Replay of factorized temporal journey

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Abstract

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 post-retrieval 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.

Keywords: replay; time; conjunctive representation; sharp wave ripple; episodic memory

Introduction

Episodic memories are inherently spatiotemporal, requiring the brain to represent both where and when events occur (Tulving, 2002). In rodents, hippocampal place and grid cells encode spatial maps (O'Keefe & Nadel, 1978; Tolman, 1948; Moser, Kropff, & Moser, 2008) that can be replayed to support navigation and memory (Foster & Wilson, 2006; Diba & Buzsáki, 2007). However, how the brain encodes and replays temporal sequences remains less understood. Recent studies suggest a shared coding principle between space and time (MacDonald, Lepage, Eden, & Eichenbaum, 2011; Umbach et al., 2020; Eichenbaum, 2014; Buzsáki & Llinás, 2017). If so, we would expect sequential reactivation of temporal representations, independent of or in conjunction with other variables.

Here, we used intracranial EEG (iEEG) and multivariate decoding to examine whether abstract temporal trajectories are encoded and replayed during memory retrieval and rest. We further assessed whether these cortical replays are coordinated with hippocampal sharp-wave ripples (SWRs), long thought to mediate hippocampal–cortical communication (Ji & Wilson, 2007; Buzsáki, 2015).

Method

Participants and experimental design

Intracranial recordings were obtained from 18 epileptic patients (age 24.67 ± 1.94, 5 females) when they performing a temporal order judgment task (TOJ) using naturalistic videos. In experiment, each trial began with a unique 4-6 s video depicting a primate or non-primate animal, following by a memory test in which participants judged the temporal order of two frames extracted from the video. A 5-s rest period followed each retrieval. Participants then rated their confidence on a 4-point scale. Incorrect or missed responses were excluded from further analyses. All procedures were approved by the institutional review board, and no seizures occurred during testing.

Cortical and SWR-associated replay detection

Electrode contacts were localized by co-registering post-implant CT scans to pre-implant T1-weighted MRI using Brainstorm. Contacts were identified manually and projected to MNI space after cortical surface reconstruction. Channels in epileptic loci or outside brain parenchyma were excluded.

We applied the Temporally Delayed Linear Modeling (TDLM) framework (Liu et al., 2021) to identify sequential reactivation of decoded temporal states during retrieval and post-retrieval rest. Trial-wise reactivation of each temporal state was used to compute sequenceness, defined as the degree to which neural transition probabilities between decoded states matched the hypothesized transition matrix. Significance was assessed using 1000 permutations of the transition matrix, with maximum sequenceness across lags used for multiple comparison correction.

To examine hippocampal–cortical coordination, we aligned cortical replay events with hippocampal sharp-wave ripples (SWRs). SWRs were detected via band-pass filtering (70 – 180 Hz) and thresholding the ripple-band power at 4 SD (Norman et al., 2019) in five participants with hippocampal contacts. Replay within each SWR was quantified using a weighted linear correlation between decoded time and actual time (Wu & Foster, 2014). For ripple bursts (adjacent peak-to-peak gap $<$ 100 ms), we computed the score across the full burst duration. Significance of each event was determined by 1000 circular shuffles of decoded time probabilities.

Results

Factorized temporal journeys

We recorded iEEG signals from whole-brain space across 18 participants while they viewed naturalistic videos. Spectral features from each 4-s encoding period were extracted, and eight one-vs-rest L1-regularized logistic classifiers were trained to decode temporal states. To avoid overfitting, we used nested 5-fold cross-validation: the inner loop randomly sampled 100 regularization values ($C \in \left[10^{-4}, 10^{-2}\right]$ from a log-uniform distribution, selecting the one that minimized log-loss.

Time codes generalized across video content with above-chance decoding accuracy in 17 of 18 participants ($65.20 \pm 3.01\%$, Fig. 1a); one participant was excluded due to chance-level decoding performance. Much like time cells, most decoding errors occurred between adjacent time bins, especially later in the sequence, resembling the temporal compression seen in time cells. This was further supported by pairwise Mahalanobis distances between temporal states, which decreased over time, indicating reduced temporal resolution as the sequence unfolded.

Beyond successful cross-category decoding, we tested how temporal and content dimensions interact using representational similarity analysis (RSA) on confusion matrices from a joint content × time decoder. The results favored a linear conjunctive model over non-linear entangled alternatives

(Fig. 1b), suggesting that content and time contribute jointly yet independently to the neural code.

To rule out passive timing mechanisms such as counting, we conducted cross-condition decoding between cognitive states. Temporal decoders trained during active viewing failed to generalize to post-trial rest, and vice versa, indicating that the observed temporal codes are specifically tied to memory encoding, not context-free time tracking.

Distinct roles of on-task and off-task replay

We applied trained temporal decoders to memory retrieval and post-retrieval rest periods to assess replay using the TDLM framework. Both forward and reversed replay were detected (Fig. 1c), with peak state-to-state lags between 110 to 150 ms. These peaks were consistent across sequence length, content category, and participants.

We summed up forward and reversed sequenceness to quantify overall replay strength and found that on-task and off-task replay show distinct roles in predicting memory performance. At the group level, stronger off-task replay was associated with slower memory response, while on-task replay showed a trend toward faster response. Trial-by-trial multilevel modeling revealed a slightly different picture: on-task replay strength was significantly related to faster retrieval, whereas off-task replay did not significantly correlated with reaction time (Fig. 1d). These results suggest distinct mechanisms underlying on-task and off-task replay, with on-task replay facilitating memory retrieval per se and off-task replay potentially compensating for weaker memory performance.

Cortical replay associated with hippocampal SWRs

Finally, we examined whether hippocampal sharp-wave ripples (SWRs) were temporally coupled with cortical replay in five participants with hippocampal electrodes. SWR spectral signatures and ripple rates remained stable across task phases (mean ripple rates: 0.40 (Encoding), 0.42 (Delay), 0.43 (TOJ), 0.33 (Rest)).

Given limitations of the TDLM as a state model in detecting fragmented or discontinuous replay patterns, we applied a weighted correlation approach to detect ripple-aligned replay. Around 10% of SWRs met the replay criteria, significantly exceeding the 5% chance levels.

To test whether replay events could span multiple ripples, we combined the adjacent ripples with peak-to-peak lag less than 100 ms into ripple bursts. Replay was substantially more likely during ripple bursts (63%of events, Fig. 1 e-f), consistent with rodent findings that replay can chain across ripples (Davidson, Kloosterman, & Wilson, 2009; Wu & Foster, 2014). However, when controlling for event duration, replay strength and detection likelihood did not differ significantly between ripple types (Fig. 1g), suggesting that bursts enhance replay primarily through extended temporal windows rather than intrinsic signal differences.

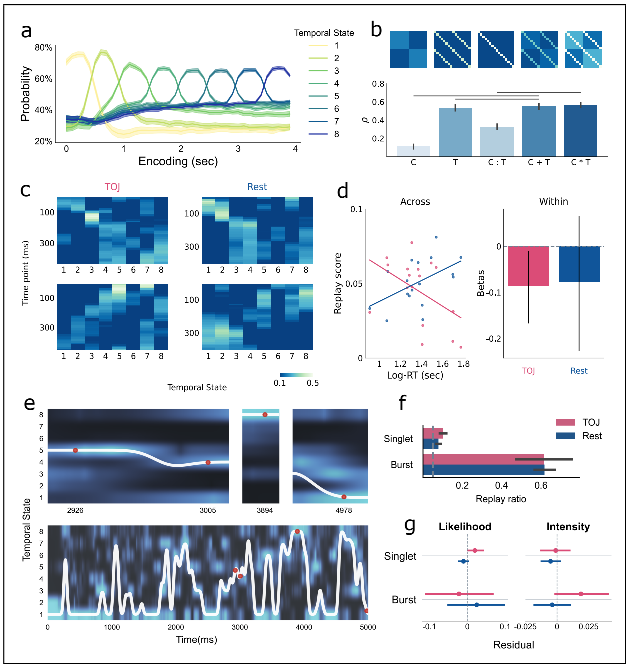

Figure 1: a. Predicted probabilities for each temporal state. b. Model-based RSA comparing five models: content-specific (C), time-specific (T), entangled (C:T), orthogonal (C+T), and full interaction (C*T). Horizontal bars mark significant contrasts (FDR < 0.05). c. Example reactivation heatmaps from single trials showing forward (top) and reversed (bottom) replay. d. On-task and off-task replay play distinct roles in memory. Left: group-level analysis; Right: trial-level analysis. e-g. Cortical replay aligns with hippocampal SWRs. Replay is more frequent in ripple bursts than singular ripples, but this difference is explained by event duration.

Conclusion

Our findings reveal human time-cell-like population codes that generalize across content, compress over time, and form conjunctive what × when representations. Replay of these codes during retrieval and post-retrieval rest show a functional dissociation – on-task replay strength is associated with faster retrieval, suggesting a real-time role in guiding memory access, whereas off-task replay is stronger in participants with weaker memory, implying a role in post-hoc consolidation. Notably, we found that neocortical replay events were temporally aligned with hippocampal sharp-wave ripples, supporting the idea that replay is coordinated between the hippocampus and neocortex.

Together, we demonstrated the replay of factorized temporal trajectories in human episodic memory in a manner similar to the well-established spatial replay phenomenon. Our findings indicate that the hippocampal-cortical replay mechanism supports not only the reconstruction of “where” and “what” but also “when”, revealing an important but previously overlooked dimension in the generalized cognitive map.

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