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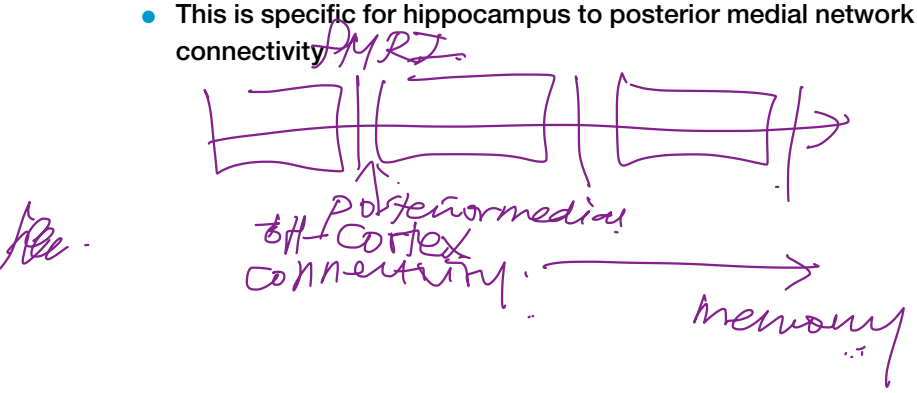
Hippocampal-cortical interactions during event boundaries support retention of complex narrative events

Highlights

- Humans divide ongoing experiences into discrete events
- We tested how the hippocampus communicates with cortex during encoding using fMRI
- Connectivity at the end of events is associated with better subsequent memory
- This is specific for hippocampus to posterior medial network connectivity



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In brief

Barnett et al. explored functional connectivity of the hippocampus during the encoding of naturalistic events. Counter to many previous memory theories, communication between the hippocampus and neocortex was particularly important at the offset of events.

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Hippocampal-cortical interactions during event boundaries support retention of complex narrative events

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SUMMARY

According to most memory theories, encoding involves continuous communication between the hippocampus and neocortex, but recent work has shown that key moments at the end of an event, called event boundaries, may be especially critical for memory formation. We sought to determine how communication between the hippocampus and neocortical regions during the encoding of naturalistic events related to subsequent retrieval of those events and whether this was particularly important at event boundaries. Participants encoded and recalled two cartoon movies during fMRI scanning. Higher functional connectivity between the hippocampus and the posterior medial network (PMN) at an event's offset is related to the subsequent successful recall of that event. Furthermore, hippocampal-PMN offset connectivity also predicted the amount of detail retrieved after a 2-day delay. These data demonstrate that the relationship between memory encoding and hippocampal-neocortical interactions is dynamic and biased toward boundaries.

INTRODUCTION

Since the pioneering work of Ebbinghaus,[1] researchers have studied memory by investigating recognition or recall of lists of verbal stimuli or pictures. Neuroscience research in this tradition has shown that memory for this kind of arbitrary episodic information is supported by the hippocampus, which is thought to index neocortical representations during encoding of an event.[2–6] Real-world events, however, are far from arbitrary. Considerable evidence suggests that we can use our prior knowledge of how structured events typically unfold to generate mental models (called event models) that enable inferences about current experiences and predictions of upcoming information.[7–9] When we encounter information that violates the expectations of the current model, we experience an event boundary—a transient moment in time that has been linked to hippocampal encoding[10,11] and a shift to a new event model.[12]

Recent work investigating encoding and retrieval of structured events in films and stories[13–16] has indicated that default mode network (DMN) regions, including the medial and lateral parietal cortex, medial prefrontal cortex (mPFC), and medial temporal cortex, carry event information in multivariate fMRI activation patterns, which may represent our internal event models.[10,17–19] During encoding of naturalistic events, DMN regions accumulate information on the scale of minutes,[16] form stable activation patterns within events, and greatly shift their patterns at points that coincide with subject-identified event boundaries.[10,20,21] Together, the evidence suggests that the DMN may accumulate and carry event model information.[22] Hippocampal activity, on the other hand, increases at event boundaries,[23,24] which, in turn, coincide with pattern shifts in the DMN.[10] This hippocampal activity at the end of an event is reliably correlated with successful encoding of event details.[11,25,26]

Based on this evidence, new computational models of memory have used simulations to show that event information (that gradually accumulates in the DMN) is indexed by the hippocampus preferentially at event offset.[22,27] Further, indexing during the middle of an event was associated with poor model performance. This is in contrast to traditional models and theories of episodic memory that have highlighted the importance of constant, obligatory hippocampal encoding of all conscious material,[5,28–31] with little or no consideration of event structure. Thus, these differing models produce conflicting predictions regarding memory indexing at event offsets versus middles. Here, we sought to empirically test the hypothesis that hippocampal-DMN interactions at boundaries are especially important for encoding using functional connectivity (FC) as participants encode complex, naturalistic narratives.

Importantly, memory for narrative content contains a rich combination of information. Recalled content can be divided into

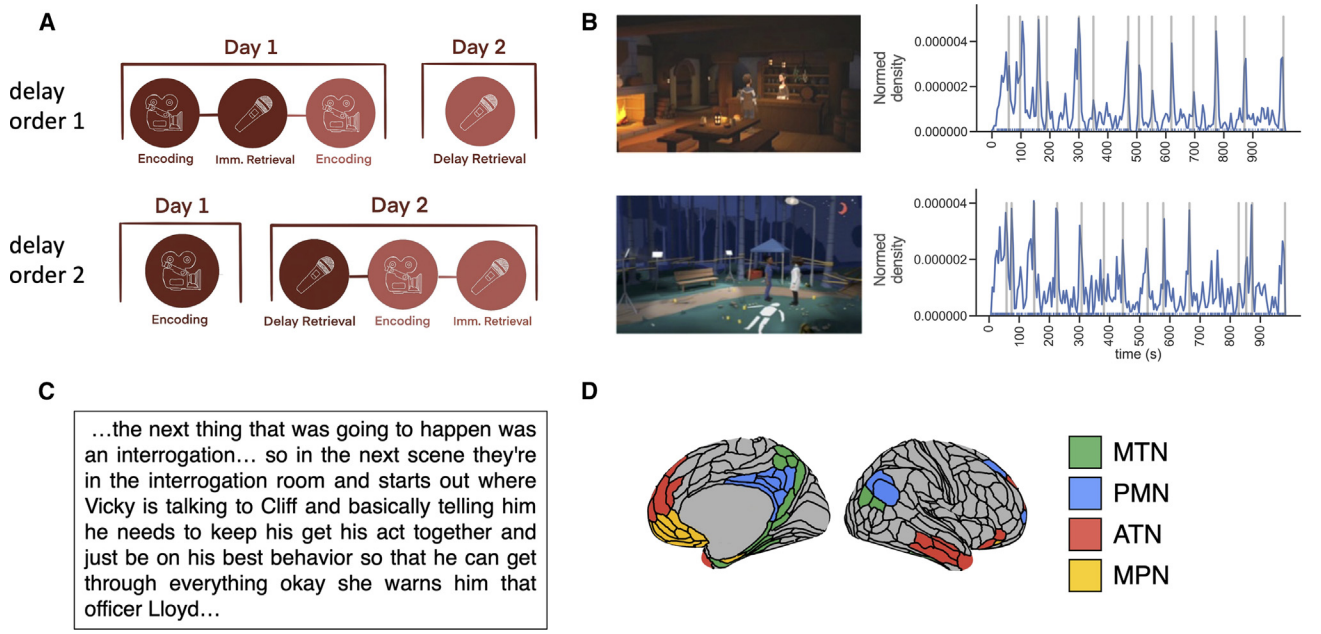

Figure 1. Study design and stimuli characteristics

(A) Overview of the procedure. Participants viewed and recalled two ~16-min cartoon movies during fMRI scanning. The order of the delay and movie was counterbalanced across participants.

(B) A screenshot from each movie with accompanying kernel density estimates of event boundaries from 62 online participants. Vertical gray lines indicate where event boundaries were used in fMRI analysis.

(C) Example excerpt of recall transcription from the recall session during fMRI.

(D) Regions of interest from the Human Connectome Project-Multimodal Parcellation (HCP-MMP) atlas,[40] color-coded by the cortico-hippocampal network to which they belong, as identified in Barnett et al.[35]

details that are central to a narrative (details that may fit an event model) and details that are peripheral or are not crucial to progressing the narrative.[32,33] Central and peripheral details are thought to differ both in retention and neural underpinnings within the hippocampus and subnetworks of the DMN.[32–34] Central details tend to be better retained over time and may depend more on the anterior hippocampus,[33] which shows higher FC with the medial prefrontal (MPN) and anterior temporal (ATN) subnetworks (see Figure 1D) of the DMN,[35–37] whereas peripheral details may depend on the posterior hippocampus, which connects more to the medial temporal network (MTN).[34] Both the anterior and posterior hippocampus strongly connect with the posterior medial subnetwork (PMN) of the DMN,[35,37,38] which consists of the posterior cingulate cortex (PCC), retrosplenial cortex, and angular gyrus (not to be confused with the parietal memory network[39]). We sought to examine whether interactions between the hippocampus and these DMN subnetworks at the offset of events during encoding are important for subsequent recall of details. Because the type (central vs. peripheral) and amount of details recalled vary over time, we examined how hippocampal interactions relate to the recall of central and peripheral details at short and long retention intervals.[32,33] Newer computational models considering event structure have not explicitly made predictions about these different detail types, nor have they made predictions regarding the different DMN subnetworks; thus, we aim to expand on these models and harmonize them with existing network frameworks and memory quality findings.

Here, using fMRI, we tested the idea that the encoding of structured events is supported by cortico-hippocampal interactions at event boundaries. Participants were scanned while viewing two custom-made animated films and subsequently recalled events from these films either in the same scanning session or after a 2-day delay (Figure 1A). We tested the prediction that FC between the hippocampus and DMN subnetworks (Figure 1D) is associated with subsequent retrieval success, and this association is specifically pronounced at the offset of an event. Based on evidence that the recall quality of naturalistic events changes over time,[32,33,41] we also examined whether functional interactions at encoding were particularly important for detailed memory after longer (2 days) versus shorter (5 min) delays.

RESULTS

FC between the hippocampus and PMN at event offset during encoding relates to subsequent retrieval success for events

We tested how FC of DMN subnetworks with the hippocampus during naturalistic event encoding relates to subsequent retrieval success for these events and whether this connectivity is particularly important at the offset of an event, as predicted by Lu, Hasson, and Norman.[27] Events were defined as the time in between

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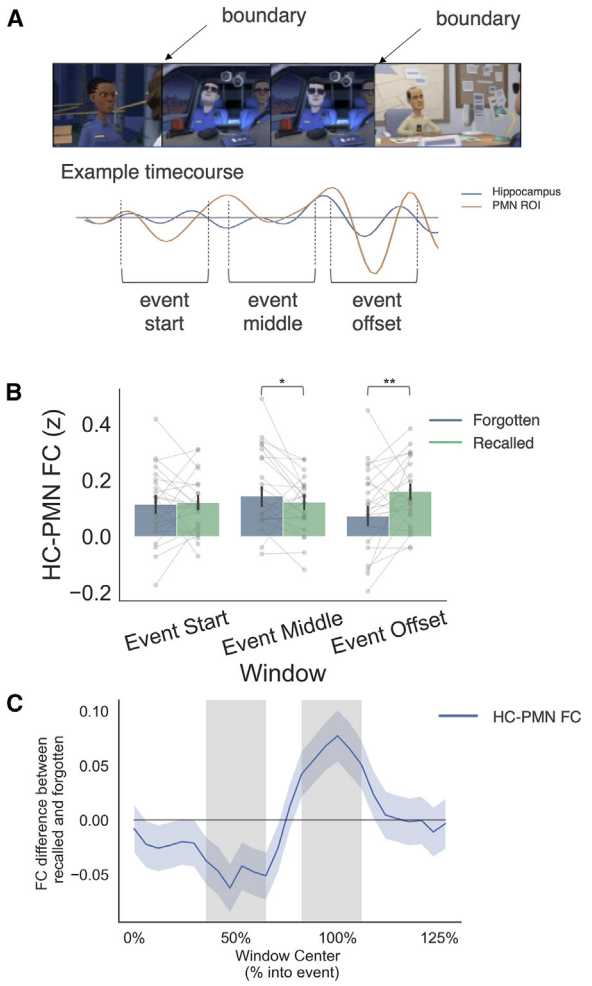

Figure 2. Functional connectivity between the hippocampus and posterior medial network at the end of events is associated with subsequent recall

(A) Schematic example of windows used for FC analysis. 10 TRs on either side of event start, middle, or offset (20 TR total window) were used to estimate FC between the hippocampus and PMN.

(B) FC between the hippocampus and PMN at the event start, event middle, and event offset, split based on whether the event was subsequently recalled or not. Each point represents a participant's mean hippocampal-PMN FC, and each bar with error bars represents the model estimate and 95% confidence interval of the estimate.

(C) Plot showing the estimated mean difference in functional connectivity between events subsequently recalled and forgotten plotted for 20 TR windows centered at increments across events. The blue-shaded bar around the line represents the standard error of the estimate. The gray vertically shaded areas represent clusters of consecutively significant windows that occur at a frequency greater than expected by chance. 0% on the x axis represents the event start plus 5 TRs, whereas 100% represents the event offset plus 5 TRs to account for hemodynamic lag. *$p < 0.05$, false discovery rate (FDR)-corrected. **$p < 0.01$, FDR-corrected for the generalized linear mixed model. See also Figure S3 and Table S1.

event boundaries that were designed into the stimuli and confirmed by an independent sample of 62 online participants who performed event segmentation on the movies (Figure 1B; see STAR Methods for event segmentation task details). Each movie contained 14 events unique events that formed a narrative. For the participants who underwent scanning, we calculated FC between the hippocampus and each region of interest (ROI) within the PMN, MTN, and ATN during encoding for each subject and each event. These networks were examined because we observed that they carried multivariate event representations at encoding and retrieval (see Figure S1). FC values were calculated at 20-time point (TR) time windows (24.4 s per window) centered around each event's start, middle, and offset after accounting for the hemodynamic lag (see STAR Methods). We averaged the hippocampal-ROI FC within networks to get a measure of hippocampal to cortical network FC (Figure 2A). Because the long axis of the hippocampus has differential FC and specialization, we performed this separately for the anterior and posterior hippocampus.[36,42,43] The hippocampal-network FC for each network was entered as a regressor to predict subsequent recall success using a generalized linear mixed-effects model. Memory for an event was determined by examining the free recall of each participant (Figure 1C). If a participant recalled an occurrence from an event, then it was classified as recalled in a binary fashion. In the model, we tested how delay (immediate vs. 2 days), hippocampal long axis (anterior vs. posterior), and temporal window (start vs. middle vs. offset) interacted with encoding FC to explain subsequent retrieval success by including these variables as regressors. We also included hippocampal boundary activity and cortical network boundary activity as regressors to control for univariate activity effects (see STAR Methods) because univariate activity in the hippocampus at stimulus offset has previously been shown to predict subsequent memory.[11]

For the PMN, our analyses revealed a significant interaction between FC and window on subsequent recall success (Wald $X^2(2, n = 24) = 14.15$, $p = 0.0008$), but no interaction of FC with delay, hippocampal long axis, or any combination of these factors (all $p > 0.1$; see Table S1 for test statistics and p values). The significant interactions observed in this analysis reflected the fact that FC was differentially predictive of subsequent memory across different time windows, with significant effects at the event middle and event offset (Figure 2B). At the event start, FC was not significantly related to subsequent recall ($z = 0.6$, $p = 0.55$), but during the middle window, we observed a significant effect such that higher FC was predictive of subsequent recall failure ($z = 2.17$, $p = 0.045$ false discovery rate [FDR]-corrected). To determine the consistency of this effect within the ROIs of this network, we repeated this analysis for each ROI in the PMN individually, finding that the estimated slope showed a negative relationship with memory in 21/24 ROIs, suggesting that nearly all ROIs in the network shared this effect (Figure S2A). Conversely, at the event offset, increased FC between the hippocampus and PMN was predictive of subsequent recall success ($z = 3.21$, $p = 0.004$, FDR-corrected). To determine the consistency of this effect, we repeated this analysis for each ROI in the PMN individually, finding that the estimated slope was positive in 24/24 ROIs, demonstrating a consistent pattern of effects across the network (Figure S2A). These results indicate that the event offset is a critical moment for event encoding processes.

In this model, we also observed that univariate activity in the PMN at the event offset was associated with subsequent recall

Event 정의: 62 온라인 참여자들이 확인한 EB 사이의 시간.
실제 Recall

success (Wald $X^2(1, n = 24) = 17.2$, $p = 0.00003$). This effect was qualified by an interaction with delay (Wald $X^2(1, n = 24) = 15.8$, $p = 0.00007$), in which activation at encoding was positively associated with subsequent recall success after a delay of 2 days ($z = 3.3$, $p < 0.001$) but not after an immediate delay ($z = 0.12$, $p = 0.9$). These effects are independent of the FC effects because they were included in the same model. Univariate hippocampal activity, however, was not a significant predictor in subsequent recall success after accounting for PMN univariate activity, retention delay, or hippocampal-PMN FC (Wald $X^2(1, n = 24) = 0.078$, $p = 0.78$).

A subset of the events in the movies were shorter than 40 TRs in length and, therefore, had overlapping connectivity windows (four events in movie 1, two events in movie 2). Repeating this analysis with those events removed did not change the findings (Table S1). Further, repeating the analyses, calculating FC using larger (30 TRs) or smaller (10 TRs) window sizes, or using more inclusive temporal filtering minimally changed the results (the hippocampal-PMN FC event middle result was no longer present with a window size of 10 TRs; Table S1).

Given that the choice of using windows centered on the onset, middle, and offset may miss the finer dynamics of the FC-memory relationship over the course of an event, we performed a sliding window analysis. Here, we recalculated FC between the hippocampus and PMN for the window centered on the TR at the beginning of an event (after accounting for hemodynamic delay). The center TR of the window was then "slid" through the event incrementally, and FC was calculated at each increment (see STAR Methods). Because we did not observe an interaction across the hippocampal long axis (anterior vs. posterior ROIs) in the prior analysis, the anterior and posterior hippocampus FC values were averaged together. Using a linear mixed model, we calculated the model estimated FC difference between subsequently recalled and subsequently forgotten events at each window. To assess statistical significance, we performed a permutation test in which we randomly shuffled event labels and reran the analysis 1,000 times. We then calculated the maximum number of consecutive windows that were significant at $p < 0.05$ for each permutation to create a null distribution. We then compared the actual number of consecutive windows that were significant at $p < 0.05$ with the null distribution. The results of the sliding window analysis reaffirm the dynamics of the targeted window analysis, showing that FC at the event offset is higher in subsequently recalled vs. subsequently forgotten events ($p = 0.026$) and the reverse is true in the middle of an event ($p = 0.026$) (Figure 2C).

Additionally, one may ask whether these results are specific to hippocampal-PMN interactions or whether they are broadly related to within-PMN interactions. We thus repeated the analysis, examining the average FC between each PMN ROI and every other PMN ROI (excluding itself) to determine whether within-network PMN FC could explain these effects. There was no relationship between PMN-PMN FC and subsequent recall success (Wald $X^2(1, n = 24) = 0.78$, $p = 0.38$) and no interaction with window (Wald $X^2(1, n = 24) = 2.2$, $p = 0.33$) or delay (Wald $X^2(1, n = 24) = 1.07$, $p = 0.3$; see Table S1).

For the MTN, we observed a significant FC by window-by-delay interaction ($X^2(2, n = 24) = 12$ $p = 0.003$), but there was no interaction with the hippocampal long axis ($p > 0.1$; see Table S2 for test statistics and p values). Follow-up testing showed that higher FC between the hippocampus and MTN in the middle of an event during encoding was associated with failure to recall that event after an immediate delay ($z = 3.6$, $p = 0.0007$, FDR-corrected). To determine the consistency of this effect, we repeated this analysis for each ROI in the MTN individually, finding that the estimated slope was consistently negative in 28/30 ROIs, suggesting that nearly all ROIs in the network shared this pattern of effects (Figure S2B). No other relationship between FC and memory was found at any other delays or windows (all $p > 0.05$, FDR).

In this model, we also observed that univariate activity in the MTN at the event offset was associated with subsequent recall success (Wald $X^2(1, n = 24) = 10.4$, $p = 0.001$). This effect was qualified by an interaction with delay (Wald $X^2(1, n = 24) = 18.8$, $p = 0.00001$), in which univariate boundary activation was positively related to subsequent recall success 2 days later ($z = 3.1$, $p < 0.003$) but not with memory immediately after encoding ($z = 0.7$, $p = 0.48$). These effects are independent of the FC effects because they were included in the same model. Univariate hippocampal activity was not a significant predictor of subsequent recall success after accounting for MTN univariate activity, retention delay, or hippocampal-MTN FC (Wald $X^2(1, n = 24) = 0.74$, $p = 0.39$).

Again, restricting this analysis to events longer than 40 TRs did not change the findings, nor did altering the window size (see Table S2). Altering the low-pass filtering threshold did have an influence on the significance of the interaction terms, but the effect of hippocampal-MTN FC in the middle of an event at the immediate delay was still significant at uncorrected levels (Table S2).

For the ATN, we did not observe any significant relationship between FC with the hippocampus at encoding and subsequent recall success, nor any interactions with delay or hippocampal long axis (all $p > 0.05$).

FC between the hippocampus and PMN relates to the number of subsequently retrieved details

Having observed that increased FC between the hippocampus and PMN was predictive of subsequent recall success, we then asked whether hippocampal-PMN FC at encoding related to the number of verifiable details participants reported from the events that were successfully recalled. The audio recordings of each participant's recall were transcribed and scored for the number of details by trained raters (J.S. and R.Y., unpublished data) using the scoring methods from the autobiographical interview[44] to delineate the details a participant recalled for each event they successfully reported. We focused our analysis on "verifiable details," which were details that could be confirmed from the movie.[45] If hippocampal-PMN FC is a measure of successful encoding, then we should expect that events with higher FC will be recalled with more verifiable detail than those with low FC.

A mixed linear model predicting the number of details reported from a retrieved event showed a significant interaction between hippocampal-PMN FC, delay, and window ($F(2, 2{,}566.6) = 5.63$, $p = 0.0008$). There was no interaction with hippocampal long axis ($p > 0.05$; see Table S3 for test statistics and p values). When

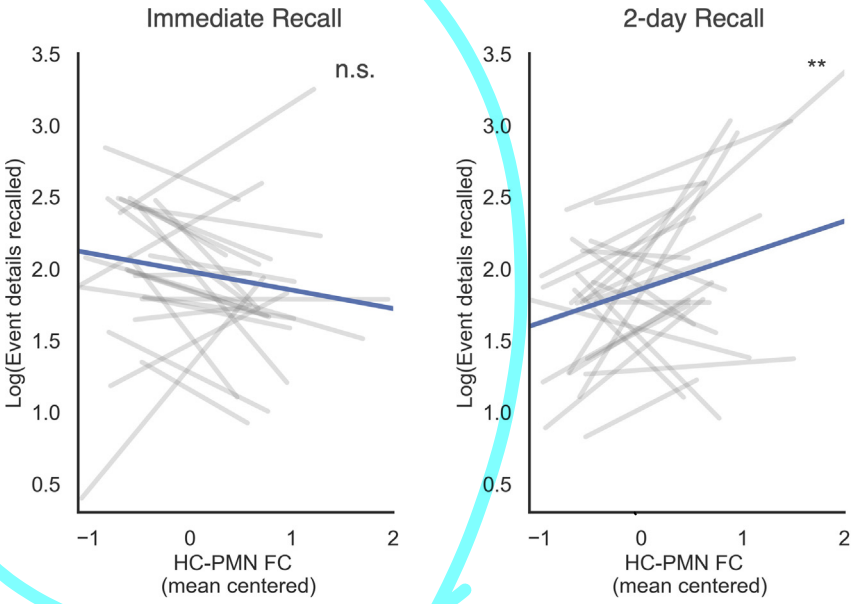

Figure 3. Functional connectivity between the hippocampus and posterior medial network at the end of events is associated with more detailed subsequent memory

Relationship between hippocampal (HC)-PMN FC and the number of subsequently recalled details (log-transformed) for events that were successfully recalled at the immediate and 2-day delayed recall sessions. Each gray line represents the regression line of an individual participant, and each blue line represents the group regression line produced from the linear mixed model. n.s., not significant; **p < 0.01. See also Figure S3 and Table S3.

breaking down the significant interactions, we observed that hippocampal-PMN FC at the event offset was positively associated with the number of details subsequently retrieved from that event 2 days later (t(2,684) = 3.3, p = 0.003, FDR-corrected; Figure 3) but was not associated with the number of details retrieved at the immediate recall phase (t(2,684)= −1.1, p = 0.42, FDR-corrected; Figure 3). This finding dovetails with the above analysis and suggests that the coordinated activity between the hippocampus and PMN at event boundaries is particularly important for forming detailed, retrievable memories. To determine the consistency of this effect, we repeated this analysis for each ROI in the PMN individually, finding that the estimated slope showed this pattern in 22/24 ROIs, suggesting that nearly all ROIs in the network shared this pattern of effects (Figure S2C). We did not observe an association between hippocampal-PMN FC and the number of retrieved events for FC at event onsets (immediate delay: t(2,566) = 0.9, p = 42; 2-day delay: t(2,566) = −1.9, p = 0.09) and middles (immediate delay: t(2,567) = −0.8, p = 0.42; 2-day delay: t(2,567) = 1.4, p = 0.18).

Hippocampal boundary activity is related to the memory quality in a delay-dependent fashion

Previous work has shown that people tend to retain details central to a narrative, or " the gist," longer than details that are peripheral to a narrative.[32] Given that previous work has linked memory granularity to the long axis of the hippocampus,[36,46,47] with the anterior hippocampus playing a role in memory for gist and the posterior hippocampus playing a role in memory for finer-grained details, we hypothesized that encoding FC of the anterior and posterior hippocampus would be differentially related to the number of central and peripheral details recalled. Specifically, we predicted that anterior hippocampus-MPN FC at encoding would relate to the number of subsequently recalled central details because the anterior hippocampus plays a role in gist memory and the mPFC has been linked to schema processing.[48] Further, we hypothesized that FC between the posterior hippocampus and MTN might relate to fine-grained or peripheral details recalled because the posterior hippocampus and medial temporal lobes have been linked with fine-grained, arbitrary detail memory.[48,49] To investigate this, we categorized the verifiable details into central details (details that, if omitted, would alter the interpretation or comprehension of the narrative) and peripheral details (all other verifiable details; see STAR Methods). We tested whether hippocampal to MPN FC predicted central details and whether hippocampal to MTN FC predicted peripheral details, using linear mixed models. However, we did not observe any relationship between recall of these different detail types and hippocampal connectivity with the MPN (central: F(1, 2,646) = 1.4, p = 0.24; peripheral: F(1, 2,640) = 2.8, p = 0.09) or MTN (central: F(1, 2,646) = 0.19, p = 0.66; peripheral: F(1, 2,640) = 0.98, p = 0.32) and no interaction with hippocampal long axis (MPN by long axis for central details: F(1, 2,651) = 0.03, p = 0.87; MPN by long axis for peripheral details: F(1, 2,641) = 0.19, p = 0.66; MTN by long axis for central details: F(1, 2,653) = 1.5, p = 0.22; MTN by long axis for peripheral details: F(1, 2,641) = 1.99, p = 0.15).

Although the overall number of central and peripheral details was unrelated to our hypothesized brain activity, we did see an effect on the proportion of central relative to peripheral details. Specifically, we observed a significant interaction between hippocampal boundary activity and delay in predicting the proportion of central details subsequently recalled (F(1, 849) = 11.6, p = 0.0007). Follow-up on this interaction showed that hippocampal boundary activity was related to a higher proportion of peripheral compared with central details subsequently recalled during immediate retrieval (t(842) = 2.7, p = 0.01, FDR-corrected). After a 2-day delay, however, events that had higher hippocampal boundary activity at encoding were recalled with a higher proportion of central compared with peripheral details (t(843) = 2.2, p = 0.03, FDR-corrected). This suggests that univariate hippocampal boundary activity at encoding impacts the subsequent memory quality for events in a delay-dependent fashion. However, although we may have expected anterior and posterior hippocampal activity to differentially relate to central and peripheral details, we did not observe an interaction with hippocampal long axis (F(1, 835) = 0.08, p = 0.78).

DISCUSSION

Using dynamic, naturalistic stimuli, we demonstrated that interactions between the hippocampus and neocortical networks may be critical for successful encoding. FC between the hippocampus and the PMN at event encoding was associated with subsequent recall success of the event. Critically, the timing of the interactions had a significant impact on this relationship, such that hippocampal-PMN FC at the event offset was positively associated with recall success, but interactions in the middle of an event were inversely related to recall success. Further, the amount of detail retrieved after a delay was influenced by hippocampal-PMN interactions at the event offset at encoding. Our findings suggest that durable memory formation depends on interactions between the hippocampus and neocortex at event boundaries, not for the event that is about to begin but for the event that just finished.

Theories of episodic memory posit that event information represented in the neocortex is translated into a memory trace in the hippocampus.[2–5] The term "neocortex" is remarkably broad in these models because much of the brain is important to our ongoing experience, but there is good reason to believe that a subset of the neocortex, the DMN, plays a specialized role, particularly for event memory. The DMN is functionally connected to the hippocampus[35,50] and has been discussed in terms of memory processing and retrieval[34,51,52] because it is known to be especially active during retrieval of autobiographical memories and recollection[53] but has not been considered to be reliably linked to encoding in traditional memory experiments[54] (although see Ranganath et al.[55]). In traditional memory experiments, lower activity in the DMN has been associated with better subsequent memory.[54,56,57] In the angular gyrus, a primary region of the DMN, lower encoding activity has been linked to better classifier accuracy in distinguishing stimuli category in this area and better subsequent memory.[58] These findings may seem counter to our results that show univariate activity in DMN subnetworks is related to subsequent recall success. Importantly, these effects are often found when taxing memory for arbitrary associations. The use of prior knowledge, however, may impact the DMN's role in encoding. Liu et al.,[59] for example, had participants form face-scene associations using either famous faces or non-famous faces. DMN regions (medial prefrontal, medial parietal, lateral parietal, and parahippocampal) activated more strongly for famous faces at encoding and were linked with subsequent retrieval success in the famous face condition.[59] Similarly, narrative stimuli, such as the stimuli used here, often allow for prior knowledge of event situations to interpret ongoing information and aid in encoding.[12,13,22] In this study, we demonstrated that PMN and MTN boundary activity is related to subsequent memory for narrative events. This is congruent with previous work linking DMN activity to subsequent memory when prior knowledge can be used.[59] Thus, the DMN is likely of particular importance when employing prior knowledge, such as building internal event models, in service of encoding. In contrast, when task demands tax the binding of arbitrary elements, focus on stimulus features in the external world may be more critical, and broad DMN activity may be reflective of internal cognition that is less focused on encoding these features.

Recent work from our group and others has shown that the DMN can be subdivided into subnetworks[35,60–62] that play a role in the representation of naturalistic events.[10,17–19] Among the DMN subnetworks, our findings demonstrated that functional connections between the hippocampus and the PMN supported subsequent memory for events. This finding is consistent with the idea that event model features represented in the PMN are encoded in the hippocampus.[22] One recent computational modeling study has suggested that it might be optimal to selectively encode episodic information at the event offset, particularly when that memory will be subsequently used for comprehension and prediction.[27] This model had a component that tracked features of the ongoing event, akin to event models represented in the PMN. The model also had a component for long-term storage, similar to the hippocampus, in which information from the ongoing event model was encoded into long-term storage at either the middle of events or event offsets. Encoding at the event offset was ideal for model performance,[27] which dovetails with our findings that PMN-hippocampal FC at the event offset during encoding was associated with higher subsequent retrieval success and, at the 2-day delay, more detailed retrieval of the events. Thus, the event offset may represent a window of time for features that have accumulated in the ongoing event model to be encoded into accessible long-term memory representations, as was the case in the model proposed by Lu et al.[27] In rodents and primates, detailed electrophysiological studies have also supported the idea that neocortical input into the hippocampus is gated via the rhinal cortex, such that not all neocortical input that reaches the rhinal cortex is subsequently passed to the hippocampus.[63] Additionally, the model proposed by Lu et al.[27] also found that encoding in the middle of an event was detrimental to model performance, which dovetails with our findings that higher FC between the hippocampus and PMN during the middle of events was negatively associated with recall success. Functional interactions at the middle of events between the hippocampus and the PMN and MTN may reflect the hippocampus encoding incomplete event information, it may reflect the hippocampus reinstating information into these networks, or it may reflect a reset of the event models due to off-task processing (e.g., mind-wandering or future thinking), which could negatively impact comprehension and retrievability of the rest of the event. Although the data here cannot speak to the specific processing occurring, they do suggest that coordinated activity of the hippocampus and PMN during encoding is beneficial to retrieval, particularly when this coordination occurs at the event offset.

An alternative account of event encoding hypothesizes that event models are represented in the hippocampus instead of the PMN.[64,65] For example, according to the model outlined by Griffiths and Fuentemilla,[64] as features of an event are encountered, unique populations of hippocampal neurons are activated to represent those features. The authors claim that this allows the hippocampus to build an ongoing event model of an event that is steadily and proactively encoded as it unfolds. At an event boundary, the sequence of features is rapidly replayed to facilitate retroactive encoding of the final event representation. This logic suggests that ongoing interactions between the hippocampus and neocortex should be necessary and important for encoding, but it makes no strong predictions about these

interactions at the boundary. These predictions do not fit with our observations because we found that hippocampal-cortical FC at the beginning and middle of an event were unrelated to memory (or related to worse memory) and only processing at the end related to subsequent retrieval success. There are several possible explanations that can reconcile these accounts. First, the model proposed by Griffiths and Fuentemilla[64] is largely influenced by studies in which an event is described as a period in which a sequence of arbitrary stimuli is encoded in a stable context.[66–68] Because participants cannot form a predictive model of what to expect in these sequences based on any prior event schemas, the hippocampus may play a much stronger role in binding this sequence of arbitrary stimuli, and the impact of PMN representations is low. When the sequence of events conforms to a familiar structure or schema, such as the sequence of events when one visits an airport or restaurant, the PMN may have a more significant role in forming an event model with a limited role for the hippocampus, as was shown in Baldassano et al.[69] Further, when a sequence of information can be reliably predicted from a PMN event model, the hippocampus may not need to encode each encountered feature, but rather can simply index the PMN model that can accumulate and reconstruct the elements. For example, people with hippocampal damage retain immediate recall of prose information,[70] can tell globally coherent stories,[71] and even show similar multivariate patterns in posterior medial and lateral parietal cortex during movie viewing when compared with controls.[72,73] This suggests that extrahippocampal regions such as the posterior medial cortex represent event models, especially when prior knowledge of events can inform episodes and memories. A modified version of Griffiths and Fuentemilla's account could potentially fit our findings. It may be that, when encoding is particularly successful, the rapid replaying of features represented in the hippocampus at event boundaries leads to increased FC between the hippocampus and PMN. This could be true if the rapid hippocampal replay leads to a rapid replay of event features in neocortex. Given the temporal and spatial resolution limitations of fMRI, we are not able to examine rapid neuronal firing rates within a theta cycle in the hippocampus to determine if event features are incorporated into a sequence of population firings. However, using EEG, Silva et al.[74] have shown that event boundaries trigger rapid replaying of multivariate patterns present in the just-completed event.[74] Thus, future studies using imaging techniques with higher temporal resolution should investigate whether the relationship between memory and hippocampal-PMN interactions at event boundaries is related to the rapid replay of hippocampal sequences that reinstate PMN representations.

Boundaries may also be an optimal time to integrate previously learned information with new events that are narratively linked or semantically related. Prior work from our lab has shown that hippocampal multivoxel patterns show high reactivation at event boundaries when viewing an event that is narratively coherent with a previous event,[45] and, at retrieval, reinstatement is higher for coherent events, leading to better memory. A recent study has shown a similar reactivation result, such that the multivoxel patterns of past events tend to be reactivated at event boundaries, and this is modulated by the similarity of their semantic content.[75] This pattern was shown in the hippocampus, medial temporal lobes, and posterior medial cortex. Forming a coherent narrative has a large effect on the memorability of events.[7,8,76] Although we did not explicitly manipulate narrative coherence in our stimuli, it is possible that variations in coherence and memorability could create the appearance of subsequent memory effect in neural activity[77] such that highly memorable events result in higher hippocampal-PMN offset connectivity. Future work should examine how communication between the hippocampus and DMN affects the integration of coherent vs. non-coherent events in memory and whether causally manipulating this communication impacts memory.

The findings presented here seem to demonstrate a privileged role of the PMN in event memory because we did not observe robust memory effects in other cortico-hippocampal networks. Based on prior memory theories, we hypothesized that MPN FC with the hippocampus would relate to memory for the central aspects of an event. However, we did not observe this effect. Episodic memory studies have highlighted mPFC-hippocampal interactions as a major contributor to schema-related memory,[47,49,78,79] and research using naturalistic stimuli has shown that multivariate patterns in the mPFC generalize between videos that share similar situations[19,69] during viewing. The movie stimuli used in this study depicted narratives that tended to follow classic tropes of either a crime show or a fantasy show. Thus, MPN representations may have pertained to broader fantasy show vs. crime show schemas, which could not differentiate between events within a movie.

FC of the MTN and ATN with the hippocampus was also not associated with subsequent memory retrieval. Previous work has shown that the MTN may play a special role in memory precision and perception[61,80,81] and the ATN plays a special role in object, person, and social processing.[19,52,82] For the MTN, we specifically investigated whether FC with the hippocampus would relate to peripheral details (details that were not essential to the narrative and may reflect more vivid memory). We did not observe this to be the case. Memory assessment in this study was examined as overt free recall of the movies and did not impose any specific focus on precision, social elements, or conceptual elements of memory because participants were encouraged to retrieve every detail they could possibly remember. A memory task focused more on the perceptual or social elements may be more related to hippocampal-MTN or hippocampal-ATN FC, respectively, during encoding and could be the subject of future research.

PMN event representations, in contrast, may be more generalized than MTN and ATN representations. For example, Zadbood et al.[83] scanned participants as they both viewed narrative movies and verbally recalled those movies. They then played the verbal recall of the initial participants to a new set of participants during scanning. Remarkably, multivariate representations in the PCC and angular gyrus were shared in the brains of people watching the movies, those same people recalling the movies, and the new people listening to the recall of the movies[83] suggesting that these areas carry modality-invariant event representations. Even during episodic simulation, when participants must generate an event based on a cue, activation in the PCC and angular gyrus exclusively correlates with the

number of generated details despite the fact that medial and anterior temporal regions are active for this type of task.[84] This broad involvement in event-based processing suggests a privileged role of the PMN in maintaining internal event representations necessary for encoding and reconstructing complex naturalistic memory.

Our findings did not demonstrate any effect of the hippocampal long axis and its preferred connectivity to the subnetworks of the DMN. Although previous studies have shown an impact of granularity[36,42,46,47] and retention delay[33,85–88] on the involvement of the anterior vs. posterior hippocampus, we did not find such effects in our study. To investigate this, we examined how FC in the anterior and posterior hippocampus related to the subsequent recall of central and peripheral details, respectively. Although previous studies have shown a greater drop in peripheral details reported across multi-day delays compared with central details,[32,33] we did not observe a proportional drop in these details. However, these previous reports had used longer delays (7-day delays), which may have allowed for more forgetting of peripheral details or more difficulty in accessing such details, which may explain why we did not observe differentiation along the long axis. We did, however, observe that hippocampal boundary activity at encoding was related to the proportion of central vs. peripheral event details that were subsequently remembered, and this effect varied based on delay. Higher hippocampal boundary activity at encoding of an event was associated with a higher proportion of peripheral compared with central details recalled immediately after encoding. However, for events recalled following the 2-day delay, higher hippocampal boundary activity at encoding was associated with a higher proportion of central compared with peripheral details. This suggests that the same activity that may lead to rich recall at a short delay can lead to a more gist-like memory representation at a longer delay. Previous work has suggested that offline processing between the hippocampus and neocortex can lead to a transformation in the quality or focus of memory transformations.[47,85,89] Boundary activity at encoding may tag these memories for further offline processing, leading to this interaction with memory quality over time. Although we initially hypothesized that the anterior and posterior hippocampus would contribute differently to central and peripheral details, we did not observe an effect of hippocampal long axis in terms of subsequent memory effects.

Our study demonstrates that the influence of hippocampal-PMN FC on memory is dynamic. However, fMRI requires a relatively large window size for estimating FC,[90] which, combined with low temporal resolution, limits the ability to reliably infer the directionality of information transfer. Computational models and theories of memory would predict that event features represented in the cortex or PMN are bound by the hippocampus.[2,22,27] However, we cannot infer the directionality of FC with our data. Further, given the time window used here to calculate FC, we may be capturing back-and-forth interactions between the hippocampus and multiple brain regions of the PMN or MTN rather than a one-time information packet transfer. However, one study that used intracranial recordings found that, at event boundaries during story listening, information flows from the cortex to the hippocampus, which is what we would predict if this time point is important for encoding.[91] Additionally, although the hippocampus shows connectivity with these networks at encoding, it will also increase connectivity with these networks during retrieval, and this increase is related to memory success.[92] Understanding how these interactions vary during spoken recall of naturalistic events, however, requires caution because movement can heavily influence connectivity measures. Finally, we grouped regions together into subnetworks based on a group-averaged community detection solution from an independent sample of participants scanned at rest.[35] Although we were able to find robust effects, recent work has shown that there are individual differences in network organization across participants.[62,93] These individual network estimations are mostly overlapping with group-estimated networks,[94] but future work may be able to rely on individually estimated networks to characterize subtler memory effects.

In conclusion, the present study has presented evidence to extend our understanding of how the brain translates experience into memory by examining the time course of interactions between the hippocampus and neocortex. We discovered that interactions between hippocampus and PMN at the offset of an event, but not at the onset or middle, are beneficial for subsequent recall success and are also associated with more detailed retrieval when events are retrieved after a longer delay. This suggests that the event offset is a critical moment in time for encoding complex, narrative events.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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AUTHOR CONTRIBUTIONS

Conceptualization, A.J.B. and C.R.; methodology, A.J.B., M.N., J.S., R.Y., B.I.C.-S., and C.R.; investigation, A.J.B. and M.N.; analysis, A.J.B., M.N., J.S., R.Y., and C.R.; software, A.J.B.; writing – original draft, A.J.B. and C.R.; writing – review & editing, all authors; funding acquisition, C.R., A.J.B., and B.I.C.-S.; supervision, C.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and code	This paper	https://doi.org/10.5281/zenodo.8411900
Software and algorithms		
fMRIprep	Esteban et al.[95]	https://fmriprep.org/; RRID:SCR_016216
Nipype	Gorgolewski et al.[96]	https://nipype.readthedocs.io/en/latest/; RRID:SCR_002502
Emmeans package for R	Russell V. Lenth	https://cran.r-project.org/web/packages/emmeans/index.html; RRID:SCR_018734
PsychoPy v3.0.0	Peirce et al.[97]	https://www.psychopy.org/; RRID:SCR_006571
SpeechRecognition tool for Python	Anthony Zhang	https://github.com/Uberi/speech_recognition#readme
FreeSurfer	Dale et al.[98]	https://freesurfer.net/; RRID:SCR_001847
AFNI	Cox and Hyde[99]	https://afni.nimh.nih.gov; RRID:SCR_005927
SPM12	Functional Imaging Laboratory	https://www.fil.ion.ucl.ac.uk/spm/software/spm12/; RRID:SCR_007037
lme4	Bates et al[100]	https://cran.r-project.org/web/packages/lme4/index.html; RRID:SCR_015654

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Alexander Barnett (alexander.barnett@utoronto.ca).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Upon publication, data and analysis code will be available via GitHub (https://github.com/ajbarn/hc-pmn-boundary-fc). Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Participants

Functional MRI study

Twenty-nine healthy, young adult participants were recruited from the University of California, Davis, and surrounding area. Five participants were excluded due to scanner artifact or audio recording failures during recall leaving a final sample size of twenty-four ($N_{Females}$ = 14, mean age = 23.5 years [SD = 4.1 years]). All participants were right-handed and neurologically healthy. The study was approved by the Institutional Review Board of the University of California at Davis (IRB #1352490 & IRB # 637028) and adheres to all principles of The Belmont Report. All participants provided written informed consent prior to participation. Participants were compensated $20/hour for their time.

Event boundary estimation

An independent sample of 97 participants ($N_{Females}$ = 45, mean age = 19.9 years [SD = 1.5 years]) from the University of California, Davis, viewed one of the two stimulus movies via the online platform Testable (www.testable.org). After data inspection, participants who made no response (29 participants) and those that responded more than 1.5 times the interquartile range above the third quartile (6 subjects) were excluded resulting in a sample of 62 participants.

METHOD DETAILS

Experimental stimuli

We constructed a set of animated, short movies using Plotagon (https://www.plotagon.com/desktop/). All movies were scripted and produced by the first author (AJB) with voice acting provided by volunteers in the center and with assistance from author (BICS) for audio preprocessing in Audacity v2.4.2. All movies depicted a continuous narrative. A practice movie was created that depicted two characters in conversation and was one-minute in length. The two experimental movies used in scanner were approximately 16.5 minutes in length each (Movie 1, 16:47; Movie 2, 16:22). Both movies consisted of a series of events that each depicted two characters at a time interacting. Each had a total of seven unique characters, and each had a total of eight spatial locations. One movie was set in a medieval, fantasy-like world and the other depicted a crime scene investigation narrative. The movies were designed such that each would elicit 13 event boundaries corresponding to changes in location, changes in time, or changes in the combination of characters shown.

Behavioral tasks

Event boundary rating

An independent sample of 97 online participants viewed one of the two stimulus movies via the online platform Testable (www.testable.org). Participants were presented with one of the two movies, and during viewing, were asked to press the spacebar whenever they perceived that a meaningful event had ended, and another event had begun. Online participant response data was examined for data quality and participants who made no response (29 participants) and those that responded more than 1.5 times the interquartile range above the third quartile (6 subjects) were excluded resulting in a sample of 62 participants. Summed participant inputs over time were modelled with a kernel density function with a 5s bandwidth for each movie and confirmed the temporal location of the intended event boundaries (Figure 1B). One unplanned, but reliable, event boundary was observed in both movies. One unplanned event boundary pertained to characters changing positions within the same scene as they continued the same conversation (characters moved from standing at a bar to sitting at a table). The other unplanned event pertained to a fade to a black screen with written text describing a change in location. The periods in between event boundaries were considered events with each movie having a total of 14 events that were an average of 72 seconds (range 22s – 137s).

Practice recall

Prior to scanning, participants completed a brief example trial of the experiment to get accustomed to the type of task they would be performing in the scanner. After providing written consent, participants viewed a one-minute cartoon video on a desktop personal computer. They were instructed to "watch the video as you would a television show you are interested in" and that they would be asked to remember the video after. They were asked to recall, in as much detail as possible everything they could from the video. They were also asked to recall in temporal order, if possible, but completeness and detail were considered more important than temporal order and, so, if at any point they realized they had missed something, they were instructed to return to that detail. They were instructed to mention every detail they could recall, even if it seemed irrelevant. After participants performed this recall, the experimenter provided a general probe to the participant asking if there was anything else they could recall. Recall data was not recorded, but participants were encouraged to push themselves to retrieve all details they could once they performed the task in the scanner.

Character familiarization

After responding to the practice video, participants were then familiarized with a set of characters that they would subsequently view in upcoming movie stimuli in the MRI scanner task. This was undertaken to improve participant recall of character names during narrative recall to allow better designation of events for memory scoring. Participants were presented with a total of 14 character-avatars using PsychoPy v3.0.0.[97] Participants were told that they would see a series of cartoon people with a name and a fact about each character and they were instructed to try to memorize the names. The 14 characters were split into two blocks of seven characters, based on the two movies in which they would subsequently feature. Each character avatar was presented one at a time, for 3000ms, in the center of the computer screen and the character's name was printed underneath the character's avatar. In between each character presentation was a 1000ms interstimulus interval. Following encoding of each character and name, participants performed a two-alternative forced-choice decision task for each of the character's names. Participants were shown each character avatar individually, in random order, with two names (one originally shown with the displayed character, and one from another character that was previously shown) underneath the character. Participants were instructed to indicate which name belonged to the displayed character. A 1000ms inter trial interval was present between each testing trial. After this testing block, participants were once again shown each character avatar, with their name printed underneath, along with a fact about that character's role in the upcoming videos. For example, the character named "Arlene" was presented underneath the cartoon avatar of the Arlene character alongside Arlene's role in the video of "Barmaid". This provided feedback on the names for the participant and added an additional semantic fact for the participants to encourage memory formation for the characters.

Pre-scan set-up

Participants were fitted with MRI-compatible earbuds with replaceable foam inserts (https://www.sens.com/products/model-s14/) and were provided with additional foam padding inside the head coil for hearing protection and to mitigate head motion. Participants were additionally given bodily padding, blankets, and corrective lenses as needed. An MRI compatible microphone (Optoacoustics FOMRI-III; https://www.optoacoustics.com/medical/fomri-iii) with bidirectional noise-cancelling was affixed to the head coil, and the

receiver (covered by a disposable sanitary pop screen) was positioned over the participant's mouth. Participants were given a description of strategies to remain still while speaking during functional image acquisition. Participants were told to avoid nodding or shaking their head and have minimal jaw movement—by keeping their top and bottom teeth touching—during speaking. During MRI data acquisition, an eye tracker was operational to monitor participants' wakefulness and head motion during spoken recall, but no eye tracking data were recorded.

fMRI task overview

Participants were tasked with encoding and recalling two, 16.5-minute animated videos. One video was recalled after a brief 5-minute delay (during which participants underwent a T1 anatomical scan), and the other was recalled after a 48-hour delay. Participants were split into four groups to counterbalance video order and retention delay order—half of the participants performed the short delay recall first, and half performed the 48-hour delay recall first (Figure 1A).

Encoding block instructions: Prior to each encoding scan, participants were instructed to: "Watch the following movie as you would a television show you are interested in. We will ask you to remember the movie at a later time." Participants then viewed the first of the two animated videos. After encoding, participants underwent a 3.5-minute anatomical scan.

Recall block instructions: During recall scans they were instructed to: "In as much detail as possible tell me everything you can remember about the last movie we showed you. Try to recount the events in the original order in which they occurred. Completeness and detail are more important than temporal order. If at any point you realize that you have missed something, return to it. Try to describe EVERY detail that you have about the movie you just watched, even if it seems irrelevant." The participants then spoke into the scanner safe microphone and recalled details from the video they had most recently viewed during a functional scan. Participants received additional instructions regarding head movement prior to recall: "Remember to stay as still as possible. Try to speak while moving only your lips and not your jaw; Sometimes people tend to nod or shake their head when they are talking. Avoid these tendencies as much as possible."

If the video was scheduled for the short recall delay, the participant would perform the recall block immediately after the anatomical scan. If the video was in scheduled for the 48-hour delay first recall group, the participant would then undergo a reverse phase encoding functional scan, followed by a diffusion weighted scan, and a reverse phase encoded diffusion weighted scan (to be reported elsewhere). The participant would then leave the scanner and return two days later to complete the recall block in the scanner and undergo an additional anatomical scan.

After completing the encoding and recall of both movies, participants then watched an 11-minute documentary-style video and were instructed to watch the following video as they would a television show they are interested in. This final video was not recalled by the participants and was not processed as part of the current study.

Recall scoring

Audio recall from each participant's fMRI recall run was transcribed automatically using the python tool SpeechRecognition (https://github.com/Uberi/speech_recognition#readme) and the automatic transcription was examined, and any transcription errors were corrected by two trained research assistants (J.S. and R.Y.). These two trained research assistants parsed the transcripts into details using an adapted version of the autobiographical interview.[44] A detail "was defined as a unique occurrence, observation, or thought, typically expressed as a grammatical clause. Additional information in the clause was scored separately".[44] Details that were errors or were did not pertain to verifiable events in the movie were excluded from further analysis. Verifiable details were then categorized as either central details, or peripheral details to determine whether details that are central to the narrative plot are better retained than those that are peripheral.[32] For example, a central detail might be something like "Officer Lloyd asks for Cliff's help" which is a critical turning point in solving the case in the narrative. A peripheral detail would be something like "Cliff has bird tattoos on his chest" which is a detail that is inconsequential to the narrative. The combination of central and peripheral details make up all total verifiable details or "total details".[45] To categorize central and peripheral details, four research assistants watched each video and created an annotation file for each line of dialogue and occurrence they viewed. This was then combined into a single document and the research assistants ranked each detail/occurrence on a scale of 1-5 in terms of detail centrality. Raters were instructed that a detail would be considered central if removal of that detail would affect their interpretation or comprehension of the narrative. A rating of 5 would be given if removal of the detail significantly affected their interpretation or comprehension and a 1 was to be given if removal of the detail would have no effect at all on their interpretation or comprehension of the narrative. Details that were given an average score greater than 3.5 were considered central details and summary statements of these details were produced via conferencing among the group. During scoring, details were classified as central if they matched a detail that was identified as central by the central detail rating group, and all other verifiable details were classified as peripheral. While this scoring provided a fine-grained approach to evaluating memory, we also examined whether events were recalled in a binary fashion. If any event-specific details were recalled from an event, that event was said to be successfully recalled and events for which no details were recalled were classified as forgotten or unsuccessfully recalled. The Shapiro–Wilk test was used to evaluate normality on the distribution of details.

MRI acquisition

MRI scanning for the primary dataset was performed using a 3T Siemens Skyra scanner system with a 32-channel head coil. Two T1-weighted structural images were acquired using a magnetization prepared rapid acquisition gradient-echo pulse sequence (TR = 1900 ms; TE = 3.1 ms; field of view = 256 mm^2; flip angle = 7°; image matrix = 256 × 256, 208 axial slices with 1.0 mm^3 voxel

size). Functional images were acquired using a gradient EPI sequence (TR = 1220 ms; TE = 24 ms; field of view = 192 mm^2; image matrix = 64 × 64; flip angle = 67°; multiband factor = 2; 38 interleaved axial slices, voxel size = 3 mm^3 isotropic), phase encoding: anterior-posterior. Reverse phase-encoded EPI data was also acquired using the same parameters to correct for phase encoding distortion in preprocessing (below).

MRI preprocessing

Anatomical data preprocessing

A total of 2 T1-weighted (T1w) images were found within the input BIDS dataset. All of them were corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection,[101] distributed with ANTs 2.3.3[102] (RRID:SCR_004757). The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast[103] (FSL 5.0.9, RRID:SCR_002823). A T1w-reference map was computed after registration of 2 T1w images (after INU-correction) using mri_robust_template[104] (FreeSurfer 6.0.1). Brain surfaces were reconstructed using recon-all[98] (FreeSurfer 6.0.1, RRID:SCR_001847), and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle[105] (RRID:SCR_002438). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (ANTs 2.3.3), using brain-extracted versions of both T1w reference and the T1w template. The following template was selected for spatial normalization: ICBM 152 Nonlinear Asymmetrical template version 2009c[106] (RRID:SCR_008796; TemplateFlow ID: MNI152NLin2009cAsym). Surface-based registration to the HCP-MMP1.0 atlas[40] was performed, and subject-specific cortical regions of interest (ROIs) were calculated according to atlas boundaries. Surface-based cortical regions were converted to volumetric ROIs and transformed into functional native space. The hippocampus was segmented in FreeSurfer in an automated fashion. Manual adjustments were done to correct mis-classified voxels, and the hippocampus was divided into anterior and posterior segments based off the disappearance of the uncal apex,[36] with the posterior hippocampus designated as all of the hippocampus posterior to the disappearance of the uncal apex on a coronal slice.

Functional data preprocessing

For each of the BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep.[95] A B0-nonuniformity map (or fieldmap) was estimated based on two (or more) echo-planar imaging (EPI) references with opposing phase-encoding directions, with 3dQwarp[99] (AFNI 20160207). Based on the estimated susceptibility distortion, a corrected EPI (echo-planar imaging) reference was calculated for a more accurate co-registration with the anatomical reference. The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer) which implements boundary-based registration.[107] Co-registration was configured with six degrees of freedom. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt[108] (FSL 5.0.9). The BOLD time-series were resampled onto the following surfaces (FreeSurfer reconstruction nomenclature): fsaverage5. The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. The BOLD time-series were resampled into standard space, generating a preprocessed BOLD run in MNI152NLin2009cAsym space. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following[109] (absolute sum of relative motions) and[108] (relative root mean square displacement between affines). FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by[109]). The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. Frames that exceeded a threshold of 0.5 mm FD or 3.0 standardised DVARS were annotated as motion outliers. All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using antsApplyTransforms (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels.[110] Non-gridded (surface) resamplings were performed using mri_vol2surf (FreeSurfer). Following preprocessing from fMRIprep, a set of nuisance regressors was made for each participant. Translational motion in the x, y, and z direction and rotational motion in pitch, roll, and yaw were calculated for each run for each subject. Finally, the global signal of each TR was calculated. Mean FD during recall was 0.21mm which was higher than mean FD during encoding (Mean = 0.12mm; $t(22) = 8.1$, $p < .001$).

For the functional connectivity analysis, each of these nuisance regressors (motion, flagged TRs, global signal) was entered into a model and regressed out from the fMRI timecourse of the participants and the timecourse was bandpass filtered to restrict frequencies to.009 —.08Hz using the tproject function from AFNI[99] via nipype version 1.4.0[96] to create a confound corrected timeseries for each participant, for each run.

For the intersubject pattern similarity analysis, nuisance regressors (motion, flagged TRs) were entered into a model and regressed out from the fMRI timecourse of the participants and the timecourse was high-pass filtered minimally to remove frequencies

below.001Hz using the tproject function described above. While there is no agreed upon conventions for preprocessing of naturalistic imaging data, minimal high-pass filtering has been recommended,[111] as many of the regions of interest in our study have been shown to have long temporal receptive windows.[16]

Intersubject pattern similarity analysis

Prior to addressing our primary hypotheses, we first confirmed that the cortico-hippocampal networks in our sample showed event specific representations. To do so, we adopted the intersubject representational similarity analysis used in Chen et al.[17] We focused these analyses the MTN, PMN, ATN and MPN (Figure S1), based on previous work showing that these networks show high functional connectivity with the hippocampus[35,60,112] the MTN and three DMN subnetworks. The mean BOLD timecourse of each ROI in a network was calculated for each run. The ROI timecourse was then z-scored across the entire run. A regressor was made to model event activity by creating a time block corresponding to each event and convolving the block with the hemodynamic response function from AFNI.[113] A linear regression was then used to estimate the mean activity in each event for each ROI in a network. This resulted in a "multi-ROI activity pattern" per event, per subject, per network (see Figure S1 for an overview). The multi-ROI activity pattern of a network for each participant *i* was correlated with the averaged multi-ROI activity pattern for the rest of the group (excluding subject *i*) for each matching event and Fisher z-transformed. The average Fisher transformed z-value for the matching events was calculated and compared to a null distribution that was calculated by repeating this procedure 5000 times, scrambling the event labels on each iteration. If a network carried event-specific information, then the average correlation of the matching events should be significantly higher than the null distribution of randomly correlated events. The values of the true correlations for the group were thus compared to the null distribution to assess significance. This was done for both movie encoding and recall, separately. For recall, for each subject *i*, we calculated the multi-ROI activity pattern for every event *e* that was recalled by subject *i* and correlated it to the average multi-ROI activity pattern for the rest of the group that also remembered event *e*, as was done in Chen et al.[17] Recall transcripts were inspected and blocks of time corresponding to recall of a given event were labelled. Participants generally recalled events in order. However, they would sometimes recall out of order and recall information from events more than once. Thus, for some participants, they would have multiple, discontinuous blocks set for recall of an event.

Functional connectivity analysis

Pairwise FC was estimated between every pair of ROIs in the brain by correlating the confound corrected timeseries between each pair of ROIs, for each subject, during each functional run. The resulting Pearson's correlations were then Fisher z-transformed. To assess the FC between the hippocampus and a cortico-hippocampal networks of interest, we calculated the average FC of the hippocampus with all the ROIs in the cortico-hippocampal network. FC estimations were performed at three time-windows of interest—the event onset, middle and offset. For each event, we took a 20 TR window (24.4s) around the event onset, a 20 TR window around the event offset, and a 20 TR window around the event middle—a window length previously shown to be sensitive to BOLD signal correlations using naturalistic movie stimuli.[114,115] The onset, middle, and offset locations were adjusted 5 TRs forward to account for hemodynamic lag. Functional connectivity was calculated separately for anterior and posterior hippocampus, as some evidence suggests that there are different functions and different network connections along the hippocampal long-axis.[36,42,116]

A sliding window analysis was additionally performed to understand the dynamics of the functional connectivity to memory relationship. The above functional connectivity calculations were repeated, iteratively. The window center started at the event onset (shifted 5 TRs forward) a was incrementally shifted forward in $1/18^{th}$ increments of the total length of the event. This increment was chosen because the shortest event was 18 TRs long and, therefore, we could match the increments across events when examining the relationship between FC and event memory within subjects.

To further understand whether the FC results are specific to hippocampal-PMN interactions, we examined whether FC between PMN ROIs could explain subsequent memory results. To do so, we calculated the mean FC between every ROI within the PMN. FC estimations were performed at three time-windows of interest—the event onset, middle and offset. For each event, we took a 20 TR window (24.4s) around the event onset, a 20 TR window around the event offset, and a 20 TR window around the event middle. The onset, middle, and offset locations were adjusted 5 TRs forward to account for hemodynamic lag.

Univariate boundary activity

The anatomically registered functional data was entered into single subject general linear models for each subject and each movie using SPM12. A separate regressor was made for each event boundary and each event middle (the arithmetic middle of the event) having durations of 0s and were convolved with the canonical hemodynamic response function in SPM12. Nuisance regressors for motion (pitch, roll, yaw, x-translation, y-translation, z-translation) along with regressors flagging outlier TRs of high motion (FD > 0.5 or DVARS > 3) were entered as regressors of no interest. We also attempted to control for low-level visual information in our GLM by using the routine outlined by Reagh et al.[23] Edge pixels were calculated via a python routine, which read in each video stimulus, split it into its constituent frames, and in an automated fashion performed edge-detection on each frame (using python package opencv). The proportion of edge pixels to total pixel count was calculated (NumPy) for each frame, and was output into a comma-separated value file. We then resampled frame-wise edge information to correspond to the temporal scale of the fMRI data by averaging across adjacent frames within the interval of each TR (1220 ms). This resultant temporally smoothed vector served as our estimate of

low-level visual information in each timepoint of the video. This visual information vector for each video was entered into the GLMs as a regressor of non-interest. Data underwent a high-pass filter with a cut-off of 128s.

For each subject GLM, for each movie, we estimated the beta values for each event boundary and event middle at every voxel in the brain. We extracted the beta values for these regressors averaged within the anterior and posterior hippocampus, as well as each of the cortical networks (PMN, MPN, MTN, ATN) of each subject using the nipype apply_mask function.[117]

Subsequent memory effects analysis

The hippocampal-network FC values were mean centered within each participant for each cortico-hippocampal network of interest that showed event-specific multivariate patterns. These mean-centered values were entered into our statistical models. A generalized linear mixed model was used to run a logistic regression determining whether subsequent recall success could be predicted from FC, delay condition (immediate vs. two-day delay), the interaction of these two terms, and whether these interacted with FC window (beginning vs. middle vs. offset), and hippocampal long-axis (anterior vs. posterior) using glmer from the lme4[100] package in R. Since hippocampal boundary activity has previously been associated with recall success, we included boundary activity as a regressor in the model. We also included univariate boundary activity averaged across the network of interest (e.g. PMN, MTN, ATN). Significance for terms in the logistic generalized linear mixed model was determined using Wald Chi-square tests. A random intercept was entered into the model for each participant. Movie label was entered as a covariate of no interest. Follow-up effects were calculated using emtrends from the emmeans package in R and adjusted for multiple comparisons, within each network model, using the FDR method[118] implemented in the emmeans package.

To examine how the FC-memory relationship varied across the course of events, separate linear mixed model was made for each sliding window period to estimate the mean difference between FC for subsequently recalled compared to subsequently forgotten events. To assess significance, we performed a cluster size analysis. To do so, we compared the number of consecutive windows that showed a significant difference in FC between subsequently recalled and forgotten events at $p < .05$ (in both the negative and positive direction) to a null distribution created by randomly shuffling the event labels 1000 times. At each permutation we recalculated the model for each window and recorded the max number of consecutive windows significant at $p < .05$. We then compared the max number of consecutive windows in the actual data to the null distribution of max consecutive significant windows to determine significance.

Subsequent memory effects analysis controls

Multiple analysis choices were made to examine the relationship between functional connectivity and subsequent memory. Here, we repeat our analysis using a variety of alternatives. Given that with the window size of 20TRs there were some windows in some events that had overlap with adjacent windows. Thus, we repeated the above subsequent memory effect analysis and restricted this analysis to events that had more than 40TRs to exclude these overlaps.

Given that the FC results could be affected by the choice of window size, we also repeated the FC calculations using a window size of 10TRs and 30TRs. A window size of 10TRs may increase the specificity of the window, but significantly reduces the reliability of the timecourse correlations, allowing for more spurious FC fluctuations. A window size of 30TRs reduces the odds of aberrant timepoints creating spurious FC estimates, but significantly increase the overlap in event windows and makes it difficult to tease apart the different contributions of FC at the start, middle, and offsets of events.

Finally, our original analysis selected a frequency band that was consistent with the frequency at which these functional networks tend to fluctuate and frequencies above 0.1 seem to relate to vasomotor activity[119] and do not reflect the network organization we sought to examine.[119,120] However, it is possible that higher frequencies could contribute to the functional connectivity-memory relationship. Thus, we repeated the subsequent memory analysis including frequencies up to 0.15Hz and 0.2Hz.

To understand whether the FC results are specific to hippocampal-PMN interactions, PMN-PMN FC values were mean centered within each participant. A generalized linear mixed model was used to run a logistic regression determining whether subsequent recall success could be predicted from FC, delay condition (immediate vs. two-day delay), the interaction of these two terms, and whether these interacted with FC window (beginning vs. middle vs. offset) using glmer from the lme4 package in R. We also included univariate boundary activity averaged across the network of interest. Significance for terms in the logistic generalized linear mixed model was determined using Wald Chi-square tests. A random intercept was entered into the model for each participant. Movie label was entered as a covariate of no interest. Follow-up effects were calculated using emtrends from the emmeans package in R and adjusted for multiple comparisons, within each network model, using the FDR method[118] implemented in the emmeans package.

Event memory detail analysis

A second model was constructed using only events that were successfully recalled to determine the influence of FC on the amount of detail remembered from events. Here the dependent variable was the log-transformed total numbers of details recalled from events and the predictors were the same as above. Details were log-transformed since a Shapiro-Wilk test revealed that the detail distribution was not normal, $W = .72$, $p < .001$. This analysis was modelled using a linear mixed model with lmer from the lme4 package in R. Thus, rather than examining how FC relates to success of recall of events, we examined how it relates to the amount of detail retrieved when the event is recalled. Follow-up effects were calculated using emtrends from the emmeans package in R. Statistical probabilities were adjusted for multiple comparisons using the FDR method[118] implemented in the emmeans package.

To test the hypothesis that hippocampal-MTN FC was related to fine-grained detail memory, we repeated the above analysis using peripheral details only and to test the hypothesis that hippocampal-MPN FC was related to coarse-grained memory, we repeated the

above analysis using central details only. Finally, rather than using raw detail numbers, we also investigate the proportion of details that were central or peripheral. To do so, we calculated proportion as (central details – peripheral details) / (central details +peripheral details). Values closer to +1 for an event means that there is a greater proportion of central details compared to peripheral details, and values closer to -1 means that there is a greater proportion of peripheral details compared to central. These values were entered as the dependent variable to be predicted using lmer as above.

QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical tests were performed with R using generalized linear mixed models with glmer from lme4 and using linear mixed models with lmer from lme4. Significance for terms in the logistic generalized linear mixed models was determined using Wald Chi-square tests. Significance for terms in the linear mixed models was determined using car::Anova F-tests. Follow-up fixed effects statistical tests were performed using emtrends from the emmeans package in R (Figure 2B, Figure 2C, Figure 3). P-values were adjusted for multiple comparisons using the FDR method[118] implemented in the emmeans package.