Narratives as Networks: Predicting Memory from the Structure of Naturalistic Events

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ABSTRACT

Human life consists of a multitude of diverse and interconnected events. However, extant research has focused on how humans segment and remember discrete events from continuous input, with far less attention given to how the structure of connections between events impacts memory. We conducted an fMRI study in which subjects watched and recalled a series of realistic audiovisual narratives. By transforming narratives into networks of events, we found that more central events—those with stronger semantic or causal connections to other events—were better remembered. During encoding, central events evoked larger hippocampal event boundary responses associated with memory consolidation. During recall, high centrality predicted stronger activation in cortical areas involved in episodic recollection, and more similar neural representations across individuals. Together, these results suggest that when humans encode and retrieve complex real-world experiences, the reliability and accessibility of memory representations is shaped by their location within a network of events.

INTRODUCTION

Remembering the experiences of our lives requires collecting and connecting the pieces and reasons for what transpired. When we tell each other about the minutes and hours leading up to this moment, the tale will be composed of a string of time periods, "events"[1,2], distinguished by properties such as their locale or mood, and by our companions or goals at the time. Traditional experimental memory paradigms[3,4] rely on isolated stimuli in which meaningful connections between memoranda across time are removed via trial randomization. Yet in reality, each event exists within, and is to some extent defined by, a dense network of connections across time. These connections come in multiple forms: different timepoints could share properties to greater or lesser degrees, and actions earlier may have consequences later. When remembering and retelling, we often need to recapitulate not only the most important individual events, but also the overall structure of the experience, i.e., the pattern of connections across time[5,6]. Thus, it is important to understand in what ways the web of interrelations between events contributes to our memories of those experiences.

In order to test how inter-event structure relates to later memory, experimenters must use study material which contains inter-event structure. Recently, researchers have sought to incorporate the complex, multi-event nature of real-world input into laboratory experiments by using auditory and/or visual narratives[7,8]. Since narratives are temporally continuous, a major question in the literature has been how the human brain identifies and remembers discrete events from continuous experiences[2,9,10]. As input arrives from the world, the perceiver constructs a mental model of the situation, which consists of agents, objects, spatiotemporal contexts, and the relations between these components[11]. Changes in the ongoing situation trigger the registration of the just-concluded event into long-term memory, evoking transient responses in the hippocampus and its cortical partners[12,13]. The boundaries between events are also associated with shifts in neural activation patterns in higher associative areas in the default mode network (DMN[14])[15]. DMN activity patterns specific to individual events are thought to represent situation models[16], and are reinstated during narrated memory recall[17,18]. However, these studies focus on how each event is segmented from its temporally adjacent neighbors. How do the myriad connections between events, both temporally proximal and distal, impact the cognitive and neural underpinnings of naturalistic memory?

Inter-event connections could benefit both memory encoding and retrieval. At encoding, events with strong connections to numerous other events might be frequently reactivated by these links to form robust and integrated representations[19,20]. At retrieval, events with many

connections might be more likely to be cued by other events, enhancing their accessibility. These enhancing effects of inter-event connections on memory have been demonstrated in the reading comprehension literature, which focused on casual relations in relatively short and carefully designed text passages[21,22]. For example, statements that form causal chains are better remembered than isolated statements, and memory accuracy for a statement increases with the number of causal connections that it has[22,23]. Causal connectivity between statements also predicts how important readers will deem a given statement to be, and what they will judge to be the gist of the narrative[22,24]. The current study aims to examine the mnemonic benefits of inter-event connections in light of the burgeoning cognitive neuroscience of memories for events. Using previously unavailable neuroimaging approaches, we investigate the effect of inter-event structure on brain functions supporting the encoding and retrieval of event representations. In addition to testing the influence of causal relations, we take advantage of natural language processing techniques which allow effortless quantification of semantic similarity between text descriptions of complex events[25,26]. These non-causal ("semantic") relations, based on shared meaning and overlapping components between events, may constitute a previously underexplored pathway through which inter-event connections enhance memory.

Here, we propose that when people view and recall realistic, continuous audiovisual stimuli (e.g., movies), events with stronger and more numerous semantic or causal connections to other events will be better remembered, with concomitant hippocampal and DMN activity reflecting enhanced encoding and retrieval-related processing for these events. We conducted a functional magnetic resonance imaging (fMRI) study in which participants watched a series of movies and then verbally recounted the movie plots. To quantify and assess the semantic relationship between events within a movie, we employed a novel approach scalable and easily generalizable to different types of narratives (Figure 1). In this method, each narrative is transformed into a network of interconnected events based on semantic similarity measured from sentence embedding distances. Behavioral results revealed that events with higher centrality (i.e., connected to a larger number of other events) were more likely to be recalled, without showing primacy and recency effects typical in traditional random list memory experiments[3,27]. High centrality events were also associated with the neural signatures of stronger and more accurate recall: greater activation and more consistent neural patterns across individuals in the DMN areas including the posterior medial cortex (PMC). The hippocampus showed higher activation following the offset of high centrality events, suggesting that stronger hippocampus-mediated encoding contributed to the high centrality advantages.

Causal relations, defined by human judgments, predicted memory success and neural responses in a similar way to semantic relations, but also made an independent contribution to each. Overall, our findings demonstrate that memories for events are shaped by their location within a narrative network, highlighting the importance of considering inter-event structure when studying the cognitive and neural mechanisms of complex and continuous real-world memory.

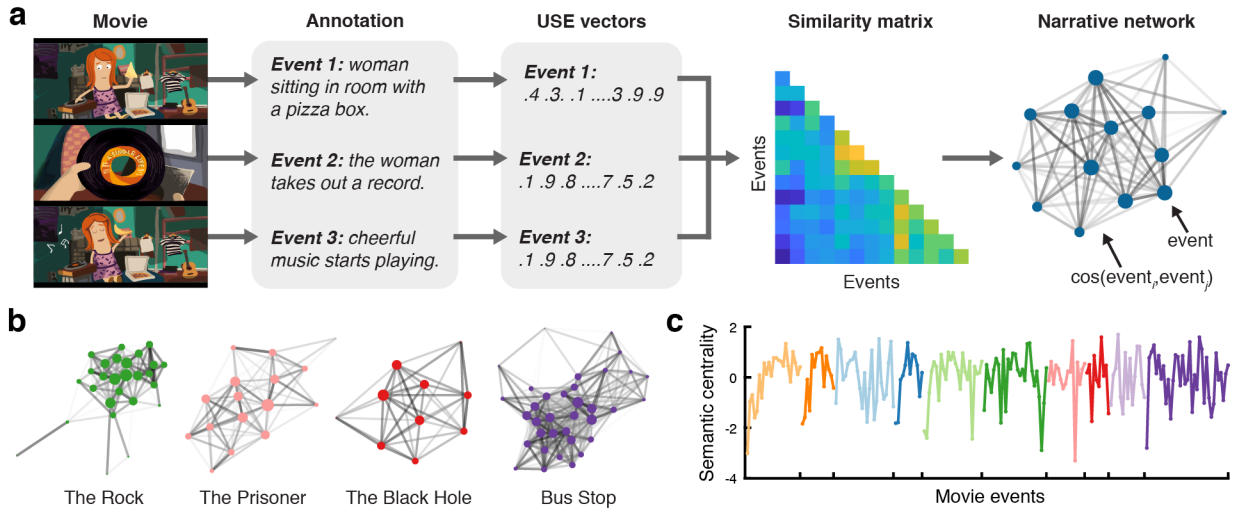

Figure 1. Semantic narrative networks. a. To create semantic narrative networks, each movie was split into events, and independent annotators provided text descriptions of the events. The text descriptions were transformed into sentence embedding vectors using Google's Universal Sentence Encoder (USE)[25]. Semantic similarity between events was computed as the cosine similarity between the USE vectors. A semantic narrative network was defined as a network whose nodes are movie events and the edge weights are the semantic similarity between the events. **b.** Semantic narrative networks of four example movies used in the fMRI experiment. Edge weights were thresholded at cosine similarity = .6 for visualization purposes. Node size is proportional to centrality. Edge thickness is proportional to edge weights. **c.** Semantic centrality (normalized degree) for individual movie events of the 10 movies used in the fMRI experiment. Different colors denote different movies.

RESULTS

Behavioral characteristics of unguided narrative recall

We first examined the behavioral characteristics of free spoken narrative recall. Subjects watched a series of short movies with unique narratives (Supplementary Table 1) and then verbally recalled the movie plots while undergoing functional MRI. Subjects were instructed to

describe what they remembered from the movies in their own words in as much detail as they could, regardless of the order of presentation. No external cues or experimenter guidance were provided during recall.

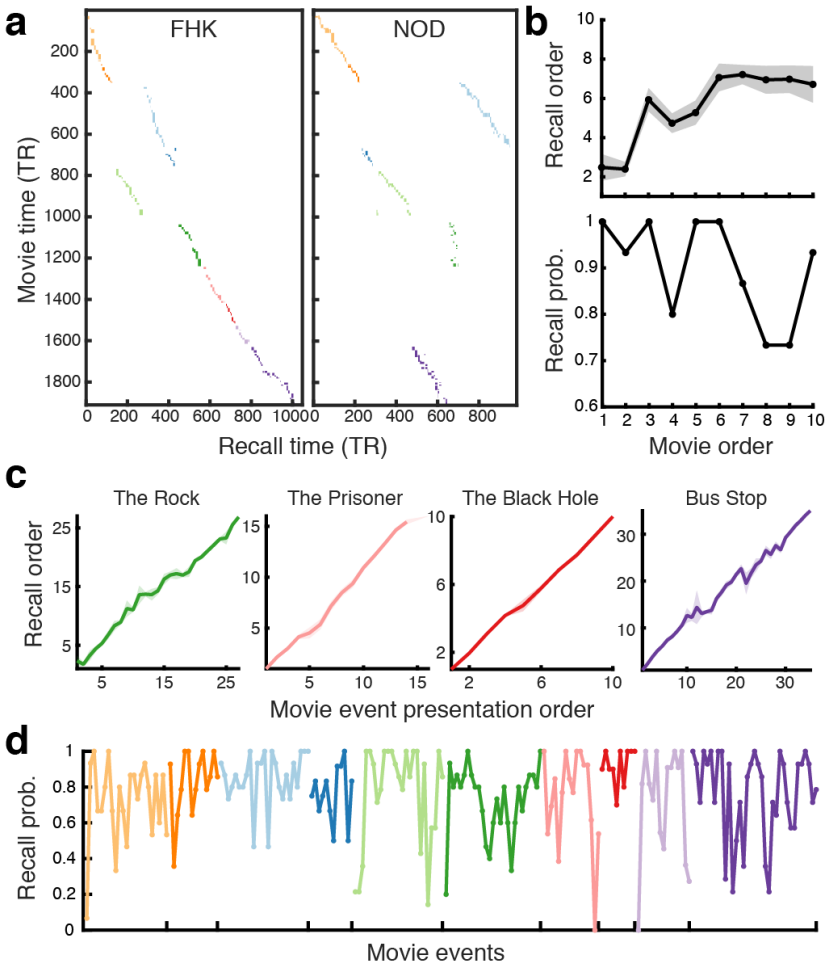

Figure 2. Unguided spoken narrative recall behavior. a. The duration and order of spoken recall for two example fMRI subjects. Each colored rectangular dot represents a movie event. Different colors denote different movies. The *x* and *y* coordinates of a dot represent the temporal position of the event during recall and movie watching, respectively. The width and height of a dot represent the duration of the event during recall and movie watching, respectively. **b.** Recall order (top) and recall probability (bottom) of the ten movies used in the fMRI experiment. **c.** Recall order of individual movie events in four example movies. **d.** Recall probability of individual movie events for the ten movies shown in different colors. In **b** and **c,** recall order was defined as the rank among recalled movies or events (i.e., 1 = recalled first, *N* = recalled last, where *N* is the total number of movies or events). Shaded areas indicate SEM across subjects. In **b** and **d,** recall probability was calculated as the proportion of subjects who recalled each movie or event.

Two example subjects' recall behaviors are depicted in Figure 2a. On average, subjects recalled 9 out of the 10 movies (s.d. 1.2) and the recall lasted 32.4 minutes in total (s.d. 14.5 min). Each movie was divided into 10 – 35 events by an independent coder based on major shifts in the narrative (e.g., time, location, action). Subjects on average recalled 77.6% of the events within each recalled movie (s.d. 11.2%). Movies tended to be recalled in the original presentation order (mean Spearman's ρ between the presentation order and the recalled order = .52, s.d. across subjects = .55; Figure 2b, top panel). Although subjects were not explicitly instructed to perform serial recall, events were recalled strictly in the order in which they occurred within each movie (mean ρ = .97, s.d. = .03; Figure 2c). Thus, recalling an event likely served as a strong cue for the following event which was often semantically/causally related.

Contrary to traditional random list memory experiments[3,27], we did not observe the classic primacy and recency effects on recall probability[3] either at the movie level or the event level. The proportion of subjects who successfully recalled a movie was not higher for the first or last few movies compared to the movies presented in the middle of the list (Figure 2b, bottom panel). Likewise, the recall probability of the first/last few events was not higher than that of the events presented in the middle, either within each movie or across all movies (Figure 2d). Specifically, there was no difference between the mean recall probabilities of the first/middle/last three events of each movie ($F(2,18) = .78$, $p = .47$, $\eta^2 = .05$). These results suggest that memorability of a movie event was largely influenced by narrative properties beyond the serial position of events.

Narrative network centrality predicts what people will remember later

One important factor that may have affected the behavioral characteristics of movie event recall is the inter-event structure inherent in narratives. We used a novel approach to quantify narrative structure by transforming each movie plot into a network of events (Figure 1), in which the connections between events were determined by their similarity based on semantic contents. To measure semantic similarity between movie events, we first converted the text descriptions of the events, generated by independent annotators, into vectors of 512 numbers using Google's Universal Sentence Encoder (USE[25]). Consistent with a recent study[26], the trajectories of movie annotations in the high-dimensional vector space were highly consistent across annotators (Supplementary Figure 1), demonstrating that the text embeddings captured the semantic gist despite the differences in specific words used to describe the events. Likewise, the USE vectors of recall transcripts were similar to those of movie annotations and were also similar across subjects (Supplementary Figure 2). Semantic similarity between events

was defined as the cosine similarity between their USE vectors.

Our main variable of interest reflecting the inter-event narrative structure was the centrality (i.e., normalized degree) of individual events within a narrative network (Figure 1c). By definition, events with stronger (higher semantic similarity) and greater numbers of connections with other events had higher centrality. Critically, semantic centrality positively predicted subsequent event recall probability measured as the proportion of subjects recalled each event ($r(202) = .20$, $p = .004$, 95% confidence interval (CI) = [.07, .33]; Figure 3a). To further test the effect of semantic centrality in individual subjects, we grouped events into high or low centrality conditions within each movie (i.e., events whose semantic centrality values are within the top/bottom 40%), and measured the proportion of successfully recalled events in each condition. The recall probability averaged across movies was higher for high than low semantic centrality condition ($t(14) = 6.12$, $p < .001$, Cohen's $d_z = 1.58$, 95% CI of the difference = [.06, .12]; Figure 3b).

We next demonstrated that inter-event semantic relation and causal relation each uniquely explains narrative memory performance. Classic studies on story comprehension have reported that the number of causal connections with other events predicts the perceived importance and memorability of an event[22,24]. To test the effect of causal relations, we created the causal narrative networks of the movies (Supplementary Figure 3) by having independent coders identify causally related events within each movie (see Supplementary Figure 4 for detailed descriptions of causality responses). The connection strength between a pair of events was defined as the proportion of coders who responded that the pair is causally related. Centrality (i.e., normalized degree) of each event was then computed within each causal narrative network. The causal centrality was positively correlated with semantic centrality ($r(202) = .28$, $p < .001$, 95% CI =[.15, .41]) and recall probability ($r(202) = .29$, $p < .001$, 95% CI = [.16, .42]; Figure 3c). Recall probability was also higher for high than low causal centrality events within each subject ($t(14) = 8.23$, $p < .001$, Cohen's $d_z = 2.12$, 95% CI of the difference = [.1, .17]; Figure 3d), replicating earlier studies[22,23]. Importantly, a mixed-effects logistic regression analysis (see Methods) revealed that semantic centrality explains successful event recall even after controlling for causal centrality ($\beta = .17$, standard error (SE) = .05, $\chi^2(1) = 12.24$, $p < 0.001$) and vice versa ($\beta = .38$, SE = .05, $\chi^2(1) = 55.04$, $p < 0.001$).

We conducted a pre-registered online experiment ($N = 393$) and replicated the same behavioral characteristics of narrative recall using a new set of 10 short movies (Supplementary Figure 5). Each subject watched one of the movies and then performed a free written recall of the movie plot. Consistent with the behavioral results from the fMRI experiment, semantic

centrality (β = .17, SE = .03, $\chi^2(1)$ = 48.52, p < 0.001) and causal centrality (β = .44, SE = .03, $\chi^2(1)$ = 255.67, p < 0.001) each uniquely predicted the successful recall of an event, without any clear evidence of serial position effects (i.e., no difference between the mean recall probabilities of the first/middle/last three events of each movie, $F(2,18)$ = .85, p = .44, η^2 = .04).

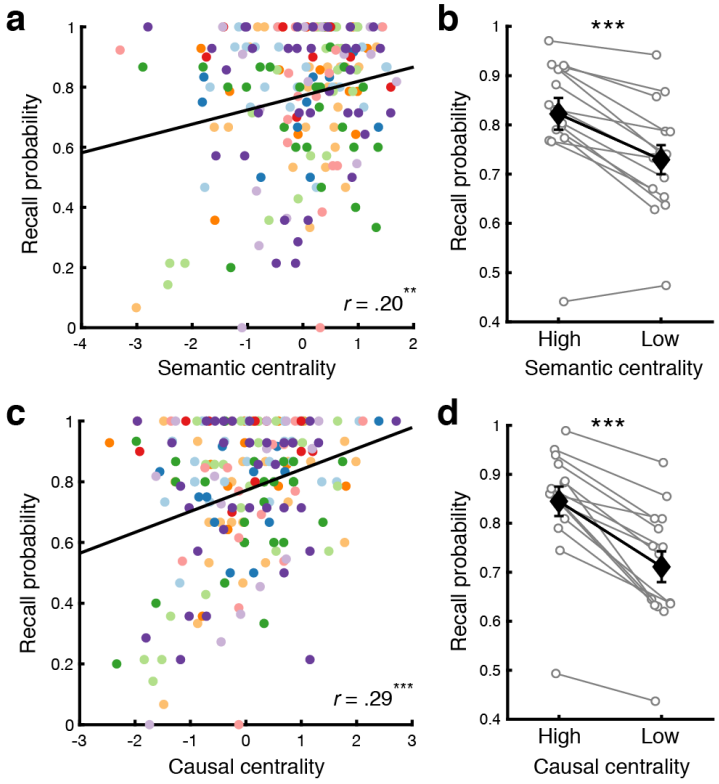

Figure 3. Effects of narrative centrality on recall performance. a. Correlation between semantic centrality and recall probability. **b.** Recall probability for High (top 40%) vs. Low (bottom 40%) semantic centrality events defined within each movie (averaged across movies). **c.** Correlation between causal centrality and recall probability. **d.** Recall probability for High (top 40%) vs. Low (bottom 40%) causal centrality events defined within each movie (averaged across movies). In **a** and **c,** each dot represents an individual movie event. Different colors denote different movies. In **b** and **d,** white circles represent individual subjects. Black diamonds represent the mean across subjects within each condition. Error bars show SEM across subjects. **p < .01, ***p < .001.

High centrality events more strongly activate DMN during recall

Narrative network centrality predicted successful memory recall of movie events. Does it also predict brain responses associated with movie watching and recall? We first identified brain regions whose activation scaled with the semantic centrality of events. In this and all following

analyses, we excluded the first event of each movie from the movie watching data. This was to minimize the influence of transient changes in activation associated with the boundaries between narratives[12,28]. The movie boundary-related responses also disrupted event-specific neural patterns by creating similar activation patterns across all movies (Supplementary Figure 6).

We performed a whole-brain general linear model (GLM) analysis designed to predict the mean activation of individual events with their semantic centrality. Group-level analysis of the subject-specific beta maps showed that, at a liberal threshold (uncorrected $p < .001$), higher semantic centrality of an event was associated with stronger activation in several regions including visual and auditory association cortices and precuneus during *movie watching* (Supplementary Figure 7a). The involvement of sensory areas may reflect potential high-level perceptual differences between the high and low centrality events, although low-level visual and auditory features including luminance, contrast, and audio amplitude were not significantly modulated by semantic centrality (all $\chi^2(1)$s < 1.94, *p*s > .16). More importantly, during *recall*, events with higher semantic centrality more strongly activated default mode network (DMN) areas including the angular gyrus (ANG) and PMC (Supplementary Figure 7b). DMN areas have been strongly associated with episodic recollection[16,29]. We also observed higher activation during recall for high than low semantic centrality events in the bilateral hippocampus ($t(14) = 2.71$, $p = .017$, Cohen's $d_z = .7$, 95% CI of the difference = [.01, .05]). These results are in accordance with the positive relationship between recall performance and semantic centrality, and may suggest that high centrality events were more strongly recollected with rich episodic details.

We used causal centrality as a regressor in the GLM analysis and again found greater activation in the same DMN areas for higher centrality events during recall (Supplementary Figure 7d). In this and following fMRI analyses, the effects of causal centrality were generally comparable to those of semantic centrality, except that causal centrality effects were weaker in analyses involving intersubject similarity. Thus, we focus on the semantic centrality effects and report the causal centrality effects in Supplementary Figure 8. We consider potential differences between semantic and causal centrality in Discussion.

Neural patterns in DMN reflect both event-specific representations and narrative network structure

Prior studies have shown that narrative events are represented as distributed patterns of activation in DMN[17,18]. How does the inter-event structure relate to the neural representations of

events during movie watching and recall? To answer this question, we performed an intersubject pattern correlation (pISC) analysis[17]. Within a brain region, event-specific pISC was computed as the mean spatial similarity (i.e., Pearson correlation) between a subject's activation pattern of an event and each of the other subjects' activation pattern of the matching event (Figure 4a). By measuring neural signals *shared* across subjects, the intersubject correlation method was expected to reduce the influence of task-unrelated idiosyncratic noise[30,31].

We first created whole-brain pISC maps to identify brain regions that showed robust event representations shared across subjects. For each cortical parcel of an atlas[32], we computed the mean pISC averaged across events and subjects. We then performed a nonparametric randomization test to determine whether the mean pISC was significantly different from a null distribution generated by randomly shuffling event labels across all movies. Replicating our prior study[17], positive pISC was observed in widespread cortical regions during both movie watching and recall (FDR corrected $q < .05$). During movie watching (Supplementary Figure 9a), the strongest pISC was found in sensory cortices, as all subjects processed the same audiovisual stimuli. During recall (Figure 4d), DMN areas, especially PMC, showed the strongest pISC, consistent with the view that PMC and functionally connected areas are engaged in the episodic construction and representation of events or situation models[16].

We next demonstrated that neural patterns in the DMN areas reflect not only the situations specific to individual events within each movie, but also the semantic relationships between them during recall. We used whole-brain representational similarity analysis (RSA[33]): for each cortical parcel and movie, we correlated the event-by-event similarity matrix based on the text descriptions of events (i.e., USE vectors from the movie annotations) and the similarity matrix based on neural responses during recall (Figure 5). The neural similarity was again computed as intersubject pattern correlation, but here the pISC was computed between different events rather than matching events. Statistical significance was determined by randomization tests using event labels randomly shuffled within each movie, and then corrected for multiple comparisons across parcels (FDR $q < .05$). We found positive correlations between the semantic similarity and neural similarity in parcels mostly within DMN, especially those in and around PMC (Figure 5). We also observed similar but stronger effects in DMN using the semantic similarity matrix generated from subjects' recall transcripts rather than movie annotations (Supplementary Figure 10b).

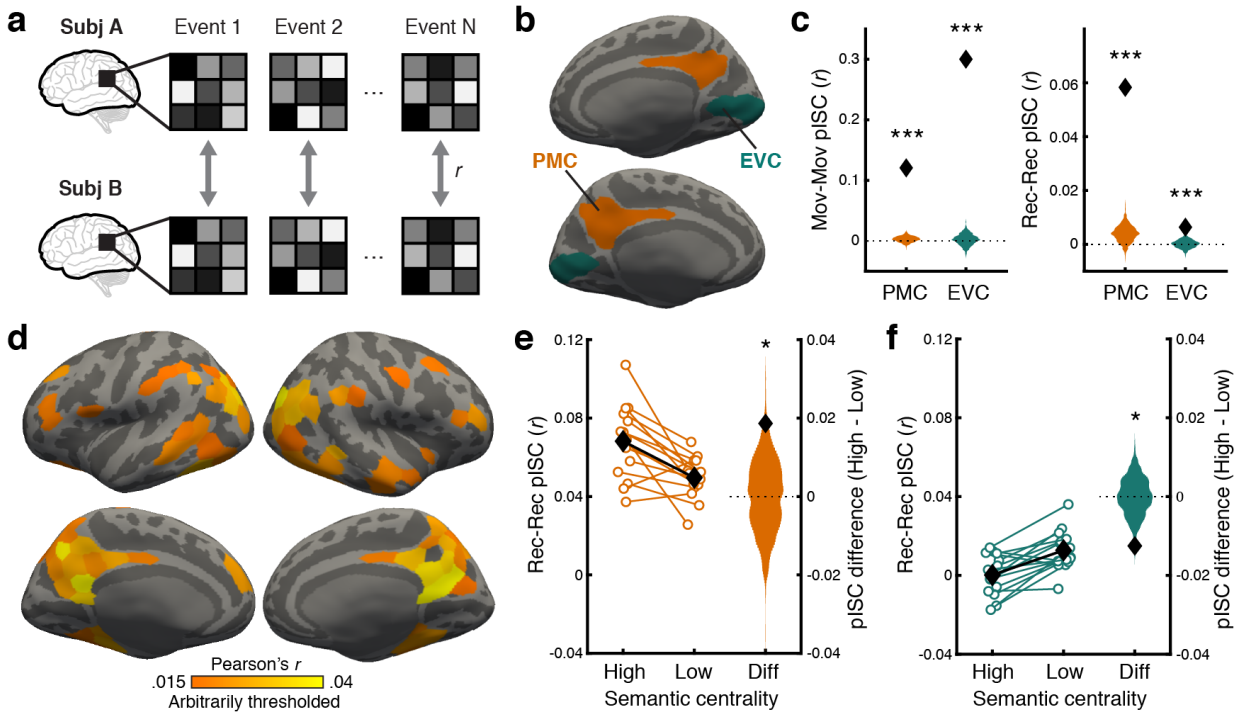

Figure 4. Event-specific intersubject pattern correlation. a. Intersubject pattern correlation (pISC) was computed for each movie event by correlating the event-specific activation pattern (averaged across times within the event) of a subject and that of each of the other subjects. **b.** Posterior medial cortex (PMC; orange) and early visual cortex (EVC; green) regions-of-interest visualized on the inflated surface of a template brain (medial view). **c.** pISC in PMC and EVC during movie watching (left) and recall (right). Black diamonds show the mean pISC averaged across all subjects and movie events. Orange and green histograms show the null distributions of the mean pISC in PMC and EVC, respectively. **d.** Whole-brain surface map of mean pISC during recall. pISC was computed for each of 400 parcels in a cortical atlas[32]. The pISC map was arbitrarily thresholded at $r = .015$ for visualization purposes. pISC values in all visualized parcels were significantly greater than zero based on randomization tests (FDR-corrected $q < .05$ across parcels). **e & f.** pISC for High vs. Low semantic centrality events during recall and the difference (Diff) between the two conditions in PMC (**e**) and EVC (**f**). For High and Low semantic centrality conditions, white circles represent individual subjects. Black diamonds represent the mean across subjects within each condition. Error bars show SEM across subjects. For the difference between High and Low conditions (Diff), black diamonds show the true subject average, and histograms show the null distribution of the mean difference. In **c**, **e**, and **f**, statistical significance reflects difference from zero based on randomization tests. *$p < .05$, ***$p < .001$.

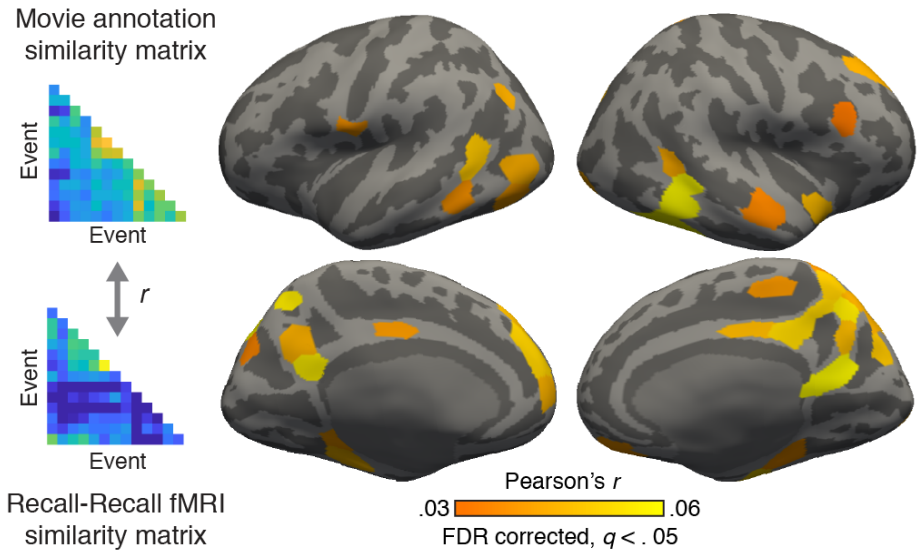

Figure 5. Representational similarity during recall. To identify brain regions whose activation patterns during recall reflect the whole semantic narrative network structure, we performed a representational similarity analysis (RSA[33]). For each cortical parcel, the representational similarity between the fMRI patterns and movie annotations was computed within each movie by correlating the cross-event intersubject pattern similarity matrix and the USE sentence embedding vector similarity matrix. The correlation coefficients were averaged across movies and subjects. The resulting mean representational similarity was tested for statistical significance against zero using a randomization test. The whole-brain RSA map was thresholded at $q < .05$ (FDR-corrected across parcels).

Narrative network centrality predicts the between-brain similarity of event representations

Our next key question was whether the centrality of events modulates the quality of event-specific neural representations in DMN measured as pISC. Here, we used a region-of-interest (ROI) approach (Figure 4b) and focused on PMC, which showed the strongest effects in the whole-brain pISC and RSA analyses above. As a lower-level control region, we used the early visual cortex (EVC). Both regions showed event-specific neural patterns (i.e., significantly positive pISC) during movie watching (pISC in PMC = .12, EVC = .3, one-tailed randomization *p*s < .001; Figure 4c, left panel) and recall (pISC in PMC = .06, EVC = .01, *p*s < .001; Figure 4c, right panel).

For each ROI, we compared the mean pISC of high vs. low semantic centrality events defined within each movie. Randomization tests were used to test the statistical significance of the difference between conditions. During recall, higher semantic centrality of an event was associated with higher pISC in PMC (high − low difference = .019, two-tailed randomization *p*

= .036; Figure 4e), whereas lower semantic centrality was associated with higher pISC in EVC (difference = −.013, p = .011; Figure 4f). These findings indicate that high semantic centrality events were represented in a more reliable and convergent manner across brains within a higher associative region supporting situation model representations, but not within a sensory control area. In contrast, no significant difference between conditions was observed in either ROI during movie watching, although the direction of effect was consistent with that during recall in both ROIs (PMC difference = .019, p = .17; EVC difference = −.031, p = .12; Supplementary Figure 9b). While speculative, the diminished effect of centrality on pISC during movie watching may reflect that the structure of the whole narrative becomes apparent only after subjects finished watching the movies (i.e., during recall).

In this and all the above analyses involving pISC during recall, twelve events recalled by fewer than five subjects were excluded. However, our main pISC analysis results remained qualitatively identical when all events were included in the analysis (Supplementary Figure 11).

Narrative network centrality modulates hippocampal encoding signals during movie watching

Hippocampus has been known to play a crucial role in encoding continuous narratives as discrete events[34]. Hippocampus activation increases at the offset of a movie event, and the magnitude of the activation predicts subsequent remembering and neural reactivation of the event[12,15,35]. This offset response has been interpreted as the registration or consolidation of the just-concluded event into long-term memory. We tested whether the centrality of events influences the offset-triggered hippocampal encoding signal during movie watching, potentially mediating the behavioral effect of narrative network centrality. We measured the time courses of hippocampal BOLD activation locked to the boundaries between events, and found that hippocampal responses were higher following the offset of high than low semantic centrality events (Figure 6a). In contrast, hippocampal responses following the onset of high vs. low centrality events were not significantly different from each other (Figure 6b), confirming that semantic centrality specifically affected the encoding of information accumulated during just-concluded events. These results may support the idea that rich connections between events lead to stronger hippocampus-mediated encoding.

Hippocampus also interacts with higher associative cortices when encoding naturalistic events[36], and increased hippocampus-cortex connectivity during encoding is associated with successful learning and memory formation[37,38]. Does the centrality of events affect hippocampal-cortical coupling as well? We used intersubject functional connectivity analysis

(ISFC[31]) to measure the interaction between the hippocampus and cortical ROIs during movie watching. ISFC computes correlations between activation time courses of different brain regions across subjects rather than within subjects, which makes it possible to isolate stimulus-locked activity from background noise[31]. We first computed ISFC between the hippocampus and PMC during the 26 movie events which were 22.5 seconds (15 TRs) or longer, and then correlated the ISFC values with the semantic centrality of the events. We found that the hippocampal-PMC interaction was stronger for higher centrality events ($r(26) = .49$, $p = .01$, 95% CI = [.13, .74]). No such relationship with centrality was observed for the hippocampal-EVC interaction ($r(26) = .01$, $p = .95$, 95% CI = [−.38, .4]). We observed comparable results when expanding the analysis to the 44 events which were 19.5 seconds (13 TRs) or longer (PMC $r(44) = .29$, $p = .06$, 95% CI = [−.01, .54]; EVC $r(44) = .05$, $p = .75$, 95% CI = [−.25, .34]). The stronger hippocampal-PMC connectivity during higher centrality events might reflect greater reinstatement of other event representations cued by overlapping components (e.g., ref.[39]). However, due to the limited number of movie events included in the analysis, it will be important to replicate these findings with a larger dataset.

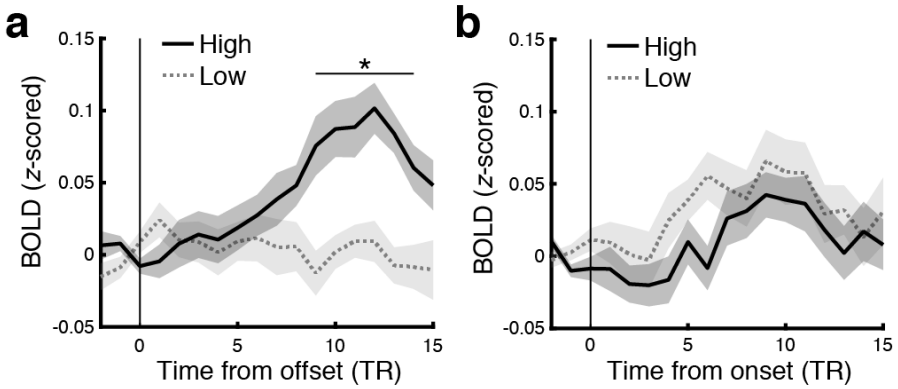

Figure 6. Effects of semantic centrality on hippocampal event boundary responses. a & b. Mean hippocampal BOLD response time courses aligned at the offset (**a**) or onset (**b**) of events during movie watching. Solid lines and dotted lines show responses for the high and low semantic centrality events, respectively. The BOLD time course of each event was first baseline corrected by subtracting the mean response of the two TRs immediately preceding the offset/onset of the event from each time point. The baseline-corrected time courses were averaged across events within each movie and then across movies and subjects. Shaded areas indicate SEM across subjects. Statistical significance reflects the difference between High vs. Low centrality events at each time point. *$q < .05$ (FDR corrected across time points).

DISCUSSION

In this study, we found that the structure of inter-event connections in complex naturalistic experiences predicts the behavioral and neural signatures of their memory traces. We applied a novel approach of transforming audiovisual movies into networks, whose nodes are events and whose edges are based on semantic similarity or cause-effect relationships between events. Subjects watched and recounted the movies in their own words; events highly connected with other events within the narrative network, i.e., “high centrality” events, were more likely to be recalled. Consistent with this behavioral effect, higher centrality was associated with greater hippocampal activity at event boundaries, as well as with increased hippocampal-cortical interaction during movie watching. Furthermore, recalling high centrality events more strongly recruited high-order cortical regions in the DMN involved in episodic recollection, and the multivoxel patterns of high-centrality events were reinstated in a more convergent manner across individuals, relative to lower-centrality events. These findings demonstrate that the specific structure of relations between events in a natural experience predicts both what will be remembered and what the properties of hippocampal and DMN regions will be during later recollection.

Recent years have seen an explosion in the use of naturalistic stimuli such as movies and narratives in exploring the behavior and neuroscience of human memory, as they provide an engaging laboratory experience with strong ecological validity compared to isolated words or pictures[7,8,40]. These studies have suggested that findings from traditional random-item list paradigms, which have dominated the field for decades, do not always fully extend to naturalistic recall (e.g., ref.[26]). In line with this, we observed that the recall probability of events from a movie does not show serial position effects typically reported in random-item list learning[3,27] where the first and last few items in a list tend to be better remembered than items in the middle. This finding was consistent regardless of whether each subject watched a single movie (Supplementary Figure 5c) or a series of movies in a row (Figure 2d). The lack of clear primacy or recency advantages may be due to the inter-event dependencies which made each narrative a coherent structure, supporting memories for central events which did not necessarily occur at the beginning or end of the story. At the same time, centrality effects may not be specific to narratives; semantically related items in a random list trigger recall of each other[4,41], which could lead to better memory performance for those items. Furthermore, the event complexity of narratives is not likely to be the main reason for the lack of serial position effects: in a highly realistic encoding setting (a real-world walk) where the events consisted of unrelated

activities (e.g., visiting a number of artworks), naturalistic recall showed similar characteristics to random-item list recall[42]. Further studies are needed to determine the roles of structural coherence and event complexity in centrality effects on memory. Understanding when and how classic list-based memory effects fail to extend to narratives and other natural stimuli will be essential for evaluating the results of future studies which use complex realistic conditions to study memory.

Why does higher event centrality improve memory performance? Distinct benefits may be present at recall and at encoding. During recall, high centrality events may have greater opportunity to be cued during recall, as by definition they have higher association strengths with other events. In our experiment, recall itself took the form of a narrative; under these conditions, high centrality events may have been especially likely to be recounted, because omitting them might disproportionately affect the logical structure and coherence of the reconstructed story. Inter-event connections may also benefit encoding. During movie watching, events highly connected with other events are more likely to reactivate and be reactivated by the other events containing shared components[39,43]. Consistent with this, we found that the coupling between the hippocampus and a cortical region involved in representing events (PMC[16,44], see below) was stronger when subjects were watching events with higher semantic centrality. The reactivation of high centrality events during encoding may result in more robust memory for those events by functioning as repeated encoding, and/or integrating the interconnected events to form joint representations[19,20,45]. The benefit of high centrality during encoding is also reflected in the greater hippocampal responses following the offset of high than low centrality movie events (Figure 6a). Such hippocampal event boundary responses have been linked to successful encoding, and have been suggested to reflect the consolidation of just-concluded episodes[12,13,34]. It has been shown that DMN connectivity during movie-viewing is modulated by surprise[46]; one possibility is that the conclusion of a higher centrality event produces greater uncertainty in the ongoing narrative, thereby resulting in a more salient boundary and stronger boundary-evoked encoding signals.

We demonstrated for the first time that DMN activity during remembering was modulated by the recollected event's position in the narrative network. High level associative areas in the DMN[14], especially the PMC and its functionally connected subregions, have been implicated in the episodic construction and representation of events[16,17,44]. In accordance with this view, we observed event-specific neural activation patterns in DMN areas during recall, and representational similarity analysis revealed that the relational structure of these neural event patterns could be predicted by human-generated descriptions of the movie and by recall

transcripts (for a similar approach, see ref.[26]). Critically, higher semantic centrality predicted greater activation (Supplementary Figure 7b) and between-subject pattern convergence in PMC (Figure 4e), neural signatures of stronger and more accurate recall of episodic details[17,29,47]. Additionally, higher intersubject similarity for high centrality events might arise from "design pressure" on narratives. Highly connected events are likely to be logically important in a story; indeed, we found that semantic centrality was positively correlated with the perceived importance of events as retrospectively rated by independent coders ($r(202) = .22$, $p = .002$, 95% CI = [.08, .34]). Thus, to aid the understanding of their linked events and eventually the whole story, high centrality events need to be designed in a way that minimizes the variability or ambiguity in how people interpret them. This adoption of a similar canonical interpretation of an event across people gives rise to more similar neural responses across individuals[48–50]. Future work may investigate whether real-life everyday events without such design pressure would show similar centrality effects to what we observed here using fictional narratives.

In contrast with the pattern in the DMN, we observed that a low-level sensory region (EVC) showed higher between-brain convergence for low semantic centrality events during recall (Figure 4f). This result should be interpreted with caution as the overall pISC was extremely low in EVC during recall due to the absence of shared visual stimulation (below the level typically considered reliable signal, in line with prior reports[17,18,51]). Nonetheless, we can speculate that the opposite effects obtained in PMC and EVC may reflect switching between internal and external modes of processing, primarily involving higher-order cortices in the DMN and sensory areas, respectively[52,53]. Subjects are more likely to be in internal mode that prioritizes retrieval[54,55] while watching high centrality events that reactivate associated events, whereas external mode is more likely to prevail during low centrality events as subjects would focus primarily on the novel current input. This may result in more visually-driven memory reinstatement (e.g., involving salient visual fragments rather than the gist of the event) and thus stronger pISC in EVC for low centrality events. EVC indeed tended to show higher activation for low semantic centrality events during movie watching (Supplementary Figure 7a), even though low-level visual features such as luminance and contrast were not modulated by semantic centrality. Similarly, a recent study[56] reported that the visual sensory network is more activated when subjects report a lower understanding of an ongoing narrative.

One might have expected that the effects of narrative structure would not be apparent in brain responses measured during ongoing movie watching, as the full structure of inter-event connections is only available after all movie events are completed. Still, as discussed above, event centrality significantly influenced hippocampal and cortical univariate responses during

movie watching. A simple explanation for these results is that centrality based on partial narrative networks (i.e., a network that excluded events not-yet-presented) was sufficiently similar to the full-narrative centrality values, especially later in a movie. Another interesting, and not mutually exclusive, possibility is that subjects were able to predict the full-narrative centrality of a current event by anticipating the potential connections with future events. In support of this interpretation, we found a strong positive correlation between the perceived importance of events obtained *concurrently* with watching the movies and those obtained *retrospectively*, after the movie ended ($r(202) = .67$, $p < .001$, 95% CI = [.58, .74]). Predictions of event centrality could be based on the learned schema of canonical story structures[57,58] as well as on director's cues used in popular movies such as luminance and shot motion[59]. Future work will explore how brain responses are driven by the temporally evolving, rather than static, inter-event structure when subjects consume unpredictable stories, or actively engage in selecting upcoming narrative events.

Causal relations have long been considered an important organizing factor for event and narrative memories[22,57,60]. Consistent with earlier work, we found that events with stronger causal connections with other events are better remembered (Figures 3c-d). Yet, while the effects of causality on univariate responses during movie-viewing (see also ref.[56]) were comparable to the effects of semantic centrality (Supplementary Figures 7c, 8c), multivoxel pattern effects of causality during recall were not as clear as those of semantic similarity (Supplementary Figures 8b, e). Several characteristics of causal relations in movie stimuli might have reduced the reliability of the effects of causal narrative network structure. First, causal relations were sparse and mostly identified between adjacent events (Supplementary Figures 3a, 4d). Causal relations also have directionality (i.e., cause vs. effect) which was not considered in the current study. In addition, causality judgments may be more idiosyncratic: average across-coder correlation was lower for causal (mean $r(202) = .34$) than semantic centrality (mean $r(202) = .52$) when centrality was computed from each individual coder's causality rating or movie annotation. It is also noteworthy that semantic and causal connections reflect different types of information: semantic connections are based on similar or shared features such as people, places, and objects, whereas causal connections additionally require an action, its outcome, and internal models providing a logical dependency between the two[61,62]. In this study, we did not focus on dissociating semantic and causal relations, as they are correlated in the movie stimuli and other naturalistic experiences. Future studies designed to orthogonalize different types of inter-event relations, including semantic and causal relations as well as other dimensions such as emotional similarity[63,64], will be able to further clarify their

unique influences on the behavioral and neural signatures of memory.

In summary, we applied a recently developed natural language model and neuroimaging techniques to a universal and natural form of human memory recall: telling stories about the past. This approach allowed us to demonstrate that rich connections between events in complex realistic experiences protect against forgetting and predict the neural responses associated with successful memory encoding, as well as the properties of brain activity during spoken recall. Consideration of the effects of inter-event structure on real-world memory may benefit practical applications such as the development of memory interventions for clinical and healthy aging populations[65] or promoting learning in educational settings[66–68]. In addition, our work demonstrates that holistic metrics which capture the interrelations of events within episodes may be important to incorporate into models of learning and comprehension, especially as these models grow in their sophistication and power to explain complex experiences in the real world[69,70].

METHODS

Participants

Twenty-one healthy subjects were recruited from the Princeton community (12 female, ages 20 – 33 years, mean age 26.6 years). All subjects were right-handed native English speakers and reported normal hearing and normal or corrected-to-normal vision. Informed consent was obtained in accordance with procedures approved by the Princeton University Institutional Review Board. Data from 6 of the 21 subjects were excluded from analyses due to excessive head motion (absolute displacement greater than 4 mm) in at least one scanning run.

Stimuli

The audiovisual stimuli consisted of 10 short movies including 3 animations and 7 live-action movies. The movies were on average 4.54 minutes long (ranged 2.15 – 7.75 minutes) and had narratives that varied in content and structure. Two of the movies consisted of short clips edited from longer full movies (Catch Me If You Can, The Prisoner). Detailed information about each movie is provided in Supplementary Table 1. Each movie was prepended with a 6-second long title scene in which the title in white letters appeared at the center of the black screen and then gradually disappeared. Five movies were presented in the first movie watching phase scanning run and the other five were presented in the second run. The movies were played consecutively

within each scanning run without gaps in between other than the title scenes. The presentation order of the ten movies was fixed across subjects. As in our prior study[17], an additional 39-second audiovisual cartoon (Let's All Go to the Lobby) unrelated to the movie stimuli was prepended at the beginning of each movie watching scanning run. The introductory cartoon was excluded from analyses.

Experimental procedures

The experiment consisted of three phases: movie watching, free spoken recall, and cued spoken recall. All three phases were performed inside the scanner. Before the movie watching phase, subjects were told that they would be watching a series of short movies. As in our prior study[17], we instructed subjects to pay attention to the movies as they would normally do in real life. Subjects were also told that they would be asked to verbally describe the movie plots later. The movie watching phase consisted of two consecutive scanning runs. Subjects watched five movies in each run (first run video duration = 24.9 minutes, second run video duration = 22.9 minutes). No behavioral responses were required from the subjects during scanning.

The free spoken recall phase immediately followed the movie watching phase. Subjects were instructed to describe aloud what they remembered from the movies in as much detail as they could, regardless of the order of presentation. We encouraged subjects to speak for at least ten minutes and told them that if they chose to speak for longer, that would be even better. Subjects were also allowed to return to a movie that they had described earlier in case they realized they had missed something while speaking about another movie. We instructed subjects to verbally indicate that they were finished by saying "I'm done" after recalling everything they could remember. A white fixation dot was presented on the black screen while subjects were speaking; subjects were told that they did not need to fixate on this dot. In case subjects needed to take a break or the duration of the scanning run exceeded the scanner limit (35 minutes), we stopped the scan in the middle and started a new scanning run where subjects resumed from where they had stopped in the previous run. 4 of the 15 subjects included in the analysis had such a break within their spoken recall session.

During the cued spoken recall phase immediately following the free spoken recall phase, subjects viewed a series of titles of the ten movies they watched. For each movie, subjects were instructed to first read the title out loud and then describe the movie. Subjects were told to provide a short summary of a few sentences in case they previously described the movie during the free spoken recall, but describe the movie in as much detail as they could if the movie was previously forgotten. The cued spoken recall phase was not analyzed for the current study.

All visual stimuli were projected using an LCD projector onto a rear-projection screen located in the magnet bore and viewed with an angled mirror. The Psychophysics Toolbox (http://psychtoolbox.org/) for MATLAB was used to display the stimuli and to synchronize stimulus onset with MRI data acquisition. Audio was delivered via in-ear headphones. Subjects' speech was recorded using a customized MR-compatible recording system (FOMRI II; Optoacoustics Ltd.).

Behavioral data collection and preparation

Movie event segmentation. Each of the ten movie stimuli was segmented into 10 – 35 events (mean 20.2, excluding the title scenes) by an independent coder who was not aware of the experimental design or results. The coder was instructed to identify event boundaries based on major shifts in the narrative (e.g., location, topic, and/or time). The coder gave each event a descriptive label (for example, "girl inside room alone with a pizza"). The start and stop timestamps of each event were recorded. There were 202 movie events in total and the duration of events ranged from 2 to 42 s (s.d. = 7.4 s). The number and the mean duration of events for individual movies are summarized in Supplementary Table 2.

Movie annotations. Movie annotations were provided by three independent annotators who did not participate in the fMRI experiment. Each annotator identified finer-grained sub-event boundaries within each of the 202 movie events based on their subjective judgments. The beginning and end of the fine-grained sub-events were also timestamped. For each sub-event, the annotators provided written descriptions about what was happening in the movie at that moment in their own words. No edits were made on the written descriptions other than correcting typos and removing/replacing special characters not recognized by our text analysis scripts. Supplementary Table 2 summarizes the number of fine-grained sub-events and the number of words generated by individual annotators for each movie.

Recall transcripts. The audio recording of each subject's free spoken recall was transcribed manually. Each recall transcript was segmented into discrete utterances based on pauses and changes in the topic. The recall transcripts were segmented such that each utterance was not longer than 50 words. Timestamps were also identified for the beginning and end of each utterance. Each utterance was categorized as one of the followings based on its content: 1) recall of specific movie events, 2) general comment about the movie, 3) memory search attempt (e.g., "Let's see…"), 4) end of recall (e.g, "I'm done."), and 5) speech unrelated to the task (e.g.,

“Can I start now?”). In case an utterance was a recall of movie events, the specific movie events described in the utterance were identified. Among the different types of utterances, only the recall of specific movie events was used in the behavioral and fMRI analyses in the current study.

Importance ratings. Importance ratings for each of the 202 movie events were collected from four independent raters who did not participate in the fMRI experiment. The raters watched each movie and then retrospectively rated how important each event was for understanding what happened within the movie on a scale from 1 (not important at all) – 10 (very important). The ratings were averaged within each event across raters for analyses (range 1.5 – 10 across events, mean 6.09, s.d. 1.92). We additionally collected importance ratings from a separate group of four independent raters while they were watching the 10 movies for the first time. At the end of each movie event, the movie stopped playing, and the raters rated the importance of the just-played event on a scale from 1 – 10. These rate-as-you-go importance ratings averaged across the raters were positively correlated with the retrospective ratings ($r(202) = .67$, $p < .001$, 95% CI = [.58, .74]).

Narrative networks

To quantify and assess the inter-event structure of the movie stimuli, we transformed each movie plot into a graph/network. In this narrative network, the events within a movie (nodes) form connections with each other (edges), and the connection strength between a pair of events (edge weight) is determined by their content similarity or causality. The narrative network edges were unthresholded (except for the visualization of semantic narrative networks) and undirected. The centrality of each individual event within a movie was defined as the degree of each node (i.e., the sum of the weights of all edges connected to the node) in the network, normalized by the sum of degrees and then *z*-scored within each movie. Events with stronger and greater numbers of connections with other events had higher centrality.

Semantic narrative networks. Movie annotations were used to generate narrative networks based on the semantic similarity between events (Figure 1). For each annotator and movie, the text descriptions for the fine-grained sub-events were concatenated within each movie event. The text descriptions were then encoded into high-dimensional vectors with Google’s Universal Sentence Encoder (USE[25]) such that each movie event was represented as a 512-dimensional vector. The USE vectors from the three annotators were highly similar to each other (mean

event-wise cross-annotator cosine similarity between all possible annotator pairs = .78; Supplementary Figure 1); thus the USE vectors were averaged across annotators within each movie event. For each movie, the narrative network was generated by using the cosine similarity between the USE vectors of movie event pairs as the edge weights between nodes (events).

Causal narrative networks. To generate narrative networks based on the causal relationship between events (Supplementary Figure 3), we had 18 independent coders identify causally related event pairs (the 'cause' event and the 'effect' event) within each movie. Each coder coded different subsets of the ten movies and each movie was coded by 12 (Catch Me If You Can) or 13 coders (all the other movies). The coders watched the movies and were given the movie annotation with sub-event segmentation by the annotator JL. The coders were instructed to consider two movie events as causally related if any fine-grained sub-event of an event is a strong cause of any (at least one) sub-event of the other event. Whether a causal relationship was strong enough to be identified depended on the coders' subjective criteria; the coders were instructed to keep the criteria as consistent as possible. The coders were also told to ignore any causal relationship between the sub-events within the same event. Thus, an event pair always consisted of two different events. For each movie, the edge weights between nodes in the narrative network was defined as the proportion of coders who identified a movie event pair as causally related, regardless of the cause-effect direction.

Mixed-effects logistic regression analysis of recall behavior

We performed a mixed-effects logistic regression analysis to test the unique effect of semantic centrality and causal centrality on recall performance after controlling for each other. Each event from each subject served as a data point. Data were concatenated across all subjects. The dependent variable of each data point was the event recall success (1 = recalled, 0 = not recalled). Normalized semantic and causal centrality were included as fixed effects. Individual subjects and movie stimuli were included as random effects. Statistical significance of the unique effect of each type of centrality was tested by performing a likelihood ratio test for the full model against a null model including all independent variables except for the variable of interest.

fMRI acquisition

fMRI scanning was conducted at Princeton Neuroscience Institute on a 3T Siemens Prisma scanner with a 64-channel head/neck coil. Functional images were acquired using a T2*-

weighted multiband accelerated echo-planar imaging (EPI) sequence (TR = 1.5 s; TE = 39 ms; flip angle = 50°; acceleration factor = 4; shift = 3; 60 oblique axial slices; grid size 96 × 96; voxel size 2 × 2 × 2 mm^3). Fieldmap images were also acquired to correct for B0 magnetic field inhomogeneity (60 oblique axial slices; grid size 64 × 64; voxel size 3 × 3 × 2 mm^3). Whole-brain high-resolution anatomical images were acquired using a T1-weighted MPRAGE pulse sequence. Scanning parameters for the anatomical images varied across subjects (15 subjects had 176 sagittal slices with voxel size 1 × 1 × 1 mm^3; 6 subjects had 192 sagittal slices with voxel size .9 × .86 × .86 mm^3), as the anatomical images of a subset of subjects were originally obtained for other projects unrelated to the current study.

fMRI preprocessing

Preprocessing of high-resolution anatomical images and cortical surface reconstruction were performed using FreeSurfer's recon-all pipeline. For each scanning run, functional images were corrected for head motion and B0 magnetic inhomogeneity using FSL's MCFLIRT and FUGUE, respectively. Functional images were then coregistered to the anatomical image, resampled to the fsaverage6 template surface (for cortical analysis) and the MNI 305 volume space (for subcortical analysis), and then smoothed (FWHM 4 mm) using the FreeSurfer Functional Analysis Stream. The smoothed functional data were then high-pass filtered within each scanning run (cutoff = 140 s). For intersubject functional connectivity analysis, we additionally projected out the following nuisance regressors from the filtered functional data: the average time courses (z-scored within each run) of 1) high s.d. voxels outside the grey matter mask (voxels in the top 1% largest s.d.), 2) cerebrospinal fluid, and 3) white matter[31]. The resulting time series were z-scored within each vertex or voxel across TRs. The first 2 TRs of movie watching scanning runs were discarded as the movies were played 2 TRs after the scanning onset. The first 3 TRs of both movie watching and free spoken recall scanning runs were additionally removed, shifting the time-courses by 4.5 s, to account for the hemodynamic response delay.

Cortical parcellation and region of interest (ROI) definition

For whole-brain pattern-based analyses, we used a cortical parcellation atlas based on fMRI functional connectivity patterns[32]. Specifically, we used the atlas where the cortical surface of the brain is divided into 400 parcels (200 parcels per hemisphere) which are clustered into previously reported 17 functional networks[71]. For region-of-interest analyses, we defined the bilateral posterior-medial cortex (PMC) and the bilateral early visual cortex (Figure 4b) by

combining parcels from the 400-parcel atlas that correspond to the areas of interest. The PMC ROI consisted of the posterior cingulate cortex and precuneus parcels in the default mode network. The early visual cortex ROI consisted of parcels around the primary visual cortex (see Supplementary Table 3 for the list of parcels used to create the ROIs). The bilateral hippocampus mask was extracted from FreeSurfer's subcortical (Aseg) atlas on the MNI volume space.

Univariate activation analysis

We performed whole-brain univariate activation analysis on the cortical surface to identify regions whose activation scales with the narrative network centrality (Supplementary Figure 7). The analysis was performed separately for the movie watching phase and the recall phase. For each vertex of each subject, we first computed the mean activation for each movie event by averaging the preprocessed BOLD signal across TRs that correspond to the event. The first event of each movie was excluded from this and all other univariate analysis of the movie watching phase (see Supplementary Figure 6). For the recall phase, only the events successfully recalled by the subject were included in the analysis. We then performed a linear regression where the event-by-event activation (combined across all 10 movies) was explained by the semantic or causal centrality of the events, after regressing out the overall movie-level activation from the event-by-event activation. Finally, one-sample *t*-tests against zero (two-tailed) were applied on the subject-specific vertex-wise parameter estimate maps to generate the group-level *t*-statistic map.

We also compared the ROI-specific univariate activation for high vs. low centrality movie events during each experimental phase. High and low centrality events were defined as the events whose semantic/causal centrality metrics were within the top and bottom 40% in each movie, respectively. For each subject and event, the preprocessed BOLD signals were first averaged across voxels or vertices within an ROI and across all TRs corresponding to the event. The mean signal was then averaged across events in the same condition and then across movies, resulting in a single value per subject and condition. Two-tailed paired *t*-tests were used to test the statistical significance of the difference between the high vs. low centrality conditions.

To compare hippocampal activation following the onset/offset of high vs. low centrality events during movie watching (Figure 6), we averaged TR-by-TR BOLD signals across voxels within the hippocampus for each subject. We then extracted time series around the onset/offset (-2 – 15 TRs) of each high/low centrality event. The first and last events of each movie were

excluded to minimize the effect of between-movie transitions. Each time series was baseline corrected by subtracting the mean activation of the two TRs immediately preceding the onset/offset of the event from each time point. The subject-specific time series were then averaged across events within each condition and then across movies. Two-tailed paired *t*-tests were used for each time point to compare the high vs. low centrality conditions. We applied the Benjamini-Hochberg procedure ($q < .05$) to correct for multiple comparisons across time points.

Intersubject pattern correlation analysis

Whole-brain intersubject pattern correlation (pISC[17,30]) maps were generated for the movie phase (Movie-Movie similarity; Supplementary Figure 9a) and the recall phase (Recall-Recall similarity; Figure 4d) separately. pISC was calculated in a subject-pairwise manner using the following procedures. For each cortical parcel of each subject, first the mean activation pattern of each event was generated by averaging the preprocessed movie or recall phase BOLD data across TRs within the event in each vertex within the parcel. Note that as recall BOLD data existed only for successfully recalled events, each subject had a different subset of recall event patterns. For each subject and event, we computed the Pearson correlation between the event pattern of the subject and the pattern of the matching event from each of the remaining subjects, which resulted in $N - 1$ correlation coefficients (N = the total number of subjects who watched/recalled the event). The correlation coefficients were then averaged to create a single pISC (r) value per event per subject. These pISC values were averaged across events (combined across all 10 movies) and subjects, resulting in a single pISC value for each parcel. We performed a randomization test for each parcel to test the statistical significance of the mean pISC. Parcel-wise mean pISC values were obtained using the same procedures as described above, except that we randomly shuffled the event labels before computing the between-subjects pattern similarity. That is, one subject's neural pattern of an event was correlated with another subject's neural pattern of a non-matching event. This procedure was repeated 1000 times to generate a null distribution of pISC. A one-tailed *p*-value was defined as the proportion of values from the null distribution equal to or greater than the actual mean pISC. The *p*-values from the entire cortical surface were corrected for multiple comparisons across all 400 parcels using the Benjamini-Hochberg procedure ($q < .05$).

We also computed pISC in the PMC and early visual cortex to test the relationship between the semantic/causal narrative network centrality metrics and event-specific neural representations in the ROIs. The subject-specific, event-by-event pISC values were computed for each ROI in the same way we computed pISC for each parcel of the whole-brain pISC map

above (Figure 4a), separately for movie watching and recall. We compared the pISC for high vs. low centrality events, defined as the events whose centrality metrics were within the top or bottom 40% in each movie. The pISC values were first averaged across events within the high/low centrality condition for each movie and then across movies, resulting in a single pISC value per condition per subject. We then ran a randomization test to assess whether the difference of pISC between the high vs. low centrality conditions, averaged across subjects, was significantly different from zero. A null distribution of the mean difference between the conditions was generated by randomly shuffling the event labels of the event-specific pISC values within each movie and then computing the difference 1000 times. A two-tailed *p*-value was defined as the proportion of values from the null distribution equal to or more extreme than the actual difference.

In all analyses involving intersubject neural similarity (including the representational similarity analysis and the intersubject functional connectivity analysis), the first event of each movie was excluded from movie phase analyses to minimize the effect of movie onset (Supplementary Figure 6). For recall phase analyses, we excluded twelve events recalled by fewer than five subjects (1 – 3 events per movie from 6 movies). However, we obtained qualitatively identical results when we included all events in the analyses (Supplementary Figure 11).

Representational similarity analysis

We performed representational similarity analysis[33] by comparing the event-by-event similarity matrices based on two different types of event representations: the text descriptions of events (i.e., movie annotations or recall transcripts) and neural activation patterns measured during recall (Figure 5, Supplementary Figure 10b). The similarity matrix based on movie annotations was generated for each movie by computing the pairwise cosine similarity between the USE vectors of all events within the movie. This matrix was identical to the adjacency matrix of the semantic narrative network. To create the similarity matrix based on recall, we first extracted the sentences from each subject's recall transcript describing each event and then converted them into USE vectors. The similarity matrix was generated for each subject and movie by computing the cosine similarity between the USE vectors of all events recalled by the subject. The matrices were then averaged across all subjects. As subjects recalled different subsets of events, the number of subjects averaged was different across event pairs.

The fMRI recall pattern similarity matrix was generated for each parcel of the Schaefer atlas. Within each of the ten movies, we computed pattern correlations (Pearson *r*) between all

possible pairs of events between all pairs of subjects. For each subject and movie, this resulted in $N - 1$ fMRI pattern similarity matrices with the size of $M \times M$, where N is the total number of subjects and M is the number of events within the movie. We took the average of each matrix and its transpose to make the similarity matrix symmetric (i.e., similarity between events *a* and *b* across subjects *i* and *j* = average of corr(subject *i* event *a*, subject *j* event *b*) and corr(subject *j* event *a*, subject *i* event *b*)), and then averaged the $N - 1$ similarity matrices to generate a single fMRI similarity matrix per movie and subject.

The representational similarity between a text-based similarity matrix and an fMRI pattern-based similarity matrix was measured by computing the Pearson correlation between the lower triangles (excluding the diagonal values) of each matrix. The correlation coefficients were next averaged across movies and then across subjects to create a single value per parcel. For each parcel, a randomization test was performed to test whether the mean representational similarity was significantly greater than zero. We randomly shuffled the event labels of the text-based similarity matrix within each movie and then computed the mean representational similarity as described above. This procedure was repeated 1000 times to generate a null distribution, and a one-tailed *p*-value was defined as the proportion of values from the null distribution equal to or greater than the actual mean representational similarity. The whole-brain *p*-values were corrected for multiple comparisons across parcels using the Benjamini-Hochberg procedure ($q < .05$).

Intersubject functional connectivity analysis

We performed intersubject functional connectivity analysis (ISFC[31]) to test the relationship between narrative network centrality and the hippocampus-cortex interaction during movie watching. We first averaged the TR-by-TR time courses of the preprocessed (non-neuronal signals removed; see fMRI preprocessing) functional data across all voxels/vertices within each of the hippocampal and cortical ROIs (PMC, early visual cortex). For each movie event as long as 22.5 seconds or longer (total number of events used across all movies = 26), we computed the ISFC between the hippocampus and a cortical ROI. Functional connectivity patterns computed within windows as short as 22.5 seconds have previously been shown to robustly predict cognitive states[72]. For each subject, we correlated the subject's *hippocampal* time series of the event and the cortical ROI time series averaged across all other subjects. We then averaged the Pearson correlation coefficients across all subjects. This procedure was repeated by correlating each subject's *cortical* ROI time series and the hippocampal time series averaged across all other subjects. Again, the correlation coefficients were averaged across subjects. We

then took the mean of the two averaged correlations to produce a single ISFC between the hippocampus and the cortical ROI for each event. Finally, we computed the Pearson correlation between the event-wise ISFC and the semantic/causal narrative network centrality.

Low-level sensory characteristics of movie events

We measured the low-level visual and auditory features of movie events to examine whether the sensory characteristics can explain the effects of centrality on neural responses during movie watching. For visual features, we measured luminance and contrast averaged across grayscale-converted movie frames within each event. In each frame, luminance was defined as the mean of pixel values, and contrast was defined as the difference between the maximum and minimum pixel values. For an auditory feature, we measured the mean amplitude of sounds played during each event. We extracted the single-channel downsampled (8000 Hz) version of audio signals from the movie clips. Within each event, the audio signals were divided into 100-ms segments, and each segment's amplitude was computed as the difference between the maximum and minimum signal intensities. The amplitudes were then averaged across all segments within each event. The first events of each movie were excluded from the analysis to be consistent with the movie phase fMRI analyses. All sensory features were z-scored across events. We performed mixed-effects linear regression analyses to test whether each of the event-wise low-level sensory features was modulated by semantic centrality, using semantic centrality as a fixed effect and movies as a random effect. Statistical significance of the effect of centrality was tested via likelihood ratio tests for the full models against the null models including the random effect of movies only.

Pre-registered online experiment

We conducted an online experiment to replicate and generalize the behavioral results of the fMRI experiment with a larger number of subjects and a new set of movie stimuli (Supplementary Figure 5). The online experiment was pre-registered at AsPredicted (https://aspredicted.org/fw59g.pdf). We recruited a total of 393 subjects on Amazon's Mechanical Turk using the psiTurk system[73]. Each subject watched one of 10 short movies and then provided a written recall of the movie plot. The audiovisual movie stimuli were different from the ones used in the fMRI experiment and included both animations and live-action movies. The movies were on average 9.1 minutes long (ranged 5.9 – 12.7 minutes). Each movie was watched by 38 – 49 subjects (mean = 39.3). Additional 99 subjects were excluded from the analysis because their recall was too short (< 150 words) or they had watched the

movie before the experiment. All subjects were provided with an informed consent form approved by the Johns Hopkins University Institutional Review Board.

The experiment was run in web browsers using JavaScript. After reading instructions, subjects watched a 2-minute-long example video clip. An example recall of the example video clip was also provided to inform subjects about the level of detail they need to produce during recall. Subjects then watched a short movie and performed the written recall task by typing in a text box to retell the movie plot in their own words. To mimic the irreversible nature of the spoken recall used in the fMRI experiment, subjects were not allowed to backspace beyond the current sentence and correct already-written sentences. Subjects were encouraged to take as much time as needed to provide as much detail as they can remember. During the delay between movie watching and recall, subjects completed a short demographic questionnaire and the Mind-Wandering Questionnaire[74], and then practiced using the text box by providing written descriptions of simple shapes. Subjects also completed a series of questionnaires at the end of the experiment, including the Survey of Autobiographical Memory[75] and the Plymouth Sensory Imagery Questionnaire[76]. Findings from the delay period and post-experiment questionnaires will be reported elsewhere.

As in the fMRI experiment, independent coders segmented each movie into discrete events (mean number of events per movie = 25.2) and provided written descriptions of each event. The written recall of each subject was also segmented into sentences, and the movie events that each sentence describes were identified. The semantic and causal narrative networks of the movies were generated using procedures identical to those used in the fMRI experiment, except that 1) the USE vectors were not averaged across annotators as each movie was annotated by a single coder, and 2) a total of 16 independent coders identified the causally related events and each movie was rated by 10 coders.

DATA AVAILABILITY

The fMRI and behavioral data for this work will be publicly available via OpenNeuro (https://openneuro.org).

CODE AVAILABILITY

The analyses in the current manuscript used code available through MATLAB, R, and Python. All custom scripts used in the manuscript are available upon request from the corresponding author.

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AUTHOR CONTRIBUTIONS

H. L. and J. C. conceived and designed the experiments. H. L. and J. C. performed the experiments. H. L. analyzed the data. H. L. and J. C. wrote and edited the paper.

CITATION DIVERSITY STATEMENT

Recent work in several fields of science has identified a bias in citation practices such that papers from women and other minority scholars are under-cited relative to the number of such papers in the field[77–81]. Here we sought to proactively consider choosing references that reflect the diversity of the field in thought, form of contribution, gender, race, ethnicity, and other factors. First, we obtained the predicted gender of the first and last author of each reference by using databases that store the probability of a first name being carried by a woman[81,82]. By this measure (and excluding self-citations to the first and last authors of our current paper), our references contain 10.45% woman(first)/woman(last), 14.93% man/woman, 25.37% woman/man, and 49.25% man/man. This method is limited in that a) names, pronouns, and social media profiles used to construct the databases may not, in every case, be indicative of gender identity and b) it cannot account for intersex, non-binary, or transgender people. Second, we obtained predicted racial/ethnic category of the first and last author of each

reference by databases that store the probability of a first and last name being carried by an author of color[83,84]. By this measure (and excluding self-citations), our references contain 4.56% author of color (first)/author of color(last), 12.06% white author/author of color, 18.89% author of color/white author, and 64.49% white author/white author. This method is limited in that a) names, Census entries, and Wikipedia profiles used to make the predictions may not be indicative of racial/ethnic identity, and b) it cannot account for Indigenous and mixed-race authors, or those who may face differential biases due to the ambiguous racialization or ethnicization of their names. We look forward to future work that could help us to better understand how to support equitable practices in science.

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SUPPLEMENTARY TABLES

Supplementary Table 1. Movie stimuli details.

Order	Title (*animation)	Duration (min:sec)	Original title	Release year	Director(s)
1	Catch Me If You Can	5:46	Catch Me If You Can	2002	Steven Spielberg
2	The Record*	2:12	A Single Life	2014	Marieke Blaauw, Joris Oprins, Job Roggeveen
3	The Boyfriend	7:45	High Maintenance	2006	Phillip Van
4	The Shoe	2:09	How They Get There	1997	Spike Jonze
5	Keith Reynolds*	5:48	Keith Reynolds Can't Make It Tonight	2008	Felix Massie
6	The Rock*	5:25	An Object at Rest	2015	Seth Boyden
7	The Prisoner	4:20	Arrival (First episode of the TV series "The Prisoner")	1967	Don Chaffey
8	The Black Hole	2:22	The Black Hole	2008	Philip Sansom, Olly Williams
9	Post-It Love	2:41	Post-It Love	2009	Simon Atkinson, Adam Townley
10	Bus Stop	6:54	Stray Dogs	2015	Minka Farthing-Kohl

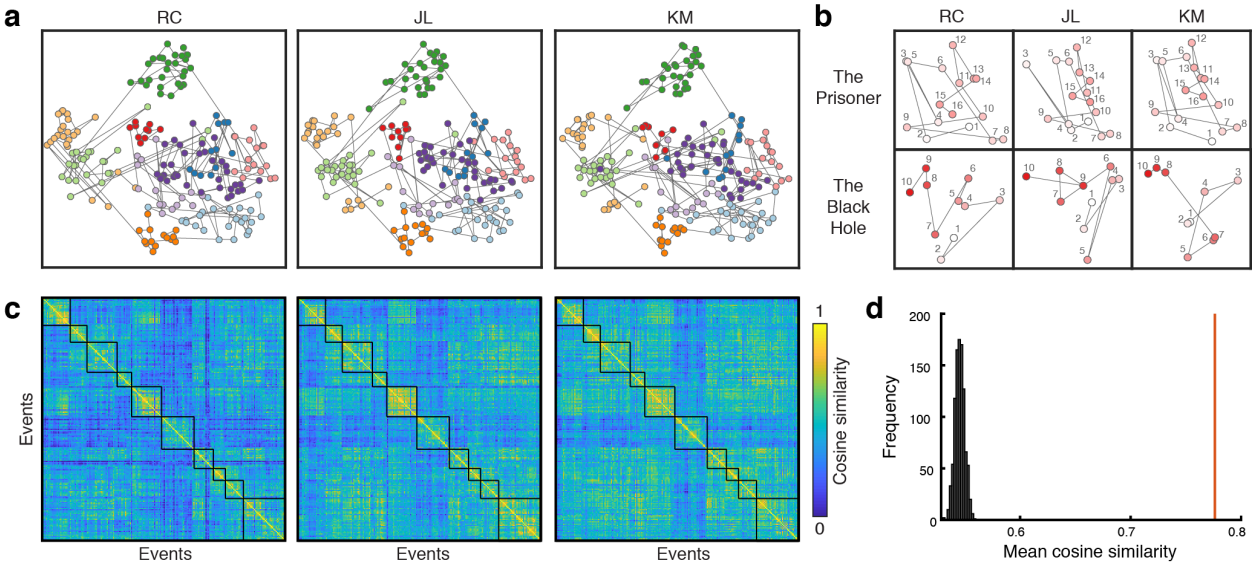
Supplementary Table 2. Descriptive statistics for movie annotations (title scenes excluded).

Movie	Number of events	Mean event dur. (sec)	Mean number of words used to describe each event				Mean number of sub-events within each event			
			RC	JL	KM	Mean	RC	JL	KM	Mean
Catch Me If You Can	23	15.1	50.3	52.7	71.8	58.3	2.6	2.5	2.5	2.5
The Record	14	9.4	37.3	65.7	78.4	60.5	2.1	3.5	2.8	2.8
The Boyfriend	25	18.4	48.3	71.4	89.1	69.6	2.9	4.1	3.4	3.5
The Shoe	12	10.8	66.2	46.4	49.7	54.1	3.2	2.4	2.2	2.6
Keith Reynolds	25	14.1	30	61.2	70.4	53.9	2.0	2.3	1.7	2
The Rock	27	12.0	35.6	53.4	44.8	44.6	1.9	3.2	1.9	2.3
The Prisoner	16	16.3	53.4	66.4	97.8	72.5	2.8	3.1	3.2	3.0
The Black Hole	10	14.3	88.3	67.1	87	80.8	3.6	4.2	3.2	3.7
Post-It Love	15	10.7	31.6	42.5	41.5	38.5	1.7	2.3	1.7	1.9
Bus Stop	35	11.9	30.4	59.7	48.5	46.2	1.6	2.7	1.9	2.1
Mean across movies	20.2	13.3	47.1	58.7	67.9	57.9	2.4	3.0	2.5	2.6

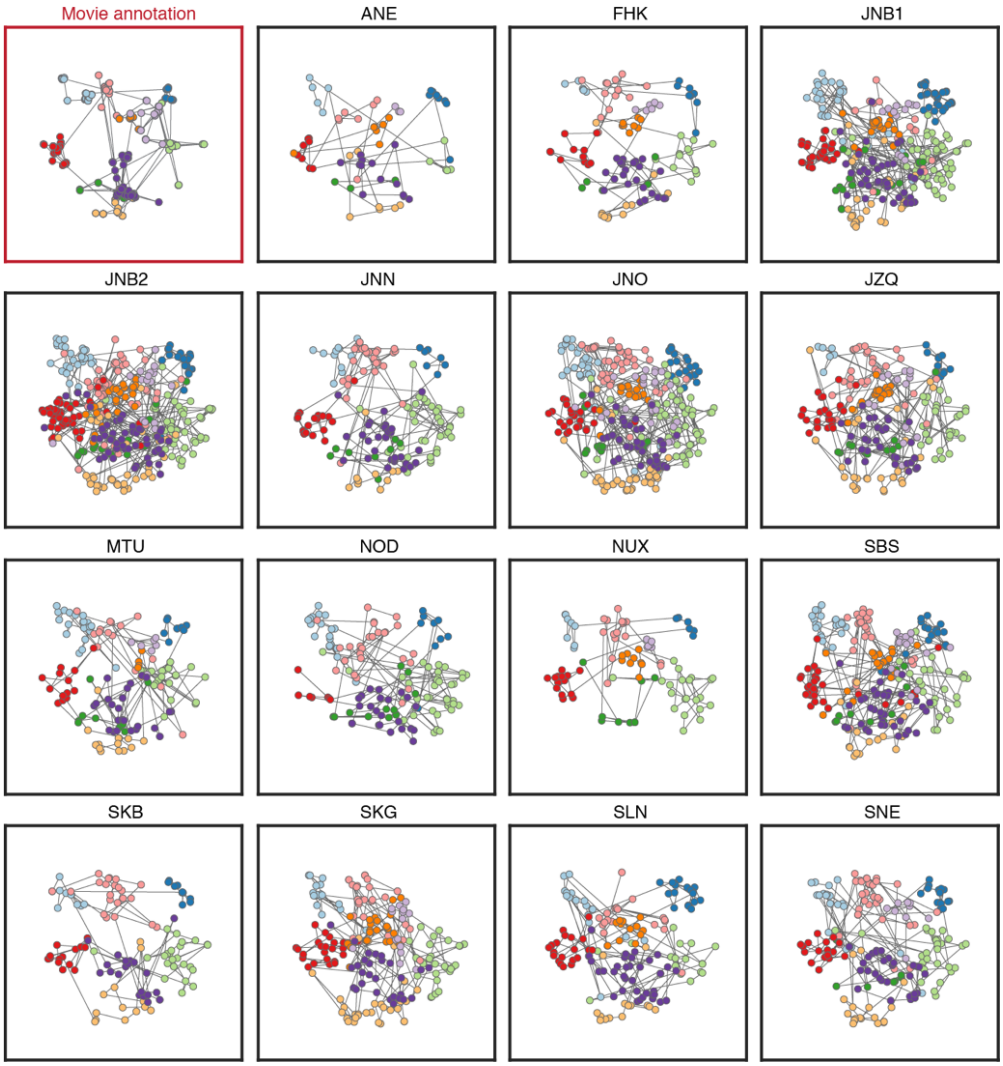
Supplementary Table 3. List of Schaefer 400 parcels used to create regions of interest.

Region of interest	Hemisphere	Schaefer parcel ID	Schaefer parcel name
Posterior medial cortex	Left	154	17Networks_LH_DefaultA_pCunPCC_1
		155	17Networks_LH_DefaultA_pCunPCC_2
		156	17Networks_LH_DefaultA_pCunPCC_3
		157	17Networks_LH_DefaultA_pCunPCC_4
		158	17Networks_LH_DefaultA_pCunPCC_5
		159	17Networks_LH_DefaultA_pCunPCC_6
		160	17Networks_LH_DefaultA_pCunPCC_7
	Right	363	17Networks_RH_DefaultA_pCunPCC_1
		364	17Networks_RH_DefaultA_pCunPCC_2
		365	17Networks_RH_DefaultA_pCunPCC_3
		366	17Networks_RH_DefaultA_pCunPCC_4
		367	17Networks_RH_DefaultA_pCunPCC_5
Early visual cortex	Left	7	17Networks_LH_VisCent_Striate_1
		18	17Networks_LH_VisPeri_StriCal_1
		19	17Networks_LH_VisPeri_StriCal_2
		20	17Networks_LH_VisPeri_ExStrSup_1
	Right	207	17Networks_RH_VisCent_Striate_1
		218	17Networks_RH_VisPeri_StriCal_1
		219	17Networks_RH_VisPeri_StriCal_2

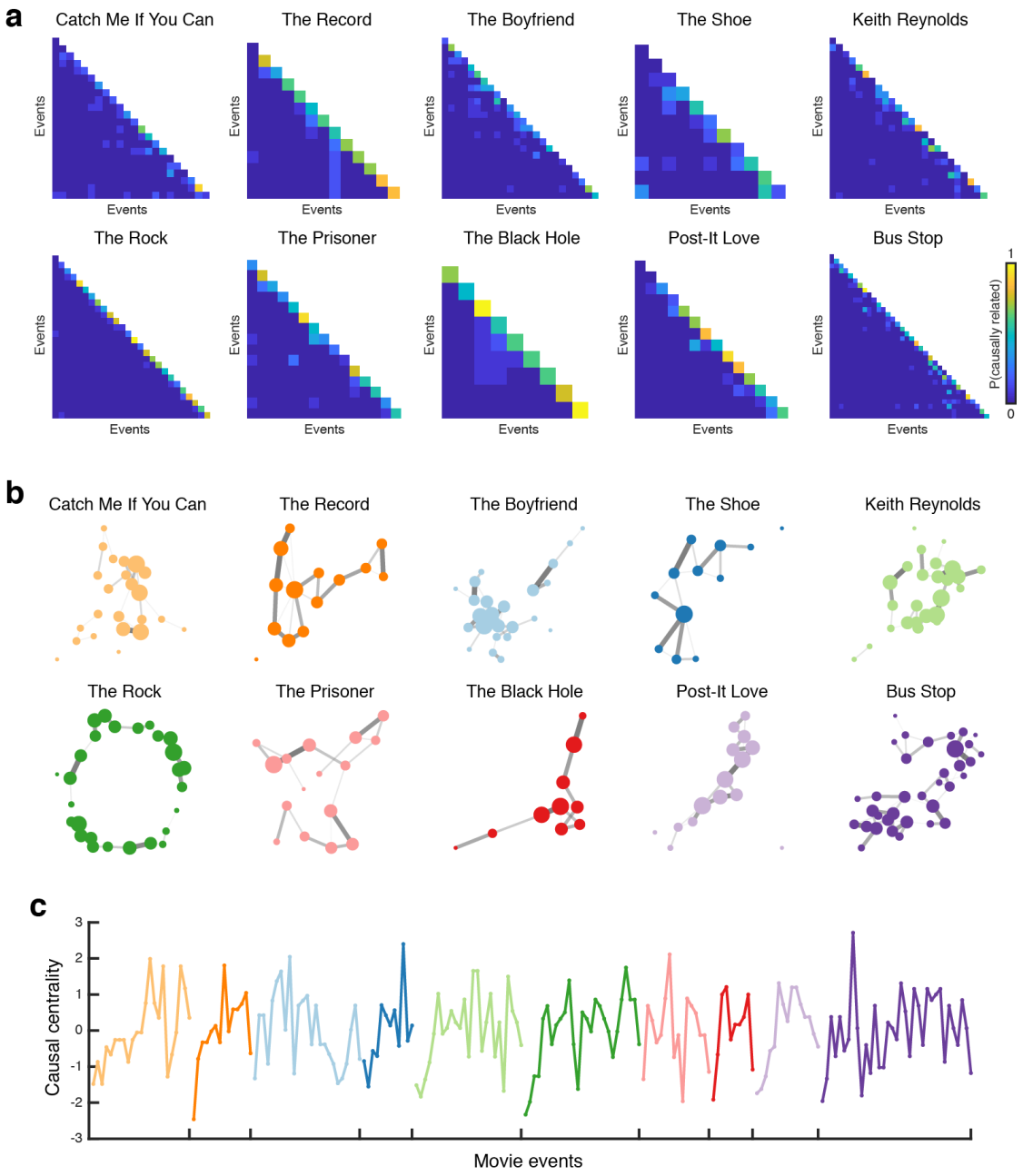
SUPPLEMENTARY FIGURES



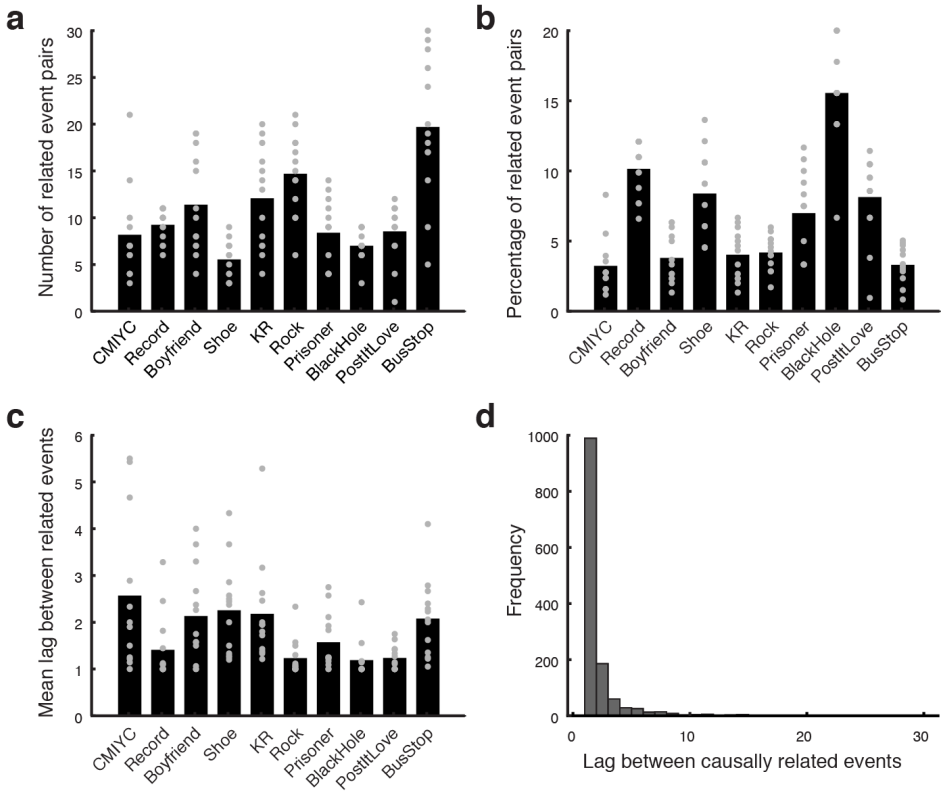
Supplementary Figure 1. Similarity of movie event descriptions across annotators. a. Visualization of three independent annotators' movie event descriptions as trajectories in the Universal Sentence Encoder (USE)[25] text embedding space (for a related method, see ref.[26]). T-distributed stochastic neighbor embedding (t-SNE) was applied on the USE vectors (concatenated across annotators) for dimensionality reduction into a two-dimensional space. Events within each movie formed visible clusters in the space, and the overall configuration of the trajectories was highly similar across annotators. Each dot represents a movie event. Temporally adjacent events are connected with gray lines. Different colors indicate different movies. **b.** Two example movies' annotation trajectories from the three annotators (isolated from the trajectories in **a**). Numbers and the color of dots indicate the order of events within each movie. Dots (events) in brighter colors were presented earlier in the movie. **c.** Cosine similarity between the USE vectors of all 202 events (combined across 10 movies) generated from each annotator's movie event descriptions. Each black square on the diagonal indicates an individual movie (i.e., within-movie similarities). **d.** We performed a randomization test to test the statistical significance of the cross-annotator similarity between movie event USE vectors. The red line shows the true mean event-wise cross-annotator cosine similarity between all possible annotator pairs. The histogram shows the null distribution of the mean cross-annotator similarity (N = 1000), generated by shuffling the event labels within each movie and annotator. The mean cross-annotator similarity was significantly greater than zero (p < .001, two-tailed).



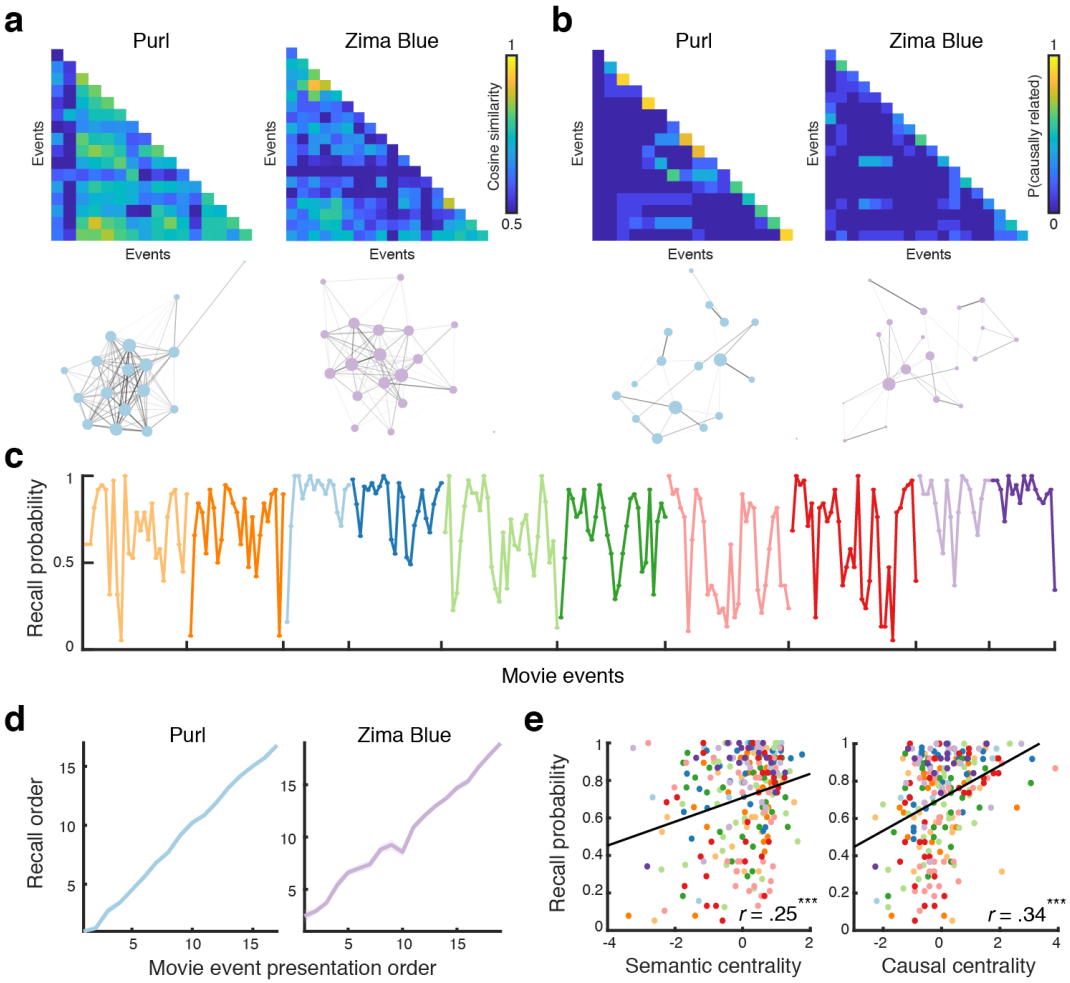
Supplementary Figure 2. Individual subjects' recall trajectories in a text embedding space. Each subject's recall transcript was segmented into utterances based on pauses and changes in the topic. Each utterance was transformed into vectors using the Universal Sentence Encoder (USE)[25]. T-distributed stochastic neighbor embedding (t-SNE) was applied on the USE vectors concatenated across all subjects' recall transcripts and the movie annotation vectors (averaged across annotators). This allowed us to visualize the USE vectors of the movie annotation (top left cell in the red frame) and recall transcripts (all the other cells in black frames) into a shared two-dimensional space. Each dot in the movie annotation trajectory represents a movie event. Each dot in the recall trajectories represents an utterance during recall. Temporally adjacent events/utterances are connected with gray lines. Different colors indicate different movies. Consistent with a prior study[26], the overall configuration of the recall trajectories was similar to that of the movie annotation trajectory. The recall trajectories were also similar across subjects, although the number of movies recalled and the number of utterances made varied across subjects.



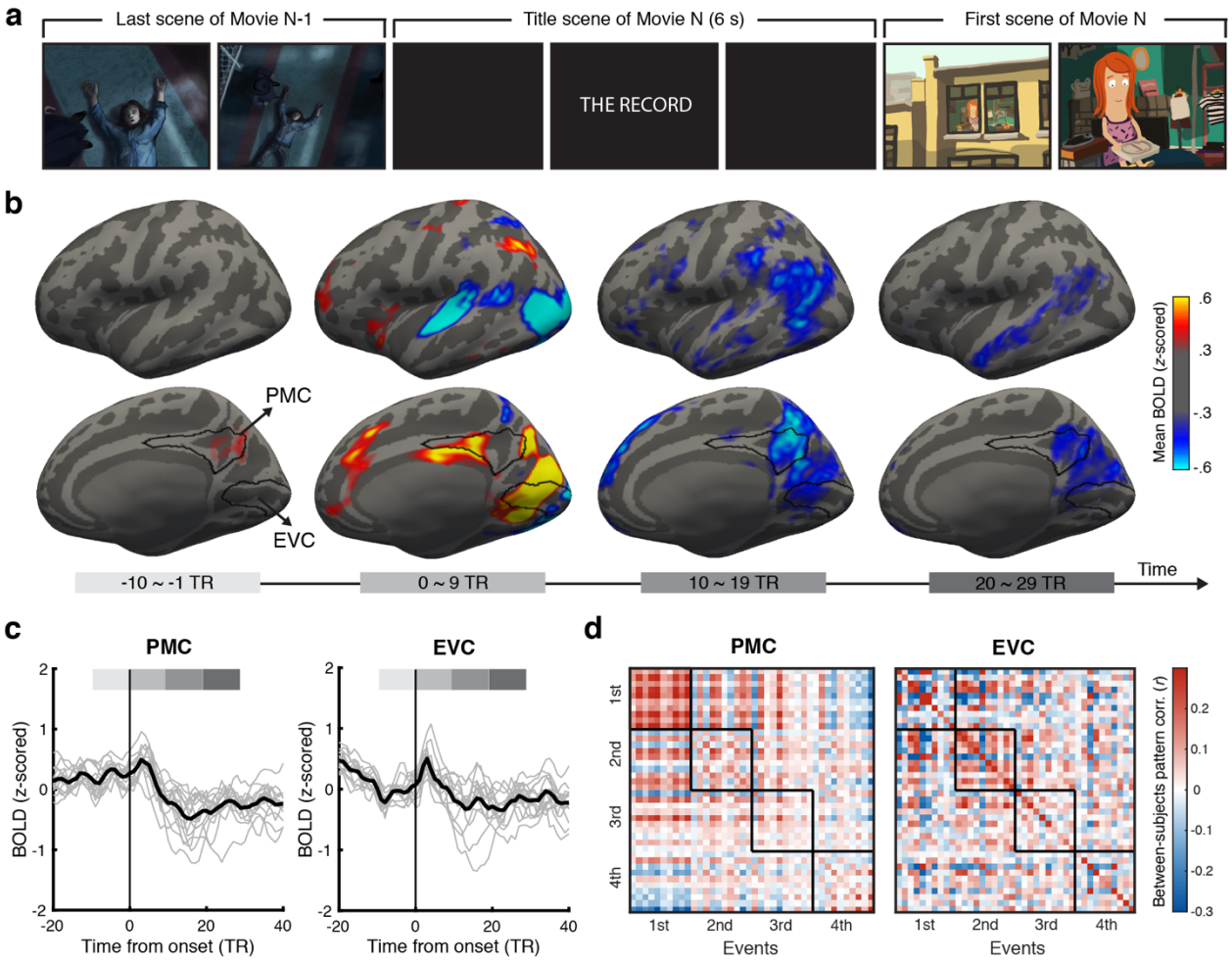
Supplementary Figure 3. Causal narrative networks. a. Causal relationship matrices of the 10 movies used in the fMRI experiment. Causal relatedness between a pair of events within a movie was computed as the proportion of independent coders who identified the pair as causally related. **b.** Causal narrative networks whose nodes are movie events and edge weights are the causal relatedness shown in **a**. Node size is proportional to centrality (normalized degree). Edge thickness is proportional to edge weights. **c.** Causal centrality for individual movie events concatenated across the 10 movies. Different colors denote different movies.



Supplementary Figure 4. Causality rating responses. a. Average number of event pairs identified as causally related within each of the 10 movies used in the fMRI experiment (mean across movies 10.47, s.d. 4.18). **b.** Average percentage of event pairs identified as causally related among all possible event pairs within each movie (mean 6.78 %, s.d. 3.95 %). **c.** Average distance between a pair of causally related events (i.e., the number of events between the two events) within each movie. Lag = 1 if the events are adjacent to each other (mean 1.79 events, s.d. .51 events). **d.** The distribution of lags between causally related events, combined across all movies and coders. Most (73.1%) identified causal relationships occurred between temporally adjacent events. In **a**, **b**, and **c**, gray dots represent individual coders and black bars show the mean across coders. CMIYC = Catch Me If You Can, KR = Keith Reynolds.

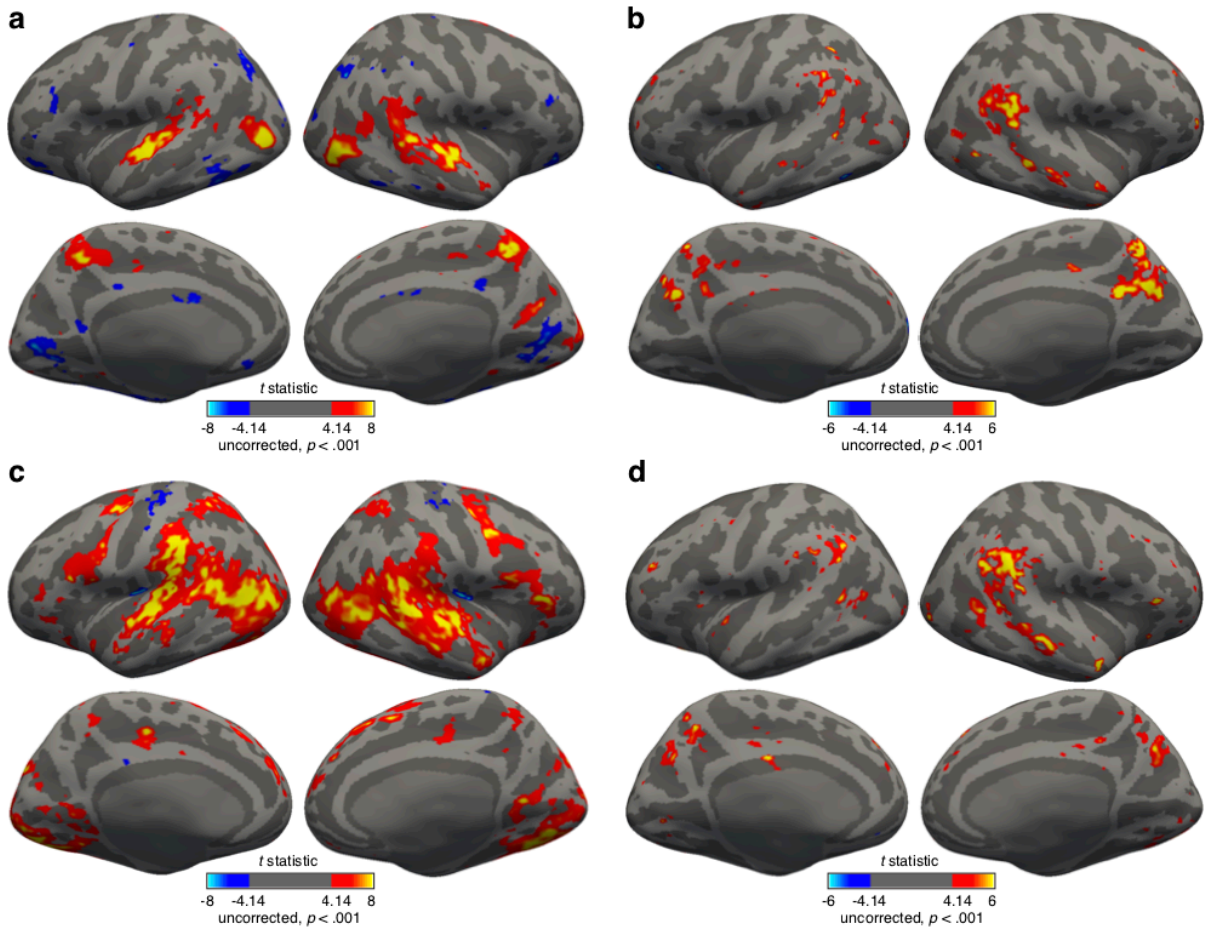


Supplementary Figure 5. Online behavioral experiment. a. The semantic similarity matrices (top) and semantic narrative networks (bottom) of two example movies used in the pre-registered online behavioral experiment. **b.** The causal relationship matrices (top) and causal narrative networks (bottom) of the same two example movies shown in **a**. **c.** Recall probability for individual movie events of the ten movies used in the online behavioral experiment, concatenated across movies. As in the fMRI experiment, primacy/recency effects were not observed. Different colors indicate different movies. **d.** Recall order of individual movie events in two example movies. Recall order was calculated as the rank (1 = recalled first, *N* = recalled last, where *N* is the total number of events in the movie) among recalled events. Subjects' written recall strictly followed the original event presentation order. **e.** Recall probability was positively correlated with semantic centrality (left) and causal centrality (right). Each dot represents a movie event. Different colors denote different movies. ***$p < .001$.

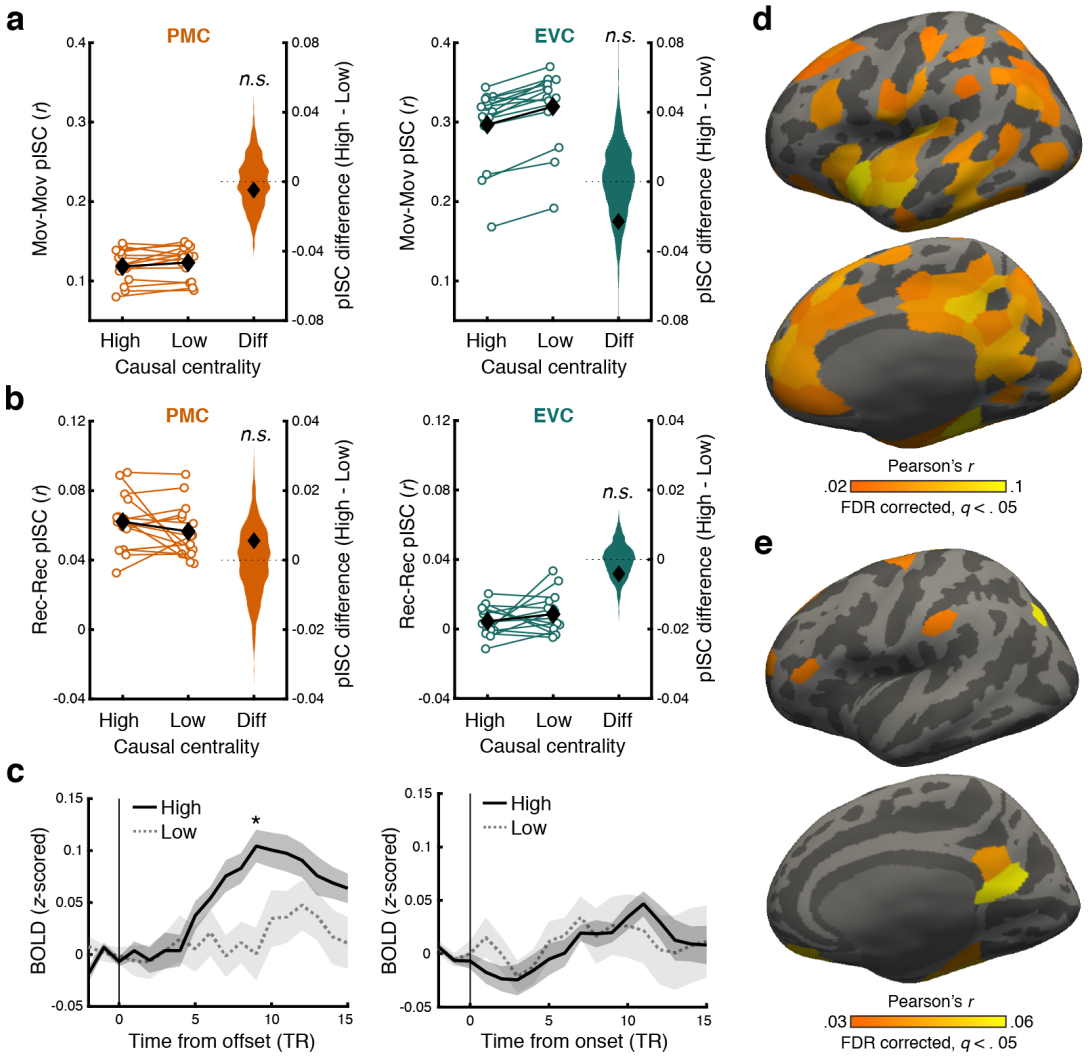


Supplementary Figure 6. Cortical responses at between-movie boundaries during movie watching. a. Example movie frame images around a boundary between two movies presented in the movie watching phase of the fMRI experiment. At between-movie boundaries, the last scene of the preceding movie was followed by a 6-second-long title scene of the upcoming movie. The transition between the 39-s introductory cartoon (presented at the beginning of each scanning run) and the first movie of each scanning run was also counted as a between-movie boundary. **b.** Whole-brain maps of cortical activity (*z*-scored BOLD signals) from 10 TRs before to 29 TRs after between-movie boundaries during movie watching (1 TR = 1.5 s). The BOLD signals were averaged across times within each 10-TR time window and then across movies and subjects. Time 0 means the onset of the movie title scene. The maps were arbitrarily thresholded to visualize brain areas whose activation was relatively higher (red-yellow) or lower (cyan-blue) than the mean activation across all time points within a scanning run (z = 0). Between-movie boundaries evoked transient changes in activation across widespread cortical areas. The black outlines indicate the posterior medial cortex (PMC) and early visual cortex (EVC) regions-of-interest. **c.** Activation time courses around between-movie boundaries in PMC (left) and EVC (right). Gray lines show individual subjects' time courses, averaged across all between-movie boundaries. Black lines show the averages across subjects. The four shades of the gray bars at the top of each panel correspond to the four time windows used in **b**. **d.** Intersubject pattern correlation between the mean activation patterns of the first four events in each of the 10 movies.

Each row and column of the similarity matrix represents an event, and the events are grouped by their temporal positions in the movie (i.e., row/column 1 – 10 = the first events of the 10 movies, row/column 11 – 20 = the second events, etc.). The black squares on the diagonal indicate cross-movie similarity within the first, second, third, and fourth events of the movies. In PMC (left), all first events showed similar patterns regardless of specific movies, and this tendency decreased in later events further away from between-movie boundaries. EVC (right) showed relatively weaker pattern similarity across movies within the first events compared to PMC.

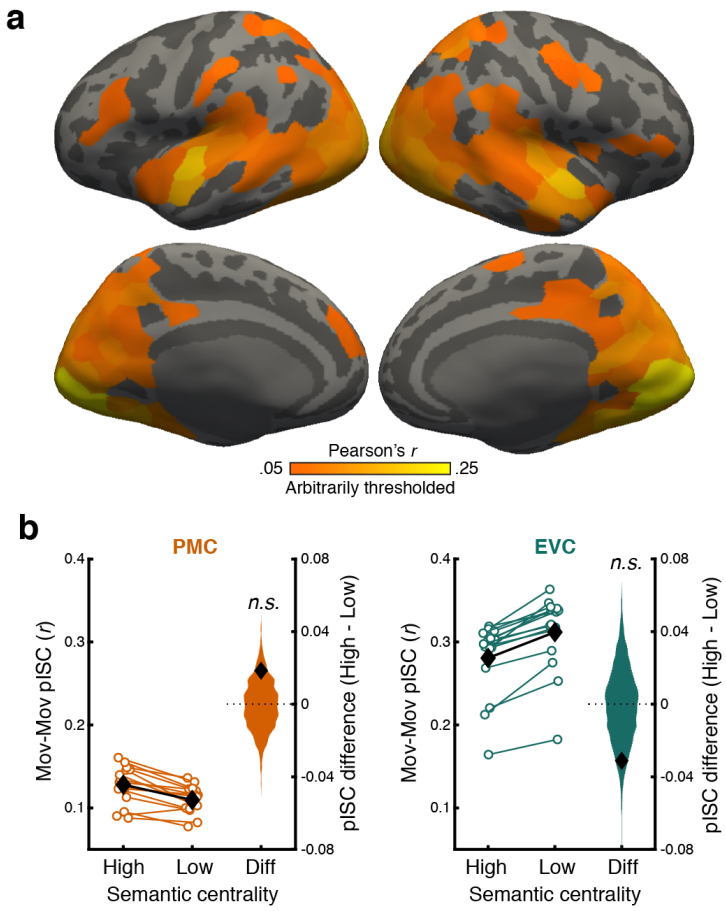


Supplementary Figure 7. Univariate activation. a & b. Whole-brain *t*-statistic maps showing the brain regions whose activation scale with semantic centrality during movie watching (**a**) and recall (**b**). **c & d.** Whole-brain *t*-statistic maps showing the brain regions whose activation scale with causal centrality during movie watching (**c**) and recall (**d**). All maps were liberally thresholded at $p < .001$ (uncorrected).

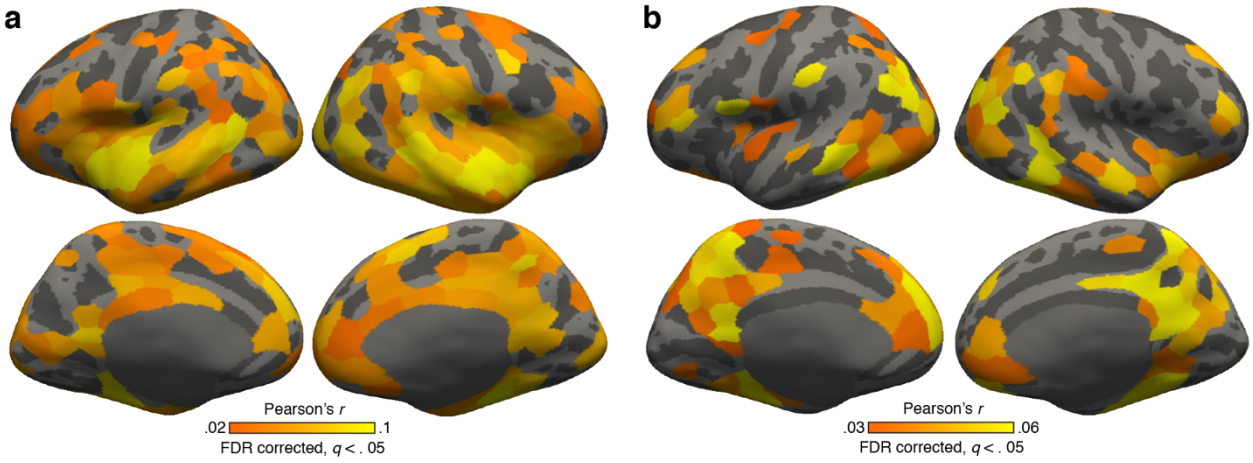


Supplementary Figure 8. Effects of causal narrative structure on neural responses. a & b. Intersubject pattern correlation (pISC) for High vs. Low causal centrality events and the difference (Diff) between the two conditions during movie watching (**a**) and recall (**b**) in the posterior medial cortex (PMC; left panels) and early visual cortex (EVC; right panels). For High and Low causal centrality conditions, white circles represent individual subjects. Black diamonds represent the mean across subjects within each condition. Error bars show SEM across subjects. For the difference between High and Low conditions (Diff), black diamonds show the true subject average, and histograms show the null distribution of the mean difference. Randomization tests showed that the difference between High vs. Low causal centrality conditions was not significantly different from zero in any of the experimental phases and ROIs (*p*s > .05, two-tailed). **c.** Mean hippocampal BOLD response time courses aligned at the offset (left) or onset (right) of events during movie watching. Solid lines and dotted lines show responses for the high and low causal centrality events, respectively. Shaded areas indicate SEM across subjects. Statistical significance reflects the difference between High vs. Low centrality events at each time point (two-tailed paired *t*-tests). Higher hippocampal responses were observed following the offset, but not onset, of high causal centrality events. *$q < .05$ (FDR corrected across time points). **d & e.** Whole-brain RSA maps showing the brain regions whose activation patterns reflect the whole causal

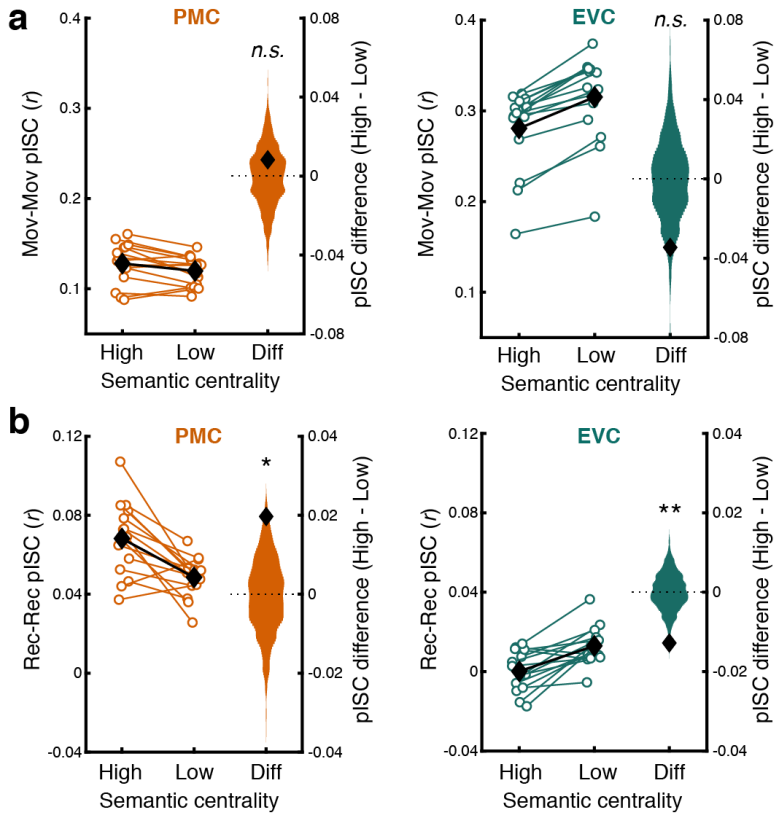
narrative network structure during movie watching (**d**) and recall (**e**). For each cortical parcel, the causal relationship matrix (Supplementary Figure 3a) of a movie was correlated with the movie's cross-event intersubject fMRI pattern similarity matrix. The correlation coefficients were averaged across movies and subjects and then tested for statistical significance against zero using a randomization test (one-tailed). All maps were thresholded at $q < .05$ (FDR-corrected across parcels).



Supplementary Figure 9. Intersubject pattern correlation during movie watching. a. Whole-brain surface map of mean pISC across matching events during movie watching. The pISC map was arbitrarily thresholded at $r = .05$ for visualization purposes. pISC values in visualized parcels were all significantly greater than zero (FDR-corrected $q < .05$ across parcels, one-tailed). **b.** pISC for High vs. Low semantic centrality events during movie watching and the difference (Diff) between the two conditions in the posterior medial cortex (PMC; left) and early visual cortex (EVC; right). For High and Low semantic centrality conditions, white circles represent individual subjects. Black diamonds represent the mean across subjects within each condition. Error bars show SEM across subjects. For the difference between High and Low conditions (Diff), black diamonds show the true subject average, and histograms show the null distribution of the mean difference. The difference between High vs. Low semantic centrality events was not significantly different from the null distribution in either ROI (*p*s > .05, two-tailed).



Supplementary Figure 10. Representational similarity analysis using movie watching phase data and recall transcripts. a. Brain regions that show positive correlations between the movie watching phase cross-event intersubject pattern similarity matrix and the movie annotation sentence embedding vector similarity matrix. **b.** Brain regions that show positive correlations between the recall phase cross-event intersubject pattern similarity matrix and the recall transcript sentence embedding vector similarity matrix. The recall transcript similarity matrix was first generated within each subject by computing the cosine similarity between the USE vectors of the subject's recall of movie events. The subject-specific similarity matrices were then averaged across subjects. In both **a** and **b**, representational similarity (i.e., fMRI–text correlation averaged across movies and subjects) for each parcel was tested for statistical significance against zero using a randomization test (one-tailed). All maps were thresholded at $q < .05$ (FDR-corrected across parcels).



Supplementary Figure 11. Effects of semantic centrality on event-specific intersubject pattern correlation including all events. a & b. Intersubject pattern correlation (pISC) for High vs. Low semantic centrality events and the difference (Diff) between the two conditions during movie watching (**a**) and recall (**b**) in the posterior medial cortex (PMC; left panels) and early visual cortex (EVC; right panels). All movie events were included in the analysis. The results were qualitatively identical to those obtained after excluding the first events from movie watching data and after excluding the events recalled by fewer than five subjects from recall data. For High and Low causal centrality conditions, white circles represent individual subjects. Black diamonds represent the mean across subjects within each condition. Error bars show SEM across subjects. For the difference between High and Low conditions (Diff), black diamonds show the true subject average, and histograms show the null distribution of the mean difference. Randomization tests were performed to test whether the differences between High vs. Low semantic centrality conditions were significantly different from zero (two-tailed). *$p < .05$, **$p < .01$.