Emotional arousal enhances narrative memories through functional integration of large-scale brain networks

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Abstract

Emotional events tend to be vividly remembered. While growing evidence suggests that emotions have their basis in brain-wide network interactions, it is unclear if and how these whole-brain dynamics contribute to memory encoding. We combined fMRI, graph theory, text analyses, and pupillometry in a naturalistic context where participants recalled complex narratives in their own words. Across three independent datasets, emotionally arousing moments during the narratives were associated with an integrated brain state characterized by increased cohesion across functional modules, which in turn predicted the fidelity of subsequent recall. Network integration mediated the influence of emotional arousal on recall fidelity, with consistent and distinct network interactions supporting the mediation across datasets. Together, these results suggest that emotional arousal enhances memory encoding via strengthening functional integration across brain networks. Our findings advance a cross-level understanding of emotional memories that bridges large-scale brain network dynamics, affective states and ongoing cognition.

Keywords: Emotional arousal, memory, network neuroscience, narratives, fMRI

Events that induce emotional arousal are often better remembered than those that are emotionally neutral[1–4]. For instance, a person is more likely to recall the details of a car accident they witnessed than what they saw on a routine drive home. Enhanced memory for arousing events prioritizes the recall of experiences that are motivationally significant, such as those relevant to potential threats and rewards[5,6]. This prioritization facilitates the efficient allocation of cognitive resources towards events that impact well-being, enabling individuals to respond more rapidly and effectively to similar events in the future[7,8].

How does emotional arousal enhance memory encoding? Prevailing theories propose that heightened arousal triggers the release of norepinephrine in the amygdala, which interacts with other memory-related regions, most prominently the hippocampus, to enhance the encoding of emotional experiences[9–12]. Consistent with this account, human functional magnetic resonance imaging (fMRI) studies have found that enhanced memory of emotional stimuli is associated with amygdala and hippocampal activation[13–17], as well as increased amygdala-hippocampal connectivity[18,19]. These findings have been recently corroborated in intracranial recordings in patients[20,21]. The administration of the β-adrenergic antagonist propranolol, which interferes with norepinephrine binding, reduces amygdala and hippocampal response to emotional stimuli and diminishes the associated memory enhancement, suggesting a causal role of arousal-dependent norepinephrine release in mediating these effects[22–25].

Current models of arousal-dependent memory enhancement have made foundational contributions to our understanding of the brain regions and circuitry involved, but they generally do not consider the role of the large-scale functional network organization of the brain (c.f. [26]). There is growing recognition that the dynamic reconfiguration of distributed functional brain networks in response to task demands is crucial for adaptive behavior[27–32] and underlies emotional responses and affective states[33–37]. Converging evidence suggests that heightened arousal promotes brain network integration - a brain state characterized by increased connectivity and cohesion across functional brain systems[38–40], which have in turn been associated with memory encoding and retrieval[41,42]. Building on this work, we propose the novel hypothesis that functional network integration facilitates the enhanced encoding of emotionally arousing memories, above and beyond the contribution of the amygdala and the hippocampus.

While earlier behavioral and pharmacological studies on emotional memories utilized narratives as stimuli[1,2,25], neuroimaging studies have primarily focused on the encoding and recall of static stimuli such as emotionally arousing images[13,14,18,19] or words[16,17]. Consequently, less is known about the relationship between neural activity and the emotional enhancement of narrative memories. Unlike static stimuli, narratives represent complex experiences where interconnected events unfold dynamically, requiring the accumulation and updating of information over time. Advances in neuroimaging techniques and natural language processing now allow for the study of how the brain encodes and recalls these naturalistic episodes[43]. Here, we take advantage of these

advances to investigate the neural basis underlying how emotional arousal enhances what is remembered from temporally extended narratives.

We utilized two publicly available fMRI datasets where participants watched dynamic audiovisual narratives and verbally recalled what they remembered. Arousal ratings of the movies were obtained by analyzing annotations of videos using large language models and from subjective ratings collected in separate behavioral experiments. Applying graph theoretic analyses to the fMRI data, we computed a dynamic measure of functional integration during narrative perception. We assessed the fidelity of participants' memory by using text embedding models to measure the similarity between their recall and detailed descriptions of the corresponding event. We then tested whether functional integration during encoding mediated the effects of emotional arousal on subsequent recall fidelity. Finally, we replicated our results in a third dataset where we measured arousal using pupillometry while participants listened to and recalled a suspenseful audio story, providing converging evidence of our results with a physiological measure of arousal. Altogether, our work advances an integrative view of arousal-dependent memory enhancement of narrative memories that bridges affective states and ongoing cognition through brain network dynamics.

Results

Our first set of analyses utilized two publicly available fMRI datasets. In the first dataset ("*Film Festival*")[44], participants watched 10 audiovisual clips from various live-action movies and cartoons (range: 2min 12s–7min 45s, average duration: 4min 32s, total duration: 45min 22s). In the second dataset ("*Sherlock*")[45], participants watched a 50-minute segment from an episode of the British TV show Sherlock. In both datasets, participants were then asked to describe what they remembered from the movies in as much detail as they could. Each movie was divided into a set of events defined by major shifts in the narrative, including changes in topic, location, time, and characters (68 events in *Film Festival*, average length=38.4s, SD=18.2s; 48 events in *Sherlock*, average length=57.5s, SD=41.76s). In the current study, we examined the relationship between functional brain network organization during narrative perception and subsequent memory of the events (**Figure 1**).

We first obtained detailed annotations of the movie events as a "ground-truth" description of what occurred in each event. To assess how well participants recalled the movie events, we quantified the semantic similarity between participants' recall transcripts and these annotations. We used Google's Universal Sentence Encoder (USE)[46] to convert the annotation and recall transcripts of each event into numerical vectors in a high-dimensional embedding space (see **Methods**). Sentences with similar meanings are encoded in vectors that are closer in the embedding space. We then calculated the cosine similarity between the vector encoding the annotation and those encoding a participant's recall of an event as a measure of recall fidelity[47–49]. A high recall fidelity score thus indicated that a participant's recall closely matched the annotation of an event. **Figure**

S1 displays an example event in each of the two datasets with the transcripts and fidelity scores of the recall from two different participants.

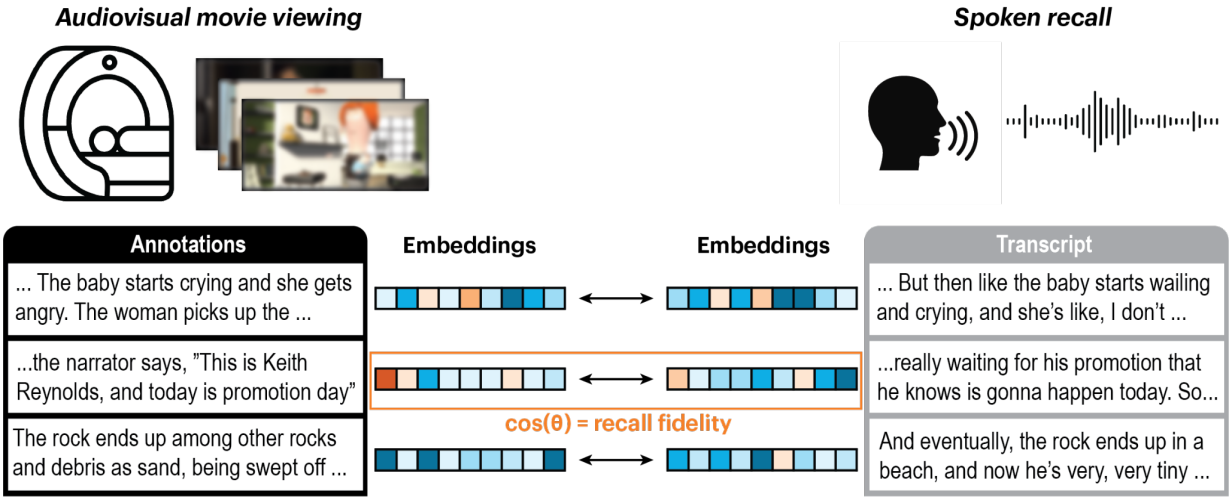

Figure 1. Schematic of task and semantic similarity analysis between movie annotations and spoken recall. Participants watched audiovisual clips in the fMRI scanner and were instructed to recall what they watched from memory. Descriptions of movie events obtained from independent coders and transcriptions of participants' verbal recall were converted to vector embeddings. Recall fidelity was computed as the cosine similarity between the vector of scene annotations from an event and the transcript from the matching event in a participant's recall.

Functional integration during movie-viewing is associated with higher memory fidelity

We first examined how dynamic changes in brain network organization during movie-viewing were associated with subsequent memory fidelity. To that end, we parcellated the brain into 216 cortical and subcortical regions. For each event in each participant, we computed the functional connectivity between each pair of brain regions as the Fisher-z transformed Pearson correlation between the BOLD time courses. The connectivity matrices were thresholded to retain the top 15% connections and binarized to create sparse graphs, where nodes represent brain regions and edges represent functional connections between regions. This approach allowed us to leverage graph theory to quantify network properties of large-scale neural dynamics and investigate how functional modules in the brain interact with one another during movie-watching.

In each graph, brain regions were assigned to communities such that regions within a community are more strongly connected to one another than to regions in other communities[50], thereby partitioning the brain into different functional modules (see **Methods**). We then quantified the diversity of intermodular connections of each brain region by calculating its participation coefficient (B_T)[51]. A brain region with a high B_T has connections distributed across multiple modules, suggesting that it may play a role in integrating information across modules[52].

Conversely, a brain region with a low B_T has most of its connections within its own module, suggesting more localized processing. High average B_T across brain regions would then reflect high levels of inter-module connectivity, indicating an integrated brain state when there is stronger cohesion across different functional modules.

For each event, we computed the average B_T across brain regions as a measure of whole-brain functional network integration[27]. Connectivity plots of events with high and low average B_T are shown in **Figure 2A**. We note that each graph was thresholded to retain a fixed number of connections, and thus all graphs had the same number of connections. As such, an increase in B_T would not be due to a greater number of connections. Instead, graphs with high average B_T had a greater number of connections *between* functional modules, indicating greater integration across networks. We hypothesized that events associated with greater functional network integration during movie viewing are more strongly encoded and are thus remembered with higher fidelity.

We used Bayesian multilevel models to test how functional network integration during movie viewing was related to subsequent event memory, which allowed us to leverage statistical pooling across participants to increase statistical power. Consistent with our hypothesis, average B_T when viewing an event was positively associated with recall fidelity in both datasets (*Film Festival*: b=0.12, 95% HDI=[0.05, 0.19], p(b>0)=0.999; *Sherlock*: b=0.11, 95% HDI=[0.03, 0.18], p(b>0)=0.998) (**Figure 2B**). Similar results were obtained with global efficiency, an alternative measure of whole-brain functional integration (*Film Festival*: b=0.17, 95% HDI=[0.1, 0.24], p(b>0)=0.999; *Sherlock*: b=0.18, 95% HDI=[0.11, 0.26], p(b>0)=0.999). To ensure the robustness of our results, we repeated the analyses with a different parcellation scheme, and also with functional connectivity matrices thresholded to retain different proportions of strongest connections (0.10, 0.20, 0.25). In all versions of the analyses, increased network integration during encoding was associated with subsequent recall fidelity (**Table S1, S2**).

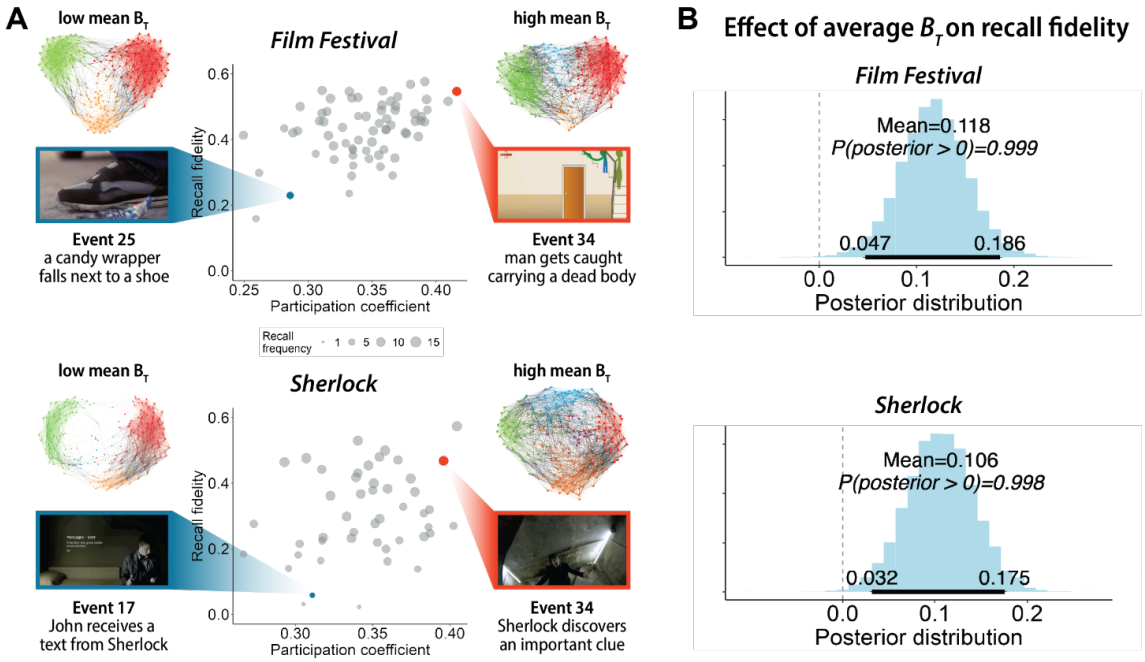

Figure 2. Functional integration during movie viewing is associated with higher recall fidelity. (A) Scatter plots depict the relationship between average participation coefficient (B_T), average recall fidelity, and recall frequency. Each datapoint is an event. The size of the circle depicts the number of participants that recalled that event. Red and blue circles correspond to example events with high (red) or low (blue) average B_T. Connectivity plots depict functional connections for the respective events, with colors denoting module assignment. Each connectivity plot contains the same number of connections, but there are more inter-modular connections during events when average B_T is high. **(B)** Posterior distribution of regressions coefficients when predicting recall fidelity from average B_T using Bayesian multilevel models for the *Film Festival* (top) and *Sherlock* (bottom) datasets. The 95% highest density interval of each distribution is indicated by the bold horizontal line.

Functional integration mediates effects of emotional arousal on narrative recall

Given the well-established role of emotional arousal in enhancing memory encoding[4,11,12], we next sought to examine the impact of emotional arousal on functional integration and narrative recall. To this aim, we obtained ratings of emotional arousal based on text descriptions of each narrative event using an open-access large-language model (LLM)[53] (see **Methods**). Additionally, we collected emotional arousal ratings from 30 participants for comparison and validation (**Figure S2A**). Human behavioral ratings, collected on a 5-point scale (median=3.2, range=1.3-4.7 for *Film Festival*; median=3, range=1.5-4.7 for *Sherlock*), were highly correlated across participants (*Film Festival*: one-to-average r=.72, p<.01; *Sherlock*: one-to-average r=.69, p<.01), indicating consistency across individuals on the level of emotional arousal of each event.

LLM-generated ratings, obtained on a 10-point scale to capture finer-grained distinctions (median=6.6, range=3.3-9.7 for *Film Festival*; median=7, range=3.8-9 for *Sherlock*), correlated strongly with the average behavioral ratings, providing convergent validity of the arousal measures (*Film Festival*: r=.60, p<.001; *Sherlock*: r=.75, p<.001; **Figure S2B)**. Subsequent analyses yielded similar results for both the LLM-generated and average behavioral ratings. For brevity, we report results using the LLM-generated ratings here, with results based on behavioral ratings reported in the supplemental materials (**Table S3**).

Relating arousal ratings to our graph measures of network integration revealed that average B_T was higher when participants viewed events rated as more emotionally arousing (*Film Festival*: b=0.13, 95% HDI=[0.06, 0.19], p(b>0)=0.999; *Sherlock*: b=0.12, 95% HDI=[0.03, 0.2], p(b>0)=0.996; **Figure 3A, Figure S3A**). In addition, events rated as more emotionally arousing were recalled with greater fidelity (*Film Festival*: b=0.13, 95% HDI=[0.07, 0.19], p(b>0)=1; *Sherlock*: b=0.15, 95% HDI=[0.08, 0.22], p(b>0)=1; **Figure 3B, Figure S3B**). In both datasets, average B_T while viewing an event mediated the effects of emotional arousal on recall fidelity (*Film Festival*: b=0.01, 95% HDI=[0, 0.02], p(b>0)=0.999; *Sherlock*: b=0.01, 95% HDI=[0, 0.02], p(b>0)=0.99; **Figure 3C**). The mediation effects were also robust when the analyses were repeated with functional connectivity matrices computed after global signal regression (**Table S4**), with a different parcellation scheme (**Table S5**) and thresholds (**Table S6**).

Demonstrating that our results replicate independently across independent datasets provides stronger evidence for the robustness of our findings than combining the two datasets. Nevertheless, to complement these analyses, we ran an additional model where we combined both datasets (total n=32), while treating each dataset as a random effect in the model. This analysis allowed us to assess the overall reliability of the observed effects across datasets, and again revealed that functional integration reliably mediated the effects of emotional arousal on recall fidelity (b=0.01, 95% HDI=[0.01, 0.02], p(b>0)=1). Altogether, these findings provide consistent evidence in support of our core hypothesis that emotional arousal enhances memory encoding by facilitating increased functional integration across brain networks.

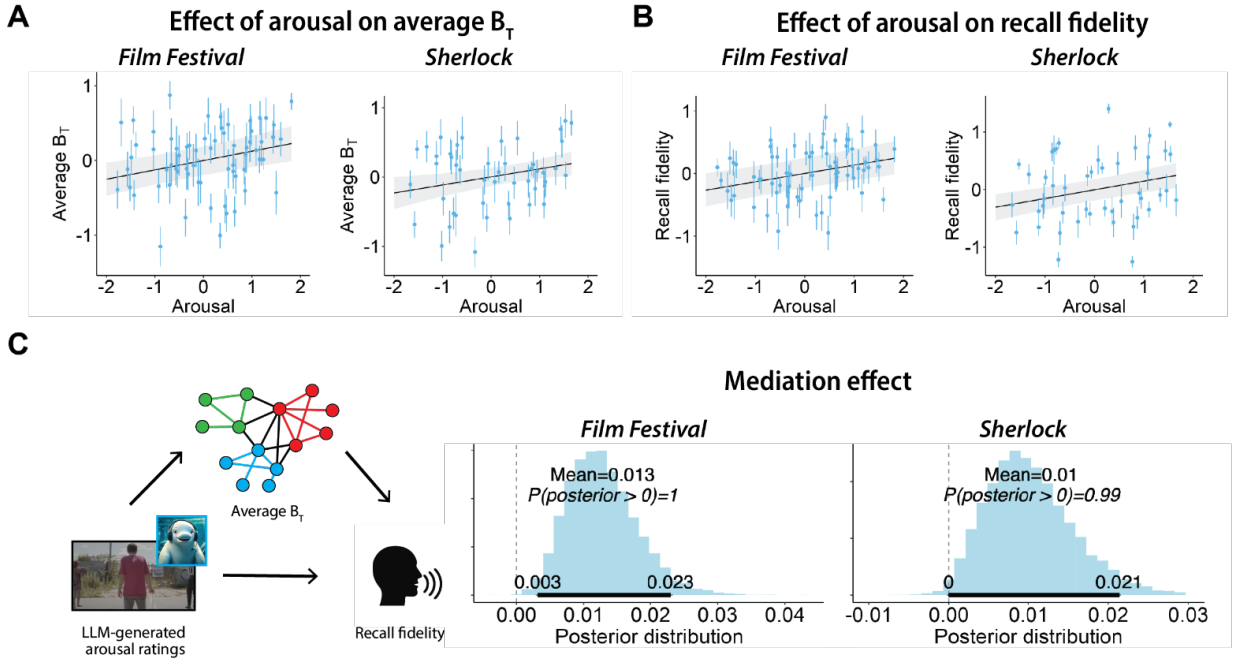

Figure 3. Functional network integration mediates the effects of emotional arousal on recall fidelity. Relationship between emotional arousal and **(A)** average participation coefficient (B_T) and **(B)** recall fidelity. All variables were z-scored across participants. Each datapoint corresponds to an event, with error bars indicating the standard error. Black line shows effect estimated from Bayesian multilevel models, with gray ribbon indicating the 95% credible interval. Posterior distributions are shown in Figure S2. **(C)** Mediation analysis testing whether average B_T during an event mediates the effect of emotional arousal on recall fidelity. Histograms depict the posterior distribution of the mediation effect estimated from Bayesian multilevel models. The 95% highest density interval of each distribution is indicated by the bold horizontal line.

Network efficiency within and between canonical brain networks mediates effects of emotional arousal on narrative recall

While average B_T provides a measure of the overall levels of network integration across functional modules in the brain, it is agnostic to the brain regions that drive this integration. Thus, different configurations of large-scale network organization might underlie the observed effects. Are there specific network interactions that consistently mediate the effects of emotional arousal on memory encoding? To address this question, we ran additional analyses to characterize the contributions of connectivity patterns within and between canonical functional brain networks.

We grouped the brain regions based on their assignment to seven functional networks defined by the Schaefer atlas, with the 16 subcortical ROIs grouped together as one network. For each network, we calculated the *within-network efficiency* as the average inverse shortest path length between every pair of regions in the network[54]. For each pair of networks, we calculated the *between-network efficiency* as the average inverse shortest path length between regions in one

network and regions in another network[41]. The within- and between-network efficiency provided measures that are often interpreted as reflecting the potential efficiency of information transfer within and across different brain networks, respectively[50,54].

We tested whether within- and between-network efficiency mediated the effects of emotional arousal on recall fidelity. To correct for multiple tests, we thresholded the results at an expected Posterior Error Probability (PEP) of 0.01[55] (see **Methods**). Our analyses identified multiple networks and network pairs that mediated the effects of emotional arousal on recall fidelity (**Figure 4A**). Notably, a subset of networks and network pairs were unique to each dataset, while several others overlapped across both datasets (**Figure 4B; Table S7**). Specifically, within-network efficiency in the dorsal attention network *(Film Festival*: b=0.02, 95% HDI=[0, 0.03], p(b>0)=0.997; *Sherlock*: b=0.03, 95% HDI=[0.02, 0.05], p(b>0)=1) and limbic network (*Film Festival*: b=0.01, 95% HDI=[0, 0.03], p(b>0)=0.997; *Sherlock*: b=0.03, 95% HDI=[0.01, 0.04], p(b>0)=0.999) mediated the effect of emotional arousal on recall fidelity in both datasets.

This was also true of the between-network efficiency between the dorsal attention network and the control network (*Film Festival*: b=0.01, 95% HDI=[0, 0.02], p(b>0)=0.999; *Sherlock*: b=0.02, 95% HDI=[0, 0.03], p(b>0)=0.977), dorsal attention and the visual network (*Film Festival:* b=0.01, 95% HDI=[0, 0.01], p(b>0)=0.974; *Sherlock:* b=0.02, 95% HDI=[0.01, 0.04], p(b>0)=0.99), the control network and the ventral attention network (*FilmFest:* b=0.02, 95% HDI=[0.01, 0.03], p(b>0)=0.999, *Sherlock:* b=0.01, 95% HDI=[0, 0.02], p(b>0)=0.0.977) the default mode network and the ventral attention network (*Film Festival*: b=0.02, 95% HDI=[0.01, 0.03], p(b>0)=0.999; *Sherlock*: b=0.01, 95% HDI=[0, 0.02], p(b>0)=0.986), the default mode network and the limbic network (*Film Festival*: b=0.02, 95% HDI=[0.01, 0.03], p(b>0)=0.999; *Sherlock*: b=0.02, 95% HDI=[0.01, 0.03], p(b>0)=0.999), and the limbic network and subcortical regions (*Film Festival*: b=0.01, 95% HDI=[0, 0.02], p(b>0)=0.993; *Sherlock*: b=0.02, 95% HDI=[0, 0.03], p(b>0)=0.998).

Together, these results identified the within-network and between-network interactions that mediated the effects of emotional arousal on memory encoding. Some network and network pairs were unique to a dataset, suggesting that the specific networks involved may be context-specific. However, several networks and network pairs were consistent across both datasets, suggesting that there may be a core set of network interactions that enhance the encoding of emotionally arousing experiences across different contexts. In both datasets, the involvement of multiple functional networks suggests that brain-wide integration supports the enhanced encoding of emotionally arousing experiences.

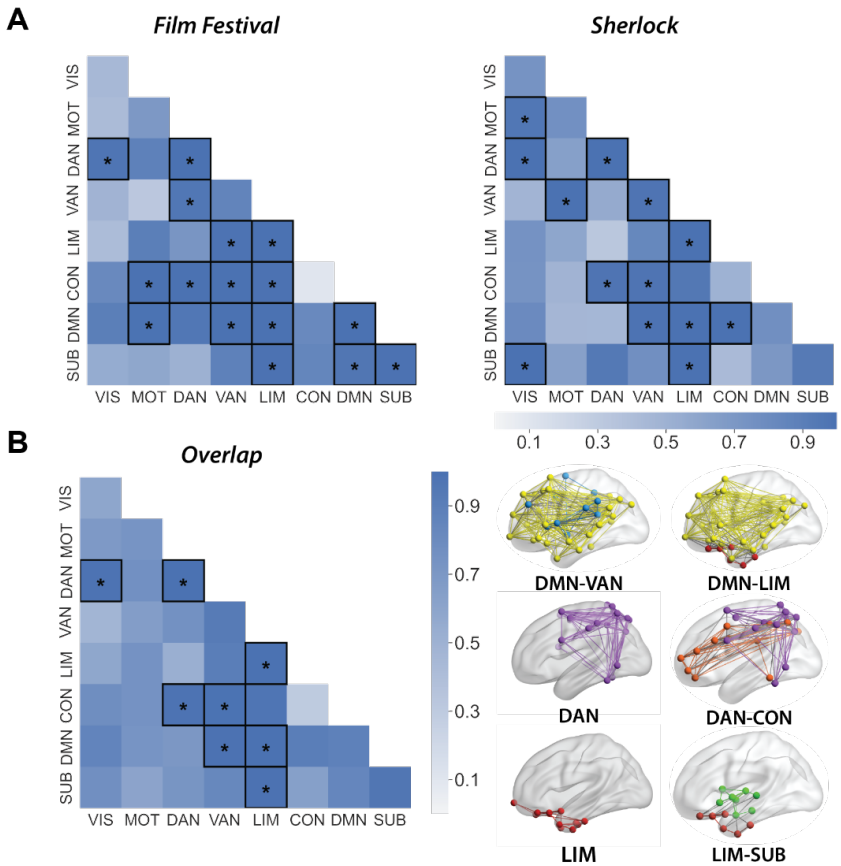

Figure 4. Within- and between-network efficiency mediates the effects of emotional arousal on recall fidelity. (A) Mediation effect in *Film Festival* and *Sherlock*. Diagonal and off-diagonal cells indicate effects of within- and between-network efficiency, respectively. Color denotes posterior probability of the mediation effect. * indicates cells that survive thresholding at average PEP of 0.01. **(B)** Plot elements are the same as (A) with colors denoting average posterior probability across both datasets. * indicates cells that survive thresholding at average PEP of 0.01 in both datasets. The right panel displays network and network pairs that mediated the relationship in both datasets. VIS-visual network, MOT-somatomotor network, DAN-dorsal attention network, VAN-ventral attention network, LIM-limbic network, CON-control network, DMN-default mode network, SUB-subcortical network.

Amygdala and hippocampus engagement during emotionally arousing events

Given the significant contributions of individual brain regions to memory and emotional processing, we focused our subsequent analyses on two specific regions of interest commonly implicated in enhanced memory encoding[15,21]: the amygdala and the hippocampus. The events in our study spanned 30 seconds to over a minute (*Film Festival* mean=38.4s, *Sherlock* mean=57.5s). As averaging amygdala and hippocampal activity over the course of an event fails to capture the time-locked neural responses evoked by dynamic stimuli, we employed intersubject correlation (ISC) analyses[56] to identify shared, stimulus-locked neural responses across participants. Notably,

prior work using the *Sherlock* dataset had found that events with higher hippocampal ISC during encoding were more likely to be remembered[45]. Here, we calculated the ISC of the amygdala and hippocampus for each event, and tested their relationship with arousal, integration, and recall fidelity.

The effects of amygdala and hippocampus ISC on arousal, network integration, and recall fidelity were consistent across both datasets, but the posterior distributions did not always exceed the 95% threshold in both datasets (see *Intersubject correlation analyses* in **Supplemental Text)**. To maximize statistical power and draw inferences leveraging results from both datasets, we report findings from Bayesian multilevel models that pooled data across both datasets, treating dataset as a random effect. Heightened arousal was positively associated with amygdala and hippocampal ISC, consistent with the engagement of these regions by emotionally arousing content (amygdala: b=0.07, 95% HDI=[0.02, 0.12], p(b>0)=0.994; hippocampus: b=0.09, 95% HDI=[0.03, 0.12], p(b>0)=0.999; **Figure 5A, 5B**). Amygdala ISC was positively associated with B_T (b=0.07, 95% HDI=[0.02, 0.11], p(b>0)=0.996), while hippocampal ISC was not (b=0.02, 95% HDI=[-0.03, 0.06], p(b>0)=0.760; **Figure 5C**). Both amygdala and hippocampal ISC were positively associated with recall fidelity (amygdala: b=0.07, 95% HDI=[0.01, 0.12], p(b>0)=0.992; hippocampus: b=0.07, 95% HDI=[0.03, 0.12], p(b>0)=0.999; **Figure 5D**). Additionally, amygdala and hippocampal ISC mediated the effects of arousal on recall fidelity (amygdala: b=0.004, 95% HDI=[0, 0.01], p(b>0)=0.976; hippocampus: b=0.005, 95% HDI=[0, 0.01], p(b>0)=0.995).

These results are consistent with prior findings indicating the importance of the amygdala and hippocampus to the enhancement of emotional memories. Importantly, the mediation effect of network integration on the relationship between emotional arousal and recall fidelity was robust to controlling for amygdala and hippocampal ISC (b=0.01, 95% HDI=[0, 0.02], p(b>0)=1), as well as average activity in the amygdala, hippocampus, and amygdala-hippocampus functional connectivity (b=0.01, 95% HDI=[0, 0.02], p(b>0)=0.999), indicating a unique contribution of large-scale functional integration above and beyond that explained by amygdala and hippocampal engagement.

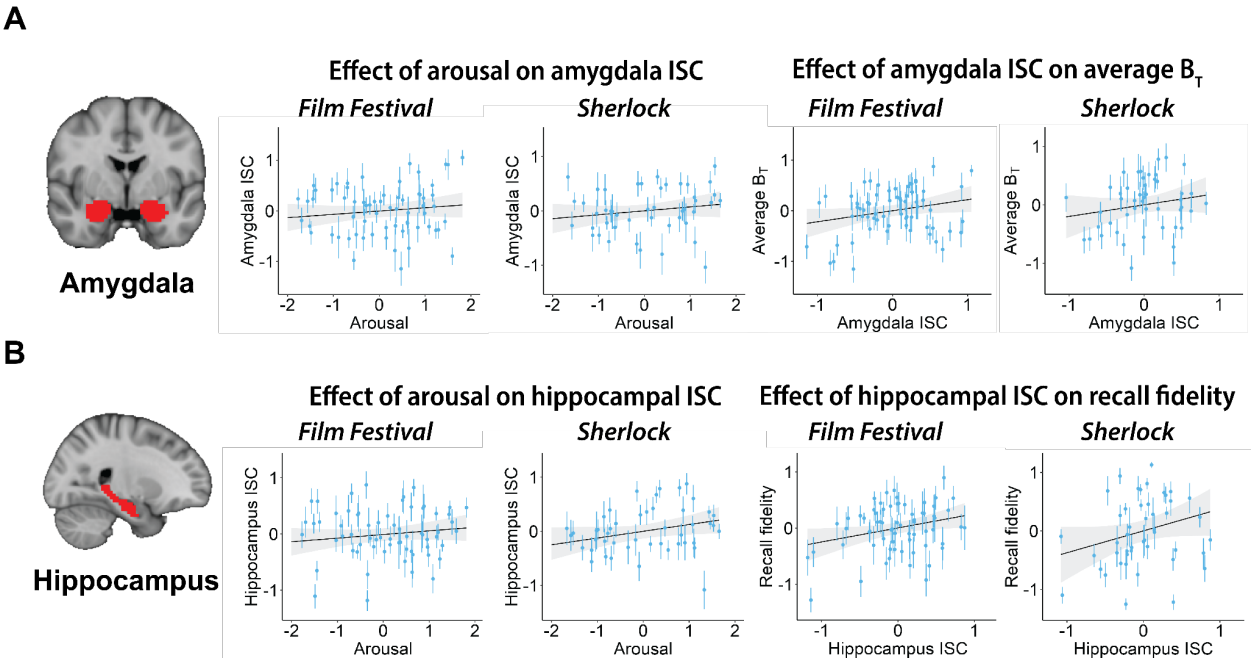

Figure 5. Emotional arousal was associated with hippocampal and amygdalar engagement during encoding. Emotionally arousing events were associated with greater inter-subject correlation (ISC) in the amygdala **(A)** and hippocampus **(B)**. In the amygdala, greater ISC was associated with greater integration in functional modules across the brain. In the hippocampus, greater ISC correlated with higher recall fidelity. Each datapoint corresponds to an event, with error bars indicating the standard error. The black line in (A) represents the estimated effects of arousal and amygdala ISC on amygdala ISC and network integration (average B_T), respectively. The black line in (B) represents the estimated effects of arousal and hippocampus ISC on average B_T and recall fidelity, respectively. The gray ribbon in both panels indicates the 95% credible interval.

Functional integration mediates effects of pupil dilation on narrative recall

Thus far, we have demonstrated that emotional arousal, as assessed through subjective ratings and large-language model-derived measures, is linked to heightened network integration and enhanced recall fidelity. Next, we assessed whether our findings would generalize to a physiological measure of arousal. Specifically, we measured physiological arousal as captured by fluctuations in pupil size during narrative listening.

We collected a new dataset (n=27) where participants listened to a suspenseful auditory story (*Paranoia*) while their pupil size was continuously measured. We further utilized an open dataset (n=22) of participants listening to the same story while undergoing fMRI[57]. The story was segmented into 24 events, and pupil size was averaged for each event. Pupil size across events was correlated between participants (one-to-average r=0.6, p<0.01), indicating that the story evoked arousal in a reliable manner across participants.

Pupil size was associated with greater recall fidelity (b=0.14, 95% HDI=[0.05, 0.22], p(b>0)=0.999; **Figure 6A**), indicating that arousing events were better remembered. Additionally, pupil size was positively associated with greater functional network integration (b=0.33, 95% HDI=[0.25, 0.4], p(b>0)=1; **Figure 6B**). Consistent with our earlier results, functional network integration at encoding was associated with subsequent recall fidelity (b=0.21, 95% HDI=[0.13, 0.29], p(b>0)=1). Finally, we found that functional network integration mediated the effects of pupil dilation on recall fidelity (b=0.06, 95% HDI=[0.03, 0.09], p(b>0)=0.999; **Figure 6C**).

Several network and network pairs that mediated the effects of pupil dilation on recall fidelity overlapped with those identified in the *Film Festival* and *Sherlock* datasets (**Figure 6D**). These include between-network efficiency between the dorsal attention network and the control network (b=0.02, 95% HDI=[0.01, 0.03, p(b>0)=1), the default mode network and the ventral attention network (b=0.02, 95% HDI=[0.01, 0.02], p(b>0)=0.999), the control network and the ventral attention network, dorsal attention network and the visual network (b=0.02, 95% HDI=[0.01, 0.03], p(b>0)=1). Altogether, these results indicate that our earlier findings generalize to a physiological measure of arousal and suggest that there is a core set of network interactions supporting the effects of arousal on memory encoding.

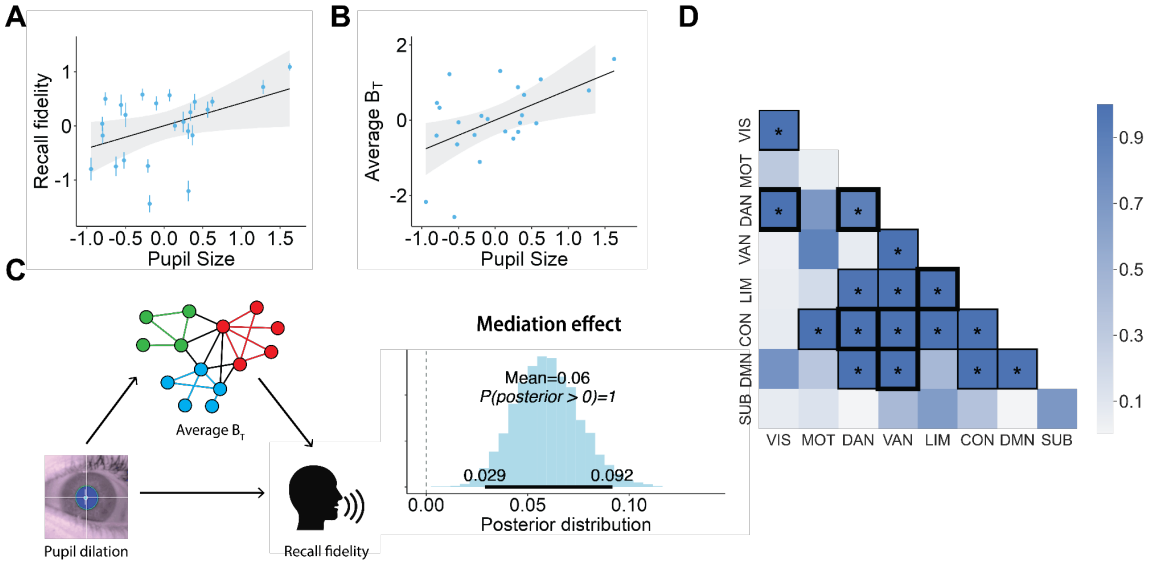

Figure 6. Functional network integration mediates effects of pupil dilation on recall fidelity. Pupil size during story listening is associated with **(A)** recall fidelity and **(B)** average participation coefficient (B_T). **(C)** Average B_T during an event mediates the effect of pupil dilation on recall fidelity. **(D)** Mediation effect in the *Paranoia* dataset. Diagonal and off-diagonal cells indicate effects of within- and between-network efficiency, respectively. Color denotes posterior probability of the mediation effect. * indicates cells that survive thresholding at average PEP of 0.01. Cells in thick borders indicate networks and network pairs that overlapped with those identified across the *Film Festival* and *Sherlock* datasets.

Discussion

Emotionally arousing experiences are often remembered with great clarity and detail[1,2]. In the present study, we combined fMRI, graph theory, and a naturalistic memory paradigm to study the emotional enhancement of narrative memories. Across three independent fMRI datasets, we demonstrated that whole-brain functional network integration during narrative perception mediated the effects of heightened emotional arousal on the fidelity at which participants subsequently remembered an event. Results replicated across measures of arousal obtained from text analyses of the content, behavioral ratings, and pupil dilation, as well as across movies and audio stories. The mediation effect was observed in interactions across multiple large-scale brain networks, indicating that emotional arousal may enhance memory by promoting coordinated activity across diverse brain regions. Together, our findings suggest that functional network integration supports the enhanced encoding of emotional memories by facilitating coordinated activity across the brain.

Our findings extend the neuroscientific investigation of emotional memories to complex, temporally-extended narratives, which are fundamental to how people make sense of experiences, share knowledge, and connect with others[43,58,59]. Prior work has demonstrated that emotionally arousing content enhances the encoding of narrative memories[1,2,25]. Here, we show that this memory enhancement is associated with increased network integration during narrative encoding. Encoding narratives involves the processing of multisensory information[60], integration with existing knowledge and schemas[61], and alignment with ongoing goals and internal states[62]. An integrated brain state, where different functional modules are highly interconnected, facilitates information exchange and coordination across regions[30,63,64]. The enhanced connectivity across perceptual, associative, and memory-related regions may support the binding of narrative events into a coherent memory representation, allowing for better encoding of event details and their broader context.

One of the strengths of graph theory is its ability to extract network-level metrics that provide insights into how the brain functions as an interconnected system. This approach allows us to capture emergent properties, such as the level of integration across functional modules, that only become apparent when considering the entire network. As a network-level property, integration can arise from various configurations of interactions between functional modules. When we examined each dataset separately, we identified network and network pairs where increased efficiency mediated the effects of emotional arousal on memory in one dataset but not the other. These results suggest that while integrated network configurations are associated with enhanced encoding of emotional memories, the specific network interactions that constitute these configurations may vary depending on stimulus content. By framing these network interactions within the broader concept of integration, our approach provides a unifying framework to explain the diverse neural pathways that strengthen emotional memories.

The findings, however, do not preclude the existence of a core set of network interactions consistently involved in the enhanced encoding of emotionally arousing memories. Indeed, we identified several networks and network pairs that mediated the effects of emotional arousal on memory fidelity across all three datasets. These include interactions between the control network and the ventral attention network (i.e., "salience" network[65]), consistent with prior work showing increased connectivity between these networks in emotionally arousing situations[37]. The ventral attention network supports the detection of salient information[66], and increased efficiency between these networks may enhance the allocation of cognitive resources toward processing emotionally significant narrative moments. We also observed consistent mediation effects involving the default mode and the ventral attention networks, which may facilitate the incorporation of externally emotionally salient information into internally constructed narrative models[67,68], prioritizing their encoding into long-term memory.

In addition, efficiency between the dorsal attention network and the control and ventral attention networks mediated the effects of emotional arousal on memory fidelity across datasets. The involvement of the dorsal attention network, which is typically associated with the top-down control of attention, aligns with prior work indicating that the enhanced encoding of emotional stimuli depends critically on attentional processes[69]. Emotional events draw attention, which in turn enhances stimulus processing. From this perspective, attention and arousal are interdependent processes that work in concert to prioritize the encoding of significant moments in a narrative. This attentional modulation is potentially supported by the locus coeruleus- norepinephrine (LC-NE) system, which is activated by arousing stimuli, and is known to enhance network integration[27,39,70] and attention control[71,72]. Consistent with this account, our study found that pupil dilation, a correlate of LC-NE activity, was associated with both network integration and enhanced memory encoding.

Our findings emphasize the importance of global brain network dynamics in enhancing memory encoding, but it is equally important to consider the role of specific brain regions within these larger networks. The amygdala and hippocampus, for instance, have been extensively studied for their roles in enhancing emotional memories[13–16,18–21]. Here, we found that emotional arousal engages the amygdala and hippocampus in a stimulus-locked manner. While the amygdala engagement was positively associated with network integration, hippocampal engagement was not, suggesting distinct roles for these regions in coordinating arousal-dependent large-scale network dynamics. Both amygdala and hippocampal engagement were positively associated with recall fidelity and mediated the effects of arousal on memory encoding, extending prior work to demonstrate the enhanced encoding of emotional moments during a temporally extended narrative. Importantly, the mediation effects of network integration remained significant when controlling for amygdala and hippocampal engagement, indicating that the effects of emotional arousal on memory encoding cannot be fully explained by activity in these regions alone.

The current results contribute to the growing body of literature relating arousal to brain network organization. Our findings are consistent previous studies that demonstrated changes in network organization following shifts in arousal states. For example, Kinnison and colleagues[73] found increased functional integration across the brain while participants viewed cues indicating potential threats (e.g., a shock) or monetary rewards. Similarly, electrophysiological studies in animal models and fMRI studies in humans have revealed that fluctuations in autonomic arousal induce changes in functional network topology [27,36,38,40,74]. Building upon these findings, our study demonstrates the functional consequences of these arousal-dependent network dynamics. Specifically, we show that arousal may prioritize information for encoding by facilitating communication across different functional brain networks, leading to greater fidelity during subsequent recall. These findings highlight the potential importance of arousal-dependent network interactions in shaping ongoing cognition.

Our findings are robust across three independent datasets, spanning both audiovisual and auditory stimuli and using distinct measures of arousal. One potential concern, however, is that the narrative events used in these studies may not have been sufficiently arousing to engage neural processes implicated in emotional memory enhancement. We consider this unlikely for several reasons. Emotional words have been shown to reliably elicit emotion-related memory effects[16,17], engaging similar neural processes as highly aversive images. All three narratives in our study contained highly arousing scenes; for example, the *Sherlock* episode included a battlefield sequence and a moment where a main character's life was seemingly under threat - events that are arguably more arousing than isolated words. Indeed, behavioral ratings of emotional arousal in the *Sherlock* and *Film Festival* datasets spanned nearly the full range of the 1–5 scale, suggesting meaningful variability in event-level arousal. Furthermore, heightened arousal was associated with increased amygdala engagement, replicating prior work using images and words. In the *Paranoia* dataset, pupil dilation was synchronized across participants, indicating stimulus-driven fluctuations in arousal that were shared across listeners. These converging behavioral, physiological, and neural measures indicate that the narrative events elicited robust and reliable arousal responses.

Taken together, our findings provide converging evidence that emotional arousal enhances narrative memories through the functional integration of large-scale brain networks. While our study focused on memory, emotional arousal is also known to influence a broad range of other cognitive processes, including attention[75,76], perception[77,78], and decision-making[79,80]. Our work lays the foundation for future research examining interactions operating at different scales, from local activity in the amygdala and hippocampus to brain-wide network dynamics, and how they facilitate the influence of emotional arousal on human cognition and behavior.

Methods

Film Festival dataset

Raw anatomical and functional data were downloaded from OpenNeuro[81]. Fifteen participants watched 10 short movie clips over the course of two functional runs (TR=1.5s, TE=39ms, flip angle=50°, voxel size=2x2x2mm^3). Each clip was approximately 5 minutes long (2.15-7.75 min) and varied in content, characters, and genre. Following movie-watching, participants were instructed to verbally describe the clips from memory. Additional details can be found in the original study[44]. MRI data were preprocessed using FSL/FEAT v.6.00 (FMRIB software library, FMRIB, Oxford, UK). The steps included motion correction of functional images, removal of low-frequency drifts using a temporal high-pass filter (100-ms cutoff), and spatial smoothing (5-mm FWHM). Functional images were registered to participants' anatomical image (rigid-body transformation with 6 DOF) and to an MNI template (affine transformation with 12 DOF). Following the original authors of this study[44], we discarded the first 2 TRs of each run to avoid the non-specific transient increase in BOLD response at the beginning of each run. Data from each run was shifted by 4.5s to account for hemodynamic lag, and then normalized by z-scoring across time within each subject.

Sherlock dataset

Preprocessed functional and anatomical data were downloaded from Princeton University's data storage repository, DataSpace[82]. Seventeen participants watched a segment from an episode of the British TV show *Sherlock* over the course of two functional runs (TR=1.5s, TE=28s, voxel size=3x3x4mm^3). Following movie-watching, participants were instructed to verbally describe the clips from memory. The preprocessed data was z-scored over time and shifted for hemodynamic lag within each run. No additional preprocessing steps were performed. Additional details about the experimental procedures can be found in[45].

Paranoia dataset

Raw anatomical and functional data were downloaded from OpenNeuro[83]. Twenty-two participants listened to a 20-minute-long story involving a mysterious social event over the course of three functional runs (TR=1s, TE=30ms, flip angle=8°, voxel size=2x2x2mm^3). Each run was approximately 7.2 minutes long (5.5-8.7 min). Preprocessing steps (motion correction, smoothing, registration) were identical to those of the *Film Festival* dataset. Data from each run was shifted by 5 TRs to account for hemodynamic lag, and then normalized by z-scoring across time within each subject.

Movie event segmentation and annotation

For the *Sherlock* stimulus, we utilized the event segmentation and annotation reported in [45]. Briefly, the 50-minute episode was divided into 48 events (M=57.5s, SD=41.7s) based on significant shifts in the narrative, such as changes in topic, location, time, and characters. An annotator then provided written descriptions about what was happening in the movie during that

event. Author K.G. repeated the procedure with the *Film Festival* stimulus, generating 68 events (M=38.4s, SD=18.2s) and corresponding written annotations of each event.

Recall transcripts

Transcripts of verbal memory recall were obtained from [44] and [45]. The transcripts were then segmented and manually matched to the corresponding events based on the annotations that best matched the verbal descriptions. For *Sherlock*, the onset and offset of the events that were remembered were provided by Chen et al. In [45]. For *Film Festival*, the associated time stamps were identified by author K.G..

Recall fidelity

We computed the fidelity of participants' recall by assessing the semantic similarity between participants' recall transcripts and movie annotations. For each event, we converted both the participants' recall transcripts and the corresponding movie annotations into separate 512-dimensional vectors using Google's Universal Sentence Encoder (USE)[46]. We chose the USE model because it generates a single embedding vector that captures the overall meaning of text spanning multiple sentences. We then calculated recall fidelity of each event as the cosine similarity between the vector encoding a participant's recall transcript and that encoding the movie annotation. USE has been frequently employed to measure semantic similarity between event descriptions[32,44,49,84]. Our approach draws on prior work computing the cosine similarity between embedding vectors encoding the annotation of an event and participants' recall as measures of memory fidelity[47–49].

Large language model measure of emotional arousal

We generated ratings of emotional arousal from the event annotations using StableBeluga-13B, (https://huggingface.co/stabilityai/StableBeluga-13B), an open access large language model (LLM)[53]. Researchers are increasingly using LLMs as tools for automated text analysis[85]. For example, LLM-generated valence and arousal ratings of text correspond well to those obtained from behavioral participants[86,87]. We provided the model with event annotations and prompted it to rate the arousal of each event on a scale from 1 to 10. As part of the model prompt, we provided a definition of arousal adapted from prior work used to obtain behavioral ratings of arousal from words, images, and films[88–90], where arousal was defined as a state of "feeling very mentally or physically alert, activated, and/or energized (see **Supplemental Materials** for the full model prompt). Due to the inherent stochasticity in the model's responses, we ran 30 iterations for each event, effectively simulating ratings from 30 "participants". These ratings were z-scored within each iteration to normalize the data and then averaged across iterations to generate an average arousal rating for each event.

Behavioral measure of emotional arousal

As a comparison and validation of the LLM-generated arousal ratings, we collected behavioral ratings of emotional arousal from thirty participants (5 male, 24 female, 1 non-binary; ages 21 to 36, mean age=26.23). Experimental procedures were approved by the University of Chicago Institutional Review Board, and participants provided informed consent prior to the start of the study. Participants were compensated with $30 for their time. Participants were provided with the same definition of arousal as the LLM, and were instructed to rate the arousal of each event on a scale of 1 to 5 after watching each event. They were allowed to pause the video to make their ratings. All participants provided ratings on both *Film Festival* and *Sherlock*, with a short break in between. The ratings were z-scored within each participant and averaged across participants to generate an average arousal rating for each event. We correlated the LLM and behavioral measures to assess the consistency across the two methods of eliciting arousal ratings.

Generating graphs from functional connectivity matrices

Cortical regions were parcellated into 200 regions of interests (ROI) taken from the Schaefer atlas[91]. Subcortical regions were divided into 16 ROIs based on the Melbourne subcortex atlas[92]. Similar results were observed when repeating our analyses with the Shen parcellation scheme that included 268 parcels encompassing both cortical and subcortical regions (**Table S1**, **Table S5**; see **Supplementary Material** for additional justification of parcellation scheme). We extracted ROI time courses by averaging all voxels within each ROI. We then regressed out mean white matter and mean cerebrospinal fluid time courses, and framewise displacement from each ROI time course to minimize the influence of motion, non-neuronal noise, and other nuisance signals on the functional connectivity estimates. Global signal regression was not included in the main analyses as it can introduce spurious correlations between brain regions[93,94]. However, we note that our results remained consistent when global signal regression was applied (**Table S4**).

For each event in each participant, we calculated the Fisher-z transformed Pearson correlation between the BOLD time courses of each pair of ROIs, resulting in a 216x216 functional connectivity (FC) matrix. Each matrix was then thresholded to retain the top 15% strongest connections and binarized to create an unweighted, undirected graph. To ensure the robustness of our findings, we replicated our results at different thresholds (10%, 20% and 25%; **Table S2**, **Table S6**). All graph theoretic metrics (see below) were then extracted using the Brain Connectivity Toolbox (BCT)[50].

Average participation coefficient

Consistent with prior studies[27,29,41], brain regions were assigned to communities (i.e. modules) using the Louvian algorithm, which seeks to identify a community structure that maximizes the number of within-community connections and minimizes between-community connections. Given the stochastic nature of the algorithm, the community assignment was repeated 1,000 times to obtain a consensus community structure for each participant and event.

We then calculated the participation coefficient (B_T) for each ROI, which quantifies the extent to which the region's connections are distributed across different communities:

$$B_{Ti} = 1 - \sum_{m \in M} (\frac{k_{i,m}}{k_i})^2$$

where k_i is the degree (i.e., total number of connections) of region i, $k_{i,m}$ is the number of connections that region i has with regions in community m. Thus, B_T ranges from 0 to 1 with higher values indicating that a region's connections are evenly distributed across communities, and lower values indicating that a region's connections are predominantly within its assigned community. To assess whole-brain network integration, we averaged B_T across all ROIs for each participant and event. The average B_T was used as our primary measure of network integration, with higher values indicating a more integrated brain state during movie-viewing.

Network efficiency measures

We calculated global efficiency (E_g) as an alternative measure of network integration[50]. E_g is defined as the average inverse shortest path length between all pairs of nodes in the network:

$$E_g = \frac{1}{n(n-1)} \sum_{i \neq j \in N} \frac{1}{d_{ij}}$$

where n is the total number of regions, N is the set of all regions in the network, and d_{ij} is the length of the shortest path between nodes i and j. Higher E_g is indicative of greater network integration where fewer connections separate any two brain regions.

Within-network efficiency was calculated as the average inverse shortest path length between all pairs of regions within a network. Between-network efficiency of network 1 and 2 was calculated as the average inverse shortest path length between each region in network 1 and each region in network 2[41]. For all efficiency measures, the shortest path was defined over all regions in the brain. In other words, when calculating between-network efficiency between networks i and j, the shortest path may include regions outside of the two networks.

Bayesian multilevel models

We used Bayesian multilevel models to analyze the relationship between brain network metrics, emotional arousal, and recall fidelity. These models were chosen for their ability to account for the hierarchical structure of the data, where events were nested within participants, and to estimate uncertainty in the parameter estimates directly. All models were implemented using the *brms* package (version 2.21.0)[95] in *R* version 4.3.2, and were run with the random seed "123" to ensure

reproducibility. The models included random intercepts and slopes for predictors to account for random variability across participants.

Models were specified with weakly informative priors to facilitate convergence, while still allowing the posterior distributions to be predominantly shaped by the data (see **Supplementary Materials** for full prior specification). Each model was run with four Markov Chain Monte Carlo (MCMC) chains, each with 4,000 samples, of which the first 1,000 samples were discarded as burn-in. The remaining samples from all chains were concatenated to form the posterior distribution of each parameter. We checked for model convergence by ensuring that the Gelman-Rubin diagnostic ($\widehat{\boldsymbol{R}}$) was less than 1.01 for all parameters. Posterior distributions were summarized by reporting the estimated posterior means and 95% highest density intervals (HDIs) [96]. We considered parameters to be credibly above zero if more than 95% of the posterior distribution was greater than zero.

Mediation analyses

Mediation effects were computed using the product of coefficients method[97]. Specifically, the posterior distribution of the mediation effect of average B_T was obtained by multiplying the posterior samples of the effect of emotional arousal on average B_T ("path a") by the posterior samples of the effect of average B_T on recall fidelity while controlling for emotional arousal ("path b").

We grouped the brain regions into the 7 functional networks defined by the Schaefer atlas, with the 16 subcortical ROIs grouped together as one network. We then assessed the mediation effect of the within-network efficiency of each network, as well as the between-network efficiency of every pair of networks. To account for multiple comparisons across networks and network pairs, we thresholded the results within each dataset at an expected Posterior Error Probability (PEP) of 0.01, corresponding to a less than 0.01 probability of making an incorrect inference (i.e., concluding that a parameter is greater than 0 when it is in fact less than 0)[55]. From a frequentist perspective, this procedure is analogous to controlling for a false discovery rate at $q < 0.01$[98]. We then identified networks and network pairs that survived thresholding at an expected PEP < 0.01 in both datasets.

Intersubject correlation analyses

We extracted the time course data from the amygdala and the hippocampus for each event. For each subject and event, we calculated the inter-subject correlation (ISC) by correlating an individual's time course data with the average of all other subjects' data. This provided an ISC value for the amygdala and the hippocampus for each subject and each event. We then tested whether ISC was associated with arousal, memory, and participation coefficient.

***Paranoia* behavioral dataset**

A total of 35 participants were recruited from the University of Chicago research participation pool (SONA systems). The experimental procedures were approved by the Institutional Review Board at the University of Chicago, and all participants provided informed consent at the beginning of the study. Three participants were excluded due to equipment failure; five additional participants were excluded due to noisy pupillometry data (see *Pupillometry* section in **Supplemental Materials**). Thus, 27 participants in total were included in the analysis. Detailed procedures regarding noise detection and preprocessing are reported in the supplementary materials.

Pupil size was recorded using the Eyelink 1000 eye tracker (SR Research, Kanata, Ontario, Canada) at a sampling rate of 500 Hz. Prior to recording, participants completed a 5-point calibration sequence. Participants were seated in front of the computer and instructed to fix their eyes on a cross displayed in front of them. After listening to the story, participants were allowed a short break before beginning the recall task. For the recall task, participants were asked to recount the story in their own words. They were encouraged to speak for at least 10 minutes and were permitted to return if they later recalled additional details.

Data and Code Availability

Raw MRI data from the *Film Festival* dataset are available on OpenNeuro,
https://openneuro.org/datasets/ds004042/versions/1.0.1
Preprocessed MRI data from the *Sherlock* dataset are hosted at DataSpace,
https://dataspace.princeton.edu/jspui/handle/88435/dsp01nz8062179.
Raw MRI data from the Paranoia dataset are available on OpenNeuro,
https://openneuro.org/datasets/ds001338/versions/1.0.0

Custom analysis scripts, as well as behavioral and pupillometry data, are available at:
https://github.com/jadynpark/arousal_integration

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