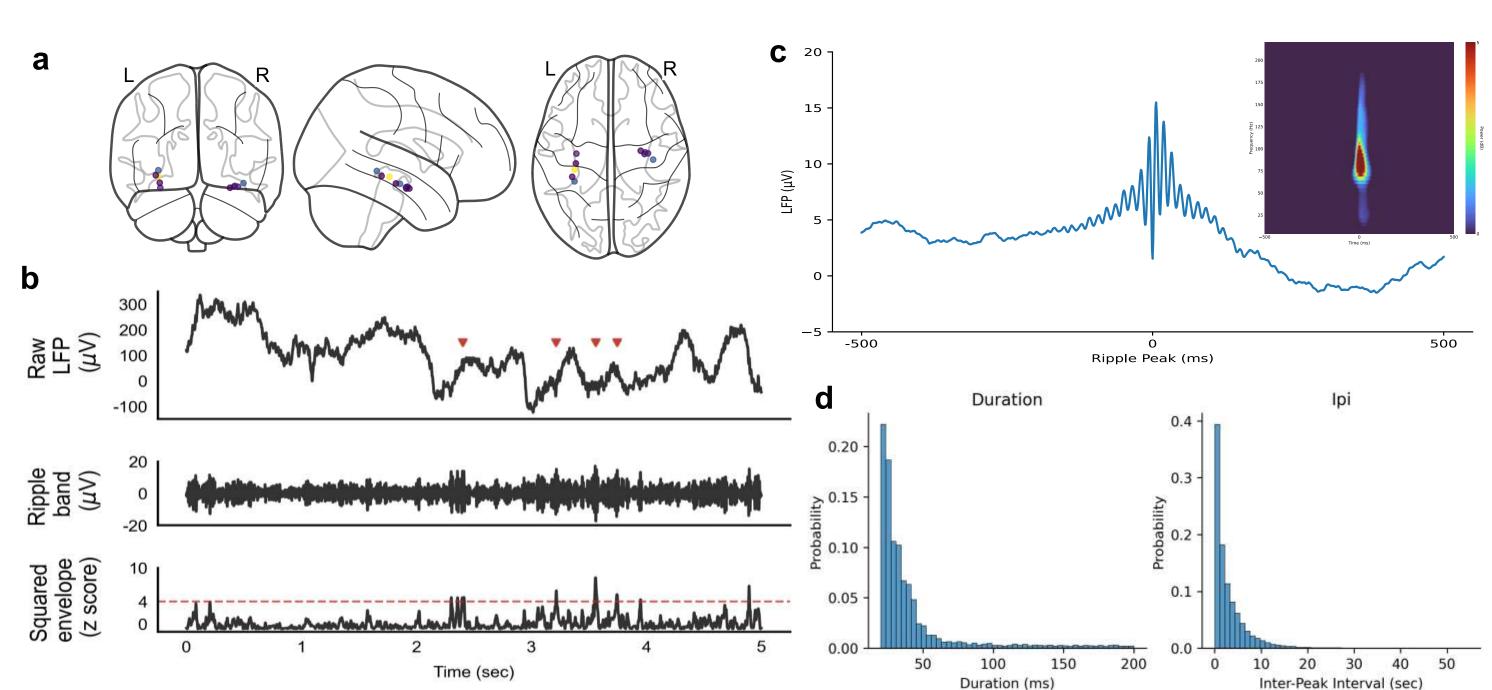


Fig 2. Sharp-wave ripple detection

- 2a. Anatomical Location. Hippocampal recording sites used for ripple detection are shown in MNI space, with marker colors indicating individual participants (n = 7).
- 2b. SWR examples during recording. From top to bottom: raw LFP, ripple-band filtered LFP (70–180 Hz), and the normalized ripple-band envelope for ripple detection. SWRs were identified as events exceeding 4 SD.
- 2c. Average peri-ripple-peak activity. Grand-average peri-ripple field potential and wavelet spectrogram are shown, centered on ripple peaks.
- 2d. Duration and inter-peak intervals.

Results

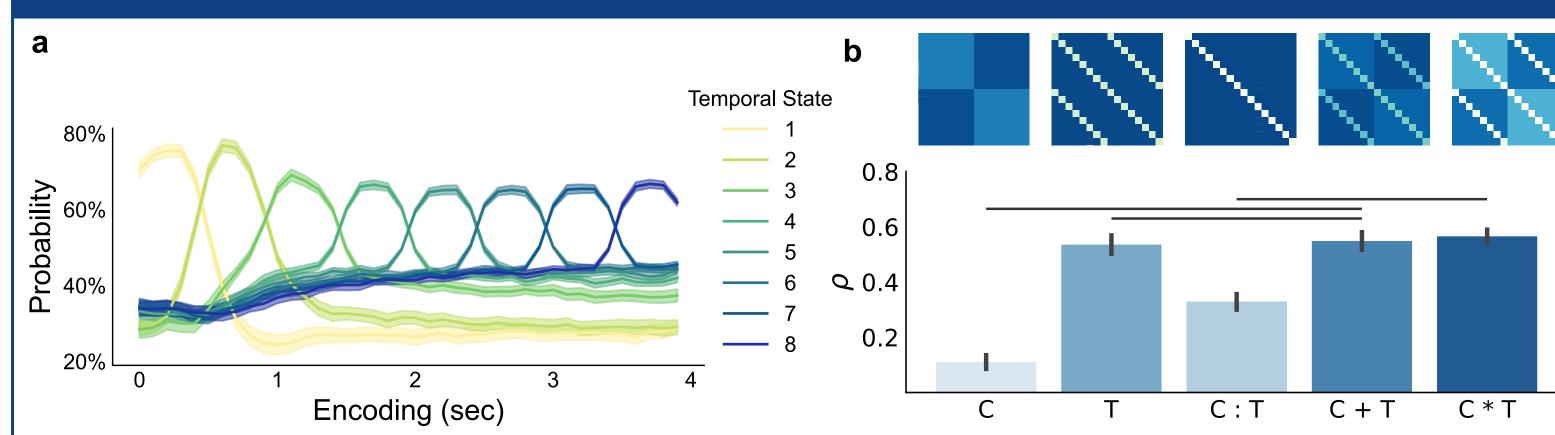


Fig 3. Neural decoding of time

3a. Decoding performance. Time decoders were trained on data from participants viewing different videos and performed successfully. Most prediction errors occurred between adjacent time states, and decoding accuracy declined over time.

3b. Decoder-derived RSA. Confusion matrices from content-and-time decoders were treated as representational similarity matrices and compared to five models: content-specific (C), time-specific (T), entangled (C:T), orthogonal (C+T), and full interaction (C*T). Horizontal bars mark significant contrasts (FDR < 0.05).

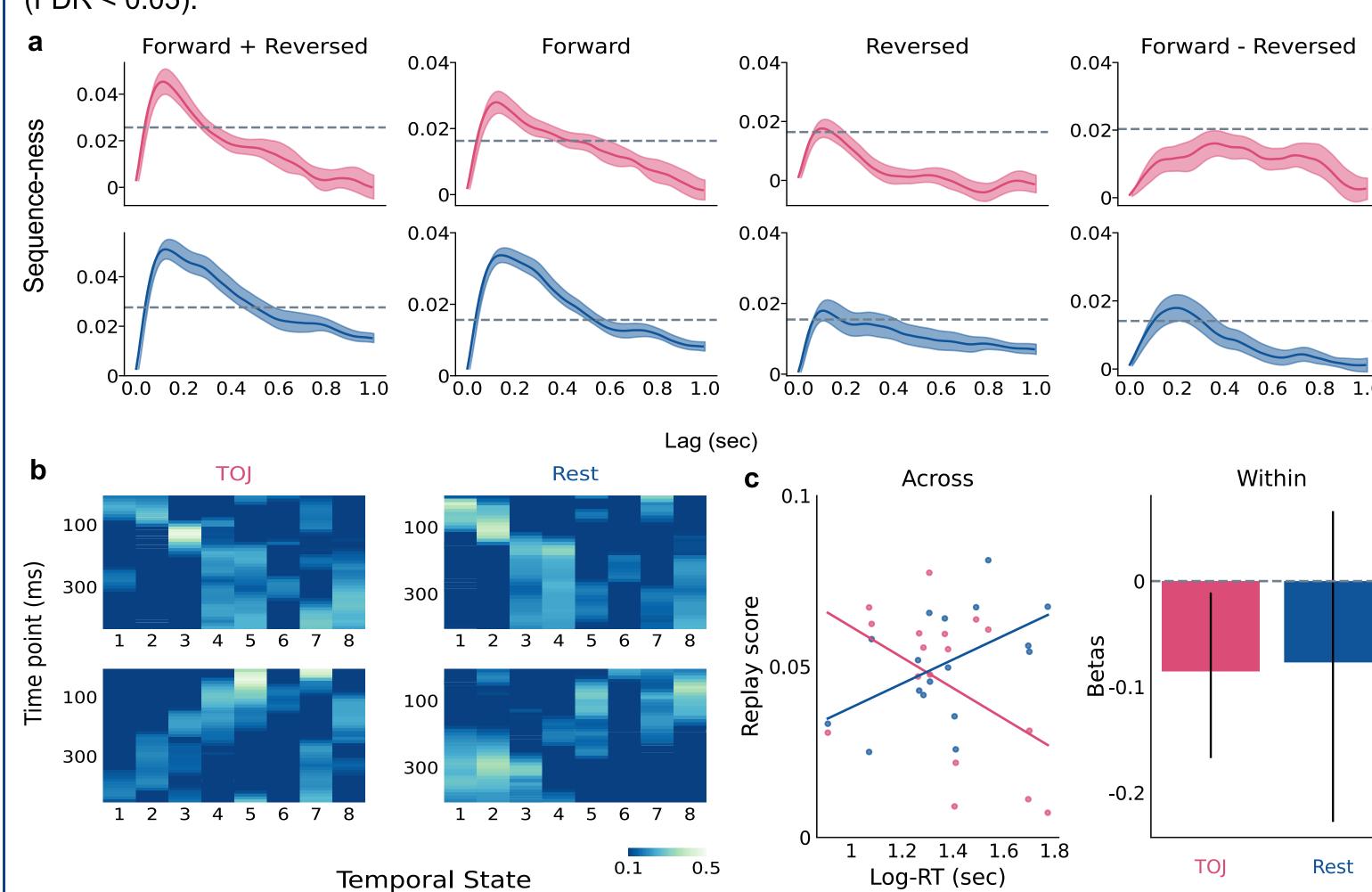
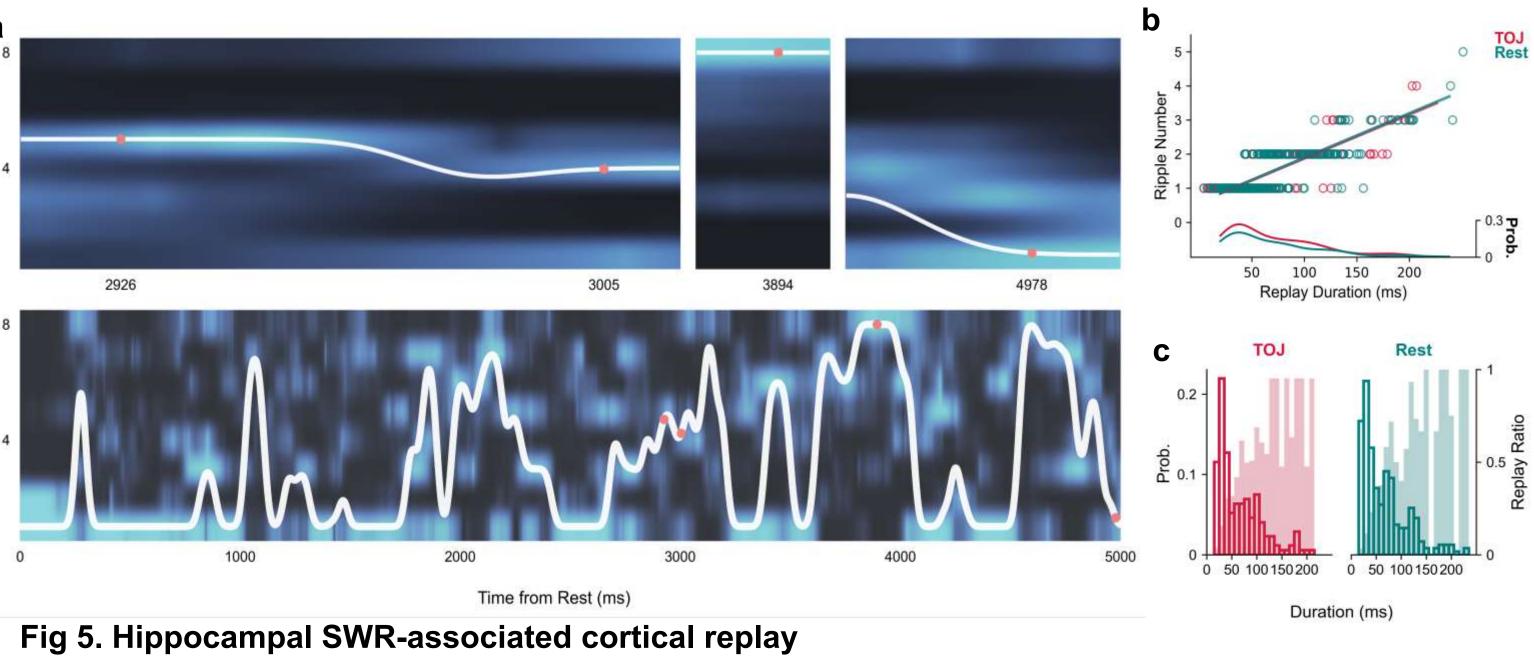


Fig 4. Bi-directional replay of temporal sequence

- 4a. On-task and off-task replay. Sequence-ness during both TOJ and post-retrieval rest was significantly above chance, with peak time lags at 120–130 ms.
- 4b. Example events. Single-trial examples show forward replay (top) and reversed replay (bottom).
- 4c. Distinct roles in memory. On-task and off-task replay contribute differently to memory. Left: group-level analysis; Right: trial-level analysis. Error bars indicate SEM across participants.



- 5a. Cortical replay in a single trial. This trial contained four hippocampal SWRs, illustrating intra- and interripple replay.
- 5b. Extended replay. Replay duration increases with the number of ripples, and most events are relatively short, as shown by the distribution.
- 5c. Replay probability. Longer ripples are more likely to co-occur with replay events.

Summary

- 1. Factorized Time code in human episodic memory.
- 2. Bi-directional rapid replay of temporal sequence during both memory retrieval and subsequent resting.
 - Distinct role of on-task and off-task replay in predicting memory performance.
- 4. Similar to hippocampal replay, cortical replay is accompanied by hippocampal SWRs, not only in isolated events but also spanning multiple adjacent SWRs.