



Neural unscrambling of temporal information during a nonlinear narrative

Clare Grall , Josefa Equita, Emily S. Finn *

Department of Psychological and Brain Sciences, Dartmouth College, 6207 Moore Hall, Hanover, NH 03755, United States

*Corresponding author: Department of Psychological and Brain Sciences, Dartmouth College, 6207 Moore Hall, Hanover, NH 03755, United States.

Email: Emily.S.Finn@dartmouth.edu

Although we must experience our lives chronologically, storytellers often manipulate the order in which they relay events. How the brain processes temporal information while encoding a nonlinear narrative remains unclear. Here, we use functional magnetic resonance imaging during movie watching to investigate which brain regions are sensitive to information about time in a narrative and test whether the representation of temporal context across a narrative is more influenced by the order in which events are presented or their underlying chronological sequence. Results indicate that medial parietal regions are sensitive to cued jumps through time over and above other changes in context (i.e., location). Moreover, when processing non-chronological narrative information, the precuneus and posterior cingulate engage in on-the-fly temporal unscrambling to represent information chronologically. Specifically, days that are closer together in chronological time are represented more similarly regardless of when they are presented in the movie, and this representation is consistent across participants. Additional analyses reveal a strong spatial signature associated with higher magnitude jumps through time. These findings are consistent with prior theorizing on medial parietal regions as central to maintaining and updating narrative situation models, and suggest the priority of chronological information when encoding narrative events.

Key words: fMRI; narratives; naturalistic stimuli; representational similarity analysis; temporal processing.

Introduction

Narratives are not bound by time. In real-world storytelling, we often communicate events in a non-chronological fashion. For example, when we talk about the events of our day with a friend, we may realize we missed a key detail and go back to fill that gap. Or when we meet someone new, we learn about their history through stories about different times in their life. Sometimes, such as in literature or film, events are presented out of order for dramatic effect (i.e., *in medias res*).

Because nonlinear narratives stand in contrast to the purely chronological way we experience our daily lives, making sense of them likely requires different or additional mental processing. Indeed, prior work suggests that we default to a chronological interpretation of events such that we assume events occur in the order they are presented, and events that are out of order induce slower reading and reaction times as well as decreased memory accessibility (Zwaan 1996; Claus and Kelter 2006; Briner et al. 2012; Xu and Kwok 2019). Notably, there is evidence that the implied time between events influences encoding such that people are slower to process higher magnitude jumps through time (Zwaan 1996).

To partially ease this processing burden, when we communicate events in a non-chronological fashion, we often use explicit temporal cues (e.g., “last week,” “earlier today,” or “several years ago”). These cues provide the necessary information for the listener to infer the relationship between events, such as their causal structure, which is key to understanding narratives

(Zwaan et al. 1995; Zacks and Tversky 2001; Whitney et al. 2009; Song, Park, et al. 2021b). Yet while past behavioral and brain imaging research has demonstrated the importance of temporal cues and context for structuring and organizing events in memory (Speer and Zacks 2005; Clewett and Davachi 2017; Cohn-Sheehy and Ranganath 2017), less is known about how a nonlinear narrative is processed in real time (“encoded,” in memory terms) from a neural perspective. How does the brain represent nonlinear narratives during ongoing experience of the narrative?

Several candidate brain regions may be sensitive to temporal cues in a narrative context. Regions of the medial temporal lobe, such as the hippocampus and parahippocampal cortex, have long been associated with processing time and space (Kragel et al. 2015; Ranganath and Hsieh 2016; Milivojevic et al. 2016). Parietal regions, including the posterior cingulate, precuneus, and angular gyrus, have also been implicated in time orientation and memory for time (Inhoff and Ranganath 2017; Skye et al. 2022). Importantly, these regions overlap with default mode regions associated with processing temporal and other types of context in paradigms using narrative and video stimuli (Whitney et al. 2009; Tylén et al. 2015; Chen et al. 2016; Chen et al. 2017; Kauttonen et al. 2018; Foudil et al. 2020; Reagh and Ranganath 2021).

Here, our aim was to elucidate how the brain uses temporal cues to encode a nonlinear narrative. We hypothesized that temporal cues prompt an “unscrambling” process in which events are reorganized into their chronological order on the fly (i.e., while experiencing the narrative). To effectively test this hypothesis,

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we needed a nonlinear narrative stimulus with explicit temporal cues. To this end, we used a functional magnetic resonance imaging (fMRI) dataset from the Naturalistic Neuroimaging Database (Ali et al. 2020), in which 20 participants were scanned while watching the movie *500 Days of Summer*, which follows two romantically involved individuals through 500 days of their relationship. The movie jumps forward and backward through time between different stages of the relationship, using written time cards (days 1–500) at the start of each scene to signal to viewers where they are in the narrative timeline. Using both univariate and multivariate approaches, we identified a set of brain areas, including parietal regions, that are sensitive to these temporal cues over and above other narrative shifts (i.e., changes in location). We found evidence that regions of the medial parietal lobe represent narrative time chronologically, despite events being presented out of order, and this chronological representation is common across participants. Furthermore, we found evidence that many of these same regions carry a unique spatial signature of activity to higher magnitude jumps through time. Overall, results suggest that the brain uses temporal cues during a nonlinear narrative to actively unscramble events in order to encode them in their chronological order.

Materials and methods

Participants

Our analyses focused on 20 participants (10 females; mean age = 27.7 years, age range = 19–53 years) from the publicly available Naturalistic Neuroimaging Database (<https://openneuro.org/datasets/ds002837/versions/2.0.0>) who watched the movie *500 Days of Summer* (duration ~91 min), which they had not seen previously (Ali et al. 2020). Participants were screened for MRI safety and met inclusion criteria such as right-handedness, English as their first language, no history of psychiatric or neurological illness, no medication, no hearing impairment, and normal or corrected vision. The study was approved by the local institutional review board.

Stimulus and procedure

Participants attended 2 sessions scheduled on separate days: one session devoted to behavioral questionnaires and one session devoted to a movie-watching fMRI scan. We focus here on the fMRI data only. Functional scans during movie-watching were conducted with as few breaks as possible. Following scanning, participants filled out other questionnaires related to the experience they had watching the movie (data not used here).

Participants watched the movie *500 Days of Summer*. We chose to use data from this stimulus for its unique nonlinear narrative structure that makes it useful for studying temporal processing during narrative encoding (Grall and Finn 2022). The movie follows two romantically involved individuals, Tom and Summer, through 500 days of their relationship. The nonlinear structure of the movie means that the scenes are not presented in chronological order and that the movie jumps forward and backward through time between different stages of the relationship. Written time cards with the upcoming day (1–500) of the relationship occur throughout the movie at these time jumps, which signal to viewers where they are in the narrative timeline. Notably, the movie is not completely scrambled: presentation and chronological order are correlated across days (Spearman's $\rho = 0.76$, $p < 0.001$) such that days that occur later in chronological time also tend to be presented later in the movie (Fig. 1A).

The movie also contains several locations that are repeatedly revisited throughout the movie (e.g., the office where both Tom and Summer work, Tom's apartment, a particular park bench, etc.). We leveraged these recurring locations to test how the brain represents spatial context in a narrative as a complement and partial control for our investigations of temporal context.

Data acquisition and preprocessing

Functional and anatomical images were obtained on a 1.5T Siemens MAGNETOM Avanto with a 32-channel head coil. Whole-brain images were acquired (40 slices per volume, 3.2 mm isotropic resolution) with a multiband echo-planar imaging (EPI) sequence (repetition time (TR) = 1 s, echo time (TE) = 54.8 ms, flip angle (FA) = 75°) with 4× multiband factor and no in-plane acceleration. For each participant, 5470 brain volumes were collected, corresponding to a movie runtime of 01:31:10. There was at least one break during the movie for each participant due to the software limitations in this EPI sequence of 1 h of consecutive scanning.

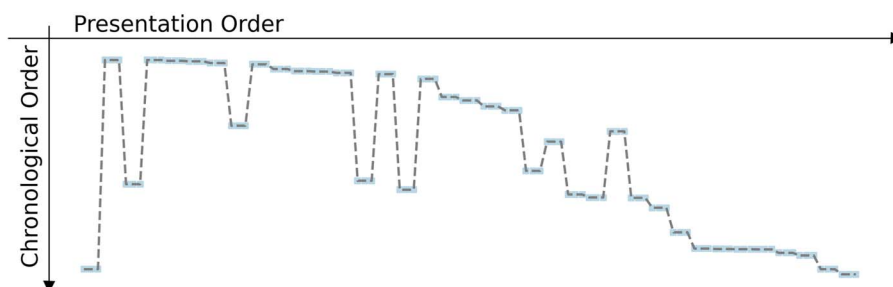
Data were preprocessed using AFNI (Cox 1996) including despiking, slice-time correction, coregistration, and nonlinear alignment to the MNI152 template brain. All analyses were conducted in volume space and projected to surface space for visualization purposes only. Time series were smoothed with isotropic full-width half-maximum of 6 mm and detrended with regressors for motion, white matter, cerebrospinal fluid, and run length. Timing corrections were applied to account for breaks in the moving viewing, and artifacts detected using spatial independent component analysis were regressed out. For more details on data acquisition and preprocessing, please refer to Ali et al. 2020. Last, we functionally aligned these preprocessed data using shared response modeling (Chen et al. 2015) as implemented in BrainIAK (Kumar et al. 2021). First, we fit a model to capture the reliable whole-brain responses to the movie across participants in a lower dimensional feature space (number of features = 50). We then applied this model to reconstruct the individual voxelwise time courses for each participant. The entire movie time series from all participants was used to train the model, which was then applied back to each full individual time series. This procedure serves as an additional denoising step and makes spatiotemporal patterns more consistent across participants.

fMRI data analysis

Estimating the effect of a nonlinear narrative: Univariate analyses

Following preprocessing, we took a general linear model (GLM) approach using AFNI (3dDeconvolve and 3dttest++ functions) to estimate the effect of time jumps and location changes for each subject with subsequent t-tests for inference at the group level (Friston et al. 2002). All first-level models included continuous regressors for luminance and audio root mean square to account for potentially confounding low-level stimulus features, both of which were derived from the movie using the *pliers* toolbox for automatic feature extraction (McNamara et al. 2017). For our primary first-level model, we wanted to identify brain regions active in response to jumps through narrative time. Therefore, we created an event-related regressor that marked all points in the narrative where there is a jump from one day-scene to another on the timeline of 500 days. “Day-scene,” here, refers to any unique instance of a day as presented on the timeline, whereas “day” refers to the point in the timeline. For example, “Day 488” appears twice during the movie and represents 1 day, but each

A. Nonlinear narrative timeline



B. Jump magnitude distribution

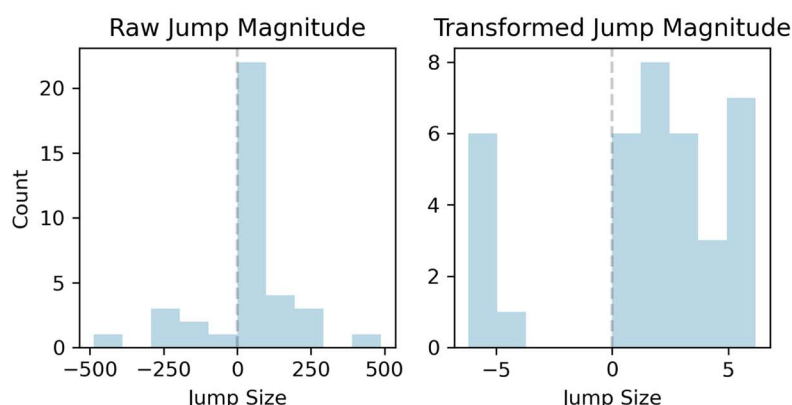


Fig. 1. Nonlinear narrative structure of the stimulus. A) The nonlinear timeline of *500 Days of Summer* depicting all day-scenes and day-scene jumps included in our analyses. This visualization uses the idea of *story curves* to compare and communicate the order in which events are narrated in the movie (presentation order) versus the order in which they actually occurred (chronological order; Kim et al. 2017). B) The distribution of jump magnitudes, visualized in terms of raw magnitude values (number of days between consecutive day-scenes) and log-transformed magnitude values.

instance that day is presented constitutes a distinct day-scene. The movie contains 37 total day-scenes; we used $n=34$ here (2 excluded for insufficient length and one excluded because the first 12 s contained brief, uncued childhood flashbacks, muddling its assignment to a particular place in the timeline). Each jump was modeled as an event lasting 1 s (1 TR) because this duration roughly corresponds to the length of time that the cue card is on the screen.

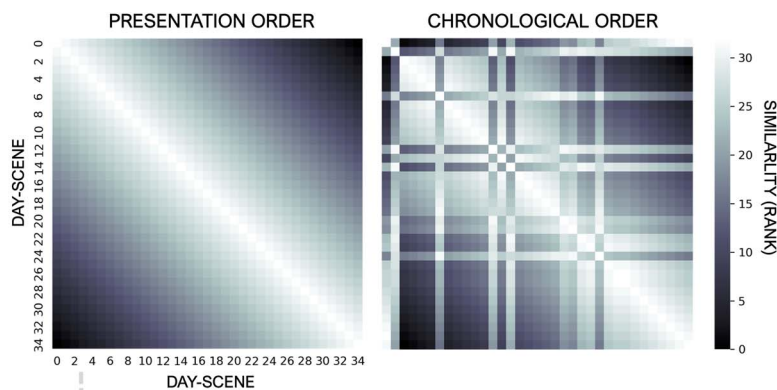
Importantly, time jumps between day-scenes are also associated with visual discontinuities (i.e., screen cuts) and changes in location in the movie. To isolate the effect of time jumps, we created another event-related regressor that marked points in the narrative where there is a change in location that occurs within a day-scene, i.e., location changes that are divorced from cued jumps in the timeline (also modeled as 1 s [1 TR] in duration since these are instantaneous scene cuts). By contrasting day-scene jumps against location changes within day-scene, we can identify regional brain responses that are particularly sensitive to jumps across time over and above changes in location. This contrast also controls for the influence of low-level scene cuts, which are present for both types of jumps. With this first-level model output, we conducted one-sample t -tests to investigate the group-level effect of day-scene jumps against baseline and location changes within day-scene against baseline. We then investigated the contrast between day-scene jumps and location changes within day-scene at the group level using paired t -tests (within-subject). All voxelwise GLM results are shown following correction for multiple comparisons using false discovery rate

(FDR, $q < 0.05$) and thresholded at a nominal cluster size of ≥ 20 voxels for visualization.

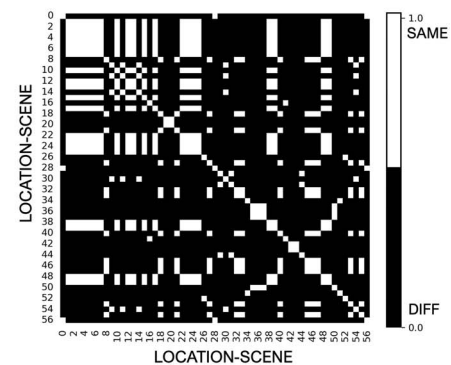
Estimating the effect of a nonlinear narrative: Within-subjects multivariate (pattern similarity) analyses

To examine how relationships across events are encoded during a nonlinear narrative, we used representational similarity analysis (Fig. 2; Kriegeskorte et al. 2008). We constructed two hypothesized models representing possible relationships between day-scenes in the movie according to either (i) the order in which those day-scenes were presented in the movie (presentation order) or (ii) the order in which those day-scenes actually occurred in the timeline (chronological order). For both models, we calculated similarity values based on day-scene ranks rather than raw day numbers to preserve an even distribution of distances between days. With these two input vectors of day-scene ranks (one reflecting the presentation order of day-scenes and the other reflecting the chronological order of day-scenes), we applied a “nearest-neighbors” approach (Finn et al. 2020) by taking the difference between each pair of day-scene ranks and inverting the values for ease of interpretation such that higher similarity scores between day-scenes correspond to pairs where we expect a higher correlation between neural representations. The two resulting temporal model matrices offer the following competing predictions: (i) day-scenes that are presented consecutively (regardless of when they occurred chronologically) are represented more similarly than those that are more distant in presentation order, or (ii) day-scenes

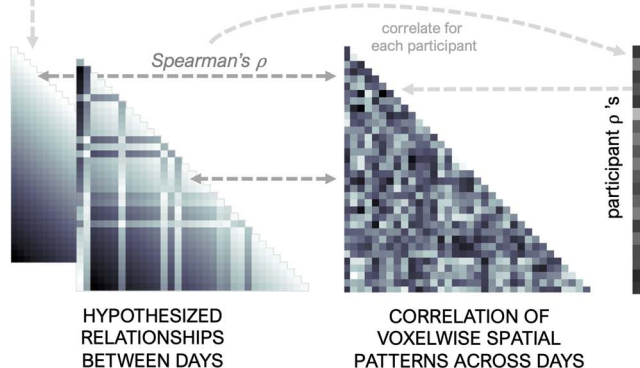
A. Predicted representations of time across day-scenes



B. Predicted representation of locations



C. Representational similarity analysis summary



D. Regions of interest

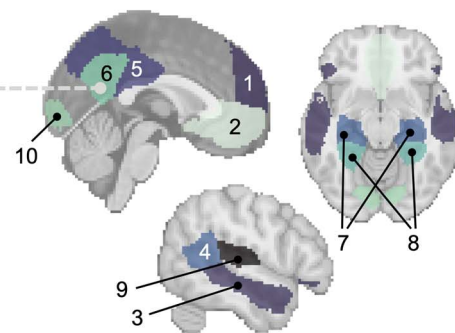


Fig. 2. Overview of within-subject pattern similarity analysis to investigate neural representations of temporal and spatial contexts. A) Models of two competing representations of time across a narrative. For the presentation order model, the day-scenes that are closer together as they are presented in the movie are predicted to be represented more similarly than day-scenes presented more distally. For the chronological order model, day-scenes that are closer together in chronological time are predicted to be represented more similarly than day-scenes that are farther apart in chronological time. B) Predicted representation of locations in the narrative such that each location is similar to itself when revisited throughout the story. C) For each region and day-scene, voxelwise data were averaged over TRs closely following each jump in time and then these spatial patterns were correlated across day-scenes. This matrix was then correlated with each model matrix (A, B; excluding the diagonal) to derive RSA ρ -values for each participant for each ROI. D) Regions of interest from the Neurosynth parcellation including (1) dorsomedial prefrontal cortex (dmPFC), (2) ventromedial prefrontal cortex (vmPFC), (3) superior temporal sulcus (STS), (4) Temporoparietal junction (TPJ), (5) precuneus/posterior cingulate cortex (prec/pCC), (6) posterior portion of the posterior cingulate cortex (post-pCC), (7) hippocampus, (8) parahippocampal cortex (PHC), (9) primary auditory cortex (A1), and (10) primary visual cortex (V1). A1 and V1 were analyzed as control regions in which we would not necessarily expect to see an influence of temporal context on neural representations.

that are closer together chronologically (regardless of when they are presented in the movie) are represented more similarly than those that are more distant in chronological order (Fig. 2A).

We calculated neural pattern similarity within *a priori* selected regions of interest (ROIs) derived from the 50-node Neurosynth parcellation (de la Vega et al. 2016; Fig. 2D). These ROIs represent regions previously associated with processing temporal and/or spatial context and/or integrating narrative information across long timescales and include the dorsomedial prefrontal cortex, ventromedial prefrontal cortex, superior temporal sulcus, temporoparietal junction, posterior cingulate, precuneus, parahippocampal cortex, and hippocampus. We biased our choice of ROIs toward regions associated with the default mode because of this network's known role in processing naturalistic narratives, although we note that other areas of heteromodal association cortex may also play a role in temporal processing (e.g., superior parietal lobe, dorsolateral prefrontal cortex). We also included ROIs in the primary auditory cortex and primary visual cortex as control/comparison regions.

We focused on the data corresponding to the 12 s immediately following each day-scene jump (TRs 3–15, where TR = 1 s;

starting at TR 3 to discard the timecard shown on screen during these jumps). We used this data segment for two reasons: one, because we are interested in brain responses to jumps across time, using data from early in the day-scene better isolates potential unscrambling processes evoked by the jump; and two, taking a matched amount of data from each day-scene removes potential confounding effects of the (often substantial) differences in total duration across day-scenes. (Twelve seconds, or 15 s/TRs following the end of the cue card, corresponds to the length of the shortest day-scene.) For each participant, we averaged voxelwise activity across these TRs for each day-scene to get a vector representing voxel activity values associated with adjusting to that day in the timeline. We then estimated neural pattern similarity matrices by correlating (Pearson's r) voxelwise values between each pair of day-scene vectors. We then correlated (Spearman's ρ) the upper triangle (excluding the diagonal) of each participant's neural similarity matrix with the upper triangle of each model matrix (presentation or chronological order) to derive the ultimate representational similarity correlation value (Fig. 2C). This within-subjects procedure was repeated for each ROI, resulting in 20 representational similarity values (1 per participant) for each model

for each ROI. Each distribution of 20 values was submitted to a one-tailed, one-sample *t*-test to determine whether the representational similarity with that model for that ROI was significantly greater than zero. For all ROI *t*-statistics that emerged as significant within model (FDR, $q < 0.05$; corrected for 10 comparisons across ROIs), we further tested whether there was a significant difference between presentation and chronological order models using paired (within-subject) *t*-tests.

We followed a similar procedure to examine the representation of spatial locations across the narrative. To do this, we identified all locations in the movie that were visited at least twice and on two separate day-scenes and their corresponding TRs ($n = 11$ unique locations). We refer to each unique visit to a location as a location-scene, similar to our day-scene distinction described above. From this list, we created a binarized model matrix which predicts that scenes taking place in the same location are represented more similarly than scenes taking place in different locations (Fig. 2B). Using the same ROIs as above, we calculated neural pattern similarity by taking the voxelwise average of all TRs associated with each location-scene and correlating (Pearson's *r*) these voxelwise values between each location-scene pair. Then, we correlated (Spearman's ρ) the upper triangle of this location-based neural similarity matrix with the upper triangle of the location model matrix for each participant and ROI. The distributions of correlation values for each ROI ($n = 20$; 1 per participant) were submitted to one-sample *t*-tests, and all estimates were FDR corrected for multiple comparisons across 10 ROIs. To compare the relative strength between models to predict representational similarity, we ran a linear mixed-effects model with "model" (i.e., presentation order, chronological order, spatial location) as the fixed factor and participant as a random factor. All post-hoc comparisons were FDR-adjusted.

Estimating the effect of a nonlinear narrative: Across-subjects multivariate (pattern similarity) analyses

To determine whether neural representations of a nonlinear timeline are similar across participants, we conducted an across-subjects analysis that accounts for relationships across days using the following steps (Fig. 3). First, for each ROI, we used the average of TRs 3–15 after each day-scene jump in each participant (the same averaging mentioned above) to build a voxel-by-day-scene-by-participant array. Next, for each participant, we correlated (Spearman's ρ) each day-scene vector with the average of all other participants' day-scene vectors following a leave-one-out procedure. Therefore, for each participant day-scene, there are 34 correlation values representing the similarity between that participant's day-scene representation and the group-average day-scene representation of all day-scenes.

If there is a common signature of either presentation order or chronological order across participants, we would expect that, as the distance between days increases, the correlation between individual and group-average spatial day-scene representations should decrease. (This is the same idea as the within-subject analysis above, but this time in a shared, across-subject context.) To then determine whether there is a stronger shared representation of presentation or chronological order, we correlated day-scene distance values (either presentation or chronological) with the ρ -values representing day-scene similarity between each participant and the average of all other participants. We calculated these for each participant and each day-scene, which resulted in correlation values (34 per participant) that summarize the relationship between across-subject day-scene spatial similarity and temporal

distance. We submitted these summative correlation values to an LME model with participant and day-scene index specified as random factors to determine which distance order (presentation or chronological) is a stronger predictor of cross-subject pattern similarity.

Encoding nonlinear timeline jump magnitude: Univariate and multivariate analyses

Given prior evidence suggesting that jump magnitude plays a role in how we process nonlinear timelines (Zwaan 1996), we conducted an additional univariate analysis to assess whether brain activity varies based on jump magnitude. In the context of our narrative stimulus, jump magnitude refers to the temporal distance between day-scene jumps such that a jump from day 1 to day 290 has a higher magnitude (289) than a jump from day 2 to day 10 (8). We re-ran the previously mentioned first-level model but with day-scene jump as an amplitude-modulated regressor, which allowed us to determine whether brain activity at day-scene jumps scales with jump magnitude. It is important to note that the distribution of jump magnitudes is uneven such that there are few large jumps and many smaller jumps (Fig. 1B, left). Moreover, we do not expect brain activity to scale linearly with jump size such that a jump of 289 days will correspond to a 289 times higher increase in brain activity amplitude compared to a jump of 1 day. Therefore, we log-transformed the distribution of jump values for both this analysis and the following multivariate analysis (Fig. 1B, right). Again, all voxelwise GLM results are shown following correction for multiple comparisons using FDR ($q < 0.05$) and thresholded at a nominal cluster size of ≥ 20 voxels for visualization.

We also tested whether the effect of jump magnitude manifests in multivariate patterns of spatial activity (rather than in activity amplitude as tested by the univariate analysis described above). There are two general possibilities for how multivariate activity patterns could encode jump magnitude. First, there could be a distinct influence of larger time jumps (as compared to smaller time jumps) as participants reorient themselves to a distal portion of the narrative timeline. This possibility could in turn manifest as either (i) a shared spatial signature for large jumps (with more variability among smaller jumps) or (ii) an idiosyncratic signature for each particular large jump (with a shared spatial signature for smaller jumps). Both of these possibilities can be tested simultaneously with a model that incorporates absolute jump magnitude into the calculation of pairwise similarity values. (This class of models has been referred to as "Anna Karenina" models; Fig. 7B, right; Finn et al. 2020). Specifically, for each pair of day-scene jumps, we calculated the average of their jump magnitude ranks. This resulted in a model that predicts that larger day-scene jumps are represented more similarly within an ROI, while smaller day-scene jumps are represented more idiosyncratically. Of note, the same model is equally capable of testing for possibility 1iii in the sense that a strong negative representational similarity value with this model would indicate evidence for a shared signature for processing smaller time jumps (but no such coherent signature for processing larger time jumps).

Second, it could be the case that jumps of similar magnitude, regardless of whether they are large or small, will have a similar multivariate signature (akin to what has been termed the "nearest neighbors" model; Fig. 7B, left; Finn et al. 2020). This possibility can be tested with a model that uses relative jump magnitude to calculate pairwise similarity values. Specifically, to construct this model, we took the difference between the magnitude ranks of each pair of jumps, which predicts that all day-scene jumps that

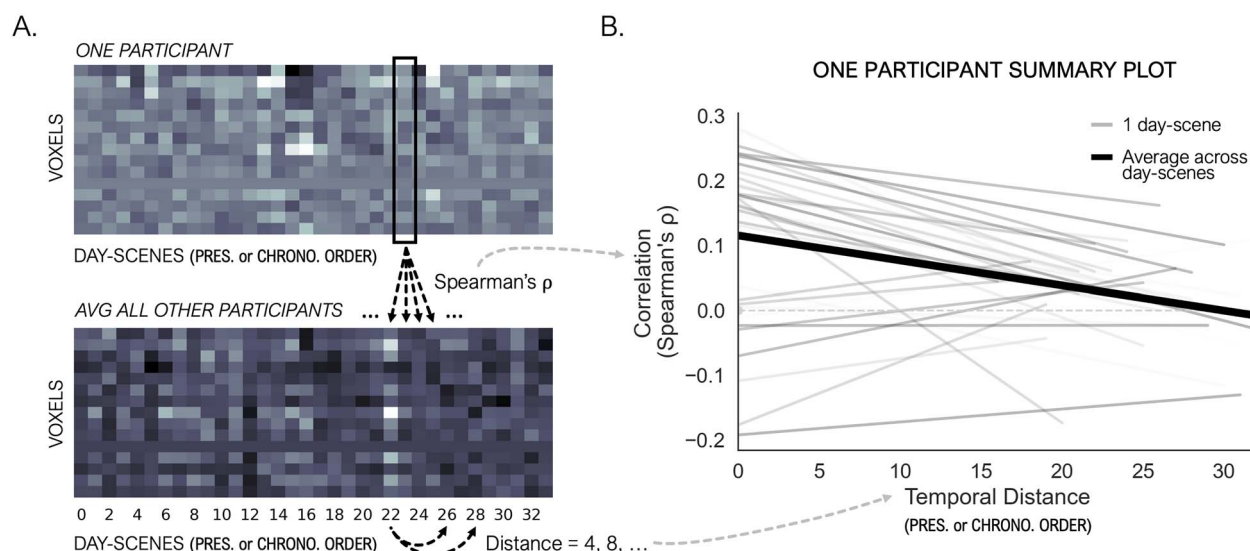


Fig. 3. Overview of across-subjects pattern similarity analysis. A) To determine whether representations of narrative time are common across subjects, we first calculated the voxelwise average of the first 12 s after each day-scene jump for a given ROI to get a voxel-by-day-scene array for each participant. Then, for each participant, we correlated each day-scene pattern from that individual with the average pattern for each day-scene from all other participants following a leave-one-out procedure. Finally, we correlated the resulting similarity values with the difference between day-scene ranks (ranked in either presentation or chronological order) to summarize the relationship between across-participant neural similarity and temporal distance. This results in 34 correlation values per participant (one for each day-scene). B) As temporal distance becomes greater, we would expect similarity values to decrease such that there should be a negative slope for each day. Therefore, comparing the strength of these negative slopes between the presentation- and chronological-order models will suggest which model better captures across-participant similarity of neural representations. Note that not all day-scenes can have the full range of temporal distances, such as those in the middle of the timeline, and therefore there are fewer values at higher temporal distances.

are similar in their magnitude will be represented similarly within ROIs.

With these magnitude models, we then applied the same within-participant RSA procedure described above (*Estimating the effect of a nonlinear narrative: Within-subjects multivariate (pattern similarity) analyses* section) to assess the evidence for each model.

Results

Our goal was to elucidate how the brain encodes a nonlinear narrative. Specifically, we sought to uncover brain regions that are sensitive to temporal cues in a nonlinear narrative and test whether neural representations of event relationships are more influenced by the presentation order or chronological order of events.

Jumps across time and space evoke widespread neural activity

To effectively represent time during any narrative, but especially a nonlinear one, the brain must first recognize when a change in temporal context has occurred. In our first set of analyses, we investigated which brain regions are sensitive to jumps in time and/or space by modeling both cued cuts to a new day-scene (time) and changes in location that happened within a day-scene (space). We then ran separate univariate contrasts against baseline for time jumps and location changes. Several regions showed increased activity to time jumps (Fig. 4A), including the posterior cingulate (pCC), bilateral intraparietal sulcus (IPS), precuneus, retrosplenial, and parahippocampal cortices. Two regions along the superior parietal and lateral occipitotemporal gyri showed decreased activity to time jumps. A similar set of regions showed heightened activity to changes in location, including the parahippocampal cortex (PHC), lateral superior occipital gyrus,

and precuneus (Fig. 4B). These results align with previous research finding a consistent role for medial parietal and medial temporal lobe structures in processing time and space (Whitney et al. 2009; Cohn-Sheehy and Ranganath 2017; Skye et al. 2022).

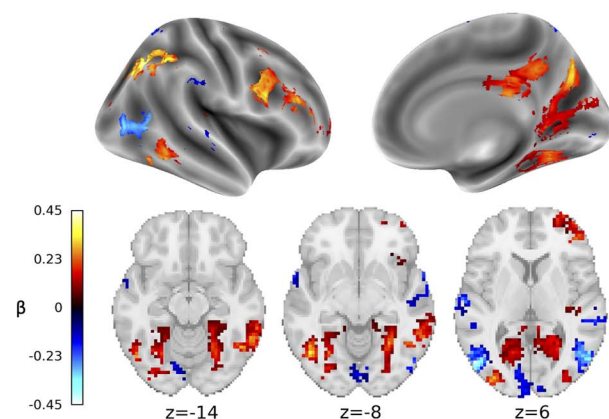
Neural activity specific to jumps across time

Having established that jumps across both time and space in a narrative are associated with heightened activity in certain cortical regions, we next investigated whether some regions show a stronger response to one type of jump (Fig. 4C). From this contrast (time jumps > space jumps), several regions emerged as more sensitive to jumps through narrative time over and above changes in location. These included the pCC, bilateral IPS, bilateral inferior temporal gyrus (ITG), and right dorsolateral prefrontal cortex (dlPFC). Several regions showed the opposite pattern, that is, greater activity to location changes over time jumps, including the retrosplenial and parahippocampal cortex as well as the lateral occipitotemporal gyrus. This is consistent with previous evidence showing the parahippocampal cortex's sensitivity to spatial information (Aminoff et al. 2013).

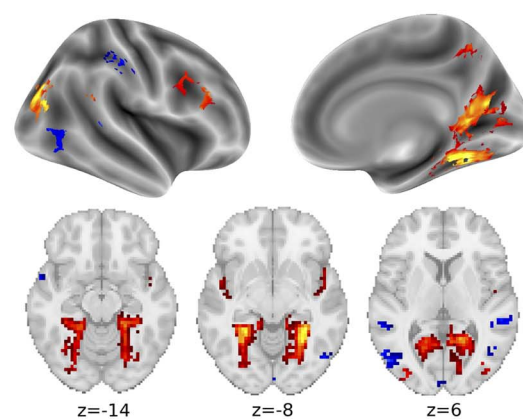
Within-subject evidence for neural unscrambling of events

Following a change in temporal context, the brain must then begin to encode the next segment of the narrative by creating a new event representation. To effectively make sense of the story, this representation likely contains information about the new event's position relative to other events. In our next set of analyses, we asked whether, in a nonlinear narrative, event representations track events' position in the narrated story order or whether the brain engages in active unscrambling of events to encode them in their underlying chronological position (Fig. 5A). Using spatial activity patterns in select ROIs during the first 12 s of

A. Day Jumps > 0



B. Location Changes Within Day > 0



C. Day Jumps > Location Changes Within Day

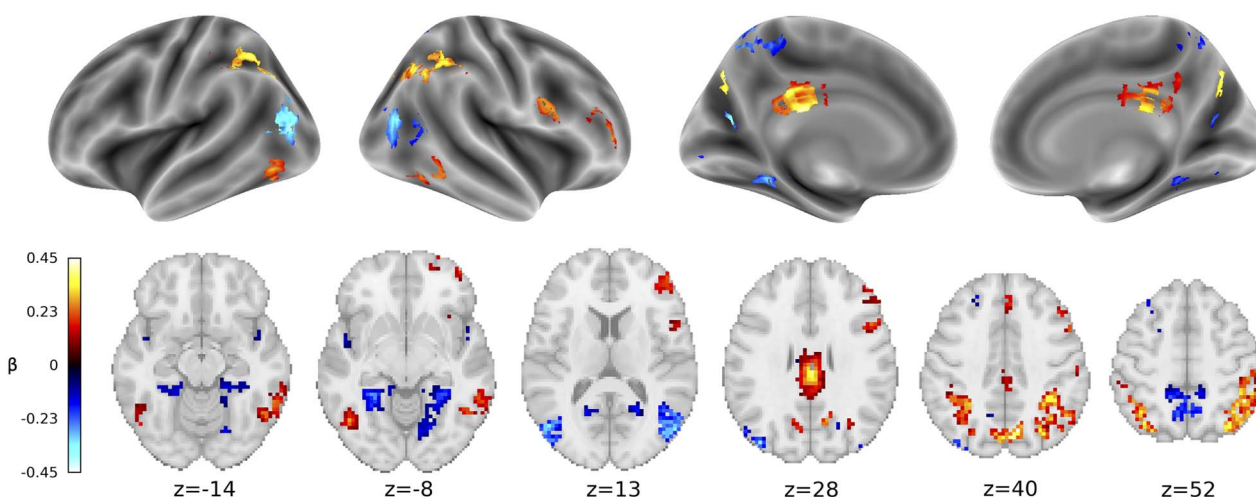


Fig. 4. Brain activity evoked by jumps in time and space. A) Brain activity to cued time jumps. B) Brain activity to jumps in space (i.e. changes in location within the same day). C) Contrast between time jumps and location changes within the same day-scene (warm colors indicate higher activity for time jumps; cool colors indicate higher activity for location changes). All results shown at an FDR-corrected threshold of $q < 0.05$ with a nominal cluster threshold ≥ 20 voxels for visualization. Surface plots and axial slices depict identical maps; the latter are included for better visualization of deep cortical regions (e.g., parahippocampal cortex).

each new day-scene (immediately following the time card that cued viewers to the new position in the 500-day narrative timeline), we assessed similarity between neural representations of day-scenes and two distinct models of temporal context (Fig. 2A): one predicting higher similarity between events presented closer together in movie time (presentation order), and one predicting higher similarity between events that took place closer together in story time (chronological order).

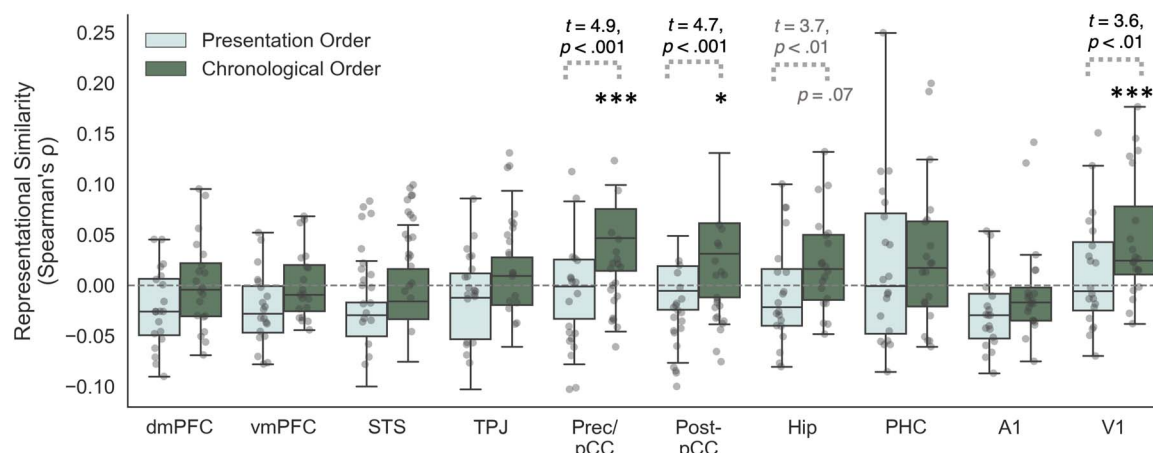
No ROIs showed significant representational similarity with the presentation order model (one-tailed t -tests, t 's = $-4.3 - 1.1$, p 's > 0.8 ; all p -values reflect correction for multiple comparisons across 10 ROIs within each model, FDR $q < 0.05$). In other words, no evidence suggests that these ROIs follow a presentation order of narrative time such that day-scenes that are presented closer together are represented more similarly. On the other hand, several ROIs showed significant representational similarity with the chronological order model, including the precuneus/pCC ($t = 4.64$, $p = 0.0009$), the posterior pCC ($t = 2.92$, $p = 0.01$), and V1 ($t = 3.28$, $p = 0.009$). The hippocampus also showed marginal representational similarity with the chronological order model ($t = 2.03$, $p = 0.07$).

Moreover, direct comparisons within these four ROIs showed that representational for the chronological model similarity is stronger than for the presentation model (paired [within-subject] t -tests, precuneus/pCC, $t = 4.97$, $p < 0.001$; pCC, $t = 4.70$, $p < 0.001$; V1, $t = 3.66$, $p = 0.002$; hippocampus, $t = 3.64$, $p = 0.002$). This provides evidence for a temporal unscrambling effect such that, in visual regions but also in higher-order association regions such as those in the medial parietal cortex, the brain reorganizes information in line with a chronological sequence of events at encoding.

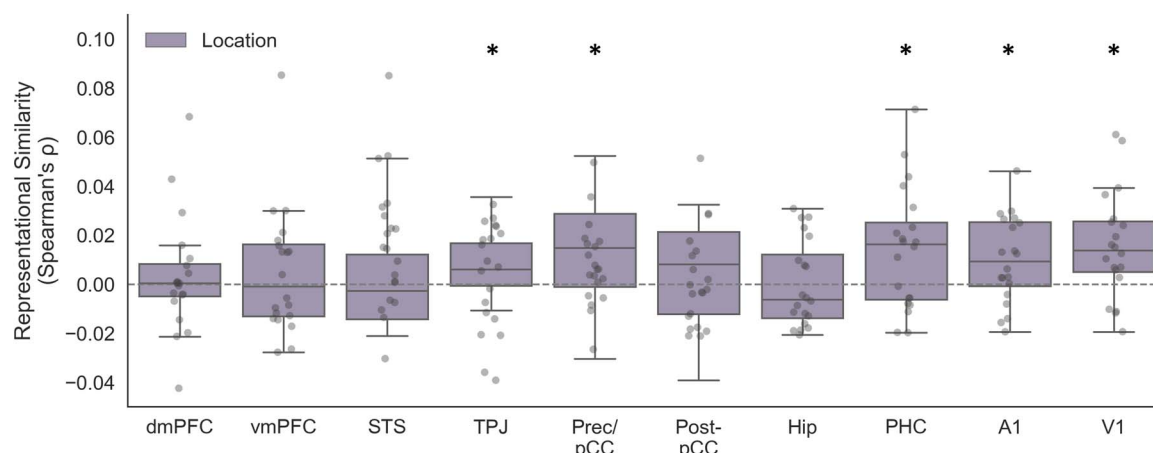
Spatial context is represented in medial parietal and temporal regions

Using the spatial context model (Fig. 2B), which predicts that scenes taking place in the same location are represented more similarly than those taking place in different locations, we identified another set of ROIs that represent location (Fig. 5B): precuneus/pCC ($t = 2.71$, $p = 0.02$), TPJ ($t = 2.17$, $p = 0.04$), PHC ($t = 2.55$, $p = 0.02$), A1 ($t = 2.52$, $p = 0.03$), and V1 ($t = 3.23$, $p = 0.02$). This aligns with previous findings on the sensitivity of the PHC to spatial context information (Reagh and Ranganath 2021).

A. Temporal model similarity across regions



B. Spatial model similarity across regions



C. Across model comparisons within regions

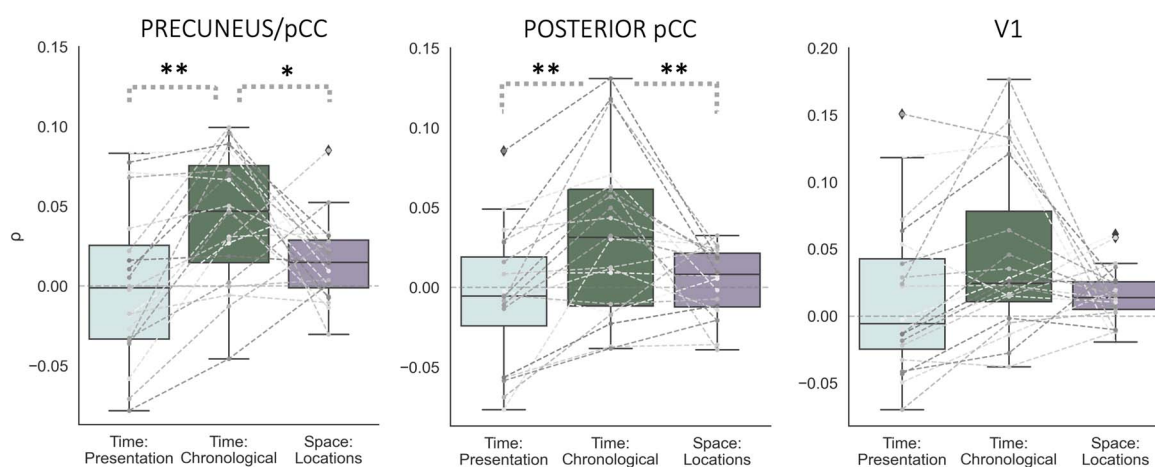


Fig. 5. Narrative events are represented chronologically over and above when those events were presented in a nonlinear narrative. A) Representational similarity (Spearman correlations) between the two different temporal models and voxelwise spatial patterns across days. The chronological model (cf. Fig. 2A) showed significant representational similarity in precuneus/pCC, posterior portion of the pCC, and V1 (FDR $q < 0.05$, corrected for multiple tests within the model), and paired (within-subject) t -tests showed that these regions represent chronological order more strongly than presentation order. B) The spatial model, which tests the degree to which revisited locations are represented similarly across visits (cf. Fig. 2B), showed significant representational similarity in the precuneus/pCC, A1, and V1 (FDR $q < 0.05$). C) Post hoc comparisons (FDR-corrected) after linear mixed-effects modeling across the 3 models within these significant regions showed that representations of the chronological model were stronger than both other models in the medial parietal regions, but there were no differences across models for V1. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Medial parietal cortex shows specificity for chronological representation of events

Follow-up linear mixed-effects models confirmed that, in the precuneus/pCC ($F_{2,38} = 7.31, p = 0.002$), representational similarity for the chronological model ($b = 0.043, SE = 0.01$) was significantly higher than for the presentation ($b = 0.001, SE = 0.01; t = 3.78, p = 0.002$) or location models ($b = 0.016, SE = 0.01; t = 2.39, p = 0.03$). There was no difference between the presentation and location models. This was also the case for the posterior pCC ($F_{2,38} = 8.62, p < 0.001$), where the chronological model ($b = 0.033, SE = 0.01$) was a stronger fit than the presentation ($b = -0.006, SE = 0.01; t = 3.98, p = 0.001$) and location ($b = 0.004, SE = 0.01; t = 3.01, p = 0.007$) models, with no difference between presentation and location models. In V1 ($F_{2,38} = 3.54, p = 0.04$), however, no significant differences were found between the chronological ($b = 0.045, SE = 0.01$), presentation ($b = 0.013, SE = 0.01$), and location ($b = 0.016, SE = 0.01$) models. All post hoc comparisons were FDR-adjusted. This demonstrates that of the models we tested, event representations during encoding in medial parietal regions (but not primary visual cortex) are relatively specific to chronological context over and above presentation or location context.

Across-subject evidence for neural unscrambling of events

To determine whether this chronological representation of events—i.e. the voxelwise patterns associated with nearby day-scenes—was common across participants, we correlated each participant's day-scene pattern with the average of all other participants' day-scene patterns in a leave-one-out procedure. As the temporal distance (either in presentation order or chronological order) increases, we would expect the individual-to-group correlations between day-scene representations to decrease. Indeed, within the precuneus/pCC ROI, all participants tend to show negative slopes for most days as temporal distance increases, and this relationship is more apparent for a chronological order of events compared to a presentation order of events (Fig. 6).

To test this relationship, we summarized data within day-scene for each participant by correlating the individual-to-group day-scene similarity values with both chronological distances and presentation distances, resulting in one correlation coefficient per day-scene per participant. Linear mixed effects modeling ($F_{1,1306} = 16.96, p < 0.001$) revealed the chronological order of distances ($b = -0.11, SE = 0.02$) to be a stronger fit than presentation order ($b = -0.06, SE = 0.02; t = -4.12, p < 0.001$) in the precuneus/pCC. This was not the case for the posterior pCC ROI ($F_{1,1306} = 2.94, p = 0.09$) for which the chronological order of distances ($b = -0.05, SE = 0.02$) was stronger than the presentation order ($b = -0.04, SE = 0.02$), but not significantly so ($t = -1.72, p = 0.09$). Notably, because we expected correlations associated with temporal distances of zero (i.e. the same day-scene) to be high, which could potentially bias results, we verified that the pattern of results does not change when excluding data points from distance zero (e.g. precuneus/pCC, $t = -4.19, p < 0.001$). Overall, these results show that, in addition to the within-subject spatial signature of chronological event order reported above, there is also evidence for an across-subject spatial signature such that participants' neural representations of days close by in chronological time are consistent with one another.

A unique multivariate signature encodes time jumps with large magnitude

If encoding temporal context during a nonlinear narrative carries a different and/or additional processing cost, it stands to reason

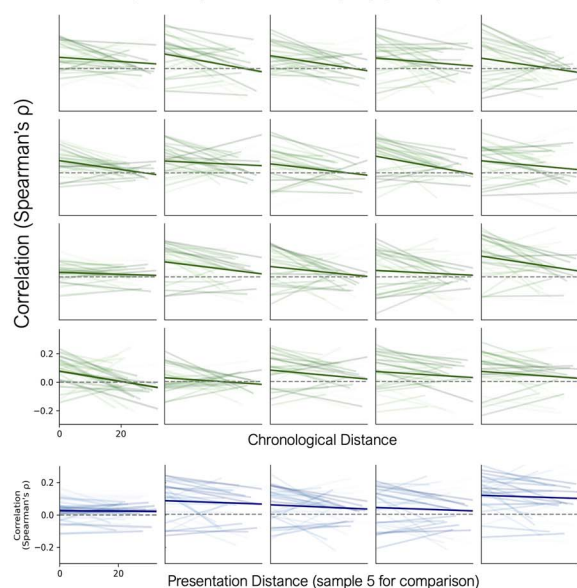
that neural activity might scale with or otherwise reflect the magnitude of each temporal shift.¹ In our final set of analyses, we sought to determine whether brain activity varied according to jump magnitude (i.e. the size of the jump through time). Notably, there is an uneven distribution of jump magnitudes with more small jumps (<100 days) than large jumps (>300 days; Fig. 1B, left). Because we do not expect brain activity to scale linearly with the size of the jump, we log transformed the jump magnitude values before using them in further analyses (Fig. 1B, right).

We first tested the possibility that jump magnitude is reflected in univariate activity: in other words, larger jumps evoke stronger neural responses (Fig. 7A). There was some evidence for increased activity to larger jumps near the auditory cortex and decreased activity in the visual cortex. A possible explanation for the effect in the auditory cortex is that there was a non-diegetic page-flipping sound cue that played at almost every time jump and lasted longer for larger jumps in time. Together, results suggest some effect of time jump magnitude on neural activity, although the limited amount of data and lack of systematic variation in this feature make it difficult to draw firm conclusions from this analysis.

While our univariate analyses did not reveal strong effects of jump magnitude in regions hypothesized to represent time, it is possible that the effect of jump magnitude is encoded in multivariate spatial patterns rather than univariate activity. To test this possibility, we conducted a representational similarity analysis using two possible model matrices (Fig. 7B). The relative or "nearest-neighbor" model (according to the framework laid out in Finn et al. 2020) predicts that any pair of day-scenes with similar jump magnitudes, no matter if the magnitude is large or small, should be represented more similarly than day-scenes with different jump magnitudes. In contrast, the absolute or "Anna Karenina" (AnnaK; Finn et al. 2020) model predicts that jump magnitudes at one end of the spectrum—i.e., either larger or smaller—will be represented more similarly than jump magnitudes at the other end of the spectrum, where there is more variance in representations. (In this formulation, a positive correlation with the model matrix would indicate higher representational similarity for larger > smaller jumps, while a negative correlation would indicate higher representational similarity for smaller > larger jumps.)

Following the same procedure as the temporal model representational similarity analysis described above, we found that the nearest-neighbor model did not capture patterns of jump-magnitude representation in any ROI (Fig. 7C). However, the AnnaK model revealed a unique signature for larger jumps in almost all ROIs including the dorsomedial prefrontal cortex ($t = 2.76, p = 0.008$), ventromedial prefrontal cortex ($t = 2.60, p = 0.01$), precuneus/pCC ($t = 4.73, p < 0.001$), posterior pCC ($t = 4.04, p < 0.001$), temporoparietal junction ($t = 5.64, p < 0.001$), superior temporal sulcus ($t = 3.99, p < 0.001$), hippocampus ($t = 4.51, p < 0.001$), PHC ($t = 5.79, p < 0.001$), and A1 ($t = 2.95, p = 0.006$). Moreover, the AnnaK model provided a stronger fit to the data than the nearest-neighbor model (paired [within-subject] t-test, $t's = 2.27-9.94, p's < 0.03$). This suggests that there is a unique signature for higher magnitude jumps across day-scenes that is spatially encoded within these regions. It is worth noting that the AnnaK magnitude model similarity estimates (precuneus/pCC: $b = 0.06, SE = 0.01$; posterior pCC: $b = 0.06, SE = 0.01$) are not significantly different from the chronological model estimates (cf. Fig. 5A; precuneus/pCC: $b = 0.04, SE = 0.01$; posterior pCC: $b = 0.03, SE = 0.01$) in the medial parietal ROIs (precuneus/pCC: $t = 1.55, p = 0.18$; posterior pCC: $t = 1.69, p = 0.13$) when all models are assessed with a mixed-effects model with model type

A. Across-subjects day-scene similarity, by participant



B. Summarizing across-subjects similarity at each temporal distance

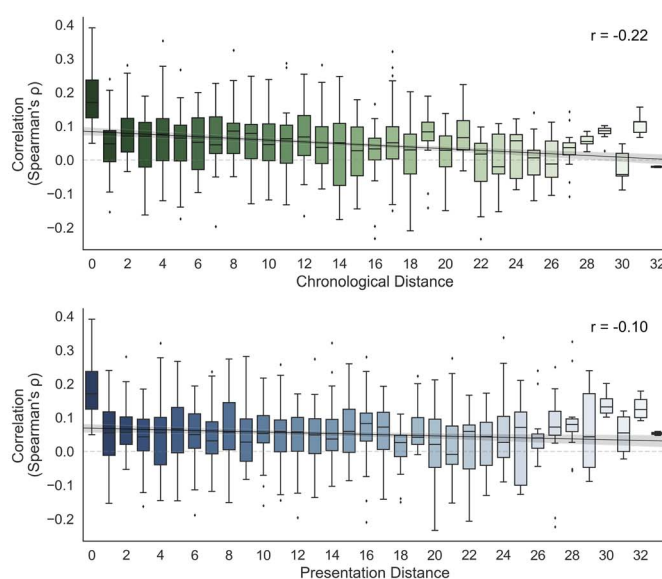


Fig. 6. Chronological representation of narrative events is consistent across participants in the precuneus/pCC. A) Across-subjects day-scene pattern similarity with a summary plot for each participant (individual green panels), in which each line represents the similarity of a single day-scene with the average of all other participant day-scenes as they increase in chronological distance. The dark line represents the average across day-scenes at each distance (x-axis value). Each participant, on average, tends to show a negative slope as chronological distance increases. This negative slope is more apparent for chronological distance than for presentation distance (5 participants shown for comparison; blue panels, bottom row), which suggests a common representation of a chronological order of events compared to presentation order. B) Summarizing across-subjects similarity values at each temporal distance for both chronological and presentation orders. Linear mixed-effects models showed that chronological distance was a better predictor of across-subject day-scene representational similarity than presentation distance ($p < 0.001$). Note that the regression line and correlation value annotated on these plots are meant for characterizing the general negative slope across temporal distances and were not used in any statistical analysis.

(chronological, presentation, spatial location, nearest-neighbor magnitude, and AnnaK magnitude) as a fixed factor and participants as a random factor (precuneus/pCC: $F_{4,76} = 8.43$, $p < 0.001$; posterior pCC: $F_{4,76} = 7.91$, $p < 0.001$). Altogether, results suggest that while processing a nonlinear narrative, medial parietal regions represent both where one is in chronological time as well as how far one jumped to get there.

Testing for confounding influence of film characteristics at day jumps

In a *post hoc* analysis, we investigated whether there was a common set of film characteristics, or semantic features, present at the beginning of each day-scene (i.e., immediately following each day jump) that could explain the chronological model results. The logic is as follows: if day-scenes nearby in chronological time are more likely to share certain semantic features—e.g., to take place in similar locations or to focus on a specific character—then increased representational similarity between day-scenes might be due to these shared features rather than to their position in the narrative timeline *per se*.

To investigate this possibility, for the first 12 seconds following each day jump (the same data that entered into all RSAs described above), we created dummy variables from annotated features such as the location after the jump, the number of faces on screen, and the characters (if named) on screen (e.g., for the “office” location variable, there is a 1 when the movie jumps to the “office,” and a 0 when jumping elsewhere). We correlated (Pearson’s r) these features with the chronological and presentation order of events and calculated the 95% confidence intervals for both correlation values to ensure that the correlation values overlap, which would indicate that they are not significantly different from each other and therefore should not exert a robust confounding influence on our pattern of results. No significant differences

were found across features of interest including, for example, the representation of the office location between the presentation ($r = -0.43$, 95% CI $[-0.66, -0.12]$) and chronological ($r = -0.54$, 95% CI $[-0.74, -0.26]$) orders or the presence of the male main character’s face between the presentation ($r = 0.17$, 95% CI $[-0.16, 0.47]$) and chronological orders ($r = -0.002$, 95% CI $[-0.33, 0.32]$). Therefore, similar semantic features likely cannot explain the advantage of the chronological order model over the presentation order model.

Discussion

Here, leveraging a unique movie stimulus with a cued nonlinear narrative structure, we investigated how the brain encodes both time and space with a particular focus on representations of temporal context. Regions in the medial parietal lobe were particularly responsive to jumps in the narrative timeline. Notably, patterns of activity in these same medial parietal regions also tracked a chronological sequence of events, which suggests that these regions engage in an “on the fly” temporal unscrambling of events when they are presented out of order. These same regions also show a special spatial signature for larger jumps within the nonlinear narrative timeline.

Much previous research on processing time focuses on memory for time and how temporal context influences recall and memory for events, but here we focus on temporal processing at the encoding stage. Results revealed several regions that are sensitive to jumps through narrative time over and above their sensitivity to changes in location, including the pCC, precuneus, IPS, ITG, and right dlPFC. This adds to a growing body of work associating medial parietal regions, and particularly the precuneus, with temporal processing (Peer et al. 2015; Cohn-Sheehy and Ranganath 2017; Skye et al. 2022). Using lesion-symptom

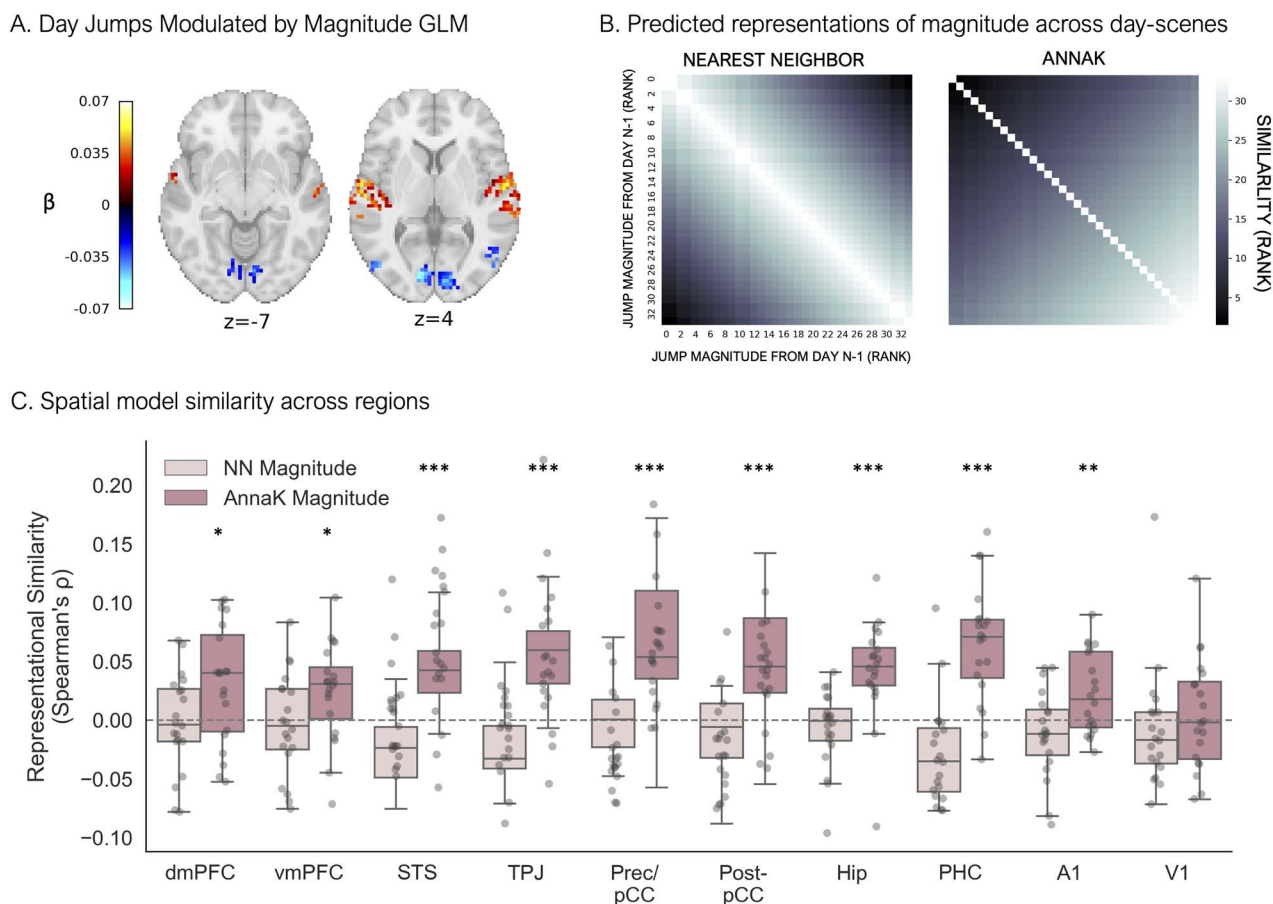


Fig. 7. Time jump magnitude is encoded in multivariate spatial patterns. A) Brain activity associated with day-scene jumps as modulated by jump magnitude (warm [cool] colors indicate increased activity for larger [smaller] jumps; FDR-corrected threshold $q < 0.05$, nominal cluster threshold ≥ 20 voxels for visualization). B) Models of 2 competing representations of time jump magnitude across a narrative. For the nearest-neighbor model, all day-scene jumps of a similar size will be represented more similarly compared to day-scene jumps of more distal sizes. For the AnnaK model, day-scenes associated with larger (smaller) magnitude jumps will be represented most similarly, and similarity will decrease as jump magnitudes become smaller (larger). Day-scenes are sorted by the (ranked) magnitude of the jump from the preceding day-scene for visualization. C) Representational similarity (Spearman correlations) between the magnitude models and voxelwise spatial patterns across day-scenes. The AnnaK model in the direction of a shared signature for larger jumps showed significant representational similarity across all ROIs except V1 (2-sided, one sample t-test; FDR $q < 0.05$, corrected for multiple tests within model), and paired t-tests showed these regions represent the AnnaK model relationships more than the nearest-neighbor model relationships. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

mapping, Skye et al. (2022) pinpointed the precuneus as well as parahippocampal cortex (PHC) as crucially involved in time orientation. Here, we see increased PHC activity in response to both time jumps and location changes. On the order of seconds or minutes, all changes in location are associated with changes in time. In our analyses, we attempted to dissociate changes in time and location on the order of days. Differential sensitivity to changes in location within a day compared to changes in location that are concurrent with day jumps suggests that spatial context is a higher priority cue for PHC activity, while temporal context is a higher priority cue for medial parietal cortex.

To elaborate on the role of the medial parietal cortex in processing time, our results suggest that when encoding a narrative that is presented in a non-chronological fashion, the precuneus and pCC actively unscramble events to represent information chronologically. Specifically, days that were closer together in chronological time were represented more similarly regardless of when they were presented in the movie, and these representations were consistent across participants. This finding fits with previous theorizing on the role of default-mode regions as the nexus for complex sense-making over long timescales through the

integration of novel external and prior internal information (Simony et al. 2016; Yeshurun et al. 2021), and it aligns with the idea that medial parietal regions act as a hub for maintaining and updating mental situation models (Speer et al. 2007; Whitney et al. 2009). We posit that this temporal unscrambling function may support our ability to embed the causal structure of events in a mental model. In other words, as a story unfolds, narrative events are discretized and stored such that, when an event is presented out of order, that event can be slotted into its correct chronological position, which corresponds to a causal order of events that must flow forward in time. Causal structure is a central feature of narratives (Briner et al. 2012; Bordwell et al. 2020), and there is evidence that people use causal networks of events to encode and retrieve complex experiences (Lee and Chen 2022), which can explain how causal connections improve narrative memory (Brownstein and Read 2007; Radvansky et al. 2014). This line of reasoning can also explain why we are sensitive to temporal cues (e.g., “immediately,” “the next day”) when comprehending purely textual narratives (Zwaan 1996; Speer and Zacks 2005), which, akin to the robust precuneus and pCC activity in response to day jumps shown here, provide the necessary information to

organize events in time and infer causal order. Of note, because our stimulus did contain explicit temporal cues in the form of day cards, it remains unclear whether the same on-the-fly unscrambling process would occur in situations absent such explicit cues where the viewer needs to use more subtle clues to guess when the present scene might have occurred in the overall timeline.

In the context of any narrative, but especially a cued nonlinear narrative such as the one used here, time jumps represent event boundaries, and a larger jump in time corresponds to a larger shift in narrative context (Speer et al. 2007; Pu et al. 2022). For example, when the movie presents Day 290 at the beginning of the film, the viewer must efficiently situate the scene as a “relationship breakup event,” which operates under distinct emotional and social conditions compared to “beginning relationship events.” The strength of these “relationship-phase schemas” may explain why days closer together in chronological time are represented more similarly. Indeed, in a recent study on temporal processing using tightly controlled conditions, Bellmund et al. 2022 found that event representations in the hippocampus were biased toward prior, constructed knowledge of event sequences over and above event presentation order and elapsed time. In the present study, prior knowledge of the structure of relationships could have facilitated the encoding of nonlinear events into their chronological sequence. Moreover, this may help explain the distinct spatial signature for higher magnitude jumps that we observed. The brain might treat higher-magnitude jumps specially compared to lower magnitude jumps because they evoke increased surprisal (Brandman et al. 2021) and perhaps, therefore, increased processing demands and/or engagement (Song et al. 2021a). Increased cognitive demands could explain slower behavioral processing times for distal events (Zwaan 1996; Claus and Kelter 2006) but increased ability to discriminate between distal events (Brown et al. 2009; Pu et al. 2022) due to their distinct narrative contexts.

One alternative explanation for our temporal unscrambling effect is that days that are close together in chronological time, whether early in the relationship timeline or toward the end, may have shared low-, mid-, and/or high-level characteristics that drive similarity between their neural representations. While we controlled for two low-level audiovisual features (namely, luminance and audio envelope) by regressing these from each subject's functional time-series before further analysis, there could be other features that are consistent across neighboring locations in the timeline. (Of note, any consistent visual information could help explain the significant V1 representational similarity values with the chronological model; cf. Fig. 5A). For example, at the beginning of the relationship timeline, there may be an overrepresentation of jumps to one particular location or the same character's face on screen. To account for this, for each day jump, we annotated features including the location, the number of faces, the characters (if named), and the shot scale for the faces (i.e., the extent to which a character's face fills the screen). We found no significant differences in these features between presentation and chronological event sequences, suggesting that these low- and mid-level features cannot explain the apparent unscrambling effect. Another potentially important, high-level characteristic is emotional valence: if valence covaried with chronological time, this could have confounded our analyses. However, we consider this unlikely because the emotional arc of the chronological narrative was not monotonic but rather roughly U-shaped (positive at the beginning of the relationship, negative surrounding the breakup, and positive again as the main character moves on and begins a new relationship; Chu and Roy 2017). Still, these alternate

explanations cannot be robustly ruled out given our single and limited stimulus, which speaks to the need to corroborate our results with additional nonlinear narrative stimuli.

In conclusion, we uncovered a set of brain regions associated with processing jumps across time in a nonlinear narrative. We found evidence that regions of the medial parietal cortex actively unscramble narrative events to encode them in a chronological fashion. These findings held in both within-subjects as well as across-subjects analyses, suggesting that temporal representations are to some extent shared across brains. We also found that higher magnitude jumps through time evoke a unique response pattern in these and other brain regions. Altogether, results emphasize the role of the medial parietal lobe as a hub for encoding temporal cues and context in narrative settings.

Notes

¹It might also stand to reason that jump direction, or whether the jump traveled forward or backward in time, might be reflected in brain activity, i.e. backward jumps might increase processing load because they are in the non-canonical direction. Unfortunately, this stimulus was not well suited to investigating this possibility because there were relatively few backward jumps ($n=7$) and most of them were of large magnitude (cf. Fig. 1B), making it difficult to disentangle the effects of magnitude and direction. Therefore, we leave an investigation of this possibility for future work using a stimulus with more systematic variation in the direction and magnitude of jumps.

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CRedit for author contributions

Clare Grall (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing), Josefa Equita (Data curation, Investigation), and Emily Finn (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing—original draft, Writing—review & editing).

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Conflict of interest statement: The authors declare no competing interests.

Data and code availability statement

The paper uses data obtained from the Naturalistic Neuroimaging Database (<https://10.18112/openneuro.ds002837.v2.0.0>; Aliko et al. 2020). Analysis scripts are available at <https://osf.io/qnwhu>.

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