

Changes in Events Alter How People Remember Recent Information

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Abstract

■ Observers spontaneously segment larger activities into smaller events. For example, “washing a car” might be segmented into “scrubbing,” “rinsing,” and “drying” the car. This process, called event segmentation, separates “what is happening now” from “what just happened.” In this study, we show that event segmentation predicts activity in the hippocampus when people access recent information. Participants watched narrative film and occasionally attempted to retrieve from memory objects that recently appeared in the film. The delay between object presentation and test was always 5 sec. Critically, for some of the objects, the event changed

during the delay whereas for others the event continued. Using fMRI, we examined whether retrieval-related brain activity differed when the event changed during the delay. Brain regions involved in remembering past experiences over long periods, including the hippocampus, were more active during retrieval when the event changed during the delay. Thus, the way an object encountered just 5 sec ago is retrieved from memory appears to depend in part on what happened in those 5 sec. These data strongly suggest that the segmentation of ongoing activity into events is a control process that regulates when memory for events is updated. ■

INTRODUCTION

As a part of ongoing perception, observers separate what is happening now from what just happened (Zacks, Speer, Swallow, Braver, & Reynolds, 2007; Newton, 1973). For example, while watching a man cross the street, an observer may divide the activity into two parts: the man waits for traffic to clear, then he walks through the intersection. This process, called *event segmentation*, can be measured in the laboratory by asking participants to press a button when they believe an *event boundary* (the moment in time that separates two events) has occurred. Event segmentation has observable effects on neural processing and long-term memory for events. When observers passively view movies of goal directed activities, the points in time that correspond to event boundaries are associated with increased BOLD activity in bilateral extrastriate cortex, including motion-sensitive and biological motion-sensitive regions, right pFC, and bilateral medial parietal cortex (MPC; Zacks, Swallow, Vettel, & McAvoy, 2006; Speer, Swallow, & Zacks, 2003; Zacks et al., 2001). In long-term memory tests, event boundaries are also better recognized than other time points in the movie (Swallow, Zacks, & Abrams, 2009; Zacks et al., 2007; Baird & Baldwin, 2001; Newton & Engquist, 1976). Although these data show that event segmentation has important consequences for the way perceived events

are processed and encoded, relatively little is known about its consequences for memory retrieval.

Several theories of perception and comprehension suggest that changes in events should lead to changes in how recent information is retrieved from memory (Zacks et al., 2007; Zwaan & Radvansky, 1998; Gernsbacher, 1985). In general, these theories propose that observers represent the current situation in a mental model that encodes features of the current event, including location of the event, the actors, their goals, and the objects that are present. According to the Event Segmentation Theory (EST; Zacks et al., 2007), models of the current event (*event models*) are actively maintained in memory until the event is segmented. Once the event is segmented, EST claims that active memory is cleared, and a new event model is built from current perceptual information.

EST entails three specific hypotheses about memory encoding and retrieval.

First, event boundaries should be better encoded into episodic memory than other moments in time. As part of setting up a new event model, information presented at event boundaries should receive additional processing and therefore should be better encoded into episodic memory than nonboundary information.

Second, event boundaries should mark when recently encountered information is cleared from active memory. If and when subsequent retrieval is needed, this information must be retrieved from episodic memory. Clearing active memory at event boundaries should have several consequences for memory for recently encountered objects.

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Because it is not processed as well as boundary information, information presented during nonboundary periods is less likely to be encoded into episodic memory and should be less accurately retrieved across events than within events (Swallow et al., 2009; Baird & Baldwin, 2001; Newton & Engquist, 1976). Indeed, relative to boundary information, nonboundary information is poorly remembered after long delays (Newton & Engquist, 1976) and appears to contribute little to an observer's comprehension of an event (Schwan & Garsoffky, 2004). In addition, because forgetting irrelevant information reduces the degree to which it interferes with the retrieval of relevant information (Kuhl, Dudukovic, Kahn, & Wagner, 2007), forgetting nonboundary information may facilitate the retrieval of boundary information that has been encoded into episodic memory (Swallow et al., 2009). Because it should be encoded into episodic memory, boundary information may be remembered as well, or better, after active memory has been cleared at a subsequent event boundary.

Finally, the proposal that active memory is cleared at event boundaries implies that the brain systems involved in retrieving recently encountered information should change when events change. Brain regions involved in episodic retrieval, such as the medial temporal lobe (MTL) and medial and lateral parietal cortex, should be more active during retrieval across events than during retrieval within events. In addition, regions that are most active during successful retrieval from episodic memory should also be most active when boundary information is retrieved across events.

Previous research on event perception provides substantial evidence in favor of the first hypothesis (Swallow et al., 2009; Baird & Baldwin, 2001; Newton & Engquist, 1976), showing that movie frames and objects that are visible at an event boundary are better recognized than those that are not. Research in narrative and discourse comprehension (Radvansky & Copeland, 2006; Speer & Zacks, 2005; Gernsbacher, 1985; Jarvella, 1979) and two studies of retrieval during film viewing (Swallow et al., 2009; Carroll & Bever, 1976) provide evidence for the second hypothesis: Changes in perceived and narrated events can impair retrieval of information encountered before the change. However, to date, no research has investigated neural activity during memory retrieval as a function of event segmentation.

To examine whether the neural systems involved in remembering recent information change in response to changes in events, we asked 28 participants to watch movies depicting goal directed activities while undergoing fMRI. The movies were rich, naturalistic stimuli excerpted from professional narrative cinema. The task was identical to that used in another study of event segmentation and memory (Swallow et al., 2009). Occasionally, the movies stopped for a recognition test on an object that was recently presented in the movie (Figure 1A). All objects were tested 5 sec after they were presented. For this test, the question "Which of these objects was just in the movie?" appeared above an old object that had been presented in the movie and an object that was contextually appropriate for but not present in the movie. As in earlier studies,

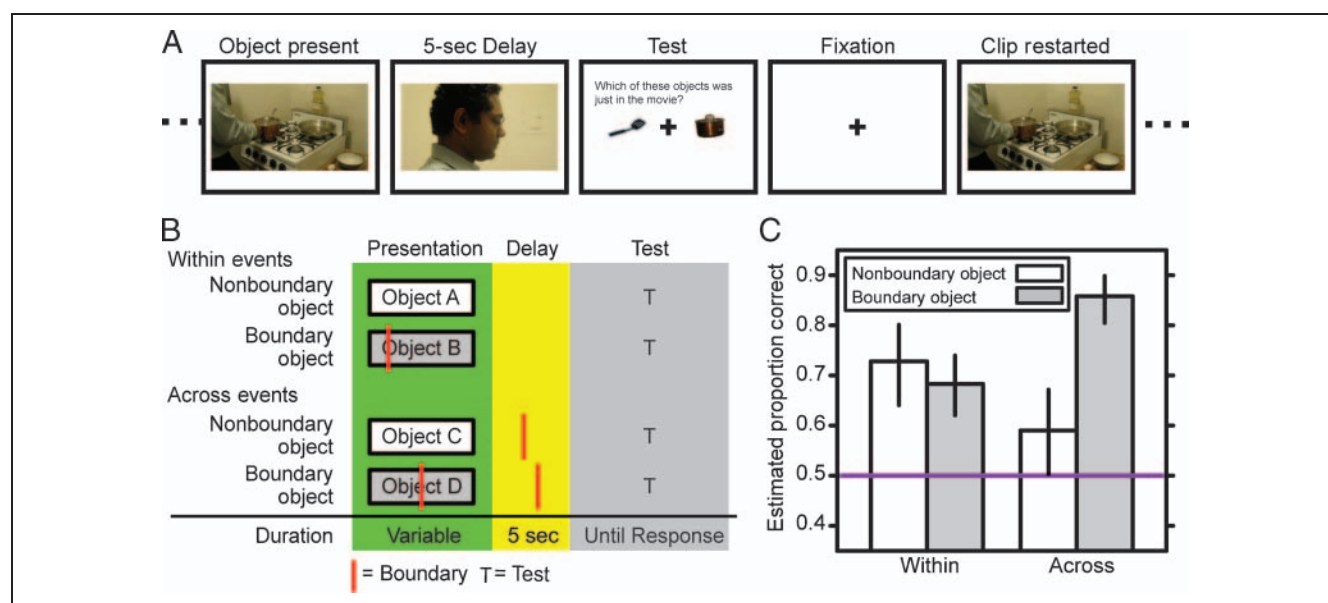


Figure 1. Design and behavioral data. (A) Participants viewed clips that depicted goal directed activities. Five seconds after an object was presented, the clip stopped for a two-alternative forced-choice recognition test. Afterward, the movie restarted at a point 10 sec before when it was stopped. (B) Object recognition tests were in four conditions on the basis of whether event boundaries occurred during object presentation and during the delay. (C) Mean estimates of accuracy for tests of an average old object (see Methods) in each of the four object test conditions. The purple line indicates chance performance. Error bars are 95% confidence intervals. Note that the images in this figure were not used in the experiments but are illustrative of what participants saw. All movies and images were displayed in full color.

several variables that could influence the memorability of each object (e.g., object size, eccentricity, and the ease with which the object is detected within the scene) were measured and statistically controlled.

We examined how recognition test performance and retrieval-related BOLD activity varied as a function of two attributes of event segmentation (Figure 1B). First, for each trial, an event boundary may have occurred during object presentation (*boundary object* trials) or not (*nonboundary object* trials). For example, in one of the stimulus movies, a man is shown aiming a toy gun at a balloon and then firing, at which point an event boundary occurs (perhaps reflecting that the actor's activity changed from aiming to firing). A wall clock is on the wall behind the man when the event boundary occurs, making it a boundary object. According to EST, the occurrence of an event boundary during the presentation of the clock should increase the likelihood that it is processed and encoded into episodic memory. Second, for each trial, an event boundary may have occurred during the 5-sec delay between object presentation and test (across event trials) or not (within event trials). In the previous example, a couple of seconds after the man shoots the toy gun, the movie cuts to a new scene in which he is shown taking a picture. An event boundary occurs at this time, perhaps reflecting the actor's change in location and activity. Because the clock is tested soon after this event boundary, it is tested across events. According to EST, anything that has not been encoded into episodic memory (less likely for nonboundary objects) should be less recognizable when it is tested across events rather than within events. Anything that has been encoded into episodic memory (likely for boundary objects) should be recognizable after an event boundary.

For all conditions, the delay between object presentation and test was held constant, whereas the presence of event boundaries during object presentation and during the delay varied.

METHODS

Participants

Participants were 28 right-handed, native English-speaking volunteers (20 women, 18–28 years old) who provided informed consent. All procedures were approved by the Washington University institutional review board.

Image Acquisition and Processing

Data acquisition was performed in a Siemens 3-T MRI Scanner (Erlangen, Germany). A high-resolution T1-weighted image (MPRAGE; $1 \times 1 \times 1.25$ mm) was acquired. BOLD data (Ogawa, Lee, Kay, & Tank, 1990) were acquired with a T2*-weighted asymmetric spin-echo echo-planar sequence (slice repetition time [TR] = 64 msec, echo time = 25 msec) in 32 transverse slices (4.0-mm isotropic voxels) aligned with the anterior and posterior commissures. To facilitate BOLD

data registration to individual anatomy, a high-resolution T2-weighted fast turbo-spin echo image ($1.3 \times 1.3 \times 4.0$ -mm voxels, slice TR = 8430 msec, echo time = 96) was acquired in the same plane as the T2* images before the BOLD data were collected. Timing offsets in the functional data were corrected with cubic spline interpolation, and intensity differences in the slices were removed to compensate for interleaved slice acquisition. Functional and structural data were aligned, warped to standard stereotaxic space (Talairach & Tournoux, 1988), and resampled to 3.0-mm isotropic voxels.

Stimulus Presentation

Stimuli were presented with PsyScope X software (Cohen, MacWhinney, Flatt, & Provost, 1993) on a PowerBook G4 (Apple Inc., Cupertino, CA). Visual stimuli were back projected onto a screen at the head of the scanner bore. Movie soundtracks were presented over headphones.

Materials

Detailed descriptions of the materials are available elsewhere (Swallow et al., 2009). In brief, five clips from four commercial movies, *Mr. Mom* (Dragoti, 1983), *Mon Oncle* (Tati, 1958), *One Hour Photo* (Romanek, 2002), and *3 Iron* (Ki-Duk, 2004) depicted characters engaged in everyday activities in natural and realistic settings, had little dialogue, and presented clearly identifiable objects. Scenes from the film *3 Iron* were presented in two clips to permit the introduction of a central character appearing in later scenes. A clip from *The Red Balloon* (Lamorisse, 1956) was used for a practice session. Five seconds of a black screen preceded and followed each clip.

A second group of 16 individuals identified event boundaries. Participants watched the clips and pressed a button whenever they believed one natural unit of activity ended and another began. Participants performed the task twice to identify events at large and small temporal resolutions (*grains*). The button-press time series for each clip and grain were smoothed (Gaussian kernel; large grain bandwidth = 2.5 sec, small grain bandwidth = 1 sec). Event boundaries were defined as the highest local maxima of the smoothed time series. The number of boundaries equaled the mean number of button presses for that clip and grain.

Thirty-five objects presented in the movie clips were selected for testing. The 35 object tests were classified according to the presence or absence of an event boundary during object presentation and during the 5-sec delay between object presentation and test (Figure 1). There were 7 objects in the nonboundary object, within event condition, 8 objects in the boundary object, within event condition, 9 objects in the nonboundary object, across events condition, and 11 objects in the boundary object, across events condition. Thirty-five additional objects were identified for a secondary analysis but were not tested (*non-test*

control). Like the objects that were tested, these objects were classified according to whether an event boundary occurred during the time the object was on the screen and during the 5-sec period that followed object presentation (equivalent to the delay period for tested objects). The number of tested and untested objects in the four conditions defined by these two factors was equivalent.

Recognition Test Alternatives

The 35 old objects that were selected for testing were continuously visible for at least 1 sec and were not presented within 5 sec of other old objects. For each old object, an object that was contextually appropriate but from a different semantic category than the old object (e.g., cat vs. chair) served as the recognition test foil. An image for the test foil was photographed, acquired on-line, or taken from stock photography and manipulated to match the properties (e.g., contrast) of the old object (for additional details, see Swallow et al., 2009).

In two pilot studies, participants performed match-to-sample tasks. For these tasks, a frame from the movie appeared above images of two objects. One group was shown the old object and an object from the same category as the old object (e.g., two different chairs). The other group was shown an object from the same category as the old object (e.g., a different chair) and the recognition test foil (e.g., a cat). Participants were told to select the object (or type of object) that most closely matched an object in the frame as quickly as they could. Only objects that were correctly matched by 80% of participants were used in the recognition tests.

Task and Procedure

Functional data were acquired in five BOLD runs (TR = 2.048 sec), one for each clip. Clip order was counter-balanced across participants. Before each run, a brief introduction was read. Runs began with 19 frames of a black fixation cross ($1^\circ \times 1^\circ$) on a white background. The clip then played at the center of the screen. About once a minute, the clip stopped for a two-alternative forced-choice recognition test. Thirty-five tests were *object tests* (Figure 1A) for which the question “Which of these objects was just in the movie?” appeared 4.17° above a fixation cross at the center of the screen. The old object and its corresponding different type object were presented 4.86° to the left and right of the fixation cross. Twelve tests were *event tests*, which consisted of a question about a recent activity (e.g., “Who started the music?”) and two reasonable alternatives (e.g., “The young man.” “The woman.”). Event tests were included to ensure that participants attended to the activities in the films but were not designed to test the hypotheses derived from EST. The delay between the end of object presentation or the end of the event and its test was always 5 sec. Participants responded to tests with their

right hand using a four key response box. After a response, the fixation cross was presented for one to five frames before the movie was restarted. Fifteen frames of fixation followed the final portion of the clip instead of a test. Five comprehension questions focusing on the activities, intentions, and goals of the characters were administered after the run. The shortest run lasted a mean of 8.73 min, and the longest run lasted a mean of 18.9 min.

A practice session performed during the structural scan with *The Red Balloon* presented primarily event tests (6/8) to encourage participants to attend to the activities. Before the scan, the volume of the soundtrack was adjusted to ensure it was audible.

Data Analysis

Matching time from the two match-to-sample pilot studies, a variable coding whether the actor interacted with the object (actor–object interactions), object size, and object eccentricity was used as covariates in the behavioral data analyses of object test accuracy and response times.¹ Actor–object interactions were defined as any change in the relationship between the actor and an object while the object is on the screen (e.g., changing the position of an object is an actor–object interaction, holding that object in the same position and manner is not).² One model was calculated for each individual. For accuracy, logistic regression coefficients for the effects of delay and presentation boundaries were obtained. The *t* tests evaluated the statistical significance of the logistic regression coefficients. Post hoc tests were performed on the logits of accuracy. For response times, residuals from linear regression models were analyzed with ANOVA. For the figures, accuracy was estimated for an “average” old object for each trial and individual. Estimates of the probability of a correct response on each trial and its associated response time were obtained by multiplying the appropriate regression coefficients from the individual regression models by the two mean-matching time values, the mean of the actor–object interaction variable, the mean object size, the mean object eccentricity, and the dummy variables coding object test condition.

BOLD data were analyzed using the general linear model (GLM) and an assumed hemodynamic response function (Boynton, Engel, Glover, & Heeger, 1996). Regressors in the GLM modeled each type of object test (one per condition, duration = response time³), each type of nontest control (one per condition, duration matched to tests in corresponding conditions), event tests (duration = response time), movie presentation (duration = clip length), linear drift in the BOLD signal during each run, and baseline differences in BOLD signal across runs. The first four frames of BOLD data were dropped, and the remaining data were spatially smoothed with a Gaussian kernel (FWHM = 6 mm). For ROI analyses, one model was estimated per region per participant. For whole-brain analyses, one model was estimated per voxel per participant. In the whole-brain analysis, regions were defined as a set of contiguous voxels,

and the percent signal change under each condition of the object test was estimated for each region.

Identification of ROIs

Using established protocols (Head, Snyder, Girton, Morris, & Buckner, 2005; Insausti, Insausti, Sobreviela, Salinas, & Martínez-Peñuela, 1998), one researcher traced each participant's right and left hippocampus (HPC) and parahippocampal gyrus (PHG) twice on coronal slices of the T1-weighted structural volumes. The HPC included the dentate gyrus and the subiculum. The PHG (including entorhinal, perirhinal, and posterior parahippocampus) was bounded by the white matter dorsally and by the collateral sulcus. Test–retest reliability was adequate (all intraclass correlations > .75). A motion-sensitive region in extrastriate cortex (MT+) was identified using data from another study. For that study, 28 participants were shown displays of moving dots (translating motion) and still dots for 1 sec. Moving dot displays were presented in low and high contrast. Right MT+ was defined as voxels in the right lateral posterior temporal cortex that were more active during moving dot displays than during still dot displays across participants ($p < .05$, $z \geq 4.0$, cluster size ≥ 5 voxels).

A third ROI in the inferior parietal lobule (iIPL) was identified independently of the current data set using coordinates of bilateral lateral inferior parietal regions reported by Vincent et al. (2006). In their study, Vincent et al. identified brain regions whose resting state activity correlated with seed regions in the HPC. Subsequent analyses confirmed that these regions showed standard old/new and remember/know effects in recognition memory. iIPL regions were defined as all voxels within 9 mm of the voxel with the peak resting state correlation in the IPL (left iIPL: $-39 -73 42$; right iIPL: $45 -69 40$; Vincent et al., 2006).

RESULTS

Behavioral Data

Participants accurately responded to the event tests and the postclip comprehension questions, indicating that they were attending to the activities presented in the movies. Mean accuracy for the event tests was 0.946 ($SD = 0.061$), with an average median response time of 3.27 sec ($SD = 0.854$). Mean accuracy and response times for the post clip

comprehension questions were 0.870 ($SD = 0.076$) and 7.05 sec ($SD = 1.54$).

According to EST, the perception of an event boundary should lead to increased perceptual processing and the construction of a new mental model describing the current situation. If this is the case, then boundary objects are more likely to be encoded into episodic memory than are nonboundary objects. In addition, EST claims that active memory is cleared at event boundaries. As a result, recognizing objects across events should depend on episodic memory representations. Furthermore, because related information is no longer in active memory to interfere with retrieval, objects encoded into episodic memory may be better remembered when they are tested across events rather than within events (cf. Kuhl et al., 2007). EST therefore predicts an interaction between presentation boundaries and delay boundaries: Both nonboundary and boundary objects should be recognizable when tested within events, but only those objects that are encoded into episodic memory (likely for boundary objects but not for nonboundary objects) should be available in memory when they are tested across events.

Figure 1C illustrates recognition test accuracy for the four object test conditions. The data support EST's predictions: When an event boundary occurred during the 5-sec delay between presentation and test, accuracy for nonboundary objects declined, $t(27) = -3.68$, $p = .001$, and accuracy for boundary objects increased, $t(27) = 6.12$, $p < .001$, resulting in a reliable interaction between event boundaries during the delay and event boundaries during object presentation: odds ratio = 1.51, mean logistic regression coefficient = 0.41, $SD = 0.44$, $t(27) = 4.9$, $p < .001$; main effect of presentation boundaries: odds ratio = 1.44, mean logistic regression coefficient = 0.14, $SD = 0.33$, $t(27) = 2.22$, $p < .04$; main effect of delay boundaries: odds ratio = 1.25, mean logistic regression coefficient = .22, $SD = 0.33$, $t(27) = 3.58$, $p < .002$. An analysis of response times (Table 1) indicated that differences in response accuracy across the four test conditions did not result from a speed accuracy trade-off. Responses were fastest when boundary objects were tested across events, slowest when boundary objects were tested within events, and comparable in the remaining two conditions. This pattern produced a reliable main effect of delay boundaries, $F(1, 27) = 7.27$, $p < .01$, $\eta_p^2 = .213$ and an interaction between delay- and presentation-boundaries, $F(1, 27) = 5.59$,

Table 1. Mean and Standard Deviation (in Parentheses) of Response Times, in Seconds, to Object Tests

	<i>Within Events</i>		<i>Across Events</i>	
	<i>Nonboundary</i>	<i>Boundary</i>	<i>Nonboundary</i>	<i>Boundary</i>
Raw mean	3.27 (0.72)	3.44 (0.74)	3.29 (0.58)	3.15 (0.69)
Average object	3.32 (0.75)	3.48 (0.78)	3.30 (0.58)	3.08 (0.62)

Average object response times were derived from the linear regression models of individual participants data (see Data analysis section) using the mean object size, mean actor–object interactions, mean object eccentricity, and mean-matching times of all the old objects.

$p < .025$, $\eta_p^2 = .172$; the main effect of presentation boundaries was not reliable.

There are two striking aspects of these data. First, recognition accuracy was low and near chance for nonboundary objects that were tested across events but well above chance for nonboundary objects tested within events. This effect is wholly consistent with the predictions derived from EST. According to EST, nonboundary objects are not likely to be stored in episodic memory, and anything not stored in episodic memory should be difficult to recognize after an event boundary. Second, the occurrence of an event boundary during the 5-sec delay between presentation and test was associated with greater recognition accuracy for boundary objects. This difference may be due to the fact that within event and across event, tests occurred at different times relative to the beginning of the current event (or the most recent event boundary). Additional information may be acquired and stored in active memory as an event progresses. Cognitive load and interference from information stored in active memory therefore should be greater later in an event, when within event tests occurred, than earlier in an event, when across event tests occurred. After the clearance of active memory at delay boundaries, decreases in cognitive load and interference would enhance recognition memory for boundary objects, which are likely to be stored in episodic memory, but not for nonboundary objects, which should be less available for retrieval. Additional research is needed to determine whether interference and cognitive load can account for better recognition of boundary objects tested across events than those tested within events. Importantly, however, the data were consistent with predictions derived from EST and replicated data from previously reported experiments (Swallow et al., 2009).

Imaging Data

If retrieval across events relies on episodic memory, then brain regions involved in episodic memory retrieval should be more active when an object is retrieved across events than when it is retrieved within an event. Such regions include the HPC and the PHG. These regions have been tied to the encoding and successful retrieval of domain general relational information about an episode and to the encoding and successful retrieval of context, scene, and layout information, respectively (Davachi, 2006; Hannula, Tranel, & Cohen, 2006; Dobbins, Rice, Wagner, & Schacter, 2003). Because HPC and PHG show greater increases in activity when encoding context is successfully retrieved from episodic memory (Dobbins et al., 2003), EST predicts that they should show larger increases in activity when boundary objects are tested across events (and purportedly retrieved from episodic memory) than within events. We defined anatomical ROIs for the left and right HPC and PHG (Head et al., 2005; Insausti et al., 1998) and used a GLM to estimate, for each participant, the degree to which BOLD activity in these regions differed across the four types of object

tests. These estimates were then submitted to a repeated measures ANOVA with four factors: event boundaries during object presentation, event boundaries during the delay interval, brain hemisphere, and anatomical region.

Estimated BOLD activity in the HPC and PHG during the four different types of object tests is illustrated in Figure 2. Overall, the PHG was more active during retrieval than was the HPC, main effect of region $F(1, 27) = 46.8$, $p < .001$. However, the PHG and the HPC showed a similar pattern of activity across the four object tests. As can be seen in Figure 2, both the HPC and the PHG were more active during retrieval across events than during retrieval within events, but only when boundary objects were tested, resulting in a reliable Delay Boundary \times Presentation Boundary interaction, $F(1, 27) = 7.42$, $p = .011$, and a main effect of delay boundaries, $F(1, 27) = 8.96$, $p = .006$. Delay and presentation boundaries did not reliably interact with hemisphere or region, largest $F(1, 27) = 1.94$, $p = .175$. Of critical importance, however, was whether retrieval-related activity in the HPC and PHG was greatest when boundary objects were retrieved across events than that in the other three test conditions. This was the case in the HPC where activity was greater when boundary objects were retrieved across events than that in the other three test conditions, smallest $t(27) = 3.46$, $p = .002$. In the PHG, activity was reliably greater when boundary objects were retrieved across events than when they were retrieved within events and when nonboundary objects were retrieved across events, smallest $t(27) = 2.11$, $p = .044$. The difference in activity for boundary objects retrieved across events and nonboundary objects retrieved within events was not reliable

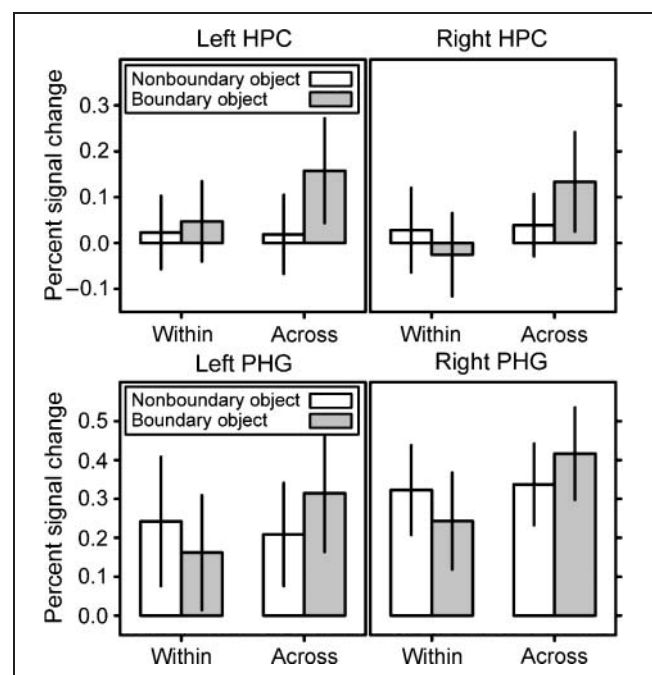


Figure 2. Activity in anatomical ROIs defined for the bilateral HPC and PHG varied across the four types of object recognition tests. Error bars indicate 95% confidence intervals.

in the PHG, $t(27) = 1.61, p = .119$. Thus, the HPC showed the largest increases in activity in the condition in which the objects should have been successfully retrieved from episodic memory. The PHG also increased in activity most when successful retrieval from episodic memory was expected, although this effect was reliable in only two of the three comparisons.

To further evaluate whether episodic retrieval systems are more engaged when retrieving objects across events than within events, we conducted a voxel-wise whole-brain analysis. As with the ROI analysis, responses for each participant were estimated using a GLM that included contrasts for each type of test. Model estimates were submitted to a 2×2 ANOVA with event boundaries during object presentation and event boundaries during the delay as within-participants factors and participant as a random effect. F values were sphericity corrected and converted to z values. The map-wise false-positive rate was held to $p < .05$ ($z \geq 4.0$, cluster size ≥ 4 voxels; McAvoy, Ollinger, & Buckner, 2001). The resulting regions are listed in Table 2.

As illustrated in Figure 3, regions in the bilateral MTL (Brodmann's area [BA] 35/36), the MPC, including bilateral precuneus (BA 31/18) and left posterior cingulate cortex (PCC; BA 23/31), and the right IPL (rIPL, BA 19) were more active during retrieval across events than during retrieval within events, smallest $F(1, 27) = 79.6, p < .001$. This delay boundary effect interacted with the effect of event boundaries during object presentation in the right MTL, left PCC, and rIPL, smallest $F(1, 27) = 6.75, p = .015$. Although the delay boundary effect was larger for boundary objects than for nonboundary objects, Tukey's post hoc tests confirmed that it was also reliable for nonboundary objects (marginal for nonboundary objects in PCC, $qs = 3.56, p = .079$; smallest $qs = 4.55, p = .017$ for all others). These data indicate that when an event boundary occurred during the 5-sec delay between object presentation and test, attempts to retrieve both boundary and nonboundary objects engaged the MTL, MPC, and rIPL.

Another region in the rIPL showed a reliable interaction between delay boundaries and presentation boundaries (Figure 4). This region was medial and superior to the rIPL region that exhibited a main effect of delay boundaries. It showed a pattern of activity very similar to that observed in the anatomically defined HPC: Changes in activity were greatest when boundary objects were retrieved across events, smallest $t(27) = 5.79, p = .001$. However, for nonboundary objects, there was no significant effect of whether they were tested within or across events, $t(27) = -1.03, p = .31$.

To further explore the relationship between the activity in the HPC and the IPL during the object tests, regions in bilateral IPL were independently defined using coordinates reported in another study (iIPL; see Methods; Vincent et al., 2006). Although activity in the HPC was greater than activity in the iIPL (which decreased in activity for most conditions; see Table 3), $F(1, 27) = 7.4, p < .011$, the overall pattern of activity in these regions was similar across test conditions (Presentation Boundary \times Delay Boundary \times

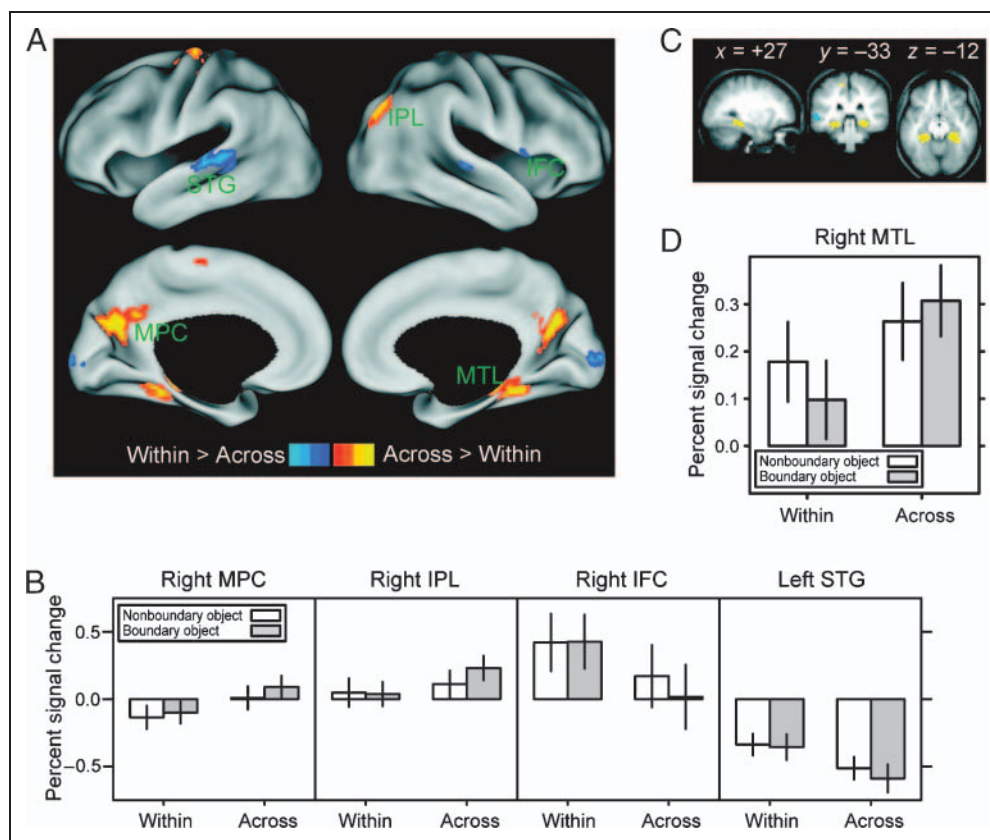
Table 2. Regions Whose Activity Varied across the Four Object Tests

<i>Cortical Region</i>		<i>BA</i>	<i>Center of Mass</i>
<i>Main Effect of Event Boundaries during the Delay</i>			
Precentral sulcus	Left	4	-20, -21, 58
Precentral gyrus	Left	4	-34, -28, 42
Inferior frontal cortex	Right	44/6	55, 6, 3
Precuneus	Left	31/18	-13, -62, 21
	Right	31/18	15, -57, 23
Posterior cingulate	Left	23/29/30	-16, -48, 6
IPL	Right	40/39	38, -72, 32
MTL	Left	35/36	-24, -39, -11
	Right	35/36	26, -38, -10
Superior temporal gyrus	Left	22	-58, -29, 1
	Left	41/42	-55, -43, 4
	Right	22	57, -25, 1
Cuneus	Both	18	0, -93, 0
Cerebellum	Left		-14, -41, -39
	Right		12, -48, 6
<i>Main Effect of Event Boundaries during Object Presentation</i>			
Precentral sulcus	Left	6	-17, -30, 51
IPL	Right	40/39	41, -63, 39
	Left	40/39	-41, -68, 36
Precuneus	Both	31/18	1, -67, 31
Posterior cingulate	Right	23/29/31	5, -45, 26
Angular gyrus	Right	22	56, -43, 18
Temporal occipital cortex	Left	39/37	-42, -68, 6
Lateral occipital cortex	Left	18	-28, -89, 8
	Right	18	31, -85, 13
Medial occipital cortex	Both	19	8, -93, 23
<i>Interaction</i>			
Precuneus	Right	31	5, -38, 38
Intraparietal sulcus	Left	39/7	-38, -56, 42
IPL	Right	40/39	36, -65, 41
Temporal occipital cortex	Left	39/37	-41, -70, 5
	Right	39/37	46, -69, 10
Lingual gyrus	Left	18	-4, -82, -10
Cerebellum	Right		7, -58, -36

Center of Mass is in (x, y, z) coordinates.

Figure 3. Retrieval-related activity in a network of regions was associated with whether an event boundary occurred during the 5-sec delay.

(A) Regions more active during retrieval across events than within events are in yellow; regions more active during retrieval within events than across events are in blue (mapped to PALS atlas with CARET; Van Essen, 2002, 2004). (B) Percent signal change during tests in four conditions for representative regions. (C) Slices showing the regions in the MTL on the average anatomy of participants. (D) Percent signal change, plotted as for (B). Error bars indicate 95% confidence intervals.



Region interaction was not reliable), $F(1, 27) = 1.08, p = .31$. Activity in bilateral HPC and iIPL was greatest when boundary objects were tested across events and similar in the remaining three test conditions, Presentation Boundary \times Delay Boundary interaction, $F(1, 27) = 16.3, p < .001$; main effect of presentation boundary, $F(1, 27) = 24.0, p < .001$; main effect of delay boundary, $F(1, 27) = 5.15, p = .031$. The main effect of presentation boundaries was stronger in the iIPL than that in the HPC, $F(1, 27) = 17.7, p < .001$.

Because event segmentation is accompanied by a transient increase in activity in medial parietal regions of the brain as well as in extrastriate regions (Zacks et al., 2001), it is possible that some of the observed effects of delay boundaries on activity reflect processing that would have occurred in the absence of retrieval attempts. A second analysis examined activity during the period that occurred 5 sec after untested objects were presented (when tests normally occurred, *nontest control period*). Activity during the nontest control period was analyzed according to whether event boundaries occurred during object presentation and during the 5-sec period that followed presentation. In addition, we defined a control region in a motion-sensitive region of right extrastriate cortex (MT+) that transiently increases in activity at event boundaries (Zacks et al., 2001). Estimates of percent signal change in the test and nontest control periods are reported in Table 3. The independent variables did not reliably interact during the nontest control period in the HPC, PHG, and

MT+ ROIs, largest $F(1, 27) = 1.04, p = .317$. For the regions identified through the whole-brain analysis (MTL, MPC, and rIPL), ANOVAs on BOLD activity after tested and untested objects showed that the delay boundary effect was greater during tests than during the nontest control period (interaction), smallest $F(1, 27) = 16.7, p = .001$. Thus, the selective pattern of responses in the HPC, PHG, MTL, MPC, and rIPL during retrieval likely reflects retrieval-related processing rather than ongoing event processing.

DISCUSSION

If event boundaries mark when active memory for the current event is reset and updated, then retrieving information from the event just before the current one should engage episodic memory systems (Zacks et al., 2007). Therefore, the MTL, MPC, and IPL should be more active when objects are tested across events than when they are tested within events. The data support this claim. The MTL, which includes the HPC and the PHG, was differentially engaged in retrieval as a function of when event boundaries occurred in the clips. Activity in the bilateral MTL, bilateral MPC, and rIPL was greater when boundary and nonboundary objects were tested across events than when they were tested within events. Furthermore, the HPC and a region in the rIPL were most active when boundary objects were tested across events, the condition in which successful retrieval from episodic memory was predicted.

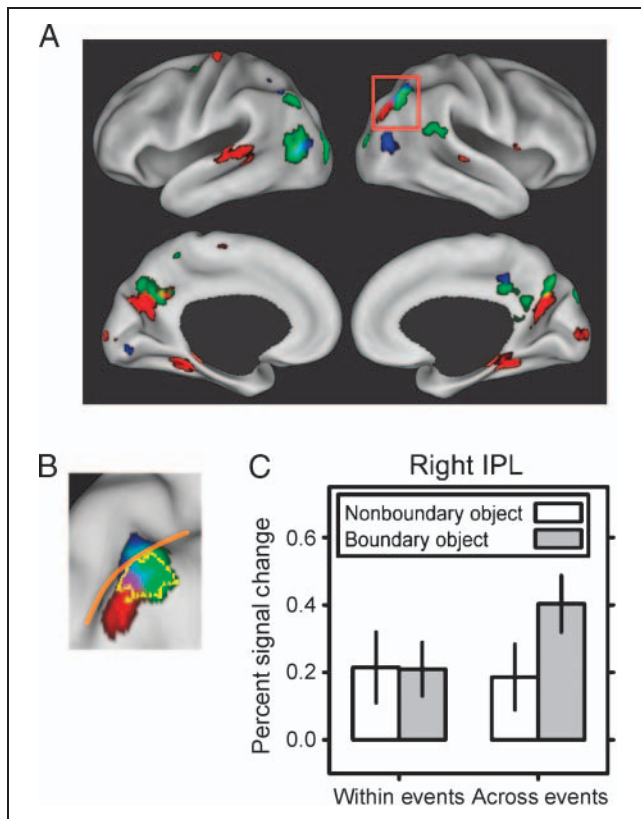


Figure 4. Regions showing the delay boundary effect, the presentation boundary effect, and an interactive effect of these two factors. (A) Regions whose activity differed between within- and across-event retrieval (red) were largely separate from those whose activity changed when an event boundary occurred during object presentation (green) and those whose activity depended on the interaction of these factors (blue). Overlap is shown in yellow, magenta, and light blue. (B) Retrieval-related activity in several adjacent regions in the rIPL (outlined in the red box in panel A and shown here from a dorsal posterior angle) immediately ventral to the posterior intraparietal sulcus (marked in orange) differed along the delay and presentation boundaries factors as well as their interaction. The yellow outline indicates the iIPL ROI defined by coordinates from a study of resting state activity in the HPC (Vincent et al., 2006). (C) Activity in the rIPL region that showed an interactive effect of delay and presentation boundaries mirrored recognition test accuracy (blue region in panel B), changing most when boundary objects were tested across events. Error bars indicate 95% confidence intervals.

These differences in activity were observed despite the fact that other potentially confounding factors were held constant (i.e., 5-sec delay between object presentation and test, equivalent testing conditions, and presumably equivalent retrieval strategies).

Retrieving Objects across Events Engages Episodic Memory Systems

Activity in the MTL, MPC, and rIPL has been repeatedly observed in neuroimaging studies of episodic memory retrieval and during the recollection of encoding context, objects, words, and visual scenes (Ciaramelli, Grady, & Moscovitch, 2008; Summerfield, Lepsien, Gitelman, Mesulam,

& Nobre, 2006; Wagner, Shannon, Kahn, & Buckner, 2005; Dobbins et al., 2003). The HPC, PHG, and rIPL are also more active when participants search for targets in visual scenes that they have previously encountered, indicating that they may be involved in retrieving the locations of objects in scenes from memory (Summerfield et al., 2006). In addition, during an episodic retrieval task, activity in an IPL region whose resting state activity is correlated with that in the MTL was greater when participants reported remembering an item than when they reported that they were familiar with the item (Vincent et al., 2006). This IPL region was similar in location to the rIPL region that was selectively active when both boundary and nonboundary objects were tested across events (Figures 3 and 4). Moreover, like the HPC, activity in bilateral IPL regions defined using coordinates from Vincent et al. (2006) was greatest when boundary objects were tested across events and similar for the remaining three types of object tests. Activity in the IPL has been associated with a variety of retrieval phenomena, including the adoption of a task set for episodic retrieval, successful recollection of an earlier experience from episodic memory, and reporting that a test item was previously studied (Ciaramelli et al., 2008; Wagner et al., 2005). The involvement of these regions in retrieval across events converges with the behavioral data and the anatomical ROI analyses, suggesting that retrieval across events relies on episodic memory systems. It is therefore plausible that the MTL, MPC, and rIPL were engaged when objects were retrieved across events to reinstate the previous event in memory.

The observed pattern of activity in the IPL, PHG, and HPC does not simply reflect successful recognition of the object being tested. In this experiment, recognition accuracy was best when boundary objects were tested across events, moderate when boundary objects and nonboundary objects were tested within events, and worst when nonboundary objects were tested across events (Figure 1C). Activity in the HPC and a region in the rIPL (Figure 4B, light blue) was also greatest when boundary objects were tested across events. However, BOLD activity in these regions was similar when objects were tested within events and when nonboundary objects were tested across events. Activity in these regions did not distinguish between objects that were recognized at near chance levels (nonboundary objects that were tested across events) and objects that were recognized moderately well (objects that were tested within events).

Rather, the data more closely conform to EST's prediction that successful retrieval from episodic memory should only occur when boundary objects are tested across events. According to EST, episodic retrieval should not be necessary when objects are retrieved within events. Any region whose activity reflects retrieval success from episodic memory should therefore show the largest increases in activity when boundary objects are tested across events and should not differentiate between the other three conditions. The pattern of activity in the HPC and rIPL, both of which have

Table 3. Mean and Standard Deviation of Percent Signal Change in ROIs

Region		Test				Nontest Control			
		Within Events		Across Events		Within Events		Across Events	
		NBO	BO	NBO	BO	NBO	BO	NBO	BO
HPC	L	0.02 (0.21)	0.05 (0.23)	0.02 (0.22)	0.16 (0.29)	-0.01 (0.2)	0 (0.15)	0.08 (0.13)	0.02 (0.16)
	R	0.03 (0.24)	-0.03 (0.23)	0.04 (0.17)	0.13 (0.28)	0 (0.2)	-0.01 (0.13)	0.01 (0.14)	0 (0.19)
PHG	L	0.24 (0.43)	0.16 (0.38)	0.21 (0.34)	0.31 (0.39)	-0.02 (0.3)	0.11 (0.31)	0.09 (0.2)	0.05 (0.17)
	R	0.32 (0.3)	0.24 (0.32)	0.34 (0.27)	0.42 (0.31)	0.03 (0.2)	0.01 (0.22)	0.01 (0.21)	0.06 (0.18)
MT+	R	-0.64 (0.57)	-0.57 (0.52)	-0.55 (0.51)	-0.7 (0.56)	0.01 (0.2)	-0.03 (0.21)	-0.03 (0.18)	0.02 (0.2)
PreC	L	0.18 (0.11)	0.1 (0.19)	0.26 (0.14)	0.31 (0.21)	0.05 (0.1)	0.03 (0.21)	0.03 (0.14)	0.01 (0.22)
	R	-0.12 (0.09)	-0.07 (0.14)	0.01 (0.1)	0.09 (0.16)	0.07 (0.12)	-0.08 (0.16)	-0.01 (0.12)	0 (0.17)
PCC	L	-0.14 (0.13)	-0.1 (0.22)	0.01 (0.12)	0.09 (0.21)	0.04 (0.16)	-0.1 (0.22)	-0.04 (0.15)	-0.02 (0.22)
IPL	R	-0.08 (0.08)	-0.11 (0.2)	-0.01 (0.1)	0.06 (0.23)	0.03 (0.11)	-0.02 (0.22)	0.00 (0.13)	0.04 (0.19)
MTL	L	0.05 (0.13)	0.04 (0.23)	0.11 (0.14)	0.23 (0.23)	0.01 (0.11)	-0.01 (0.26)	-0.04 (0.14)	0.04 (0.27)
	R	0.16 (0.1)	0.12 (0.26)	0.27 (0.13)	0.3 (0.25)	0.01 (0.11)	0.06 (0.27)	0.02 (0.14)	0.01 (0.29)
iIPL	L	-0.14 (0.45)	-0.06 (0.38)	-0.22 (0.43)	0.05 (0.38)	0.02 (0.31)	-0.06 (0.26)	-0.05 (0.22)	-0.06 (0.3)
	R	-0.21 (0.5)	-0.15 (0.33)	-0.29 (0.41)	0.04 (0.27)	0.02 (0.24)	-0.09 (0.22)	-0.1 (0.29)	-0.06 (0.3)

NBO = nonboundary object; BO = boundary object; L = left; R = right; HPC = hippocampus; PHG = parahippocampal gyrus; MT+ = putative human analog to motion-sensitive middle temporal cortex in monkey; PreC = precuneus; PCC = posterior cingulate cortex; IPL = inferior parietal lobe; MTL = medial temporal lobe; iIPL = independently identified IPL region defined by coordinates from Vincent et al. (2006).

been associated with retrieval success from episodic memory (Ciaramelli et al., 2008; Vincent et al., 2006; Wagner et al., 2005; Dobbins et al., 2003), is consistent with this prediction.

Implications for Episodic Memory

Current theories of memory suggest that at least three factors may affect which brain systems are involved in holding a piece of information in memory at a given moment in time: the *type* of information maintained in memory (e.g., words vs. faces), the *amount of time* that has elapsed since the information was encountered, and the *amount of intervening information* encountered in that period (Johnson & Rugg, 2007; Baddeley & Logie, 1999; Anderson & Neely, 1996). Recent data show that the HPC, once thought to be selectively involved in long-term episodic memory, is also necessary for retaining relational information over short periods (Hartley et al., 2007; Hannula et al., 2006; Olson, Moore, Stark, & Chatterjee, 2006). These data have reignited the debate about the relationship between episodic memory and active memory (Jonides et al., 2008; Shrager, Levy, Hopkins, & Squire, 2008; Olson et al., 2006), supporting claims that it is the *type* of information maintained in memory that is most important for predicting whether the MTL are involved in its maintenance and retrieval. However, a growing number of studies also show that the involvement of the HPC in retrieval reflects the

occurrence of *any intervening information* between encoding and retrieval (Jonides et al., 2008; Öztekin, McElree, Staresina, & Davachi, 2008; Hartley et al., 2007; Hannula et al., 2006; Olson et al., 2006; Cowan, 1999). In one study, Öztekin et al. (2008) presented a list of five consonants to participants and immediately afterward administered a two-alternative recognition test on one of the consonants. When the last item in the list was tested, activity in the HPC was significantly lower than it was when the tested item was presented in an earlier position. These data indicate that the HPC is involved in retrieval when any amount of information, even a single consonant, intervenes between encoding and retrieval.

Our data provide a unique perspective on the role of the HPC and MTL in memory. In this experiment, the type of information that was tested and the delay between object presentation and test were constant across conditions. In addition, because the film continued during the 5-sec delay between object presentation and test, some amount of intervening information occurred in all conditions. What differentiated the conditions was whether an event boundary occurred during the delay and whether an event boundary occurred during object presentation. Despite the fact that the same amount of time had elapsed and information was continuously presented during the delay, the HPC and the MTL were most active during retrieval when an object had to be retrieved across an event boundary. Therefore, these data suggest that the involvement of the HPC and MTL in memory retrieval depends not just on how much time has

elapsed or how much intervening material has been presented but also on whether a new event has begun since the information was encoded.

Although the present study examined memory retrieval, these results have implications for the encoding of episodic memories. A parsimonious proposal is that, as a result of the memory updating, successive events may constitute qualitatively different context signals. These context signals may be used to discriminate the events in episodic memory (Polyn & Kahana, 2008). Thus, event segmentation may determine the elementary units of episodic memories. If so, abnormal segmentation patterns should be associated with poorer memory for events. Indeed, memory for events is disrupted both in individuals who abnormally segment events (Zacks, Speer, Vettel, & Jacoby, 2006) and when experimental manipulations interfere with normal segmentation (Schwan & Garsoffky, 2004; Boltz, 1992). Elementary episodic memory units may be quickly forgotten or integrated into larger knowledge structures that represent knowledge goals and event structure (Conway, 2009). Research on autobiographical memory indicates that such integration is critical for delayed recall (Conway, 2009).

The data from this experiment also suggest an intriguing relationship between memory deficits associated with MTL lesions and the way perceived events are structured in time. Patients suffering lesions in the MTL demonstrate a marked impairment in the ability to remember a recent event after a brief delay (Stefanacci, Buffalo, Schmolck, & Squire, 2000). In particular, HPC damage leads to impairments in remembering the spatial, temporal, and associative relations among items (Konkel, Warren, Duff, Tranel, & Cohen, 2008; Hannula et al., 2006), all of which may be important components of the mental representations of ongoing events (Zacks et al., 2007). The present data indicate that when an event is segmented, retrieving information encountered before segmentation engages the MTL. Although this does not mean that the MTL are necessary for retrieval across event boundaries, it does suggest that event segmentation may influence when amnesiacs lose track of recent events. Specifically, patients with MTL damage may retain information about an ongoing event until the event changes. Because event segmentation has been previously associated with changes in high-level conceptual features of activity (e.g., an actor putting an object down, walking to a new spatial location, or changing his or her goals; Speer, Zacks, & Reynolds, 2007) and changes in low-level perceptual features of an activity (e.g., object velocity; Zacks, 2004), conceptual and perceptual changes in events could influence when amnesiacs are more likely to forget what just happened.

Conclusion

Information does not continuously move into and out of active memory. Rather, the present data indicate that what one remembers and for how long depends on when events are segmented as well as subsequent input. The data are

consistent with studies showing that the MTL are involved in retrieving study items over both short and long delays (Hannula et al., 2006; Olson et al., 2006). Beyond this, they offer insight into when episodic retrieval systems are involved in retrieval and when they are not. Indeed, the data point to the conceptual and perceptual changes in events that correspond to event boundaries (e.g., an actor putting an object down or changing his or her goal state; Speer et al., 2007; Zacks, 2004) as important factors in determining when people will likely forget what has just happened.

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Notes

1. Thematic relevance of the object to the scene, thematic relevance of the foil to the scene, and semantic relatedness of the target and foil to each other were also examined. These variables were not reliably related to recognition test accuracy ($r_s < .04$), $t(33) < 0.22$, $p > .83$, and were not included as covariates in the behavioral data analysis.
2. A more inclusive variable coding whether any actor in the scene touched the object was also obtained. This variable was less strongly related to recognition test accuracy ($r = .30$) than was the actor-object interactions variable ($r = .46$). Because of the high degree of overlap in these variables, only the variable that served as the strongest predictor of recognition test accuracy was included as a covariate in the analysis.
3. Response times to the object tests varied across conditions (see Table 1) and ranged from a mean minimum of 1.53 sec ($SD = .221$ sec) to a mean maximum of 6.41 sec ($SD = 1.94$ sec). The hemodynamic response function was extended by response times to account for this variability. A second analysis in which the HRF was not extended by RT was also conducted and yielded data consistent with those reported here.

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