

# Cortical reinstatement of causally related events sparks narrative insights by updating neural representation patterns

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We make sense of everyday events by reasoning about their underlying causes. When we connect causal links between events separated in time, we often experience a sudden feeling of “aha!”, or insight. To understand its cognitive and neural mechanisms, we designed an fMRI study in which participants watched a temporally scrambled TV episode. Participants pressed an “aha” button whenever they understood something new and explained their reasoning. More than 40% of insight explanations reference past events causally related to the current event. Neural patterns representing these causally related past events are reinstated across the cortex. This neural reinstatement drives sudden shifts in cortical activity patterns ~2 s prior to aha button presses, reflecting updates in situational representation. Moreover, distributed brain areas represent causally related events with similar neural patterns, beyond shared semantic or perceptual features. Together, the study suggests that we comprehend events by retrieving causally related past events, followed by updating neural patterns at moments of insight.

We understand everyday events by reasoning about their underlying causes. This process involves not only tracing causal chains of consecutive events but also connecting causes across events separated in time. While causal connections can emerge gradually as events unfold, we often experience a sudden “aha” moment when linking distant events. These moments of insight occur when remembering critical past events. For example, imagine you are stuck in unusually heavy traffic and cannot figure out why. When you suddenly recall hearing news about a big event happening downtown today, you will experience an “aha” moment and understand the congestion.

In cognitive psychology, insight has been most widely studied in problem-solving<sup>1,2</sup>, such as when participants solve the nine-dot problem by connecting all dots with four straight, continuous lines<sup>3</sup>. Insight has been defined as a sudden conscious change in a person’s representation of a stimulus, situation, event, or problem<sup>4</sup>. This notion was supported by a recent fMRI study that demonstrated changes in

neural activity patterns at moments of insight<sup>5</sup>. Shifts in visual cortical patterns were found when participants suddenly identified difficult-to-recognize Mooney images, which scaled with their reported degrees of insight. In this context, insight was considered as an all-or-none, step-function experience, in contrast to analytic problem-solving, which occurs deliberately and incrementally<sup>6</sup>.

Intriguingly, similar neural mechanisms appear to underlie moments of insight during the comprehension of everyday events and situations. When participants encountered major “twists” in stories that abruptly changed their interpretation, neural representation patterns shifted markedly, particularly within regions of the default mode network<sup>7,8</sup>.

Yet not all narrative insights unfold in such all-or-none fashion. They can also emerge gradually through incremental knowledge gain and often involve reflecting back on past events. In Song et al.<sup>9</sup>, participants pressed an “aha” button to express their moments of insight

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as they watched a hard-to-understand movie. Participants reported multiple “aha” moments as they gradually comprehended the narrative. They pressed more frequently when incoming events were causally related to past events, although no behavioral measure specific to memory retrieval was collected in this study. In another study, Miličević et al.<sup>10</sup> presented short movie clips that were either parts of coherent narratives or were unrelated to one another. Once participants discovered which clips formed coherent narratives, neural patterns in the hippocampus and medial prefrontal cortex became more similar for linked than for unlinked events. Together, these findings suggest that narrative insights are characterized not only by neural pattern shifts but also by the reorganization of neural patterns based on memories of related past events.

These studies raise further questions: What specific relationships do these past events have with the current event? How and when do people retrieve related past events during comprehension? More broadly, what neural processes underlie these memory-based insights?

Early work examined ongoing narrative comprehension by asking participants to describe their thoughts while reading or to recall stories afterward. Using a think-aloud paradigm, Suh and Trabasso<sup>11</sup> found that participants were more likely to recall past events that were causally related to the current event, implying an active causal inference process during comprehension. Studies also found that events that are more causally connected to other events were more likely to be remembered later<sup>12–16</sup>. These findings led to a theory positing that comprehension is achieved by constantly reinstating causally related past events in memory and updating causal links between events to form a coherent representation of a situation<sup>17–20</sup>. Recent fMRI studies corroborated this account by showing that neural patterns of related past events were reinstated in the brain during narrative comprehension<sup>21,22</sup>. For example, Chang et al.<sup>21</sup> presented a narrative that alternated between two storylines until their connections were revealed later. At these reveal moments, neural patterns representing related past events were reinstated, and the strength of neural reinstatement predicted how well participants integrated the two stories. Although causal relationships were not directly tested, this work suggests that neural patterns of related past events are reinstated during narrative comprehension.

Linking theories on insight during problem-solving and causal inference during narrative comprehension, we present three main findings about the underlying neural processes. First, participants retrieve causally related past events at moments of insight, reflected as the reinstatement of neural patterns representing these events. Second, situational representations are updated at moments of insight, marked by sudden shifts in neural patterns. Third, neural reinstatement of causally related past events drives these neural pattern shifts, constituting a neural signature of memory-guided insight. Using an fMRI, this study characterizes how people comprehend ongoing events by gaining insights into their causal connections.

## Results

### Comprehending a scrambled episode involves multiple moments of insight

We collected fMRI data as human participants ( $N=36$ ; fMRI data of  $N=33$  analyzed) watched a temporally scrambled episode of a TV show, *This is Us* (41 m 40 s). The episode is an omnibus-style narrative where the stories of four characters—Jack, Randall, Kate, and Kevin, each faced with their own life challenges—unfold in parallel in interleaved order. The four characters’ events play out independently, except for the biological twins Kate and Kevin, who sometimes appear in the same events. A major twist at the end reveals that Randall was born on the same day as Kate and Kevin, and he was adopted, making the three of them triplets. Jack is their father, with his story taking place 36 years in the past. This sudden reveal elicits a big “aha” moment.

We wanted to make the episode difficult to understand so that participants had to actively comprehend the narrative throughout the entire episode while experiencing multiple “aha” moments. To do this, we segmented the episode into 48 events (each  $52 \pm 21$  s) and scrambled their temporal sequence. In effect, participants watched a sequence of events that jumped back and forth in time, requiring them to connect relational links between events. The 48 events were grouped into 10 blocks in scrambled orders, such that 5 events were assigned to each of the 9 blocks. The 10th block included the last 3 events of the original episode that contained the big reveal. While fixing the order of events within each block, we scrambled the block order to create three sets of stimuli in different block orders. Block 10 was always placed at run 7 for all scrambled-order groups, and blocks 1–9 were positioned in the first one-third (run 1–3), middle one-third (run 4–6), and last one-third (run 8–10) of run orders for the three groups (Fig. 1A). This allowed us to compare behavioral responses and brain activities across scrambled-order groups as participants perceived the same audiovisual stimuli with different knowledge and contexts about the narrative.

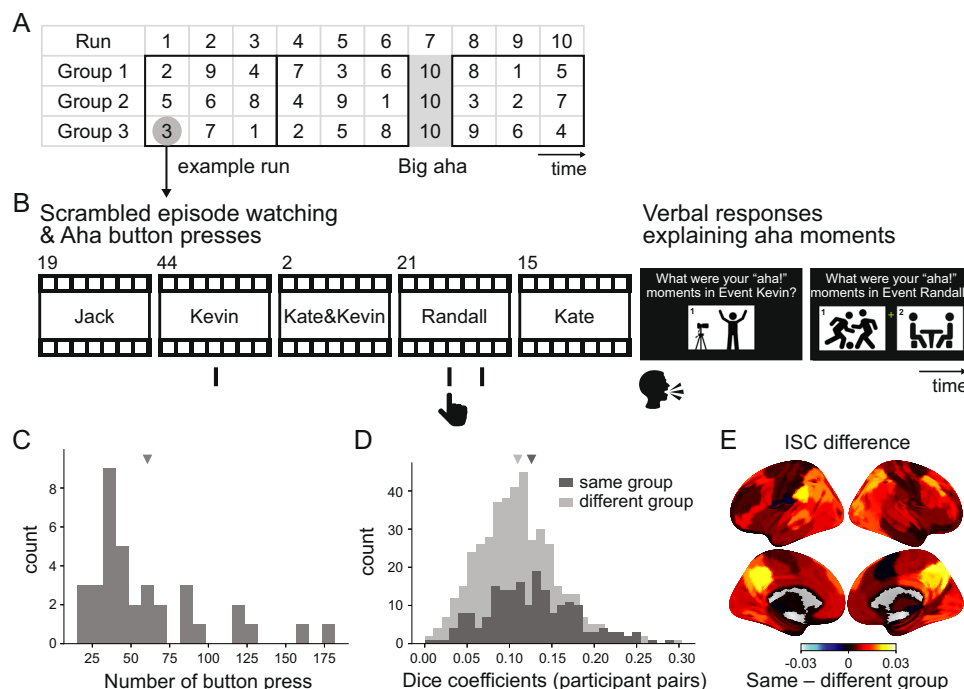
Thirty-six participants were randomly assigned to one of the three scrambled-order groups (12 participants per group). Participants were instructed to press an “aha” button whenever they understood something new about the show’s events and characters. After watching a set of events in a run, participants were shown screenshots taken whenever they pressed the aha button and were asked to verbally explain why they pressed the button at these moments (Fig. 1B). The motivation was to know the exact moments when, and the reasons why, participants experienced insight.

The frequency of aha button presses varied across participants. On average, participants pressed the button roughly once every 41 s, with a median of one press every 58 s, ranging from one press per 14 s to 2 m 47 s (Fig. 1C). Calculating dice coefficients of participant pairs’ button press moments (after unscrambling the events into their original sequence) showed that participants pressed the aha button at similar times, significantly higher than chance ( $z=35.249$ ,  $p<.001$ ; Fig. 1D). The aha button presses were more synchronized among participants within the same scrambled-order group compared to different groups (Wilcoxon rank-sum test,  $W=3.617$ ,  $p<0.001$ ; Fig. 1D), which illustrates that insight is not only driven by the stimulus but also modulated by the context and prior knowledge. This behavioral result was complemented by the fMRI result, where we estimated the intersubject correlation (ISC) of neural patterns across every pair of participants (again, after unscrambling the events into their original sequence). A majority of parcels exhibited positive ISC between pairs of participants, with stronger ISC within the same scrambled-order group than across groups (98 out of 100 cortical parcels and 11 out of 16 subcortical parcels based on ISC difference) (Fig. 1E). Together, results show that participants experienced multiple insights at similar moments in time when comprehending the scrambled episode.

### Causally related past events are retrieved at insight moments

Why did participants press the aha button in those moments? To understand this, we analyzed participants’ verbal explanations of their aha button press moments. Based on narrative comprehension theory, we hypothesized that participants retrieved past events that were causally related to the current event<sup>12,17,18</sup>.

For a data-driven, qualitative understanding of insight moments, three of the authors labeled each verbal explanation of insight moments into a set of categories (Supplementary Table S1). The categories were not defined a priori but were qualitatively derived by the first author to maximally cover the spectrum of participants’ verbal responses. Each response could be associated with multiple categories; for example, a participant may have had an aha moment about what is going on in the current event (current event understanding)

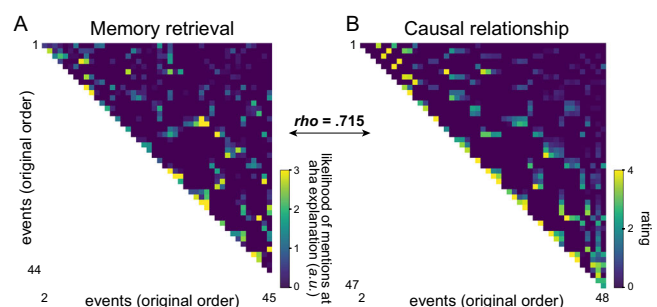


**Fig. 1 | Experimental design and behavioral results.** **A** Block order for the three stimulus groups. The episode was segmented into 48 events and assigned to one of the 10 blocks. The numbers denote block indices. Blocks 1 through 9 include 5 events in scrambled order, and block 10 includes the last 3 consecutive events of the episode, which contain the big reveal. Each block is assigned to either the first, middle, or last one-third of the runs in the three scrambled-order groups (solid contour). **B** Experimental design of one example fMRI run. Participants pressed the aha button as they watched scrambled-ordered events from the episode. For each block, an event from Jack, Kate, Kevin, and Randall stories was selected, respectively, with one additional event from either Jack event, Randall event, or Kate & Kevin event. The numbers on top of the events denote event indices. Then, participants were presented with screenshots of all the moments they had pressed the aha button and were asked to verbally explain why they pressed in these moments.

The screenshots of aha button presses that corresponded to each event were presented together. The schematic figure presents one screenshot for a Kevin event and two screenshots for a Randall event, matching the number of button presses made in the respective events. **C** Histogram of the aha button presses of 36 participants. The triangle indicates the mean number of button presses. **D** Synchrony in the aha button press moments for all participant pairs. The dark gray histogram indicates the dice coefficients of participant pairs that belong to the same group, whereas the light gray histogram indicates the dice coefficients of participant pairs that belong to different groups. The triangles indicate the mean dice coefficients for respective histograms. **E** The difference in mean intersubject correlation (ISC) values across participant pairs that belong to the same scrambled-order group versus different groups. ISC was calculated for 100 cortical and 16 subcortical parcels, respectively.

based on their memory of a past event (memory retrieval) while speculating about what may happen next (inference). We did not include the 7th run in the analysis because most of the responses were about their "big aha", which was hard to disentangle into categories. Coding of verbal responses found that  $41.15 \pm 16.64\%$  of the aha explanations included mentions of past events (ranging from 12.00 to 76.79% across participants), even when this was not an explicit instruction given to participants. The result indicates that many insight moments were achieved by comprehending the current event in relation to past events.

Then *what* past events were retrieved in memory? Were they causally related to past events as we hypothesized? To ask this, we created a memory retrieval matrix by coding past events that were retrieved when participants explained their insight moments. If a past event (or events) was mentioned when explaining an aha button press at a current event, +1 was assigned to that pair(s) of events in an event-by-event matrix (interrater reliability among three raters: pairwise Spearman's  $\rho = 0.803, 0.596, 0.640, p$  values  $< .001$  compared to chance created from shuffled matrices). This memory retrieval matrix was created for each participant, temporally unscrambled to its original sequence, and then averaged across all participants to create a single memory retrieval matrix (Fig. 2A). This matrix thus represents the degree to which every event pair is related in memory, or how likely an event is to prompt retrieval of, or to be retrieved during, another event. Additionally, we created a causal relationship matrix by having three of the authors independently rate the causal relationship



**Fig. 2 | Relationship between past event retrieval at insight moments and event causality.** **A** Memory retrieval matrix indicates the likelihood of an event retrieving, or being retrieved by, another event when participants explained their aha button presses. The events were unscrambled in order, and memory retrieval matrices created for 32 participants were averaged. Events 46–48 (in 7th run) were not included in analyses. **B** The causal relationship matrix indicates the degree of causal relationship rated for every event pair on a scale of 0–4.

between every pair of events on a scale of 0 (No causal relationship) to 4 (very high causal relationship) (interrater reliability among three raters: pairwise  $\rho = 0.701, 0.754, 0.818, p$  values  $< .001$ )<sup>13,15,16</sup> (Fig. 2B; Supplementary Table S2).

When comparing the memory retrieval matrix with the causal relationship matrix, we found a significantly high positive correlation

(Spearman's  $\rho = 0.715$ ,  $p < 0.001$  compared to chance created from shuffled matrices), meaning memory retrieval followed the causal event structure (Supplementary Text S1).

To consider alternatives other than the causal relationship, we created various narrative feature similarity matrices, including similarities in semantic contents of event annotations, which characters appeared in the event, where the event took place, low-level visual features (hue, saturation, pixel intensity, and motion energy of the video), and low-level audio features (amplitude and pitch of left and right stereos) (Supplementary Fig. S1A). We also created a time proximity matrix indicating how nearby in time the event pairs are in their original sequence. The causal relationship matrix and all alternative features we considered, with the exception of audio features, were similar to one another (pairwise  $\rho$  values ranging from 0.216 to 0.858, FDR-corrected  $p$  values  $< .001$ ) (Supplementary Fig. S1B). A multiple linear regression analysis found that the causal relationship matrix and the 6 narrative feature matrices together predict the memory retrieval matrix, with  $R^2 = 0.527$ , where the causal relationship explained the largest variance ( $t = 16.474$ , standardized coefficient = 0.615,  $p < 0.001$ ) amongst all other variables (semantic similarity:  $t = 2.517$ , standardized coefficient = 0.087,  $p = 0.012$ ; all other variables  $p$  values  $> 0.2$ ). Importantly, when predicting the memory retrieval matrix from the causal relationship matrix alone, the explained variance remained less changed compared to that of the full model, with  $R^2 = 0.519$  (model comparison,  $F = 2.664$ ,  $p = 0.014$ ). On the contrary, when predicting the memory retrieval matrix from the 6 narrative feature matrices without the causal relationship matrix, the explained variance showed a pronounced decrease, with  $R^2 = 0.396$  ( $F = 271.387$ ,  $p < 0.001$ ). The explained variance was not significantly different from the full model when only the two significant predictors, causal relationship and semantic similarity, were included ( $R^2 = 0.526$ ;  $F = 0.397$ ,  $p = 0.851$ ). These results indicate that participants' memory retrieval at moments of insight was primarily driven by causal relationships between events, above and beyond similarities in semantics, characters, places, low-level audio and visual features, or proximity in time.

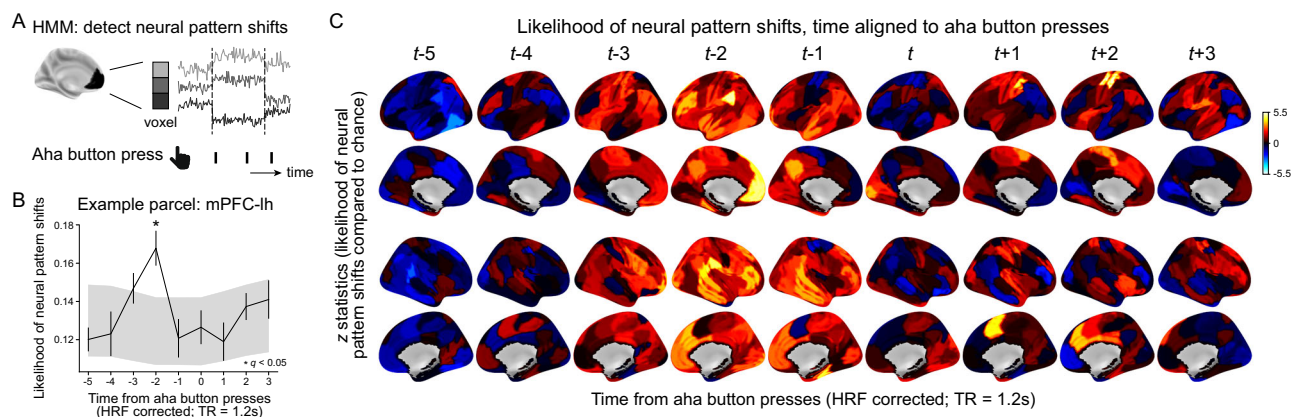
### Cortical representation patterns shift at moments of insight

What neural signature characterizes the experience of insight? Motivated by the psychological definition of insight as a sudden conscious change in representation<sup>4</sup> and in accordance with recent

neuroscientific findings<sup>5</sup>, we hypothesized that neural activity patterns would suddenly change at moments of insight. To test this, we used a data-driven hidden Markov model (HMM) to identify moments of sudden shift in voxel activity patterns<sup>23</sup> (Fig. 3A). The HMM was applied to multivoxel activity time series in each of the 100 cortical parcels<sup>24</sup>, for each of the 48 events and 33 participants, respectively.

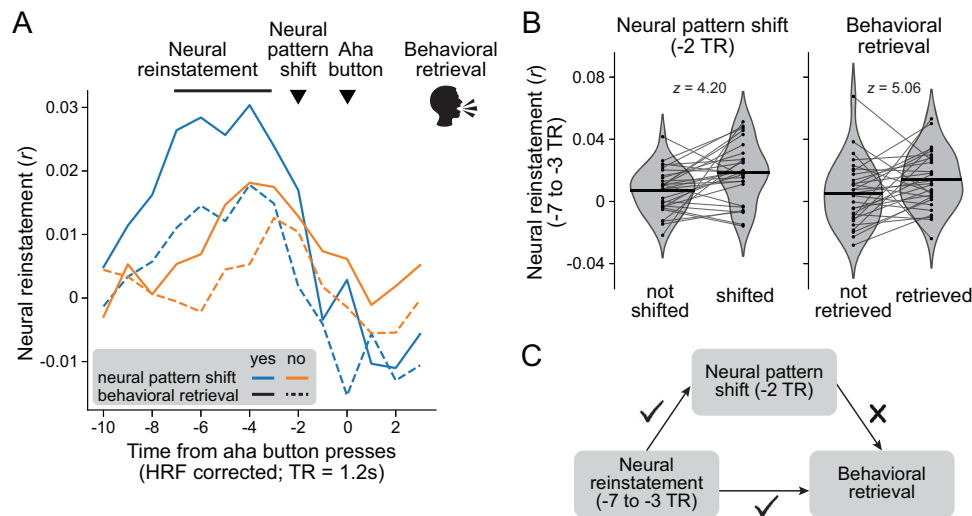
We hypothesized that participants' aha button presses would be aligned with moments of neural pattern shift detected by the HMM. To test this, we time-aligned the HMM-detected shifts to a participant's every aha button press moment ( $-5$  to  $3$  TRs from the aha button response times, after shifting  $4$  TRs [ $4.8$  s] to account for hemodynamic response delay [hemodynamic response function; HRF]), which were averaged across all button press moments. The likelihood, or the proportion, of neural pattern shift from  $-5$  to  $3$  TRs from aha button presses was compared to a chance distribution where the button press moments were randomly shuffled (Fig. 3B; Supplementary Fig. S2).

Figure 3C shows  $z$ -statistics, indicating the likelihood of representation pattern shifts compared to the chance distribution, of 100 cortical parcels, at  $-5$  to  $3$  TRs from the HRF-shifted aha button presses. An overall increase in the likelihood of neural pattern shifts was observed across distributed areas in the cortex at  $-2$  s prior to aha button presses. Specifically, 19 out of 100 cortical parcels indicated a sudden shift in representation patterns at 2 TRs ( $=2.4$  s) prior to button presses (see Supplementary Table S3 for a list of these 19 regions), and 8 out of 100 cortical parcels at 1 TR ( $=1.2$  s) prior to button presses (see Supplementary Fig. S3 for a thresholded map, FDR- $p < 0.05$ ). All of these significant parcels showed positive  $z$ -statistics. Regions indicated to be significant bilaterally were the dorsolateral prefrontal cortex, parietal operculum, parahippocampal cortex, and the temporal lobe. The number of significant parcels detected was  $\leq 4$  out of 100 parcels for the rest of the time points tested. The results indicate that representation patterns of the distributed cortical areas shifted at roughly 2 s prior to participants' aha button press moments (Supplementary Text S2). The result suggests that the change in cortical representation patterns characterizes the experience of insight, reflecting an update of the situational representation (see Supplementary Text S3 for the relationship between insights and perceived event boundaries; see Supplementary Fig. S4 for neural pattern shifts time-aligned to event boundaries).



**Fig. 3 | The likelihood of neural pattern shifts near the aha button press moments.** **A** Schematic illustration of the method. For each parcel, the hidden Markov model (HMM) was applied to identify sudden shifts in multivariate BOLD activity patterns. Moments of HMM-detected neural pattern shifts were compared to HRF-shifted aha button presses, based on the hypothesis that insight moments would correspond to changes in neural patterns. **B** Likelihood of neural pattern shifts compared to a chance distribution with randomly shuffled aha button presses, visualized in an example parcel, the left medial prefrontal cortex (mPFC)

(33 participants). The solid line indicates the likelihood of neural pattern shifts ( $\pm$ standard error of the mean). The gray area indicates the 95% confidence interval of the chance distribution (10,000 iterations). Asterisks indicate time points significantly different from chance (corrected for the number of parcels and time steps, FDR- $p < 0.05$ ). **C** The same result as **B**, but in 100 cortical parcels. Colors indicate  $z$ -statistics computed in comparison to the chance. Supplementary Fig. S3 shows a thresholded  $z$ -statistics map at FDR- $p < 0.05$ .



**Fig. 4 | Relationship between neural reinstatement of causally related past events, neural pattern shifts, and behavioral retrieval of causally related past events.** **A** Neural reinstatement time-aligned to HRF-shifted aha button presses. The aha button presses were categorized based on whether neural shifts occurred 2 TRs prior to the button presses and whether past events were behaviorally retrieved during verbal response phases (category indicated by colors and styles of the lines). Lines indicate the average across 19 regions and 29 participants. **B** Mean neural reinstatement at -7 to -3 TRs from the aha button presses, with respect to whether the neural patterns shifted vs. not at -2 TR (left), and whether past events

were retrieved vs. not when explaining the corresponding button presses (right). Dots indicate the average neural reinstatement of 19 regions for each of the 29 participants. Lines within the violin plot show the means of the distributions. Statistics were conducted using mixed effects models to account for the effects of 19 regions and the random effects of participants. **C** Schematics of the results. The neural reinstatement significantly predicts both the neural pattern shift and behavioral retrieval, whereas the neural pattern shift does not reliably predict behavioral retrieval.

### Neural reinstatement of causally related past events drives neural pattern shifts at insight moments

What drives neural pattern shifts at moments of insight? Based on behavioral results, we asked whether the reinstatement of causally related past events is related to the neural pattern shift and predicts behavioral retrieval of those past events. To calculate neural reinstatement, we summed neural patterns of past events, weighted by their causal relationships with the current event (Supplementary Text S4)<sup>25</sup>. A softmax function was applied to these weights to impose selectivity to highly causally related past events (see Supplementary Text S5 to compare results across varying degrees of selectivity)<sup>16,26</sup>. This integrated neural pattern representing causally related past events was correlated with the neural pattern near moments of aha button presses, representing the degree of neural reinstatement (see the “Methods” section). We focused our analysis on the 19 cortical regions that significantly shifted neural patterns 2 TRs prior to aha button presses.

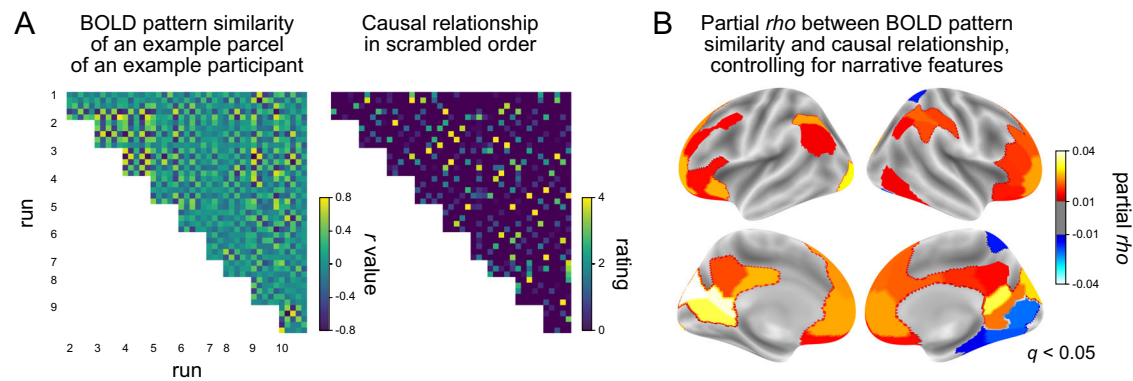
Figure 4A visualizes neural reinstatement time courses aligned to moments of aha button presses. The aha button presses were grouped into four categories based on whether (i) a neural pattern shift was detected 2 TRs prior to the aha button press and (ii) whether a participant mentioned past events when verbally explaining their insight for this button press. A neural reinstatement effect was observed from -7 (=8.4 s) to 3 TRs (=3.6 s) before the aha button presses. The effect was pronounced when a neural pattern shift occurred 2 TRs before the button press and when the press was associated with behavioral retrieval of causally related past events (solid blue line in Fig. 4A). When neither of these occurred, the average neural reinstatement effect was near zero (dashed orange line in Fig. 4A).

To test this statistically, we asked whether the degree of neural reinstatement influences the likelihood of neural pattern shift and behavioral retrieval, respectively (Fig. 4B). First, we used a logistic generalized linear mixed effect model to predict neural pattern shifts at -2 TR, given the average neural reinstatement effect at -7 to -3 TRs from the aha button presses. Neural pattern shifts were more likely to be detected when the neural reinstatement was high ( $\chi^2(1) = 17.639$ ,

$p < 0.001$ ,  $z = 4.201$ ), indicating that the neural reinstatement of causally related past events influenced updates in neural patterns. Second, we again used a logistic generalized linear mixed effect model to predict verbal retrieval of past events, given the average neural reinstatement effect at -7 to -3 TRs from the aha button presses. Participants were more likely to retrieve past events when the neural reinstatement was high ( $\chi^2(1) = 25.662$ ,  $p < 0.001$ ,  $z = 5.062$ ), indicating that neural reinstatement predicted behavioral retrieval (Supplementary Text S6 and S7).

We further asked if neural reinstatement, neural pattern shifts, and their interaction predict behavioral retrieval of causally related past events (Fig. 4C). Neural reinstatement predicted behavioral retrieval ( $\chi^2(1) = 20.779$ ,  $p < 0.001$ ,  $z = 4.555$ ), corroborating neural reinstatement as a measure of memory retrieval. We also found a main effect of neural pattern shift at -2 TR predicting behavioral retrieval in the negative direction ( $\chi^2(1) = 8.830$ ,  $p = 0.003$ ,  $z = -2.975$ ), although this effect was not significant when we included neural pattern shifts that occurred at -1 TR ( $\chi^2(1) = 0.594$ ,  $p = 0.441$ ,  $z = -0.771$ ) which refrained us from making further interpretations or conducting a mediation analysis. No interaction was found between neural reinstatement and neural pattern shift in predicting behavioral retrieval ( $\chi^2(1) = 0.062$ ,  $p = 0.804$ ,  $z = 0.249$ ).

Together, we found two distinct neural signatures involved in scrambled narrative comprehension. Neural reinstatement reflects memory retrieval of causally related past events and neural pattern shift reflects updates in situational representation at moments of insight. Neural reinstatement occurred prior to neural pattern shifts and was a significant predictor for both neural pattern shifts and behavioral retrieval. However, neither the neural pattern shift itself nor its interaction with neural reinstatement exhibited a meaningful relationship with behavioral retrieval. This corroborates our behavioral finding: Comprehension based on the retrieval of causally related past events is one among many different reasons for insight experience. Reinstatement of causally related past events drives insight, but having experienced insight does not necessarily mean that past events are retrieved in memory (Fig. 4C).



**Fig. 5 | Relationship between neural activity pattern similarity and causal event structure.** **A** (*Left*) The event-by-event BOLD activity pattern similarity matrix of an example parcel of an example participant. (*Right*) The same causal relationship matrix as in Fig. 2B, but in scrambled order. **B** Parcels that hold a

significant correlation between neural pattern similarity and causal relationship, while controlling for various narrative features such as semantic and perceptual similarities (thresholded at  $FDR-p < 0.05$ ). Colors indicate partial  $\rho$  values averaged across 33 participants.

### The brain represents causally related events with similar neural patterns

Neural patterns representing causally related past events were reinstated before moments of insight, as indicated by an increased positive correlation between past and present neural patterns. This suggests that causal relationships between events are encoded through shared representation patterns in the brain. We investigated (i) whether this representational similarity extends beyond nearby moments of insight and (ii) whether the effect is specific to causal relationships rather than other shared features between events. We employed representation pattern similarity analysis<sup>27</sup> to ask if causally related events were represented by similar BOLD activity patterns.

The BOLD activity time series were extracted from all voxels in each of the 100 cortical<sup>24</sup> and 16 subcortical<sup>28</sup> parcels as participants watched 48 events in scrambled orders. The BOLD time series were averaged across time for 48 events, respectively, resulting in a (number of voxels)  $\times$  (48 events) representation pattern matrix. A Pearson's correlation coefficient was computed to estimate the event-by-event BOLD pattern similarity matrix (Fig. 5A). To avoid spurious correlations, we only computed similarities between events that belonged to different fMRI runs<sup>29</sup>. The BOLD pattern similarity matrix was correlated with the causal relationship matrix (in the order that scrambled events were presented) using Spearman's rank correlation. Compared to chance distributions created by shuffling the BOLD pattern similarity matrix, all 100 cortical parcels and 9 out of 16 subcortical parcels exhibited significantly positive correlation above chance ( $FDR-p < 0.05$ ), meaning causally related events were represented by similar neural patterns across the whole brain.

Because causal relationships between events are intrinsically correlated with various narrative feature similarities and temporal proximity, we computed a partial correlation between BOLD pattern similarity and causal relationship, while controlling for narrative features including semantic and perceptual similarities and temporal distance (Supplementary Fig. S1). Even after this strict control, 40 out of 116 parcels significantly represented causally related events with similar neural patterns, among which 36 out of 40 parcels exhibited positive partial  $\rho$  values ( $FDR-p < 0.05$ ) (Fig. 5B). These regions included the bilateral retrosplenial cortex and the nearby visual areas which exhibited the largest  $\rho$  values, and the bilateral mPFC, ventrolateral and dorsal prefrontal cortex, intraparietal cortex, and precuneus and posterior cingulate cortex. This suggests that distributed brain regions encode events in a way that reflects the causal structure of a narrative, beyond semantic and perceptual similarities.

### Discussion

This study investigated how people comprehend narratives by piecing together causal links between events at multiple moments of insight. fMRI participants pressed an aha button while watching a temporally scrambled episode and verbally explained why they pressed in those moments at the end of each run. Participants experienced insights during comprehension, many of which included the retrieval of past events. Consistent with event comprehension theory, our behavioral results showed that causally related past events were reinstated in memory, suggesting an ongoing process of causal inference during comprehension. Aligned with the psychological notion of insight as a representational update, sudden shifts in cortical representation patterns were observed approximately two seconds before the aha button presses. Neural reinstatement of causally related past events—a neural signature of memory retrieval—occurred prior to these neural pattern shifts and predicted their likelihood. Finally, distributed areas in the brain represented causally related events with similar neural patterns, suggesting a way in which we form a causal understanding of narratives. In sum, the study provides neural evidence for how we reinstate memories to connect causal links between events and update situational representations at moments of insight.

In this study, participants indicated their moments of insight while watching a temporally scrambled narrative and provided verbal explanations for each insight at every run. This paradigm allowed us to examine neural processes underlying memory retrieval, causal inference, and insight during narrative comprehension. Behavioral findings showed that more than 40% of participants' insights included references to past events. The retrieved past events were the events that held strong causal relationships with the current event, with the correlation between memory retrieval and causal relationships exceeding 0.7. While causal relationships between events were intrinsically positively correlated with various narrative features, including semantic and perceptual similarities, causal relationships accounted for the largest variance in memory retrieval. These findings provide direct support for the theory that views comprehension as a process of retrieving causally related past events to update causal links between events<sup>12,17–20</sup>. Insight, as operationalized in this study, can be interpreted as the process of constructing and updating a coherent situational representation, often accompanied by the retrieval of causally related past events.

Cognitive theories have characterized insight as a sudden change in representation<sup>4</sup>. Supporting this notion, we found shifts in neural patterns at  $-2$  s prior to aha button presses in distributed areas of the cortex. Drawing on prior studies<sup>2,8,10</sup>, we propose that these shifts may reflect changes in narrative representation occurring at moments of

insight. However, this interpretation requires caution, as neural pattern shifts could also arise from alternative processes, such as motor preparation, motor execution, or decision-making. Furthermore, prior studies that used the same HMM analysis found neural pattern shifts at perceived event boundaries<sup>23,30</sup>. This is supported by the results of our additional behavioral experiment, which showed a significant correspondence between moments of insight (“aha” button presses) and moments of perceived event boundaries (“event boundary” button presses) (Supplementary Text S3). This raises an interesting hypothesis—whether experiencing insight creates internally-driven event boundaries. We encourage future work to further examine the distinction between external and internal event boundaries and how internal event boundaries relate to the experience of insight.

Participants retrieved causally related past events at moments of insight, an experience that was characterized by shifts in cortical patterns. Based on this, we asked whether the neural patterns of causally related past events are reinstated near moments of insight and whether they have consequences for neural pattern updates. To calculate neural reinstatement, we summed neural patterns of past events after weighing them by their causal relationships with the current event, and then correlated this integrated representation with the neural pattern of the current moment near button presses. This approach was motivated by seminal theories on memory integration<sup>10,31,32</sup>, although different integration mechanisms can be explored. In cortical areas that showed significant neural pattern shifts at 2 TRs prior to aha button presses, we found the neural reinstatement effect at  $-7$  ( $=8.4$  s) to 3 ( $=3.6$  s) TRs prior to the aha button presses, which conceptually aligns with Polyn et al.<sup>33</sup> that found neural reinstatement starting from  $-10$  s prior to participants’ verbal recall of items. Intriguingly, the neural reinstatement effect was pronounced when neural patterns shifted and when there was behavioral evidence of memory retrieval. The neural reinstatement effect not only predicted neural pattern shifts but also predicted whether participants would mention past events during the verbal response phase. To the best of our knowledge, this is the first study that has demonstrated the relationship between memory retrieval and insight during narratives: reinstatement of causally related past events occurs first, followed by a sudden change in neural patterns which marks moments of insight. Neural reinstatement predicts neural pattern shifts, but neural pattern shifts do not necessarily predict behavioral memory retrieval. This supports our behavioral observation that memory retrieval-based insight is one among various reasons why insight occurs (e.g., insights about current events, characters’ traits and behaviors, and relationships between characters).

In analyses relevant to Fig. 4, we treated neural pattern shifts and neural reinstatement as independent measures. The former indicates the degree of change in neural patterns across consecutive time steps, whereas the latter indicates the similarity between the neural pattern of the current time step and that of the causally related past events. The two measures are computed over different time windows: the former at  $-2$  TR, whereas the latter from  $-7$  to  $-3$  TRs from the aha button presses. Importantly, while reinstatement may increase the likelihood of a subsequent pattern shift, the converse does not follow: observing a pattern shift does not imply that it was driven by reinstatement. The results indicate that neural pattern shifts are likely preceded by the neural reinstatement of causally related past events. This does not rule out the possibility that neural pattern shifts may inevitably follow the cessation of neural reinstatement of past events. However, the result remains open to interpretation because such a relationship may not reflect a numerical artifact but indicate that situational updates naturally follow memory retrieval.

Moreover, distributed areas of the brain were found to represent causally related events with similar neural patterns. This remained true even after controlling for narrative features, including similarities in semantic contents, characters, places, low-level visual and audio features, as well as proximity in time. This indicates that the brain encodes

causal event structure by representing causally related events with more similar neural patterns and unrelated events with less similar patterns. Many of the brain regions identified in Fig. 5 overlapped with areas known to have long temporal receptive windows, which integrate information over extended timescales<sup>34–36</sup>. Such long-range integration may support the binding of causally related events that are separated in time. Future work can further examine whether the shared neural patterns based on causal relationships are driven by transient neural reinstatement of the causally related past events or structured reorganization of neural patterns that are sustained over time.

The generalizability of results should be tested in future work. Our experiment was based on one episode of a television series. We implemented a temporal scrambling approach to maximally recruit cognitive effort and memory retrieval and integration, which may differ from everyday narrative comprehension. Participants were instructed to speculate the original temporal sequence of the story, causal links that exist between events, and were instructed to press an “aha” button—all of which implicitly encourage participants to experience cognitive phenomena we report in this study. Nevertheless, these empirical choices were based on prior theories and behavioral studies, in service of our main goal of examining the neural underpinnings of these cognitive processes.

In sum, this study investigated the cognitive and neural processes underlying narrative insight, guided by memory and ongoing causal inference. Many insights were driven by the retrieval of causally related past events, supported by the neural reinstatement of these past events. This neural reinstatement drove changes in neural patterns at moments of insight, which suggest updates to the situational representation. Finally, causally related events were represented by similar neural patterns, suggesting a way in which the brain encodes causal event structure in narratives.

## Methods

### Participants

Thirty-six participants were recruited for the fMRI experiment from the Chicago area (21 female, 14 male, 1 non-binary; mean age  $23.42 \pm 4.01$  with range 18–33). No statistical method was used to predetermine sample size. All 36 participants were included in the overall sample. We noted in the corresponding “Methods” section if data from some participants were unavailable for specific analyses. Participants were compensated either monetarily or with the University of Chicago course credits. None of the participants had watched the TV series before the experiment. All participants were right-handed and reported fluency in English. The participants provided informed consent before taking part in the study. The study was approved by the Institutional Review Board of the University of Chicago.

### Stimulus

An episode of the TV series, *This is Us*, season 1 episode 1 (2016, directed by Requa, J. & Ficarra, G. and written by Fogelman, D.), was used as a stimulus in the study (41 m 40 s). The stimulus was chosen because it is an omnibus, multi-event, multi-character narrative, which has clear event boundaries, dynamic social relationships, and intense emotions that evolve over the course of the episode. Four short narratives play out in the episode in an interleaved order, starring Jack, Kate, Kevin, and Randall as main characters, respectively. The four characters’ events are delivered in an independent fashion, except for the connection that all four characters are 36 years old and that Kevin and Kate are siblings. At the end of the episode, there is a big reveal which shows that Jack’s events are from the past and he is the father of Kate, Kevin, and Randall, who are triplets.

The episode was segmented into 48 events and scrambled in temporal order. The duration of each segment was on average

$52 \pm 21$  s, ranging from 8 s to 1 m 37 s. The events were segmented by the first author based on the director's cut. We segmented the events if one character's event changed to another character's event. Within one character's continuous event, we segmented when there was a meaningful change in the narrative or temporal/spatial backgrounds. This resulted in 12 events from Jack events, 9 events from Kate events, 9 events from Kevin events, 4 events from Kate & Kevin events, 11 events from Randall events, and the last 3 events that contained the "big reveal". To scramble these events and group them into blocks in a manner that all blocks hold comparable degrees of importance, eight researchers in the lab (including the first and last authors) rated the importance of the 45 segmented events, excluding the last 3 events, which obviously held high importance. The researchers rated how important the events are in the story; if an event provided key information that is critical in comprehending the narrative of the episode, the event would be rated with a high score.

The temporally scrambled 45 events were grouped into 9 blocks such that each block consisted of one event from Jack, Kevin, Kate, and Randall events, respectively, plus one additional event that was either a Jack event, a Randall event, or a Kate and Kevin event. The last 3 events were grouped in the original temporal order as one block. The mean block duration was 4 m 10 s. The event assignments to blocks were done by the first author, so that the summed duration and summed importance of five events per block were comparable across blocks. Five events were ordered in a block such that there were no coincidental regularities in character event sequence (e.g., the likelihood that a Kate event is to be followed by a Kevin event) or the order of event importance (e.g., the likelihood that the blocks are likely to start with an unimportant event and end with the important event). Event assignment and order within each block were fixed.

Having fixed the event order within a block, we scrambled the sequence of nine blocks, to create three scrambled-order groups (Fig. 1A). We scrambled the order of blocks such that each block tiles the first one-third, middle one-third, and last one-third of the entire block order in the three stimulus groups (e.g., block 1 should be positioned at the beginning for group 1, middle for group 2, and at the end for group 3). Block 10, which contained the last 3 consecutive events of the episode, was always positioned on the 7th run such that the rest of the blocks could be positioned before the "big aha" for the two stimulus groups and after the "big aha" for one stimulus group. By systematically positioning the blocks in sequential order, we were able to compare the effects of contexts, or knowledge gained about the narrative, while holding the perceptual inputs of the event constant for the three stimulus groups. Participant assignment to one of the three groups was counterbalanced, following a rotating sequence (group 1, 2, 3, 1, 2, 3, etc.) based on their order of participation. The experimenters were aware of participants' group assignments throughout the study.

### FMRI experiment

The fMRI experiment consisted of 10 runs in total. Each run contained three parts: aha button presses during scrambled episode watching (one block of events per run) followed by the verbal explanation of why participants pressed the aha buttons at certain moments, and the verbal response on their personal thoughts about the characters. Participants' personal thoughts about the characters were not analyzed in the current study.

As participants watched the scrambled episode, they were instructed to pay attention to the video and try their best to speculate what the original story is: the original temporal sequence of the story, causal links that exist between events, and what characters are doing, thinking, and feeling. Participants were asked to press the "aha" button whenever they experienced a subjective feeling of "aha" or a sudden insight. They pressed the button when they grasped what was going on in the story, made sense of the past event that they previously did not

understand, realized something new, resolved initial curiosity about any parts of the narrative (even partially), came to have a better understanding of—or even just a speculation about—the general plots, the temporal sequence of the events, causal relationships between events, as well as characters' behavior, thoughts, feelings, intentions, and relationships with other characters. Whenever they realized that their previous "aha" moments turned out to be incorrect, which is a subjective feeling of "oops", they also pressed the aha button. All participants received the same instructions from the same instructor prior to the fMRI scans. They were reminded that there were no correct or incorrect answers to the aha button presses, that they should follow their subjective feelings, and that being a frequent or infrequent button presser does not matter in the experiment. The participants were asked to press the button without hesitation when they had even a tiny urge to press. Event onsets were triggered by scan pulses (thus, consecutive events were separated by 0–1.2 s of black screen), and the timings of onset and offset were recorded.

After the aha button presses during scrambled episode watching were over, participants were presented with screenshots of the events for which they pressed the aha button. The screenshots were labeled with numbers in order. Participants were asked to freely explain the reasons why they pressed the aha button at these moments; what they newly understood or learned about the events and characters from watching the events, and how their thoughts about the events and characters changed from watching the events. Participants were given the freedom to either explain their aha experience one by one for each screenshot, or describe their overall aha experience in those moments at an event. Because there were five event segments in each run (with the exception of run 7, which consisted of the last 3 consecutive events of the episode), all aha button presses made at each event were presented together as screenshots. For example, if a participant pressed the button twice in event 2 and once in event 4, they would be given two prompts. One would have two screenshots of event 2, and the next would have one screenshot of event 4. Because the participant did not press the button in events 1, 3, and 5, these prompts were not given. This means task demands for verbal responses differed depending on whether the participant was a frequent or infrequent button presser. Frequent button pressers who pressed the button at every event had to explain multiple screenshots that were consecutively presented for all five events, whereas infrequent button pressers had to explain a few screenshots for fewer than five events at which they pressed the button. The participants were instructed to talk clearly and accurately with as much detail as possible. If the participants were done talking about the screenshots, they pressed a button to move on to the next prompt. The next prompt started when the next scan pulse was recorded. The timing of the prompt onset was recorded. Only behavioral data were analyzed in this study—we did not analyze neural data acquired during the verbal response phase.

Participants were scanned with a 3 T scanner (Magnetom Prisma; Siemens Healthineers, Erlangen, Germany) with a 64-channel head coil. Anatomical images were acquired using a T1-weighted magnetization-prepared rapid gradient echo pulse sequence (repetition time [TR] = 2300 ms, echo time [TE] = 2.4 ms, field of view = 256 mm × 256 mm, and 1 mm isotropic voxels). Functional images were acquired using a T2\*-weighted echo planar imaging (EPI) sequence (TR = 1200 ms, TE = 25 ms, multiband factor = 4, field of view = 208 mm × 192 mm, and 2 mm isotropic voxels, with 68 slices covering the whole brain).

Stimuli were presented using Psychtoolbox and Matlab 2019b. Visual stimuli were displayed on a 40-inch LCD monitor with a resolution of 1920 × 1080 pixels and a refresh rate of 60 Hz. Auditory stimuli were delivered by Avotec through MRI-compatible Comply canal tips earbuds. Participants' voices were recorded using in-house Matlab software. After the acquisition of raw audio files, our customized software detected the regularity of audio signals coming from scan pulses and denoised them from participants' voice recordings. Four

participants' voice recordings were not analyzed because the files were not recorded or deleted during data collection.

Because all participants' duration for spoken response differed, the experimenters manually stopped the scan when each run ended. Participants' head motions during scans were monitored using the Framewise Integrated Real-time MRI Monitoring (FIRMM) software. After each run, participants were given appropriate feedback about their motion when needed. The duration of the fMRI experiment varied across participants depending on the number of verbal responses; it ranged from approximately 1 h 20 m to 2 h 15 m.

The fMRI study was followed by a post-scan behavioral session comprising two parts: recounting the scrambled story in its original order and a survey on what they thought about the four main characters. These data were not analyzed in the current study.

### fMRI image preprocessing

The fMRI data were converted to BIDS format. The frames from the movie start time and 3 TRs after the end of the verbal response were extracted from the BIDS output for analyses. All images were deblurred. Anatomical T1-weighted images were processed with a standard fMRIPrep pipeline with surface reconstruction<sup>37</sup>. Functional EPI images were also processed with the standard fMRIPrep pipeline, without slice timing correction, without susceptibility distortion correction, and images registered to MNI152NLin2009cAsym:res-2 template. The EPIs after the fMRIPrep were masked with each individual's MNI-aligned brain mask. We regressed out the following nuisance variables from all voxel time series within the masked brain: 24 head motion parameters, global signal, signals from cerebrospinal fluid and white matter, top-five cCompCor, top-five wCompCor, linear trend, and low-frequency signal with 128 s cut-off. The frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS, as well as frames that were detected as non-steady-state volumes, were censored as NaNs. We applied spatial smoothing using 4 FWHM.

Three participants' data had more than 10% of total frames censored during video watching due to head motion, and thus were excluded from all fMRI analyses (proportion of censored frames: 19.021%, 16.458%, 10.885%). The remaining 33 participants had minimal head motion during video watching, with an average of  $0.665 \pm 0.718\%$  of the frames censored, ranging from 0% to 2.126%. The three participants' behavioral data were still analyzed.

### Parcellation

We used the subject-specific, autogenerated EPI mask and predefined template-registered cortical and subcortical parcels to extract the BOLD time series of voxels. First, using 10 brain masks generated by fMRIPrep on the fMRI runs, we created a composite brain mask per participant by taking the intersection. Second, we used the 100 cortical parcels by Schaefer and colleagues<sup>24</sup> and 16 subcortical parcels by Tian and colleagues<sup>28</sup>. For each of the 116 parcels, BOLD activity time series were extracted from voxels that were contained in both the participant-specific mask and predefined parcels. Note that this process results in some parcels containing different numbers of voxels across participants.

### Data preparation for analysis

During the fMRI experiment, we recorded (1) the onset and offset of the video for each event and (2) the time participants spent verbally responding to every event in which they pressed the aha button. We limited all our fMRI analyses to moments when participants were watching the events, excluding the verbal response phase. We extracted the BOLD time series from the onset of the first event to the offset of the last event, which was shifted by 4 TRs (4.8 s) to account for the HRF. Each of the extracted voxel time series was z-normalized across time, with censored frames remaining as NaNs. Analyses were conducted using Python 3.12.2 and R 4.4.2.

### Aha button press synchrony

Thirty-six participants' aha button press moments in seconds were converted to corresponding TRs within each of the 48 segmented events. We recorded button presses up to 2 TRs after each event was over. Dice coefficients were calculated as a measure of button press synchrony. Specifically, 1 TR before and 1 TR after the button press were considered button press moments to compensate for individual differences in response times. Dice coefficients were calculated between every pair of participants. The average value was compared to a chance distribution obtained by randomly shuffling participants' aha button presses 10,000 times. The resulting non-parametric permutation test statistic was reported as  $z = (\text{real} - \text{mean}(\text{null})) / \text{std}(\text{null})$ , with a two-tailed  $p\text{-value} = (1 + \text{number of } |\text{real}| \leq |\text{null}|) / (1 + \text{number of null iterations})$ . (This procedure is consistent for all ensuing non-parametric permutation tests. All  $p\text{-values}$  reported in this manuscript are two-tailed.) Furthermore, dice coefficients were grouped by whether the pair of participants belonged to the same scrambled-order group vs. different groups, which were compared using a Wilcoxon rank-sum test (Fig. 1D).

### Intersubject correlation (ISC) analysis

The BOLD time series of all voxels within each of the 100 cortical and 16 subcortical parcels were averaged to represent the mean activity time series of a parcel. Pearson's correlations of the mean activity time series were calculated across all participant pairs. Participant pairs were grouped based on whether the pair belonged to the same scrambled-order group or different groups. The ISC difference was calculated as the mean of the same-group ISC minus the mean of the different-group ISC (calculated after Fisher's  $r\text{-to-}z$  transformation). The ISC difference was calculated for every parcel and visualized in the surface brain using `nilearn.plotting.plot_surf_stat_map` (Fig. 1E).

### Coding of verbal responses and causal relationship

Thirty-two participants' verbal explanations of their aha button presses (recorded inside the fMRI) were transcribed verbatim; 4 participants' data were excluded due to missing or deprecated voice recordings. After listening to the explanations, we defined eight categories that encompassed a broad spectrum of participants' verbal responses (Supplementary Table S1). Three of the authors categorized the explanations associated with each button press into one or more of these categories. If a participant explained the screenshots separately, different categories were assigned to the corresponding button presses, whereas if a participant explained multiple screenshots together with a single explanation, the same categories were assigned to the corresponding button presses.

For the "memory retrieval" category, which was labeled when there were either explicit or implicit mentions of past events, the three raters annotated which event(s) were mentioned. This allowed us to create a memory retrieval matrix for each participant by marking +1 if a past event was mentioned at the insight moment of a current event. This directed matrix was then unscrambled in temporal order and averaged across all 32 fMRI participants to create one undirected memory retrieval matrix. We did not include run 7 in the analyses, as the majority of explanations were "big aha" when participants understood the family relationship between the four characters.

Causal relationships of event pairs were mapped by the same three raters, on a scale of 0 (no causal relationship) to 4 (very high causal relationship). The instruction and definition of the causal relationship provided to the raters are shown in Supplementary Table S2<sup>13,15,16</sup>.

### Narrative feature extraction

Five narrative features—semantics, characters, places, low-level visual, and low-level audio features—were extracted to represent each of the 48 events (Supplementary Fig. S1A). To represent

semantics, the contents of each event were annotated in detail by the first author. The annotations in descriptive sentences, together with the transcripts of dialogs within each event, were fed into the pre-trained GPT-2 language model (transformers.GPT2Model)<sup>38</sup>. The 768-dimensional embeddings of the last hidden layer were extracted from every meaningful word (transformers.AutoTokenizer.from\_pretrained("gpt2")) and averaged across words within each event. This resulted in a 768-dimensional embedding vector with respect to 48 events. Which characters appeared in each event and where the event took place were coded as binary vectors by the first author. Character vectors represented the appearance of 4 main characters, Jack, Randall, Kate, and Kevin, and 9 sub-characters. Place vectors included a total of 15 unique indoor (e.g., Jack's bedroom, Randall's office, television set, hospital, support group, restaurant) and outdoor (e.g., soccer field, in front of Kate's house) settings. The low-level visual features were characterized by four features—hue, saturation, pixel intensity, and motion energy—which were estimated per frame and averaged across frames within an event. Hue, saturation, and pixel intensity were estimated with MATLAB's `rgb2hsv` function. Motion energy was estimated with `plis.extractors.FarnebackOpticalFlowExtractor` function<sup>39</sup>. The low-level audio features were represented with four features—amplitude and pitch of left and right stereos—which were estimated per frame and averaged across frames within an event. Amplitude and pitch were estimated using `audioread` and `pitch` functions in MATLAB. The event-by-event narrative feature similarity matrix was created by taking Pearson's correlation coefficient, which was Fisher's *r*-to-*z* transformed for further analyses.

Lastly, to represent how close in time the event pairs were in the narrative's original sequence, events were sorted in their original order, respectively, for the four characters' narratives. The events where Kevin and Kate appeared together were included in both Kate's and Kevin's narratives. If an event pair was continuous in time, the highest score (score 14) was given, and if an event pair was furthest in time (i.e., the first and last event within a character narrative that was separated by 13 events in between), the lowest score (score 1) was given. A score of 0 was given to event pairs of different character narratives (Supplementary Fig. S1A).

### Neural pattern shift detection

The hidden Markov model (HMM)-based segmentation model was implemented using the function `brainiak.eventseg.event.EventSegment`<sup>40</sup>. We applied the HMM on the multivariate BOLD activity of all voxels corresponding to each of the 100 cortical parcels, for each of the 48 events, and for each of the 33 participants, independently. We intentionally did not apply the model to sub-cortical parcels because subcortical voxel activity shifts rapidly at every TR, which does not meet the HMM's assumption that a latent event prolongs for a continuous time period. NaN values due to censoring were linearly interpolated from the neighboring frames. For each event's time series, we iterated over a different number of latent states (i.e., *K*) for optimal hyperparameter selection. If the event duration was smaller than 10 TRs, we did not apply the HMM and considered the event as a continuous time series. If the event duration was <20 TRs, we started event iterations from *K* = 2, whereas we started from *K* = 3 for events with durations over 20 TRs. For the maximum number of *K* in the hyperparameter search, we took the floor of each event duration divided by 3, such that the average duration of each event is at least 3 TRs. We applied the HMM across iterations over possible *K*s, and calculated the difference in voxel pattern similarity within the same event compared to different events. In this comparison, we controlled for the separation in time when computing the voxel pattern similarity between different time points. That is, if the within-event similarity was calculated between

TRs separated in 4 time steps, the across-event similarity was calculated between TRs also separated in 4 time steps. We chose *K*, which exhibited the largest within-event similarity compared to across-event similarity. However, in 2.435% of cases, we found either a monotonic decrease or increase in within- compared to across-event similarities across a range of *K*. We considered them poor model fits because this was likely to occur for events of shorter durations (Spearman's  $\rho = -0.881$ ,  $p < 0.001$ ). Therefore, we did not apply HMM for those events, i.e., the entire event was considered a single event. The "boundaries" detected by the HMM represented moments when multivariate voxel representation patterns shifted from one time segment to the next. These moments of neural pattern shifts were annotated with index 1, whereas other moments were indexed with 0.

To align these moments of neural pattern shifts with the aha button press moments, we took the boundary indices (1 for moments when the pattern shifted, 0 for the rest) at -5 to 3 TRs from all aha button presses for each participant and averaged them across button press moments. Time frames that did not exist within this range (e.g., aha button press that was made <5 TRs since the onset of the event) were treated as NaNs. For a statistical test, we iterated the same analysis 10,000 times with the aha button press moments randomly shuffled in time. The likelihood of the neural pattern shifts averaged across all 33 participants was compared to the chance distribution at each time step, which was corrected for multiple comparisons across parcels and time steps.

### Neural reinstatement of causally related past events

Twenty-nine participants' data were analyzed; 3 were excluded for head motion, and 4 were excluded for the failure of behavioral response recording. To estimate the neural reinstatement effect, for each aha button press, we compiled neural patterns of all past events that occurred in prior fMRI runs. These patterns were multiplied by their degrees of causal relationship to the current event, derived from the causal relationship matrix and weighted using a softmax transformation with temperature  $\tau = 1$  (see Supplementary Text S5 for results with varying  $\tau$ ). The weighted linear sum of the past events represented the integrated pattern of the causally related past events. Pearson's correlation between the integrated past pattern and the current pattern was calculated, ranging from -10 to 3 TRs from the HRF-shifted aha button presses. Our analyses were restricted to 19 cortical regions that significantly shifted neural patterns at 2 TRs prior to aha button presses. For the same time frame (from -10 to 3 TRs) and every button press, we extracted a binary measure of whether the neural pattern shift was detected by the HMM at -2 TR. For the same aha button press, we also extracted a binary measure of whether past event(s) were mentioned in the participant's verbal explanation of their insight. If any of the three coders judged that the insight accompanied the retrieval of past event(s), we considered it memory retrieval.

The aha button presses were categorized based on binary measures of neural pattern shifts at -2 TRs and behavioral memory retrieval. Based on the observation of Fig. 4A, we considered that neural reinstatement occurs at approximately -7 to -3 TRs from aha button presses. Neural reinstatement effects in this time frame were averaged (calculated after Fisher's *r*-to-*z* transformation).

Logistic generalized linear mixed effect models were conducted using the `lme4` library in R, since the neural shift and behavioral retrieval measures were both binary ("binomial" family in `glmer` function): (1) behavioral retrieval - neural reinstatement + 19 regions + (1|subject), (2) neural pattern shift - neural reinstatement + 19 regions + (1|subject), and (3) behavioral retrieval - neural pattern shift + neural reinstatement + neural pattern shift  $\times$  neural reinstatement + 19 regions + (1|subject). With regard to the latter model, we also ran a model where neural pattern shifts detected on either 2 TR or 1 TR prior to aha button presses were indicated as 1. Chi-squared tests were

conducted between each of these models and the reduced models as we removed each one of the main effects or the interaction effect individually. All analyses here are conducted as within-subject analyses.

### Event-by-event neural pattern similarity and causal relationship

For each of the 100 cortical and 16 subcortical parcels, we averaged the multivariate voxel activity pattern across time for each of the 48 events across 10 runs. Taking the correlation coefficients of (number of voxels)  $\times$  (48 events in a scrambled order) resulted in a (48 events)  $\times$  (48 events) BOLD pattern similarity matrix for each participant, which was Fisher's  $r$ -to- $z$  transformed (Fig. 5A). This was correlated with the causal relationship matrix in the scrambled order using Spearman's rank correlation. The average Spearman's  $\rho$  value across 33 participants was compared with a chance distribution, where  $\rho$  was calculated between the shuffled BOLD pattern similarity matrix and the causal relationship matrix (10,000 iterations). This was iterated across 116 parcels, with the significance corrected for 116 comparisons (FDR- $p < 0.05$ ).

In the same manner, we calculated partial rank correlation (pingouin.partial\_corr), where we correlated BOLD pattern similarity with causal relationship while controlling for six narrative feature matrices. To avoid collinearity, six narrative feature matrices were converted into six principal components prior to calculation.

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

Raw and processed fMRI data are shared in OpenNeuro, <https://openneuro.org/datasets/ds005658>. Behavioral data are shared in a GitHub repository, <https://doi.org/10.5281/zenodo.19389961><sup>41</sup>.

### Code availability

Codes are shared in a GitHub repository, <https://doi.org/10.5281/zenodo.19389961><sup>41</sup>.

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H.S.: Conceptualization, data curation, formal analysis, investigation, validation, resources, writing—original draft, writing—review & editing, visualization, project administration, funding acquisition. J.K.: Conceptualization, data curation, investigation, writing—review & editing. R.M.: Conceptualization, data curation, investigation, writing—review & editing. Y.C.L.: Conceptualization, investigation, resources, writing—review & editing, supervision, funding acquisition. M.D.R.: Conceptualization, data curation, investigation, resources, writing—review & editing, supervision, project administration, funding acquisition.

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## Competing interests

The authors declare no competing interests.

## Additional information

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