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What Constitutes an Episode in Episodic Memory?

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Abstract

The idea of episodic memory implies the existence of a process that segments experience into episodes so that they can be stored in memory. It is therefore surprising that the link between event segmentation and the organization of experiences into episodes in memory has not been addressed. We found that after participants read narratives containing temporal event boundaries at varying locations in the narrative, their long-term associative memory for information across event boundaries was lower than their memory for information within an event. This suggests that event segmentation during encoding resulted in segmentation of those same events in memory. Further, functional imaging data revealed that, across participants, brain activity consistent with the ongoing integration of information within events correlated with this pattern of mnemonic segmentation. These data are the first to address the mechanisms that support the organization of experiences into episodes in long-term memory.

Keywords

episodic memory, long-term memory, associative processes, cognitive neuroscience, neuroimaging

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Episodic memory allows people to remember life's defining experiences, such as a college graduation or wedding, as well as less significant events, such as a summertime concert in the park. Perhaps this is the reason that more than a century of psychological work and decades of neuroscientific work have focused on revealing episodic memory's underlying mechanisms. However, there is still an important question about memory that has received relatively little attention: What makes up an episode in episodic memory? In other words, how does dynamic, ongoing experience get transformed into meaningful units in long-term memory (LTM)?

Although this question has not been addressed directly, insight may come from theories of event perception and segmentation. Event-segmentation theory (EST) proposes that continuous actions are parsed, or segmented, into events (Reynolds, Zacks, & Braver, 2007; Zacks, Speer, Swallow, Braver, & Reynolds, 2007). EST also suggests that the perception and understanding of everyday experiences is mediated by a system that uses mental models to make predictions about how those experiences should unfold. *Event models* are proposed to be active representations that incorporate the perceptual details of the current experience with semantic knowledge of similar past experiences, as long as the current experience is congruent with the active mental model (Zacks et al., 2007). When perceptual details become incongruent with the active model (e.g., when one activity is finished and another is begun), EST proposes that the event model is updated to accommodate these changes. The points at which these updates are proposed to occur are called *event boundaries* (Zacks, Tversky, & Iyer, 2001).

Perhaps because mental models are also prominent in theories of narrative comprehension (van Dijk & Kintsch, 1983), much of the evidence supporting EST has come from the narrative domain. Researchers have shown that spatial and temporal shifts in narratives tend to be identified as event boundaries (Speer & Zacks, 2005; Speer, Zacks, & Reynolds, 2007; Zacks, Speer, & Reynolds, 2009). Furthermore, consistent with the EST hypothesis that working memory maintains recently encountered information in event models until it is updated at event boundaries, research has shown that information in a narrative becomes less accessible immediately following spatial or temporal event boundaries in a way that is not simply related to the passage of time since the information was encountered (Morrow, Bower, & Greenspan, 1989; Rinck & Bower, 2000; Speer & Zacks, 2005; Zwaan, 1996).

However, the manner in which event perception and segmentation influence the long-term mnemonic representation

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and organization of events remains largely unexplored. Prior studies measured accessibility of active representations after only brief delays and therefore did not examine LTM representations (Morrow et al., 1989; Swallow, Zacks, & Abrams, 2009). Other researchers have asked how explicit segmentation modulates the overall probability of remembering (Hanson & Hirst, 1989; but see Lassiter, Stone, & Rogers, 1988). In contrast to these previous studies, the work we report in this article examined whether event segmentation influences the structure of LTM beyond item recognition or recall.

The broad goal of our two studies was to determine how event segmentation affects the organization of information in LTM. Although previous imaging studies have identified changes in brain activity during ongoing perceptual processing at event boundaries (Speer et al., 2007; Whitney et al., 2009; Zacks, Braver, et al., 2001), this prior work did not address the relationship between event segmentation and episodic memory organization. In our study, Experiments 1 and 2 tested two potential influences of event segmentation on LTM organization. One possibility is that updating at event boundaries leads to a discontinuity in the preboundary and postboundary representations in memory; this discontinuity would be analogous to the accessibility changes that have been previously observed. Alternatively, the integration of information within an event model could result in a more tightly bound or clustered mnemonic representation of that event information.

Experiment 1 examined whether event boundaries influence information organization in LTM by comparing binding between information encountered within an event and binding between information crossing event boundaries. Participants read narratives that contained event-boundary sentences and were later given a cued-recall test designed to examine the degree of binding between sentences from the narrative. The results showed weaker mnemonic binding for sentences separated by a boundary than for sentences not separated by a boundary.

Experiment 2 was designed to identify the event-segmentation mechanism that might contribute to the behavioral effect found in Experiment 1. One possibility is that event-boundary perception, which has been shown to enhance encoding of boundary information (Schwan & Garsoffky, 2004; Swallow et al., 2009), prioritizes incoming novel information at the expense of representations from the previous event and thus directly decreases LTM binding across events. A second possibility is that weaker LTM binding across events is the indirect consequence of enhanced binding within events, an effect that occurs as a result of maintenance and integration of information in active event models. Experiment 2 employed functional magnetic resonance imaging (fMRI) to obtain measures of cognitive processing at event boundaries and within events while participants read narratives. This approach was intended to determine which of these two measures of cognitive processing is better correlated across participants with behavioral measures of LTM binding.

Experiment 1

Method

Participants. Twenty-three healthy volunteers (18 female and 5 male; mean age = 21.45 years, range = 18–29 years) participated in this study for payment. All participants were native English speakers with normal or corrected-to-normal vision. Informed consent for this experiment was obtained in a manner approved by the institutional review board at New York University.

Stimuli and behavioral procedure. Narratives were adapted from a previous study of event perception (Speer & Zacks, 2005) and were obtained from the online database of the Dynamic Cognition Laboratory (2007). Six narratives were used; each described a protagonist carrying out an everyday activity (e.g., tending to a garden). Thirty-eight sentences per narrative each described an action or thought by the protagonist. Interspersed within each narrative were two sentence types of interest: eight *boundary sentences* beginning with "A while later . . ." (these sentences marked the beginnings of events) and eight *control sentences* beginning with "A moment later . . ." (these sentences occurred within events). An independent experimental group confirmed that "A while later . . ." was more likely to be perceived as an event boundary than was "A moment later . . ." (see Independent Event Segmentation Study in the Supplemental Material available online). For counterbalancing purposes, six versions of each narrative were created so that the temporal references "A while later" and "A moment later" were added to a different set of sentences in each version (48 sentences of each type per participant).

Participants read the narratives one sentence at a time (Fig. 1a; presentation lasted for 6 s each) on a computer running E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA). To measure reading times, we asked participants to press a button when they were finished reading each sentence. Following sentence presentation, a fixation cross with a variable duration (2–10 s) was presented. These delays were included in anticipation of running the same paradigm using fMRI (see Experiment 2) to allow estimation of brain activity in response to sentence types of interest. Participants were instructed to remain attentive to the content of the narrative during these periods.

After encoding, participants were given a 10-min break before a surprise cued-recall test designed to measure binding between adjacent sentences with and without a boundary intervening. If event segmentation during encoding influences the binding of representations in LTM, the probability of recalling the next sentence in a narrative (when given a preceding sentence as a cue) should be lower if the next sentence occurs after an event boundary than if there is no intervening boundary. For example, prompting with cue sentences that immediately preceded event boundaries at encoding should result in lower recall of the next sentences (which occurred on

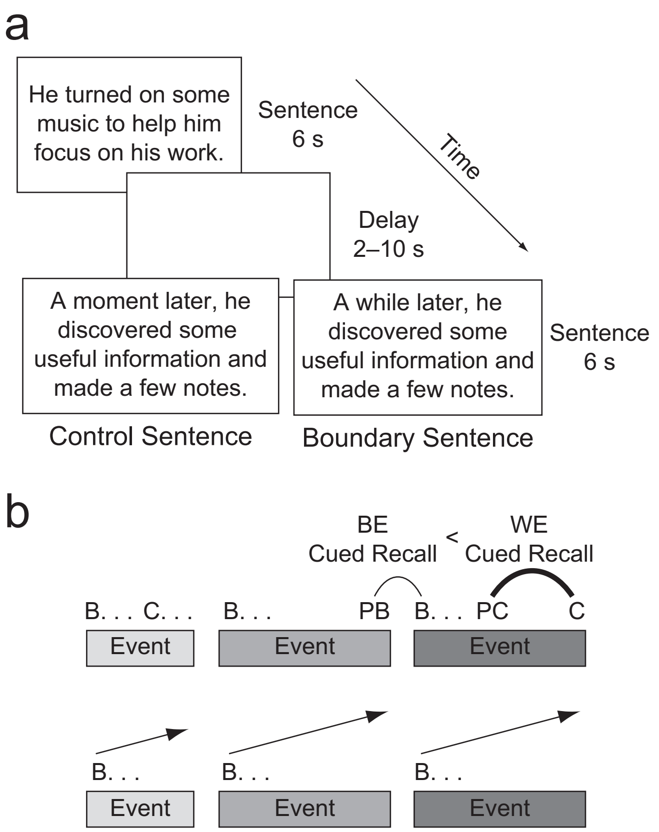

Fig. 1. Trial and experimental structure of Experiments 1 and 2. Participants were presented with sentences one at a time for 6 s each; sentences were separated by a variable-length delay period (a). A portion of the stimuli were either boundary sentences (which began with "A while later . . .") or control sentences (which began with "A moment later . . ."). Relative placement of the sentence types within events is indicated in (b). Each event began with a boundary sentence (B) and ended with a preboundary sentence (PB). Control sentences (C) were preceded by precontrol sentences (PC) within events. The top row in (b) shows the predicted behavioral differences in binding across sentences (Experiment 1). We tested whether between-event (BE) cued recall was lower than within-event (WE) cued recall. The event regressor in Experiment 2 modeled sentence-encoding activity parametrically as a function of each sentence's position within each event. The bottom row in (b) illustrates that activity was modeled as a rise within each event until the next event boundary, where it dropped back down.

the other side of the boundary) than prompting with cue sentences that immediately preceded any other sentence (which occurred within the same event's boundaries). This is because participants were required to recall information that crossed an event boundary in only the former case (Fig. 1b).

On each trial, participants were cued with a sentence from one of the narratives and instructed to recall the next sentence. If unable to do so, participants were instructed to recall the next sentence that they could remember; they were encouraged to respond to all trials. Participants performed 96 cued-recall trials (one block of 16 trials per narrative). Cue presentation was random within blocks, but to keep the study-test interval approximately constant, we matched the presentation order of the recall blocks with the order of the narratives at encoding. After cue presentation, participants pressed a key to indicate that they had recalled a sentence, and then they were prompted to type their response. In each block, participants were cued with half of the boundary and half of the control sentences from the narrative, with all of the temporal references (e.g., "A moment later") removed. Participants were also cued with half of the sentences that immediately preceded the boundary and control sentences at encoding (*preboundary sentences* and *precontrol sentences*). Each participant was tested on only one member of each boundary-preboundary pair and control-precontrol pair. This was done to avoid testing participants on the same boundary or control sentences that were also correct responses to preboundary or precontrol cues, respectively.

Two raters blind to the nature of the cues compared participants' recall responses with the original narrative sentences to determine accuracy on the cued-recall task (disagreements were resolved by discussion). A response was marked correct (hit) if it contained a direct reference to an explicitly stated detail in the narrative; verbatim sentence recall was not required. Correct responses were also coded for whether they referred to the sentence immediately following the cue at encoding (next-sentence recall).

Results

At encoding, participants read preboundary sentences ($M = 3.04$ s, $SE = 0.13$) more quickly than boundary sentences ($M = 3.19$ s, $SE = 0.13$), $t(22) = 4.76$, $p < .001$. Participants also read precontrol sentences ($M = 3.02$ s, $SE = 0.13$) more quickly than control sentences ($M = 3.26$ s, $SE = 0.13$), $t(22) = 6.40$, $p < .001$; this was expected because all boundary and control sentences began with "A while later" or "A moment later" and were therefore slightly longer than preboundary and precontrol sentences. Comparison of overall hits (proportion of cues for which the participant recalled any narrative detail) revealed no differences across sentence types (preboundary: $M = .716$, $SE = .036$; boundary: $M = .730$, $SE = .030$; precontrol: $M = .749$, $SE = .025$; control: $M = .767$, $SE = .027$), $F(3, 66) = 1.75$, $p > .16$. (See also Experiment 1 Behavioral Data in the Supplemental Material.)

The main comparison of interest was next-sentence recall for preboundary and boundary cues. This comparison allowed us to determine whether event boundaries affect LTM binding between sentences. Next-sentence recall did indeed differ across cue types, $F(3, 66) = 9.88$, $p < .001$; planned comparisons revealed that next-sentence recall was lowest for preboundary cues ($M = .175$, $SE = .026$) and that next-sentence recall for preboundary cues differed significantly from next-sentence recall for boundary cues ($M = .294$, $SE = .029$), $t(22) = 3.41$, $p < .003$, Cohen's $d = 1.35$. It is critical to note that next-sentence recall was equivalent for precontrol cues ($M = .308$, $SE = .031$) and control cues ($M = .331$, $SE = .027$), $t(22) = 0.76$, $p > .45$. These results suggest that the presence of event boundaries results in decreased LTM binding (Fig. 2a). In

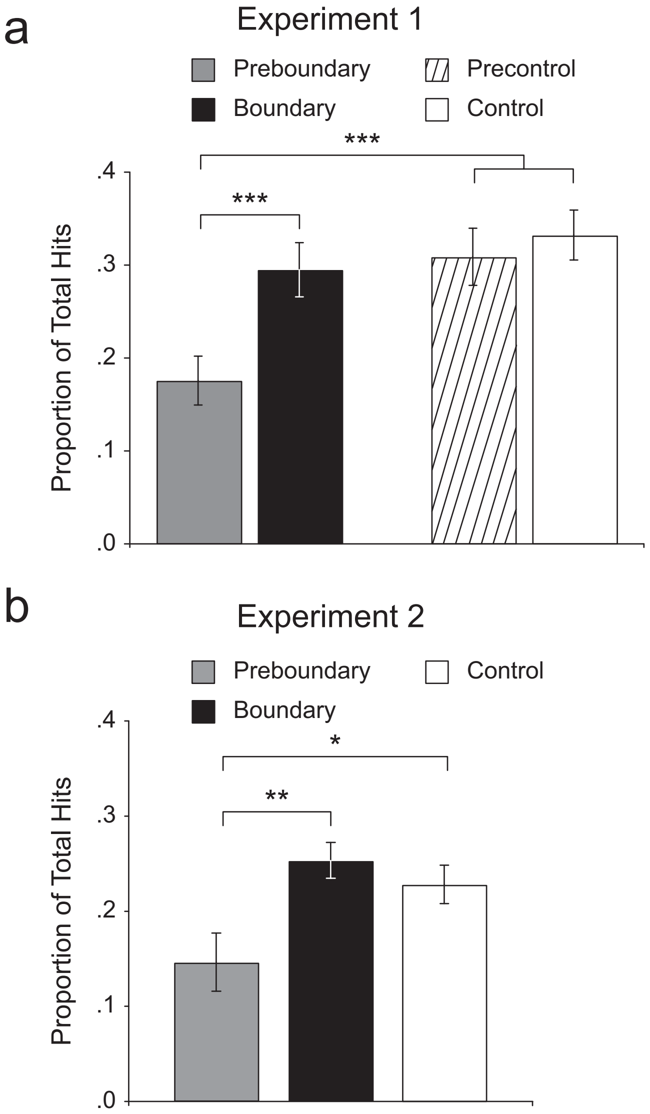

Fig. 2. Next-sentence cued-recall performance in Experiments (a) 1 and (b) 2. The proportion of all hits in which a participant recalled the sentence immediately following the cue sentence is plotted for each cue-sentence type. Significant differences between sentence types are indicated (*$p < .05$; **$p < .01$; ***$p < .005$). Error bars denote standard errors of the mean.

addition, next-sentence recall for boundary and control cues did not differ, $t(22) = 1.24$, $p > .22$; this suggests that previously reported memory enhancements for information encountered at event boundaries (e.g., Swallow et al., 2009) do not necessarily lead to enhanced binding of boundary information with subsequently encountered information, at least in the present paradigm.

Thus, the presence of an intervening boundary resulted in mnemonic binding between preboundary and boundary sentences being weaker than mnemonic binding between precontrol and control sentences, which were not separated by a boundary. On the basis of these findings, we used fMRI in Experiment 2 to determine which of two event-segmentation mechanisms—between-event (i.e., boundary) processing or within-event processing—supports these behavioral LTM binding effects. We examined patterns of reading-related brain activity that are consistent with boundary and within-event processing mechanisms, and we utilized an individual differences approach to assess the contributions of these mechanisms to mnemonic organization.

Experiment 2

Method

Participants. Nineteen healthy right-handed volunteers (10 female and 9 male; mean age = 22.64 years, range = 18–30 years) participated in this study for payment. All participants were native English speakers with normal or corrected-to-normal vision. Informed consent for this experiment was obtained in a manner approved by the institutional review board at New York University.

Stimuli and behavioral procedure. Participants read narratives while in the fMRI scanner. These narratives and the timing parameters were identical to those used in Experiment 1. Between narratives, participants performed a low-level sensorimotor baseline task for 30 s (see fMRI Sensorimotor Baseline Task in the Supplemental Material). Approximately 10 min after encoding, participants completed a surprise cued-recall test outside the scanner. This test used procedures similar to those described in Experiment 1; however, to increase the design's power to detect any possible differences in next-sentence recall between trials cued by boundary sentences and trials cued by control sentences, we used only boundary and control sentences as the recall cues in Experiment 2 (48 trials of each type). However, it is critical to note that a subset of control sentences preceded boundary sentences (and therefore were preboundary sentences); this allowed us to assess differences in next-sentence recall for preboundary and boundary cues.

fMRI procedure and analyses. Scanning was performed on a 3-T Siemens (New York, NY) Allegra magnetic resonance imaging system using a whole-head coil. Functional data were acquired using a gradient-echo echo-planar pulse sequence (repetition time = 2 s; echo time = 30 ms; 35 slices oriented parallel to the anterior commissure–posterior commissure axis; voxel size = 3 × 3 × 3 mm; interslice gap = 0.6 mm; volume acquisitions per run = 483). High-resolution T1-weighted MPRAGE (magnetization-prepared rapid-acquisition gradient echo) images were collected for anatomical visualization. Data were analyzed using Brain Voyager QX (Brain Innovation, Maastricht, The Netherlands) and in-house software. Functional images were preprocessed to correct for differences in slice-acquisition time, low-frequency noise was removed with a high-pass filter, and images were realigned within and across runs. Anatomical and functional images were spatially normalized to the Talairach stereotaxic space (Talairach & Tournoux, 1988), and functional images were coregistered to the anatomical images. Functional images were resliced to 2- × 2- × 2-mm voxels and spatially smoothed (6-mm full-width at half-maximum isotropic Gaussian kernel).

In our first analysis, a finite impulse-response (FIR) model was used to estimate the time course of the response to each sentence type. Boundary and control sentences were modeled separately with a set of seven regressors per condition that each estimated condition-specific activity for a single time point after onset. Estimates in each voxel were submitted to a 2 × 7 analysis of variance with sentence type (boundary or control) and time point as independent variables. A main effect of sentence type identified regions showing overall activation differences between boundary and control sentences, and a Sentence Type × Time Point interaction identified regions showing differences between boundary and control sentences at any individual time point.

To determine the relationship between brain activity and differential within-event LTM binding, we conducted a second analysis in which a standard epoch-based general linear model was used to obtain a single activity estimate per condition to correlate with our measure of LTM binding (boundary next-sentence recall minus preboundary next-sentence recall; this measure is hereafter referred to as *within-event binding*). We modeled three sentence types (boundary, control, and other) as boxcar regressors convolved with a canonical hemodynamic response function. A contrast of beta coefficients (boundary > control) was used to quantify processing at event boundaries. To model within-event maintenance and integration-related processing, we predicted that the processing or representational load of an event model should increase as the event unfolds in time and new representations are integrated into the model. To capture this pattern of activity, we used a parametric regressor (labeled *event*) that modeled the activity of each sentence within an event as a function of the sentence's distance from the previous boundary sentence (Fig. 1b). This distance was indexed by assigning a number to each sentence following a boundary (in sequence: 1, 2, etc.); the magnitude of the event beta coefficient was then used to index within-event processing. Mean signal and linear drift were also modeled as confounds in each run.

A statistical threshold ($p < .005$) and a spatial threshold (74 voxels) for each contrast corrected for family-wise error ($p < .05$ using a Monte Carlo simulation; see Statistical Correction Procedure for Contrast and Correlation Analyses in the Supplemental Material). For the medial temporal lobes, relaxed thresholds ($p < .005$ and 34 voxels) were used (Ojemann et al., 1997; Staresina & Davachi, 2006). To look for correlations between brain activity and within-event binding, we separately correlated the beta estimates of parametric event activity and the boundary > control contrast with behavioral measures of within-event binding across participants. This allowed us to compare the relationship between within-event binding and these two patterns of EST-related activity. A statistical threshold ($p < .005$) and a spatial threshold (25 voxels) for correlation maps corrected for multiple comparisons ($p < .05$ using a randomization simulation).

Results

Behavioral results. Reading times were equivalent for boundary sentences ($M = 3.02$ s, $SE = 0.15$ s), control sentences ($M = 3.04$ s, $SE = 0.15$ s), and preboundary sentences ($M = 3.04$ s, $SE = 0.16$ s), $F < 1$. On the memory test, overall hit rates (probabilities of recalling any sentence from the narrative) were also equivalent for boundary sentences ($M = .635$, $SE = .042$), control sentences ($M = .643$, $SE = .044$), and preboundary sentences ($M = .682$, $SE = .051$), $F < 1$. As in Experiment 1, next-sentence recall cued by boundary sentences ($M = .238$, $SE = .019$) and next-sentence recall cued by control sentences ($M = .229$, $SE = .020$) did not differ, $t(18) = 0.44$, $p > .66$. However, as in Experiment 1, next-sentence cued recall was greater for boundary cues ($M = .238$, $SE = .019$) than for preboundary cues ($M = .145$, $SE = .031$), $z = 2.958$, $p < .005$, Cohen's $d = 1.70$ (Fig. 2b).

Imaging results. Using the FIR model, we found that a right-hemisphere region spanning right posterior cingulate and precuneus ($x = 9$, $y = -54$, $z = 33$; Fig. 3a) showed a main effect of sentence type (boundary > control), which was consistent with the results of previous studies showing that this region responds differentially to event boundaries (Speer et al., 2007; Whitney et al., 2009). The Sentence Type × Time Point interaction revealed additional regions that have been implicated in narrative comprehension (Ferstl, Neumann, Bogler, & von Cramon, 2008), including right ventrolateral prefrontal cortex (PFC; $x = 40$, $y = 32$, $z = 13$), dorsomedial PFC ($x = 1$, $y = 35$, $z = 29$), and left superior temporal gyrus ($x = -56$, $y = -32$, $z = 3$; Fig. 3a and Table 1).

The parametric event regressor was used to identify brain regions showing increased activation across sentences within an event (Fig. 3b). This analysis revealed a network of brain regions, including bilateral ventromedial PFC (left: $x = -7$, $y = 36$, $z = 0$; right: $x = 15$, $y = 43$, $z = 4$) and left middle temporal gyrus (MTG; $x -57$, $y = -16$, $z = -13$). In the medial temporal lobes, a region of right parahippocampal cortex also emerged ($x = 19$, $y = -23$, $z = -16$). Combined with the FIR analysis, these data provide support for two processes hypothesized by EST: the operation of event-model maintenance and integration and the updating of the event model at event boundaries. (For additional information, see Sentence-Wise Beta Estimates for Regions Emerging From the Event Analysis in the Supplemental Material.)

Our main goal was to see whether individual variability in these two processes is linked to individual differences in the extent to which the narratives become organized into discrete episodes in LTM. To this end, we compared (across the whole brain) the extent to which activity identified in the boundary > control contrast and parametric event activity positively

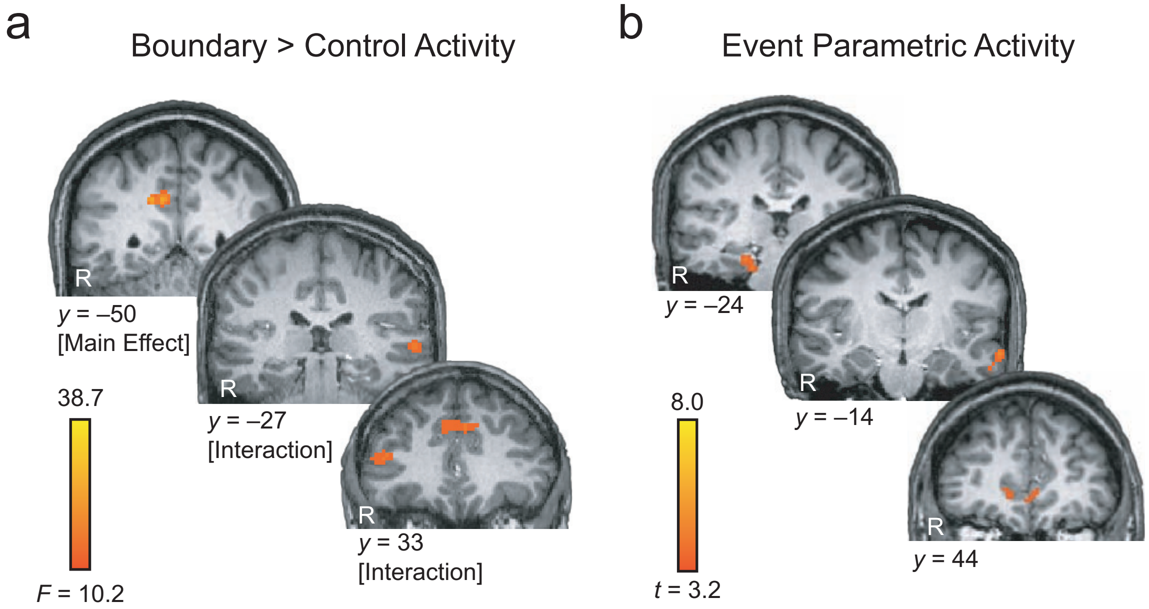

Fig. 3. Functional magnetic resonance imaging results from Experiment 2. The brain images in (a) show areas of significant activation related to main effects of sentence type and to the Sentence Type × Time Point interaction. The images in (b) show areas of significant activation for the parametric event regressor. Coordinates for each brain slice are shown. R = right.

correlated with individual participants' behavioral measures of within-event binding. It is interesting that no brain regions exhibited a significant positive correlation between event-boundary activation and within-event binding. By contrast, the correlation of parametric event activity and within-event binding revealed three regions showing significant correlations: bilateral ventromedial PFC ($x = -2$, $y = 29$, $z = 3$), right caudate ($x = 14$, $y = 15$, $z = 2$), and a region extending from right perirhinal cortex ($x = 32$, $y = -7$, $z = -20$) to right MTG ($x = 45$, $y = -8$, $z = -16$; Fig. 4a). Taken together, these results suggest that cognitive processing within events is more strongly related to within-event binding than is cognitive processing at event boundaries.

In a second analysis, we found that activity in the boundary > control contrast was positively correlated with preboundary next-sentence recall (this behavioral measure could be considered an index of boundary memory) in several regions, including left ventrolateral PFC ($x = -36$, $y = 42$, $z = 10$), right dorsolateral PFC ($x = 45$, $y = 18$, $z = 32$), and bilateral MTG (left: $x = -56$, $y = -16$, $z = -9$; right: $x = 60$, $y = -16$, $z = -9$; Fig. 4b and Table 2). Thus, the extent of activation in the boundary > control contrast predicted individual subjects' boundary memory, whereas the extent of parametric event activity predicted the increase in binding of sentences within an event. (For additional analyses, see the Supplemental Material.)

General Discussion

The findings of our study suggest that episodes in memory become organized through event-segmentation mechanisms during ongoing experience. Event boundaries weakened the long-term links between information preceding and following the boundaries, and this demonstrates that boundaries influence LTM organization and suggests that event segmentation may be responsible for organizing episodes into discrete segments in episodic memory. Furthermore, fMRI activity consistent with information integration within events significantly correlated with within-event binding, but event-boundary-related brain activity correlated only with memory for boundary information.

Prior work has identified factors other than event segmentation that influence the mnemonic binding of narrative elements. For example, actions that are associated with a common goal tend to cluster together when recalled (Lichtenstein & Brewer, 1980). This suggests that semantic knowledge of how actions are undertaken to achieve goals helps to structure memory recall. Other studies have shown that semantic knowledge for common events, or scripts, can also exert an organizing influence on LTM (Bower, Black, & Turner, 1979). However, the LTM binding effects observed in our experiments are unlikely to be a direct consequence of these types of semantic knowledge because the temporal event boundaries changed locations across participants. That is, when the semantic content remained constant, binding between adjacent elements of an ongoing narrative was additionally modulated by temporal event boundaries. A critical task for future researchers will be to understand the mechanisms by which prior semantic knowledge related to action sequences interacts with current experience to determine the large-scale structure of event memory.

Our fMRI data suggest that the increased binding of within-event representations in LTM occurs as a consequence

Table 1. Brain Regions Emerging From Contrast Analyses in Experiment 2

Model and brain region	Talairach coordinates (*x*, *y*, *z*)	No. of voxels	Peak *z*
Boundary > control FIR model: main effect			
Right posterior cingulate	9, −54, 33	160	2.911
Left lingual gyrus	−20, −85, −11	89	2.820
Boundary > control FIR model: Sentence Type × Time Point interaction			
Right lingual gyrus	9, −71, −2	6,541	5.982
Right inferior precentral sulcus	35, −2, 38	172	4.605
Right middle occipital gyrus	33, −81, −7	119	4.074
Right anterior cingulate (dorsomedial prefrontal cortex)	1, 35, 29	106	3.764
Right intraparietal sulcus	25, −60, 39	89	4.317
Right inferior frontal gyrus (ventrolateral prefrontal cortex)	40, 32, 13	84	4.210
Right intraoccipital sulcus	30, −73, 20	83	4.025
Left superior precentral sulcus	−42, −4, 46	501	5.418
Left superior temporal gyrus	−56, −32, 3	114	3.846
Left intraparietal sulcus	−25, −59, 38	98	4.073
Parametric event model			
Right inferior cingulate gyrus (ventromedial prefrontal cortex)	15, 43, 4	87	3.651
Right parahippocampal gyrus	19, −23, −16	47	3.259
Right lingual gyrus[a]	17, −77, −4	39	−3.467
Right postcentral gyrus	23, −34, 59	28	3.109
Right middle temporal gyrus	54, −7, −22	22	3.623
Left superior frontal gyrus	−22, 20, 51	193	3.559
Left calcarine sulcus[a]	−11, −82, −5	156	−3.486
Left inferior cingulate gyrus (ventromedial prefrontal cortex)	−7, 36, 0	116	3.296
Left anterior inferior temporal gyrus	−30, 9, −27	84	3.554
Left middle temporal gyrus	−57, −16, −13	78	3.922
Left lateral orbital gyrus	−34, 43, −10	35	3.266

Note: FIR = finite impulse response.

[a] These regions showed negative activity for this contrast.

of integration processes that are engaged during narrative reading. Prior imaging work on narrative comprehension and memory has examined integration processes related to situation-model construction and maintenance, typically by examining brain activation in response to narrative elements that vary in coherence or consistency (Ferstl, Rinck, & von Cramon, 2005; Hasson, Nusbaum, & Small, 2007; Xu, Kemeny, Park, Frattali, & Braun, 2005; Yarkoni, Speer, & Zacks, 2008). Because of its focus on integration-related increases in activity within events, the current approach differs from prior work and is therefore the first to show that integration-related comprehension processes operate at the scale of events. In addition, our work specifically relates a neural signal consistent with integration within events to our behavioral measure of within-event binding. Furthermore, our data showing that boundary memory correlates with activity in MTG (and other regions) are consistent with the prior findings that brain activity in regions proposed to be critical for narrative comprehension (e.g., MTG; Ferstl et al., 2008; Mar, 2004) is predictive of narrative item memory (Hasson et al., 2007; Maguire, Frith, & Morris, 1999). However, as noted in the Results for Experiment 2, no regions showed positive correlations between event-boundary activity and within-event binding. Taken together, these data suggest at least two distinct mechanisms of event segmentation that influence memory in different ways: Mechanisms operating at event boundaries enhance boundary representations (Swallow et al., 2009; Zacks et al., 2007), but mechanisms operating across sentences, albeit within the same event, contribute to LTM binding of those sentences.

The event-activity analysis suggests that event perception affects the organization of LTM through its role in integrating information into active mental models within events. This result is consistent with the findings of work examining the influence of relational working memory on LTM. This research has revealed that actively integrating information at encoding enhances LTM (Bjork, 1975; Craik & Lockhart, 1972), and this active integration has been shown to be supported by PFC processes thought to underlie maintenance and integration of active representations (Blumenfeld & Ranganath, 2006; Murray & Ranganath, 2007); these processes may allow for those representations to be bound by the hippocampus (Davachi & Wagner, 2002). It is interesting to note that this prior work used verbal material with no event structure across trials and revealed that lateral PFC is supportive of active

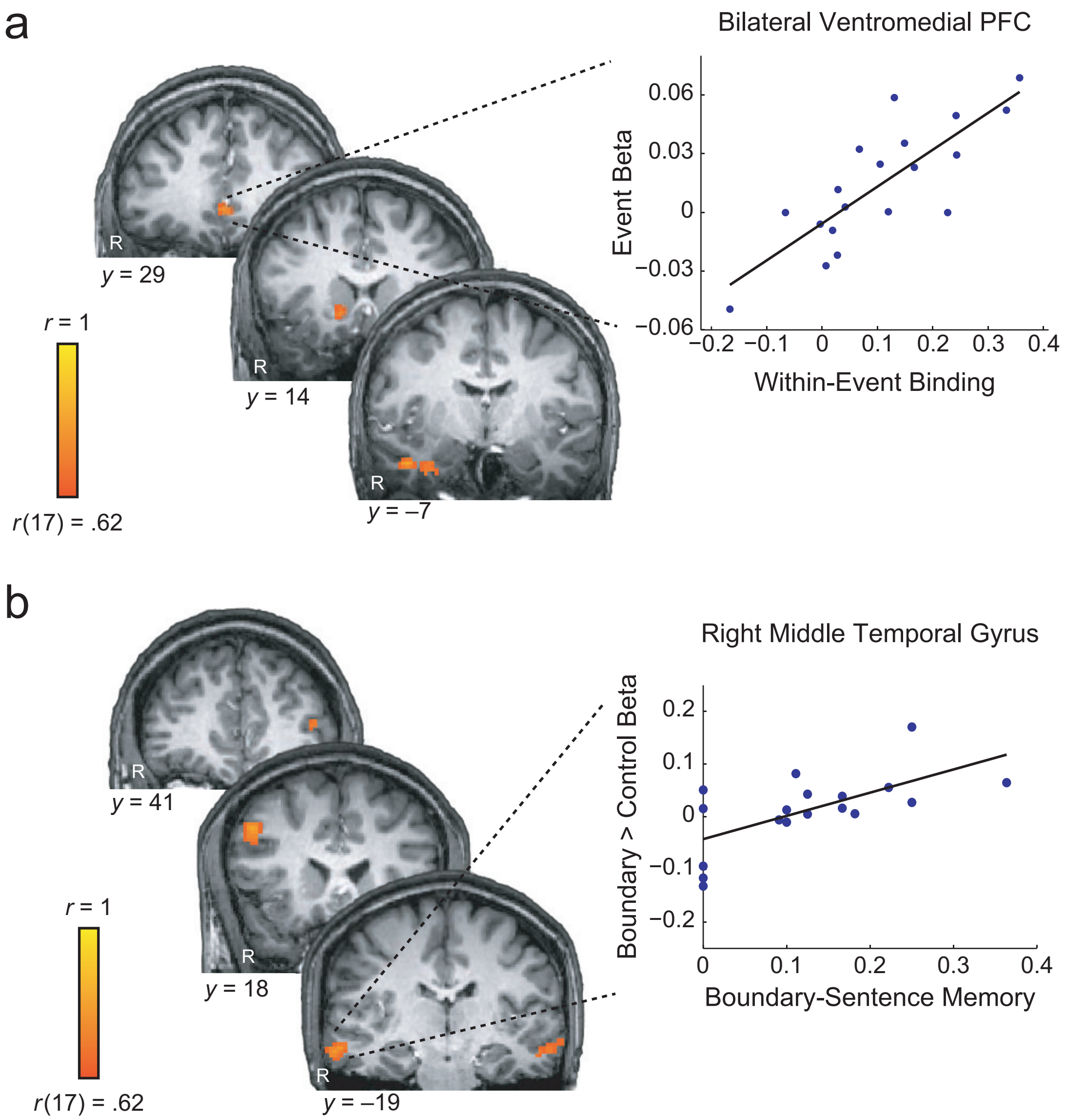

Fig. 4. Functional magnetic resonance imaging results related to memory performance in Experiment 2. Three brain regions showing correlations between parametric event activity and within-event binding are shown in (a). The scatter plot (with best-fitting regression line) illustrating correlation data from left ventromedial prefrontal cortex (PFC) is representative of the findings for other regions identified in this analysis. The images in (b) show regions with significant correlations between the boundary > control contrast and boundary-sentence memory. The scatter plot (with best-fitting regression line) illustrating correlation data from right middle temporal gyrus is representative of the findings for other regions identified in this analysis. Values on the *y*-axes of both scatter plots are in arbitrary units. R = right.

maintenance and integration. In contrast, our work and other work using stimuli with ongoing links across trials show medial PFC involvement (Hasson, Furman, Clark, Dudai, & Davachi, 2008). This suggests that the on-line representation of dynamic, ongoing experience may be mediated by medial PFC mechanisms already identified as important in social cognition (Amodio & Frith, 2006; Mitchell, Heatherton, & Macrae, 2002; Olsson & Ochsner, 2008).

Our experiments are an important step toward understanding how event perception and segmentation influence the structure of LTM. The behavioral results support the hypothesis that event segmentation shapes the organization of LTM; the fMRI results link these memory effects to brain activity consistent with information maintenance and integration within events. The results highlight an important role in episodic memory formation for cognitive processes related to tracking and comprehending the real-world structure of events.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Table 2. Brain Regions Emerging From Correlation Analyses in Experiment 2

Correlation and brain region	Talairach coordinates (x, y, z)	No. of voxels	Peak z
Within-event binding and event beta coefficients			
Right middle temporal gyrus	45, −8, −16	70	1.168
Right perirhinal cortex	32, −7, −20	65	1.042
Right caudate	14, 15, 2	26	0.895
Bilateral inferior cingulate gyrus (ventromedial prefrontal cortex)	−2, 29, 3	90	1.114
Left cuneus[a]	−1, −71, 15	44	−0.860
Boundary memory and boundary > control activity			
Right posterior middle temporal gyrus	55, −37, −10	169	1.045
Right middle frontal gyrus (dorsolateral prefrontal cortex)	45, 18, 32	129	1.101
Right intraparietal sulcus	35, −51, 42	90	0.993
Right middle temporal gyrus	60, −16, −9	74	1.132
Right posterior middle frontal gyrus	36, 3, 43	54	0.998
Right subcentral gyrus	56, 5, 17	30	0.884
Right cuneus	0, −88, 18	30	0.931
Left inferior parietal gyrus	−39, −58, 39	235	1.066
Left posterior middle temporal gyrus	−59, −33, −10	98	1.215
Left superior precentral sulcus	−33, −10, 36	79	0.996
Left middle temporal gyrus	−56, −16, −9	75	1.054
Left posterior superior temporal sulcus	−40, −50, 7	61	1.073
Left supramarginal gyrus	−54, −42, 37	54	0.912
Left transverse occipital sulcus	−24, −90, 16	31	0.973
Left inferior frontal gyrus (ventrolateral prefrontal cortex)	−36, 42, 10	28	0.843

[a] This region showed a negative correlation.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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