Title: Hippocampal ripples initiate cortical dimensionality expansion for memory retrieval

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Abstract

How are past experiences reconstructed from memory? Learning is thought to compress external inputs into low-dimensional hippocampal representations, later expanded into high-dimensional cortical activity during recall. Hippocampal ripples—brief high-frequency bursts linked to retrieval—may initiate this expansion. Analysing intracranial EEG data from patients with pharmaco-resistant epilepsy during an episodic memory task, we found that cortical dimensionality increased following ripple events during correct, but not incorrect, retrieval. This expansion correlated with faster reaction times and reinstatement of the target association. Crucially, hippocampal theta and cortical gamma phase–amplitude coupling emerged after ripples but before cortical expansion, suggesting a mechanism for ripple-driven communication. Ripple events also marked the separation of task-relevant variables in cortical state space, revealing how hippocampal output reshapes the geometry of memory representations to support successful recall.

Main Text

Episodic memory allows us to store detailed records of past experiences and consciously reconstruct those experiences at later points in time (*1*). Like any computational system though, the human brain operates with finite resources (*2*). To cope with these constraints, efficient encoding and retrieval of memories is thought to rely on compression and expansion of neural representations (*3*–*6*). During encoding, environmental information flows through cortical and subcortical regions to the hippocampus, where memories are initially stored (*7*, *8*). During retrieval, internal or external cues trigger the hippocampus to detect matches with stored traces (*9*). A partial match initiates pattern completion, leading to memory reactivation and reconstruction in cortical networks (*10*, *11*). Yet, how hippocampal pattern completion gives rise to cortical reinstatement remains poorly understood.

Recent studies have begun to conceptualise this process as shifts in the geometric relationships of points in neural state space, a framework that has found broader applications in studies of decision-making and working memory (*12*–*19*). We hypothesise that memory retrieval might likewise involve a transformation in dimensionality, such that low-dimensional hippocampal representations are expanded into a higher-dimensional cortical state, allowing mnemonic information to be decoded for successful recall (*5*, *10*, *20*, *21*). Preliminary evidence supports this hypothesis, showing a shift from semantic to perceptual representations along the ventral visual stream during retrieval (*22*–*26*). However, whether and how the hippocampus might initiate this dimensionality expansion is unclear.

One potential means to drive cortical representational expansion is through hippocampal ripples. Ripples are known to coordinate the transfer of compressed representations and changes of brain-wide functional connectivity during offline periods in rodents (*27*–*31*). In humans, an increase of hippocampal ripple rates precedes episodic memory recall (*32*–*37*) and neocortical reinstatement of previously encoded memories consistently follows hippocampal ripple events (*32*–*35*). In parallel, theoretical accounts and empirical evidence have highlighted cross-frequency interactions—particularly theta-gamma-phase–amplitude coupling (TG-PAC) —as a mechanism for coordinating long-range communication (*38*–*44*). While TG-PAC has been widely studied during mnemonic processing particularly within hippocampus (*45*–*53*), its role during retrieval, and specifically in mediating ripple-initiated cortical transformations, remains largely unexplored.

We hypothesise that the reconstruction of information in cortical regions is supported by a ripple-based mechanism, where compressed representations are expanded via PAC-based

connectivity between hippocampus and cortex. To test this hypothesis, we analysed intracranial data from 12 patients with pharmaco-resistant epilepsy as they performed an associative memory task (Fig. 1, A and B, fig. S1). We asked whether ripple events could trigger both an increase in cortical representational dimensionality and TG-PAC between hippocampus and cortex—linking local hippocampal dynamics to global cortical transformations during successful episodic retrieval (Fig. 1C).

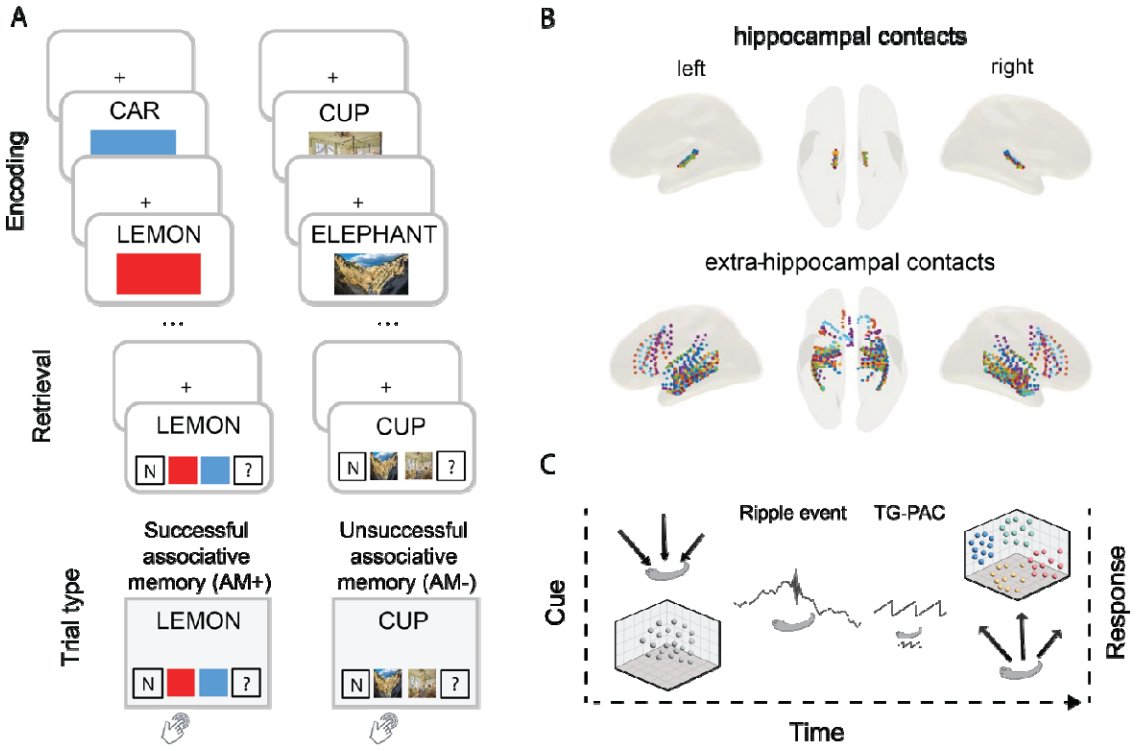

Fig. 1. Paradigm, implantation scheme, hypothesis

(A) During encoding, participants associated a noun either with one of two colours (*left*) or one of two scenes (*right*; alternating across runs). During retrieval, participants were prompted with the noun alongside response options, yielding either successful associative memory (AM+) or unsuccessful associative memory (AM-; combining incorrect and 'don't know' responses). **(B)** Hippocampal (*top*) and extra-hippocampal (*bottom*) iEEG contacts included in the analyses, highlighted in different colours for each participant. **(C)** Schematic depiction of the hypothesis: During encoding, the representation of an event is stored in hippocampus as a lower-dimensional pointer to the higher-dimensional representation in cortical areas. During retrieval, hippocampal ripples initiate a process that initiates a hippocampal-cortical connectivity through theta-gamma phase-amplitude coupling (TG-PAC), leading to the low-dimensional representation being expanded in cortical areas, which is linked to behavioural memory performance.

Behavioural results

The experiment yielded a balanced amount of successful and unsuccessful associative memory trials (AM+: M = 49.95%, SE = 5.12%; AM-: M = 50.05%, SE = 5.12%; t(1,11) = -.01,

p = .992). Response latencies for AM+ trials were faster (M = 1.90 sec, SE = .12 sec) than for AM- trials (M = 2.06 sec, SE = .12 sec; t(1,11) = -2.68, p = .021).

Greater ripple-density for successful retrieval

On average, 787.33 hippocampal ripples (SE = 145.97) per participant were detected during all retrieval trials, after excluding false positives, with a spectral mean peak at 89.17 Hz (SE = .57 Hz) (Fig. 2A; fig. S1 for participant-specific ripple plots). Previous research has shown that ripple density increases prior to successful free recall performance (e.g., (*32*)). To assess whether this finding extends to associative recognition as employed here, we extracted the ripple density for each trial, i.e., the number of ripples normalised by the trial's reaction time, and averaged across trials in each condition. Ripple density was higher during AM+ (M = .24 Hz, SE = .03 Hz) compared to AM- (M = .19 Hz, SE = .02 Hz), t(11) = 3.58, p < .01 (Fig. 2B).

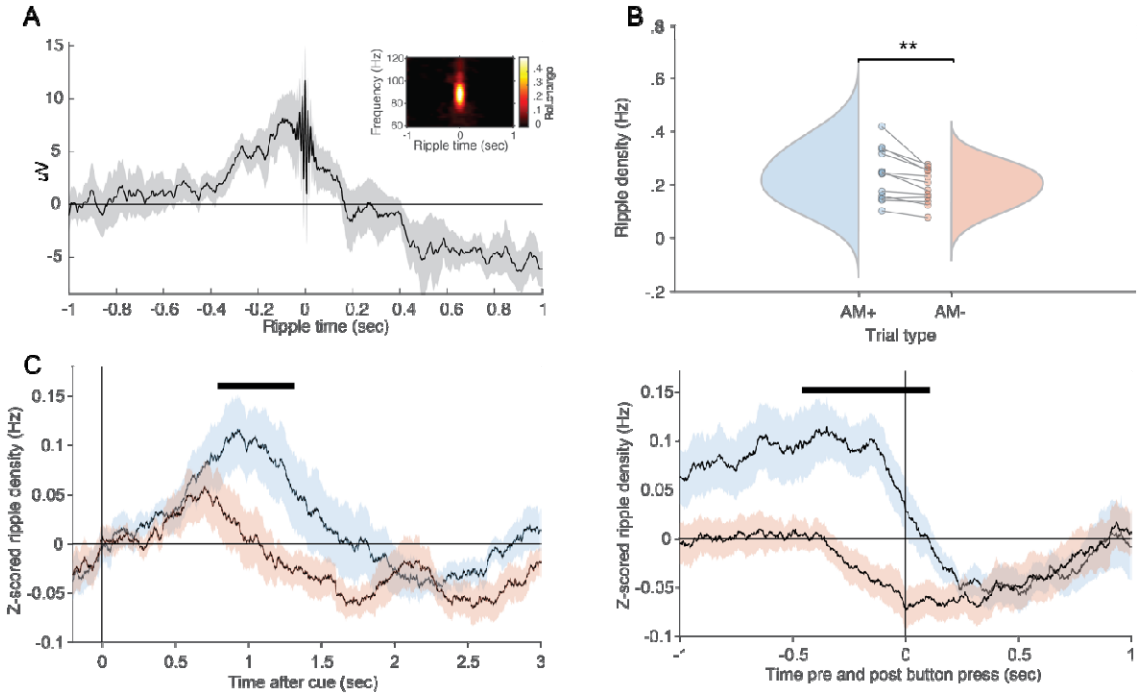

Fig. 2. Hippocampal ripple density increases during successful memory retrieval

(**A**) Grand average hippocampal ripple for all participants, aligned to ripple peak at time 0, with spectral grand average as inset, showing a peak at 89 Hz. (**B**) Ripple density significantly differed between AM+ and AM-. Circles represent participants. (**C**) Ripple density dynamics across time. *Left*: aligned to retrieval cue onset. *Right*: aligned to response time. Horizontal black lines denote significant differences between AM+ and AM- (p < .05, corrected for multiple comparisons across time).

Additionally, we examined whether the increased ripple rate occurred at specific time points during the successful retrieval and observed that ripple density was increased 800-1400ms post cue (for cue-aligned data; Fig. 2C, left) and leading up to the retrieval response (for response aligned data; Fig. 2C, right). These findings are consistent with previously reported latencies of episodic memory processes (*54*).

Neocortical reinstatement is linked to hippocampal ripple events

Building on these findings, we next examined the relationship between hippocampal ripple events and the reinstatement of information from encoding. Specifically, we assessed whether cortical patterns present during encoding re-emerged around ripple events during retrieval.

Our results confirm that ripple-locked memory reinstatement underlies successful associative recognition memory (AM+). The successful decoding of memory content was closely yoked to ripple peaks in our data and continued until the end of the analysis epoch (see figure S2 for various control analysis confirming that reinstatement was specific to the ripple latency of the current trial). This extends previous findings of the role of hippocampal ripples in the replay of encoding activity during free recall of verbal material (*34*) and suggests a generalised role of ripples in the reinstatement of information-rich cortical representations.

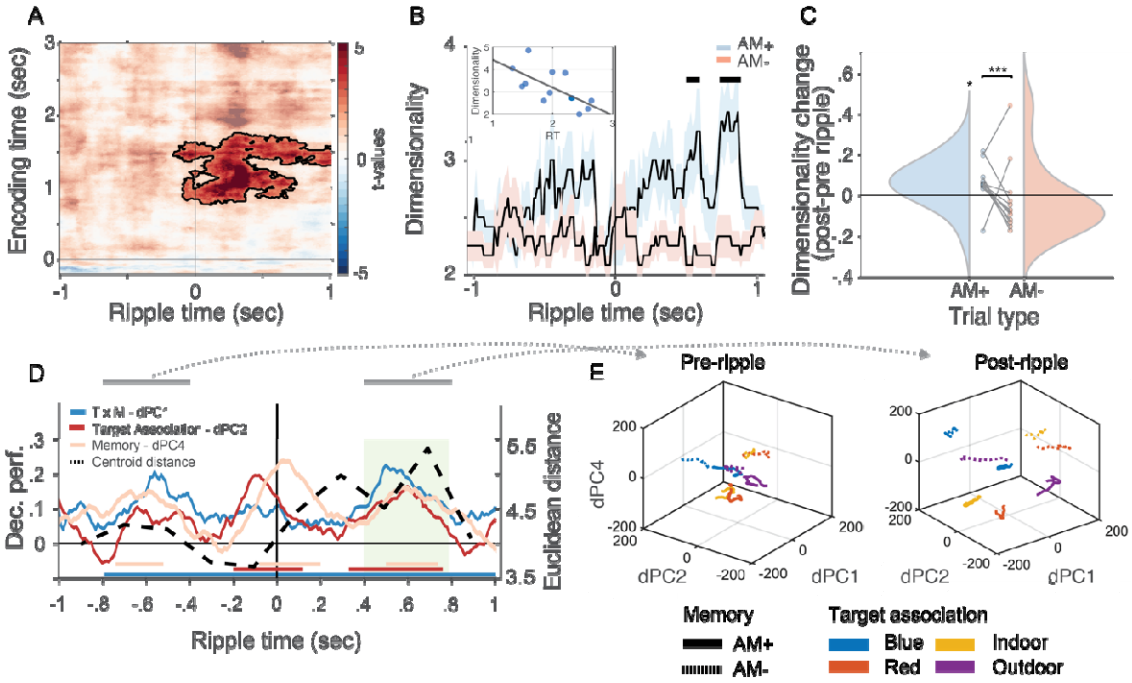

Fig. 3. Target memory decoding and dimensionality transformation are locked to ripple events.

(A) Stimulus-locked encoding x ripple-locked retrieval target decoding accuracies. Results show significant increase of cortical target decodability for successful vs. unsuccessful retrieval following hippocampal ripple events (p < .05, corrected for multiple comparisons). (**B**) Estimating dimensionality for cortical contacts yielded significantly higher dimensionality for AM+ (blue) versus AM- (red) following ripple events (time 0 on x-axis). Inset: The increase in dimensionality was significantly negatively correlated with reaction time. (**C**) Linear mixed-effects modelling (Epoch Half: pre and post ripple, Trial Type: AM+ and AM-) of cortical dimensionality revealed a significant interaction, indicating a greater increase in dimensionality post-ripple for AM+. Asterisks denote significance compared to 0 for AM+ and the interaction of pre and post ripple time-window and AM+ and AM-. **(D)** dPC1, 2, and 4 revealed significant decoding accuracy of target identity in the time window of dimensionality expansion (highlighted in green bar). Significant intervals of decodability are highlighted with horizontal lines. Euclidean distance between clusters increased around ripple onset with a peak 700ms post ripple-events (dashed line). **(E)** Plotting dPCs 1, 2 and 4, showed overlapping representations of experimental variables before ripples (left), whereas their separability increased after ripples (right).

Hippocampal ripple-induced dimensionality expansion increases the separability of cortical representations

These findings suggest that hippocampal ripples initiate a cortical "decompression" of memory representations, allowing latent information to be reconstructed during retrieval (*5*, *10*, *20*, *21*) (Fig. 1C). To formally test this, we first examined changes in representational geometry using principal component analysis (PCA), applied to iEEG data time-locked to ripple events.

We found that cortical dimensionality significantly increased following ripples during AM+ trials, compared to AM− trials, with effects emerging 470–840 ms post-ripple (two clusters; both p<.05). Dimensionality estimates were robust across parameters (fig. S3, A and B) and strongly correlated with the original signal ($r_{spearman}$ .87, p < .001; fig. S3C). Linear mixed-effects modelling confirmed higher dimensionality for AM+ trials overall (Estimate = .09, SE = .03, t(19,988) = 2.82, p = .005), and for post- vs. pre-ripple epochs (Estimate = .14, SE = .03, t(19,988) = 4.39, p < .001), with a significant interaction indicating greater ripple-induced expansion for remembered events (Estimate = -.09, SE = .02, t(19,988) = -4.16, p < .001; Fig. 3C). Paired samples t-tests supported this effect, showing increased dimensionality following ripples in AM+ trials (before: M = 2.43, SE = .05; after: M = 2.50, SE = 0.06; t(11) = 2.22, p = .049) , but no change in AM− trials (before: M = 2.44, SE = 0.06; after: M = 2.41, SE = 0.06;), t(11) = -0.45, p = .66).

Crucially, higher post-ripple dimensionality during AM+ trials was associated with faster response times ($r_{spearman}$ = -.669, p = .02; Inset Fig. 3B), and stronger cortical reinstatement ($r_{spearman}$ = .656, p = .02), linking representational expansion to both behavioural and neural markers of successful retrieval. Control analyses confirmed that these effects were specific to ripple events and not observed in surrogate data (fig. S4), reinforcing the functional role of ripple-triggered dimensionality expansion.

While PCA preserves the geometry of neural activity while maximising variance, and LDA enhances interpretability by maximising class separation, each has limitations. PCA mixes task-related variance and does not isolate the contribution of experimental variables, whereas LDA distorts the original geometry of the neural state space in service of classification. Demixed PCA (dPCA; (*55*)), addresses both limitations by simultaneously reducing population activity and disentangling it into components aligned with specific task parameters. As illustrated in Kobak et al. (*55*), dPCA separates latent structure in a way that retains both class-specific information and the original representational geometry, making it particularly well-suited for characterising the organisation and temporal evolution of memory-related cortical states. Using this approach, we could examine how ripple events affected the organisation of cortical states, not just their dimensionality (*55*).

We reconstructed neural activity using components reflecting target association (blue, red, indoor, outdoor), memory performance (AM+ and AM-), their interaction (target association x memory performance), and a condition-independent component reflecting time. According to our hypothesis, cortical representations of these variables would separate during the period of dimensionality expansion (~400–800 ms post-ripple; highlighted in green in Figure 3D), thereby enhancing decodability in high-dimensional space.

We first confirmed that our reconstruction accurately captured the data. Specifically, the first 50 dPCs accounted for as much variance as our estimated total signal (see Supplementary Materials, and figure S5A). To assess whether these demixed components carried task-relevant information, we applied cross-validated decoding, which tests whether the structure revealed by dPCA generalises to unseen data, providing a direct readout of when and how experimental variables are represented in neural population activity (*55*).

Among all components, the interaction between target association and memory performance (dPC1) explained most variance (fig. S5B), capturing retrieval-related dynamics. This component showed high decoding accuracy across almost the entire epoch and peaked shortly after ripple events. The second component (dPC2), which captured target

association-specific brain dynamics, showed significant decoding accuracy both around ripple events and during dimensionality expansion (Fig. 4A and fig. S5D). Finally, the fourth component (dPC4), linked to memory performance, significantly distinguished AM+ from AM- trials, with effects emerging shortly after ripple events and during dimensionality expansion (Fig. 4A and fig. S5F). For full output, see figure S5.

These findings confirm that dPCA effectively disentangled experimental variables in a lower-dimensional space. To quantify this representational reorganisation, we applied k-means clustering to the dPCA components and assessed the Euclidean distance between clusters. To evaluate clustering quality, we used the Silhouette score, where higher scores indicate stronger clustering. Using 200 ms time bins around ripple events, we observed increased cluster separation beginning at ripple onset and peaking ~700 ms later (Fig. 3D, dashed line). To further quantify this effect, we plotted the state-space organisation of these components during dimensionality expansion (400-800ms post-ripple events) and compared it to corresponding pre-ripple period (400-800ms pre-ripple). Before ripple events, we identified six clusters (silhouette score = .83), whereas eight clusters emerged after ripple events (silhouette score = .90) (Fig. 3E). This was accompanied by a significant increase in Euclidean distance between clusters (pre-ripple: $M = 4.06$, $SE = .044$; post-ripple: $M = 4.78$, $SE = .048$; $t(319) = 5.04$, $p < .01$). A similar pattern emerged when using dPC 1, 3, and 4 (fig. S5H, and Supplementary materials). In both visualisations, we observed a clear separation of all experimental variables following ripple events, a pattern that was less distinct before ripple onset.

Theta-gamma phase-amplitude coupling coordinates information flow between hippocampus and cortex

Our results demonstrate that hippocampal ripples initiate a cortical expansion during episodic memory retrieval in which the separation between experimental variables increases. But what mechanisms enable this transformation of information? A candidate mechanism is the coupling between hippocampal theta and cortical gamma rhythms (*38*, *39*, *44*, *56–58*). Despite theoretical accounts emphasising its importance, there is currently little direct evidence in humans that theta–gamma-phase-amplitude-coupling (TG-PAC) supports long-range communication during episodic memory retrieval.

One likely reason for this gap is the considerable variability in retrieval timing across trials, which poses a challenge for aligning neural events consistently. Our findings suggest that hippocampal ripples can be leveraged to pinpoint the exact moments of reinstatement. Thus, we hypothesised that communication between the hippocampus and cortex would occur

shortly after ripple onset, but prior to the cortical expansion of memory representations, and would be critical for reconstructing the memory trace. To test this, we examined TG-PAC in the time window surrounding ripple events.

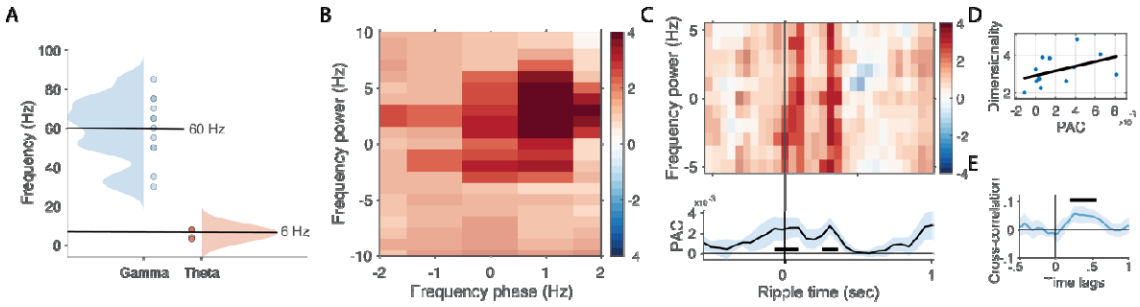

Fig. 5. Phase-amplitude coupling following ripple events are related to dimensionality expansion.

(A) On average gamma oscillations peaked at 60 Hz, whereas theta on average peaked at 6 Hz. **(B)** Significant TG-PAC around peak frequencies for respective frequency (0 on x and y axes). **(C)**. Top: A time-resolved TG-PAC commencing around ripple events and persisted for approximately 400ms after the events. Bottom: Plotting the time-resolved TG-PAC averaged across the y-axis in top panel. **(D)** A positive correlation between TG-PAC and cortical dimensionality expansion, such that stronger TG-PAC was related increased dimensionality expansion. **(F)** A cross-correlation showed that TG-PAC leads dimensionality expansion with a peak at approximately 260ms.

We identified peak theta and gamma frequencies in hippocampal and cortical signals after removing the 1/f background using the FOOOF algorithm (*59*). Time–frequency data were then aligned to these peaks (±2 Hz for theta, ±10 Hz for gamma), and phase–amplitude coupling was computed. Empirical PAC values were compared to a null distribution generated by shuffling trials 250 times per participant and time point. This allowed us to assess TG-PAC in narrow-band activity centred on peak frequencies, time-locked to ripple events (–1 to +1 s). The average peak theta and gamma frequencies were 6.08 Hz (SE = 0.69 Hz) and 59.58 Hz (SE = 4.75 Hz), respectively (Fig. 4A). This revealed significant coupling between hippocampal theta phase and cortical gamma amplitude around the identified peaks ($p_{cluster}$<.05; Fig. 4B).

To examine the timing of TG-PAC relative to ripple events, we conducted a time-resolved analysis using sliding windows. This revealed that coupling emerged shortly after ripple onset and persisted for ~300 ms ($p_{clusters}$ < .05; Fig. 4C). Notably, TG-PAC strength in this post-ripple window correlated with ripple-related increases in cortical dimensionality (r = .59, p = .04; Fig. 4D), linking cross-frequency coupling to representational transformation during retrieval.

We hypothesised that TG-PAC would follow hippocampal ripples but precede cortical dimensionality expansion. To test this, we performed a cross-correlation analysis against a null distribution of 1000 phase-shuffled surrogates. The analysis revealed a significant positive lag, peaking at ~260 ms ($p_{cluster}$ = .02; Fig. 4E), suggesting that TG-PAC may play a mechanistic role in triggering the cortical expansion of memory representations following ripple events.

Discussion

Episodic memory is thought to optimise neural processing by compressing information during encoding and expanding it during retrieval (*3–6*). In particular, the hippocampus plays a central role in this dynamic, matching retrieval cues with stored memory traces and triggering pattern completion to reconstruct the full memory in the cortex (*9–11*). Yet, the neural mechanism through which hippocampal pattern completion gives rise to cortical memory reinstatement remains poorly understood.

We hypothesised that memory retrieval involves a transformation in neural dimensionality. Specifically, that low-dimensional representations in the hippocampus expand into high-dimensional cortical activity patterns. This shift would allow higher order areas to decode rich mnemonic content (*5*, *10*, *20*, *21*). Leveraging the spatial and temporal resolution of human intracranial EEG (iEEG) while participants performed an associative memory task, we demonstrate that that successful memory retrieval was associated with stronger reactivation of encoding-related cortical patterns (Fig. 3A). Notably, this was accompanied by an increase in neural dimensionality (Fig. 3, B–C), which was linked to both faster response times (Fig. 3B) and greater reinstatement strength—suggesting a functional role for dimensional expansion in supporting retrieval.

Our findings position hippocampal ripples as key triggers of cortical reinstatement during episodic memory retrieval. While prior work has linked ripples to hippocampal–cortical communication and memory-related activity in both humans and non-human animals (*29*, *30*, *32–35*, *60–63*), we show that ripples are temporally aligned with both increased cortical dimensionality and reinstatement of encoded information. This extends previous literature by providing direct evidence that ripples mark a transition from compressed to high-dimensional cortical states supporting the reconstruction of specific mnemonic content. Moreover, our results suggest that ripple-related reflect a broader cortical mechanism for memory retrieval.

In our study, ripple-triggered cortical reinstatement occurred reliably during associative retrieval and was tightly time-locked to the onset of ripple events (Fig. 2A, fig. S2). Ripple density was also higher during correct trials, particularly in the pre-response period, suggesting that that ripples functionally drive cortical memory reactivation. Crucially, this reinstatement was accompanied by an increase in neural dimensionality. The finding puts forward a novel account of ripple events that do not simply trigger the reactivation of static memory traces, but instead facilitate an expansion of compressed representations into complex, high-dimensional cortical states. Such expansion may reflect the recruitment of a

broader set of cortical areas and the unfolding of richer, more differentiated representational patterns across the network, which then enables flexible coding of specific mnemonic content.

Our findings are also in line with recent work on the time-scales of hippocampal–cortical interactions during memory retrieval. Michelmann and colleagues (*64*) reported that hippocampal activity precedes cortical reinstatement by ~740 ms during predictive recall under naturalistic conditions, while in another study, the same authors found that hippocampal–cortical information flow precedes cortical state transitions by 500–700 ms during memory search (*65*). In line with these findings, we observed a ~400–800 ms lag from hippocampal ripples to cortical dimensionality expansion and a maximal separability of task-related variables at 700 ms post-ripples. The duration of this effect and its extended temporal window are evidence that hippocampal-driven reactivation unfolds over many synaptic transmission points to realise the expansion of a memory-trace. I.e., hippocampal outputs may initiate distributed cortical reorganisation and enable the dynamic reconstruction of mnemonic content across time and brain regions (*66*, *67*).

To characterise the representational changes that accompany this process, we used demixed principal component analysis (dPCA). Task-relevant variables, such as memory accuracy and target identity, became more separable following ripple events (Fig. 3E), with this separability peaking precisely at the time of dimensionality expansion (Fig. 3D). The neural state space also became more complex, as indicated by an increased number of optimal clusters and greater Euclidean distances between them. These results suggest that ripples support the cortical “decompression” of memory content, allowing for finer-grained separation of mnemonic features.

In our data, the increase in representational structure did not differentiate between correctly remembered and forgotten associations (Fig. 3E, right). This suggests that the ripple-mediated reorganisation of cortical dynamics alone is not diagnostic of retrieval success and other elements can cause memory processes to fail. This mirrors findings in non-human primates, where structured neural representations were observed even in error trials during working memory tasks. For example, Rigotti and colleagues found that although dimensionality collapsed in incorrect trials, task-relevant information could still be decoded—indicating an underlying structure (*68*). Similarly, in our data, incorrect trials showed lower overall dimensionality (Fig. 3B), but retained structured representations of task variables (Fig. 3E). These findings suggest that absolute separability is not the sole determinant of retrieval

success; rather, it is the richness or expressiveness of the neural state—as assessed via PCA (Fig. 3B)—that better predicts retrieval speed and accuracy.

To our knowledge, there is currently no direct evidence in humans for hippocampal theta–cortical gamma phase–amplitude coupling (TG-PAC) during episodic memory retrieval. Here, we show that TG-PAC peaks shortly after ripple events (Fig. 4C) and precedes an increase in cortical dimensionality by ~260 ms (Fig. 4E), suggesting it may act as a bridge between the initiation and reconstruction of retrieved events. This extends previous findings of TG-PAC during encoding and retrieval in the hippocampus (*45*, *47*, *58*, *69*), during spatial memory retrieval (*70*), and across distributed cortical areas during autobiographical recall (*71*).

While prior studies have linked slow and fast gamma to encoding and retrieval, respectively (*44*, *72*, *73*), we found no clear frequency split—participants showed peaks in both bands. These differences may reflect region-specific gamma dynamics outside the medial temporal lobe.

Our findings extend recent work linking neural dimensionality to flexible coding in decision-making and navigation (e.g., (13)), showing that episodic retrieval also involves dynamic, high-dimensional cortical states (5). Events with greater dimensionality during encoding are more likely to be remembered (74), raising the possibility that rich encoding geometry facilitates later reconstruction. Future work should test whether dimensionality at encoding predicts reinstatement fidelity.

We propose a framework in which ripples trigger a shift from compressed hippocampal codes to expanded cortical states. This transition may be mediated by ripple-induced synchrony (75), followed by cortical desynchronisation in alpha/beta bands (76), which has been linked to improved memory fidelity and recall (77, 78). Such desynchronisation may support low-synchrony, high-dimensional representations that promote selective decoding while reducing interference (68, 79–82). Understanding how ripple-induced synchrony interacts with cortical desynchronisation will be an important direction for future research on the temporal dynamics of memory reinstatement.

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Visualization: C.K.

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Project administration: C.F.D.

Supervision: S.M. and C.F.D.

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Competing interests

Authors declare that they have no competing interests.

Data and materials availability

The data and code that support the conclusions of this study are available upon reasonable request from C.K. (kerren@cbs.mpg.de) and are also accessible online at GitHub.

Supplementary Materials

Materials and Methods

Figs. S1 to S5

Tables S1

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