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Perceptual boundaries cause mnemonic trade-offs between local boundary processing and across-trial associative binding

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Abstract

Episodic memories are not veridical records of our lives, but rather are better described as organized summaries of experience. Theories and empirical research suggest that shifts in perceptual, temporal and semantic information lead to a chunking of our continuous experiences into segments, or 'events'. However, the consequences of these contextual shifts on memory formation and organization remains unclear. In a series of three behavioral studies, we introduced context shifts (or 'event boundaries') between trains of stimuli and then examined the influence of the boundaries on several measures of associative memory. In Experiment 1, we found that perceptual event boundaries strengthened associative binding of item-context pairings present at event boundaries. In Experiment 2, we observed reduced temporal order memory for items encoded in distinct events relative to items encoded within the same event, and a trade-off between the speed of processing at boundaries, and temporal order memory for items that flanked those boundaries. Finally, in Experiment 3 we found that event organization imprinted structure on the order in which items were freely recalled. These results provide insight into how boundary- and event-related organizational processes during encoding shape subsequent representations of events in episodic memory.

Keywords

episodic memory; event boundaries; temporal order memory; associative memory

Introduction

Although our experiences unfold in a forward and continuous manner, our memories for those experiences are structured and organized around specific events. For example, imagine spending a night out in New York City. You might go out to dinner with friends, stop at a bar for a cocktail, and then proceed to an evening concert. Prior research suggests that the experiential details within a specific event (i.e. dinner, bar, or concert) are more tightly linked in memory than details experienced in distinct events (Dubrow & Davachi, 2013; Ezzyat & Davachi, 2011). One possible explanation for this finding is that associative processes that serve to link adjacent representations of an event are enhanced when

contextual aspects of an experience are shared across time. Thus, the contents of a memory may be structured and grouped by the context in which the experience occurred. However, it is also known that contextual novelty is beneficial for some forms of encoding and, thus, memory may also benefit from distinctiveness in contextual representations (Ranganath & Rainer, 2003; Restorff, 1933). Across a series of studies, we aimed to understand how contextual stability and distinctiveness both benefit memory. Specifically, the work is focused on elucidating the different forms of associative memory that might benefit from shared and distinctive context.

A large body of prior work supports the idea that organizational processes engaged at encoding modulate the structure of our memories for those experiences (Atkinson & Shiffrin, 1971; Farrell, 2012; Lee & Estes, 1981; Lehman & Malmberg, 2013; Miller, 1956; Murdock, 1983; Raaijmakers & Shiffrin, 1981). One computational account for how this occurs suggests that the contents of our experiences are maintained in a limited-capacity buffer during encoding (Lehman & Malmberg, 2009, 2013). Item and context representations that co-occupy the buffer become associatively bound. When those maintained representations are no longer of use to the participants, a 'compartmentalization' operation is hypothesized to clear the contents of the buffer. Thus, episodic 'events' may become bound in long-term memory as a downstream consequence of encoding-related organizational processes that compartmentalize information through a selective integration mechanism.

Another conceptually related framework called Event Segmentation Theory (EST) hypothesized that 'segmentation' processes parse ongoing experience into events and serve to guide efficient allocation of cognitive processing resources in the moment (Reynolds, Zacks, & Braver, 2007; Zacks, Speer, Swallow, Braver, & Reynolds, 2007). This model proposes that incoming perceptual information and prior experience are actively integrated in working memory to generate predictions about what is likely to occur in the near future. At event boundaries, when future input may be unpredictable or 'surprising', attention is drawn to novel perceptual features in the environment and the prior event model is abandoned. Prior behavioral and neuroimaging results support the notion that people can segment ongoing experience into events and do so in a similar fashion (Radvansky, 2012; Speer & Zacks, 2005; Swallow, Zacks, & Abrams, 2009; Zacks et al., 2001, 2007). Furthermore, there is evidence that information contained at event boundaries is better remembered than information contained within an event (Boltz, 1992; Newtson & Engquist, 1976; Schwan & Garsoffky, 2004).

While somewhat different in their implementation, both of these models make the unique and interesting prediction that shifts in context may lead to enhanced memory for boundary information at the expense of ongoing integration processes. Put another way, while event boundaries may lead to a memory enhancement for information encountered at the contextual shift, they may in fact have a detrimental effect on relational, or sequential, memory for pairs of items that flank that boundary due to an interruption of ongoing maintenance/integration processes. Prior research has typically focused on the positive effects of boundaries on item memory (Boltz, 1992; Newtson & Engquist, 1976; Schwan & Garsoffky, 2004). However, this series of experiments was designed to test the idea that

contextual shifts may be good for 'in-the-moment' (within-trial) associative memory encoding at the expense of across-trial sequential integration.

First, we predicted that items encountered at event boundaries would be more tightly bound to their context, as attention may be shifted away from the maintenance of previous 'within-event' information to the changing contextual features in the environment. While previous studies suggest that that item memory at boundaries may be boosted (Boltz, 1992; Newtson & Engquist, 1976; Schwan & Garsoffky, 2004), here we explore specifically whether these items are more tightly bound to their associated contexts at event boundaries. We addressed this question in our first experiment.

Second, we predicted that integration processes across contiguous items that share the same context (i.e. an 'event') will be enhanced relative to pairs of items that were encountered in neighboring events. Put another way, while event boundaries may lead to a memory enhancement for information encountered at the contextual shift, they may in fact have a detrimental effect on relational memory for pairs of items that flank that boundary due to an interruption of ongoing item-item integration processes. Recent work using narrative cued recall (Ezzyat & Davachi, 2011), recency discrimination for sequences of visual images (Dubrow & Davachi, 2013), and temporal proximity judgments (Ezzyat & Davachi, 2014) is consistent with this prediction, showing that several measures of associative memory reduced for pairs stimuli that flank an event boundary (compared to items within the same event).

Finally, we test whether these two memory effects are in fact related. Specifically, we test whether there is a trade-off between item-context processing at event boundaries and across-event integration processes, such that a stronger boundary effect may result in worse across-event integration. We hypothesize that, at boundaries, attentional resources are redirected from the integration/maintenance of previous within-event representations to changing features in the environment. In other words, the subjective strength of the event boundary should influence associative memory for pairs of items studied across that boundary, such that a 'larger' boundary should result in worse across event associative memory.

The present set of experiments was designed to test these predictions by assessing multiple forms of associative memory. In each of these experiments, participants encoded lists of object stimuli that were grouped into smaller mini-lists (i.e. events) by a shared background color. This simple perceptual manipulation of the background color allowed us to ask whether low-level perceptual shifts in context have consequences for later memory. In Experiment 1, we tested whether items at perceptual event boundaries are more strongly bound to their context (i.e. the color background), relative to trials where there was no contextual shift. In Experiment 2, we tested whether event structuring led to reduced binding between items encountered in distinct events vs. within events, and also whether the speed of processing at boundaries is related to the cost in across-event associative memory for pairs of items. Finally, in Experiment 3 we utilize a more naturalistic retrieval task (a free recall paradigm) to ask whether and how recall behavior is organized according to the event structure of the experiment.

Experiment 1: Perceptual boundaries facilitate object-color associative memory

In Experiment 1, we sought to understand how perceptual boundaries influence associative memory for the local information presented at boundaries. Participants encoded lists of objects that were embedded in a colored frame (Figure 1). On each trial, they were instructed to imagine the displayed object in the color of the background frame and to make a pleasant/unpleasant judgment on the object-color combination. Importantly, the color of the frame did not change for six consecutive trials before switching to a new background color. We operationalized an "event" as consecutive trials where the color of the frame stayed the same. After each encoding list, participants performed an object-color associative memory test. "Boundary" trials were defined as trials on which the presented color frame was different from the previous trial; "non-boundary" trials were all other trials (i.e. the presented color matched the color from the preceding trial). Boundary objects were therefore objects that were encoded concurrently with a color frame switch, while non-boundary objects were all other objects.

The goal of Experiment 1 was to assess whether perceptual event boundaries increased object-color associative memory. We predicted that the memory enhancement would be specific to the boundary object-color pair. A pattern of this nature would suggest a transient memory effect, perhaps driven by a boundary-driven allocation of attentional resources (Kurby & Zacks, 2008).

Methods

Participants—Participants were 26 individuals (ages 18–35) recruited from New York University and the greater New York Metropolitan Area. All participants gave informed written consent in accordance with the University Committee on Activities Involving Human Subjects (UCAIHS) and participated in exchange for monetary compensation. For all three experiments, the sample size was chosen based on a power analysis (power=.8, alpha=.05) of a separate study on boundary-related memory effects from (Dubrow & Davachi, 2013).

Materials—For all experiments, we used a stimulus set consisting of 576 gray-scale pictures of objects from various online databases. A subset of these stimuli was used for Experiment 1 (432 objects). Each one was resized to a fixed size of 350×350 pixels. To generate colors for the frames, 24 unique colors were selected from color continuum ranging from [0,0,0] to [255, 255, 255] RGB values. Lists of colors for each block were generated, such that no two colors that occurred consecutively at encoding could be perceptually similar. For example, if the previous event color was red, the next color could not be orange, but it could be blue or green. Furthermore, the same color could not appear in a list more than once and colors were recycled after every four lists. Stimulus order varied for each subject and stimulus-color pairings were randomized across subject.

Design and Procedure—Before the experiment began, there was a brief practice version of the experiment to ensure that participants understood the task. For each of 12 study lists, participants intentionally encoded lists of 36 trial-unique gray-scale objects that were

embedded on a colored frame. Participants were instructed to imagine the object in the color of the frame and decide if the object-color pair was pleasing. The participants were instructed to respond as soon as they made a pleasantness decision by pressing one of two buttons on the keyboard ('j' or 'k'). The color of the frame was identical for six consecutive objects before switching to a new color for the next six objects. An 'event' was defined as six consecutive objects with the same colored frame. There were six events per study list. On boundary trials, the frame color updated at trial onset (i.e. concurrently with the object). All other trials (event positions 2-6) were called non-boundary trials. Objects were presented for a fixed time of 2.5 seconds (s) with a fixed 2 s inter-trial interval (ITI) followed by a .5 s fixation cross before the onset of the next trial. The colored frame remained on the screen continuously during the presentation of each event (including the 2 s ITI and a .5 s fixation cross) and only changed concurrently with boundary objects. It is important to note that the objects remained on the screen for a fixed period of time (2.5 seconds). Thus, encoding response times in the rest of this manuscript refer to the amount of time it took for the participant to complete the pleasantness decision, not the duration that the stimulus was on the screen.

Following each encoding list, we tested object-color associative memory. To minimize recency memory effects, the test was structured such that objects presented in the first half of the experiment (1:18) were tested first and objects presented in the second half of the experiment (19:36) were tested second. However, within each half, the test trials were randomized. For each test trial, participants were shown a previously studied object with a grey border presented above two colors that were positioned on the left and right side of the computer screen (Figure 1). One of these colors (target) was originally paired with the object while the other color (lure) was always one of the colored frames that had immediately preceded or followed the target color at encoding. The lure was counterbalanced such that it was equally likely to precede or follow the target color. Targets and lures were also equally likely to appear in the left or right positions on screen. In one step, participants were asked to indicate which of the two colors had been paired with the object at encoding and also to indicate their confidence in their decision (high/low confidence, HC/LC). Thus, there were a total of 4 possible responses during the test (HC left color, LC left color, HC, right color, LC right color). Test trials were self-paced and advanced as soon as a response was given, with a fixed .5 s ITI between test trials. Half of the items in each encoding list were tested: We alternated between testing of even and odd trials on each list.

Results

Effect of perceptual boundaries on color memory performance—We found that memory for the object-color association varied as a function of event position [Figure 2; F(5,125)=4.27, p=.001, $\eta^2=.15$]. The position by confidence interaction was not significant [F(5,125)=1.28, p>.1], so we collapsed across high and low confidence trials. A planned contrast revealed that color memory was significantly better for the boundary condition compared to non-boundary conditions [t(25)=4.68, p<.001, Cohen's d=.41] and follow up pairwise t-tests show that memory for the boundary condition was significantly better than each non-boundary condition [1 vs. 2: t(25)=2.87, p=.008, Cohen's d=.33; 1 vs. 3: t(25)=3.44, p<.002, Cohen's d=.42; 1 vs. 4: t(25)=4.29, p<.001, Cohen's d=.42; 1 vs. 5:

t(25)=3.69, p=.001, Cohen's d=.40; 1 vs. 6: t(25)=3.5, p=.002, Cohen's d=.36]. Thus, object-color associative memory at boundaries was significantly enhanced relative to trials that are not studied at perceptual boundaries. Next, we asked whether perceptual boundaries also impacted RTs during the successful retrieval of the object-color associations. We found that RTs to correctly remembered trials varied as a function of event position [F(5,125) = 4.18, p=.001, η^2 =.143]. The position by confidence interaction was not significant, so we collapsed across confidence [F(5,125)=1.23, p>.1]. A planned contrast revealed that retrieval of items from the boundary condition was significantly faster than the non-boundary conditions [t(25)=2.95, p=.007, Cohen's d=.22]. Subsequent pairwise t-tests revealed that position 1 was significantly faster than positions 3, 4 and 6, and a trend for an effect for position 2 and 5 [1 vs. 2: t(25)=1.88, p=.07, Cohen's d=.18; 1 vs. 3: t(25)=2.15, p=.04, Cohen's d=.15; 1 vs. 4: t(25)=3.62, p=.001, Cohen's d=.22; 1 vs 5: t(25)=1.84, p=.08, Cohen's d=.20; 1 vs. 6: t(25)=3.56, p=.002, Cohen's d=.35]. Thus, during retrieval, RTs to correct boundary trials were speeded relative to non-boundary trials, suggesting that information studied at boundaries is more accessible than non-boundary information.

Encoding Response times—RTs during encoding varied as a function of event position $[F(5,115)=60.7, p<.001, \eta^2=.72]$. A planned contrast confirmed that RTs to boundary trials (event position 1) were significantly slower than those on non-boundary trials (positions 2–6; t(25)=9.52, p<.001, Cohen's d=2.86). Follow-up pairwise t-tests also show that boundary RTs are significantly slower than all other tested non-boundary positions [1 vs. 2: t(25)=9.5, p<.001, Cohen's d=.97; 1 vs. 3: t(25)=9.21, p<.001, Cohen's d=1.03; 1 vs. 4: t(25)=9.44, p<.001, Cohen's d=1.14, 1 vs. 5: t(25)=8.98, p<.001, Cohen's d=1.14; 1 vs. 6: t(25)=8.29, p<.001, Cohen's d=1.07].

Discussion

Experiment 1 revealed that associative memory was enhanced for trials that appeared at perceptual event boundaries. Prior studies that have reported better overall memory for information studied at event boundaries (Boltz, 1992; Newtson & Engquist, 1976; Schwan & Garsoffky, 2004), used clips from studied movies as retrieval cues and these cues taken from event boundaries contained more diagnostic information about the clips, which could ultimately account for the memory benefit. By contrast, in the present study, the only difference between the boundary and non-boundary conditions was a change in the color of the background frame in the boundary condition. Therefore, during retrieval, the amount of available perceptual information on each test trial was the same and so, any differential effects we see in boundary memory must be related to processes that occurred during encoding. Thus, the current finding is consistent with these prior results but importantly extend them to a situation where the retrieval content is matched, which implicates that processes that occur at the time of the boundary itself are responsible for enhancing memory for boundary information. In one relevant study, Swallow et al. (2009) found that memory for objects occurring at event boundaries was better than memory for non-boundary objects when object recognition memory was probed very shortly after (5 seconds) an event boundary, but not when memory was probed within the same event. The authors interpreted this effect to suggest that retrieving across event boundaries relies on the access of long-term item representations (as opposed to accessing working memory representations). They

reasoned that since EST predicts better encoding of boundary information into long-term memory, the recognition memory difference for boundary and non-boundary objects should be maximal when the test occurs after an event boundary. The results of the current experiment are consistent with the results of this prior study. However, our study is novel in a few critical ways: First, we test memory after a substantially longer delay (3-5 minutes as compared to 5 seconds). This confirms the claim that long-term boundary memory is enhanced, rather than a difference in working memory accessibility between boundary and non-boundary information. Second, we test associative memory between an object and its accompanying color background rather than item memory. Thus, our findings extend previous work to suggest that at event boundaries, items are more strongly bound to their context (i.e. the color background). Finally, while the previous study used naturalistic movies as their stimuli, we opted for a simpler stimulus set consisting of objects and color backgrounds. While there are undoubtedly benefits to using naturalistic stimuli, our choice of simple object and color associations allowed us to carefully control for the quantity and quality of information available at event boundaries. Thus, the current experiment supports and extends previous work on boundary-related memory enhancements.

Another related study showed that switching encoding tasks midway through a short list of words resulted in a significant increase in the free recall of words that followed the task switch (specifically, n and n+1) relative to recall of items (in the same serial position) of a control list with only one task (Polyn, Norman, & Kahana, 2009b). Although interpreted as evidence for the notion that task context serves as a retrieval cue, the task switch may have additionally acted as an event boundary thus, facilitating the encoding of words that followed it. While the effect reported in (Polyn et al., 2009b) compared lists containing a task switch to lists with no task switch, the boundary-related memory enhancement reported here is relative to other non-boundary items within the same list (as opposed to lists with no boundaries). Another notable difference between the studies is that Polyn utilized a free recall task to probe memory, whereas, in the current study, we used a forced-choice associative recognition test. If free recall of the boundary item 'reinstates' its associated temporal (Howard & Kahana, 2002; Polyn, Norman, & Kahana, 2009a) or source (Frost, 1971; Hintzman, Block, & Inskeep, 1972; Murdock & Walker, 1969; Nilsson, 1974; Polyn et al., 2009b) context, the context reinstatement could act as a cue to facilitate retrieval of neighboring items, and result in enhanced memory for items that neighbored the boundary item. Thus, the enhancement of items following the boundary item in the free recall study could be driven by organizational processes during retrieval, rather than boundary-driven segmentation during encoding. In contrast, retrieval processes are unlikely to interact with the boundary enhancements reported in the current study because we probed associative recognition memory and the amount of retrieval content was matched between conditions. However, importantly, both studies employ a shift in processing during study to evoke a boundary and see that information encountered at a boundary are more likely to be remembered.

This enhancement in memory observed at event boundaries is also reminiscent of the Von Restorff effect, the empirical finding that items with features that are novel within the local context of an experiment are better remembered (Ranganath & Rainer, 2003; Restorff, 1933). However, this study is unique in that we don't test item memory, but rather we

measure associative memory between the encoded item and the contextual feature that changed (a colored background in this case). Furthermore, it emphasizes the transient nature of novelty-driven associative memory encoding: we observed an associative memory enhancement specifically that the boundaries where associative memory for the remaining non-boundary positions are reduced and not significantly different from one another. One explanation for the boundary-related memory enhancements we observed here is that the switch in context drives attention toward the novel feature in the environment (the colored background) and since attentional priority is high for this trial, binding between the object and the color is boosted. Thus, the memory benefit could be a result of novelty driven attentional priority. In summary, these results add to a growing body of literature suggesting that contextual novelty, or event boundaries, promote memory encoding.

One final, but important, point is that in this experiment and the two that follow, the color background was a task-relevant feature of the experiment. Participants made pleasantness judgments on the object color pairing. When the context is task relevant, we see a boost in item-context binding at event boundaries. Whether or not task relevance of the context is a necessary part of the experimental design should be addressed in future research.

Experiment 2: Perceptual boundaries facilitate object-color binding, but reduce across-event temporal order memory

Experiment 1 provided evidence that associative binding is enhanced for local representations encountered at event boundaries compared to those encountered in the midst of an event (i.e. non-boundary items). The enhancement in binding representations present at event boundaries is consistent with the notion that attention to boundary representations is enhanced. If this is the case, then we reasoned that another form of memory, namely temporal order memory, may be disrupted. If perceptual boundaries caused a shift in attention to the novel color information, then the associative binding between pairs of items flanking that boundary would be disrupted. Indeed, prior experiments using temporal shifts in narrative as well as category and task switches at boundaries has shown this to be the case (Dubrow & Davachi, 2013; Ezzyat & Davachi, 2011, 2014). Thus, we aimed to extend that work and see if boundaries as defined in this paradigm (i.e. the color shifts) are associated with reduced temporal order memory. Thus, in Experiment 2, we assessed the effect of perceptual boundaries on temporal order memory, as well as object-color associative memory. Furthermore, this experimental design allowed us to ask whether temporal order memory for pairs items encountered across an event boundary is related to the enhanced processing of the boundary information itself. We modified the design of Experiment 1 to include a temporal order memory test (while keeping the test of object-color background memory). The encoding task and parameters in Experiment 2 were identical to encoding during Experiment 1, except that we encouraged subjects to associate items across time to increase temporal order memory performance. After each encoding list, we tested temporal order memory for object pairs studied within the same event (the 'within-event' condition) and compared that to temporal order memory for objects studied in two adjacent events (the 'across-event' condition), keeping the actual lag between tested items the same. We also tested object-color memory after each list. We predicted that perceptual boundaries would 1)

increase object-color associative memory for boundary trials (replicating Experiment 1), and 2) result in reduced temporal order memory for objects studied in adjacent events. Furthermore, we hypothesized that the magnitude of the boundary effect (i.e. the time spent processing the boundary item) should be directly related to the decrement in across-event temporal order memory.

Methods

Participants—Participants were 31 individuals (ages 18–35) recruited from New York University and the greater New York Metropolitan Area. All participants gave informed written consent in accordance with the University Committee on Activities Involving Human Subjects (UCAIHS) and participated in exchange for monetary compensation. One participant was excluded for failure to press any buttons during encoding. The remaining 30 participants were used for all analyses.

Materials—Materials were the same as Experiment 1. The entire stimulus set was used for Experiment 2 (576 objects).

Design and Procedure—The design of the encoding was very similar to Experiment 1, except that we had 16 study/test blocks (compared to 12 in Experiment 1). Following each encoding list, we tested object-color memory followed by temporal order memory. To assess object-color memory, we tested two items from each event. Objects that appeared concurrently with a change in the color frame made up the "boundary" color condition. Objects that were studied in the middle of the list (specifically, in the 4th position of the event) made up the "non-boundary" color condition. To assess temporal order memory, participants made order judgments on pairs of items: objects studied in the second and sixth positions of each event were paired together and made up the "within-event" order condition. Objects that were studied in the fifth and third positions of two adjacent events were paired together and made up the "across-event" order condition. Note that a given item was never tested more than once. An item was either tested for color memory or temporal order memory (but never both). There were a total of 80 test trials for each of the four conditions.

The only procedural difference during encoding (compared to Experiment 1) was that participants were encouraged to adopt an associative memory strategy to promote later temporal order memory. Specifically, we told participants to imagine the objects interacting with each other over time. Critically, participants were instructed to associate objects irrespective of the presence of different color frames. We added this additional instruction since we reasoned that after the first temporal order memory test, participants may adopt this kind of strategy to be successful on temporal order memory judgments in subsequent lists. There was a short practice session to assure that subjects understood the task instructions.

After each study list, color memory was tested first, with the same design as Experiment 1. Following completion of the color memory test, participants were tested on their memory for the temporal order of pairs of objects. For each test trial, two previously studied objects appeared side by side on the screen (Figure 1). Participants were asked to indicate which of the two objects appeared earlier in the list. The tested pairs of objects were chosen such that

there had always been three intervening objects between them at encoding. Critically, this was the case for both within-event and across-event trial-pairs. Thus, the actual number of intervening items between the two conditions was constant (3 intervening items) but the across-event test-pairs were studied with a boundary between them while within-event pairs were studied with the same color frame (i.e. in the same event; Figure 1). Participants were again asked to indicate their confidence in their decision (high/low). Test trials were self-paced and advanced as soon a response was given, with a fixed .5 s ITI included between test trials.

Results

Effect of perceptual boundaries on object-color and temporal order memory—

Accuracy for object-color memory and temporal order memory was calculated in two ways: First, we looked at the overall proportion of correct responses as a function of test condition. Secondly, if the data varied by confidence, then we separated correct trials by confidence (HC/LC) and calculated memory accuracy for each condition. Finally, we assessed whether there was an interaction between boundary/non-boundary status and memory test type (color/order). We found that object-color memory accuracy for boundary trials was significantly better than non-boundary trials [t(29)=6.84, p<.001, Cohen's d=.61; see Figure 3a]. There was no condition by confidence interaction, so we did not separate the data by confidence [F(1,29)=.73, p>.1]. These analyses suggest that the event boundary significantly increased memory for the object-color association. This result replicates the boundary-related memory enhancement reported in Experiment 1.

By contrast, temporal order memory was significantly better for the within-event condition relative to the across-event condition [t(29)=4.82, p<.001, Cohen's d=1.02]. The condition by confidence interaction was not significant [F(1,29)=2.71, p>.1]. Taken together with the data above, this suggests that the boundaries led to a reduction in associative memory across events while simultaneously increasing associative binding of representations at the boundary itself. To directly test for this interaction, we performed a two-way repeated measures ANOVA and found a significant test type (color/order) by condition (Boundary/ Across-event and Non-boundary/Within-event) interaction [Figure 3a; F(1,29)=45.34, p<.001, $\eta^2=.61$]. This data shows that perceptual boundaries improved object-color memory at the boundary itself, but disrupted temporal order memory for object pairs that spanned the boundary. Together, these findings suggest a boundary-related trade-off, where memory for boundary information is enhanced, perhaps at the cost of across-event associative binding.

Across-event temporal order memory negatively related to boundary processing. As a further means for asking whether there is a trade-off between boundary processing and these different forms of memory, our next analysis assessed whether response times to boundaries at encoding were related to later color and order memory. We reasoned that increased encoding response times to boundary items might reflect greater attention to the item and color on boundary trials and may, in turn, be related to the temporal order reductions. Thus, we hypothesized that longer boundary response times may result in worse order memory for pairs of objects that spanned the boundary. Crucially, however, we expected no such

relationship between non-boundary response times and temporal order memory for withinevent trial pairs.

To test this hypothesis, we divided boundary encoding response times into terciles and assessed temporal order memory separately for each bin. This analysis allowed us to visualize the data as well as reduce some of the variance of response times driven by noise. To test whether boundary (but not non-boundary) response times are related to temporal order memory, we conducted a two-way repeated measures ANOVA. There was a significant condition (boundary/non-boundary) by response time tercile (slowest, middle, fastest) interaction [F(2,58)=3.52, p=.036, η^2 = .11]. This interaction was driven by the fact that order memory performance was the lowest in the slowest tercile of response times and was the best in the fastest tercile of boundary response times [Figure 3b; fastest vs. slowest: t(29)=2.8; p=.009, Cohen's d=.60]. Crucially, no effect of response time on order memory for the analogous intervening trial in the non-boundary condition was evident [fastest vs. slowest: t(29)=-1.01; p=.32]. That is, the response time to the item in the 4th event position was not related to within-event order memory (between the items in the 2nd and 6th event position). Furthermore, there was a significant linear trend for across-boundary temporal order memory as a function of boundary response tercile [F(2,58)=7.86, p=.007, η^2 =.12] that was not present for the analogous within-event condition [F(2,58)=.91, p=.34], suggesting that the linear trend was specific to the across-boundary condition. These data support the notion that event boundaries disrupt temporal order memory and provide evidence that response time variability on boundary trials is related to the outcome of temporal order memory for the trials that span the boundary. In contrast, response times to an intervening item within events do not appear to be related to temporal order memory.

We also performed a logistic regression using boundary response times (i.e. task responses to position 1 items) and non-boundary response times (task responses to position 4 items) to predict within-event/across-boundary temporal order accuracy (position 5 and 3 items). Neither regression was significant [boundary: coefficient=-.04, z(29)=-.51, p=.61; non-boundary: coefficient=.13, z(29)=1.61, p=.11], but the interaction was [coefficient=.45, z(29)=4.9, p<.001].

We then ran a separate control analysis to test whether this relationship between boundary response time and temporal order memory was specific to the boundary item. It's possible that rather than temporal order memory being specifically related to processing at the boundary, memory could vary as a function of the overall speed of processing across the sequence of items. In other words, order memory could vary as a function of the mean encoding response time across the tested items (i.e. all trials that intervened the later tested items), rather than to the boundary item specifically. To address this, we averaged encoding response times across sequences of items that crossed a boundary, where the flanking items of the sequence were boundary temporal order test pairs. Importantly, we excluded the boundary response itself, but included the other intervening items. Then, we again sorted the data into terciles, and computed temporal order memory separately for each response time bin. If the relationship between the speed of boundary response time and temporal order memory were specific to the processing of the boundary item, then the average response time across the sequence would not predict temporal order memory. However, if temporal

order memory co-varied with the mean response time across a sequence, than we would expect a pattern similar to the previous analysis, where longer response times predicted worse order memory performance. A one-way ANOVA revealed that mean response time for sequences of trials that crossed an event boundary was not predictive of temporal order memory [F(1,85)=1.59, p>.1], providing further evidence that boundary processing is specifically related to across-trial associative encoding. Together with the accuracy data described above, these results argue for a trade-off between boundary processing and across-event mnemonic binding.

Encoding response times—Replicating the results from Experiment 1, we see that response times during encoding varied as a function of within-event position [Figure 3c; F(5,155)=54.89, p<.001, $\eta^2=.66$], and a planned contrast revealed that task responses on boundary items (position 1) were significantly slower than non-boundary items [position 2–6; t(29)=8.60, p<.001, Cohen's d=.61].

Retrieval response times—Finally, we compared response times for correct color and order memory retrieval as a function of condition. The goal of this analysis was to see whether the relative increase in memory performance we observed in the previous color and order accuracy analyses (i.e. Figure 3a) was also accompanied by a speeding of the retrieval response. To test whether the pattern of response times across conditions was dependent on confidence, we conducted a repeated measures two-way ANOVA and assessed the condition by confidence interaction. The interaction was not significant for order [F(1,28)=.06, p>.1]or color [F(1,28)=.07, p>.1], so we collapsed across confidence. We found that response times for correct color memory retrieval trials were significantly faster for boundary trials relative to non-boundary trials [t(29)=6.07, p<.001, Cohen's d=.52; Figure 3d]. On the order memory test, better performance on the within-event trials was accompanied by faster response times relative to the across-event trials [t(29)=3.85, p<.001, Cohen's d=.40]. Additionally, a two-way repeated measures ANOVA revealed a significant memory test by condition interaction [F(1,29)=28.62, p< .001, η^2 =.50]. In sum, mnemonic representations in conditions with better memory (boundary object color and within-event temporal order) were also accessed more quickly at retrieval.

Discussion

The results of the Experiment 2 provide evidence that while associative memory was enhanced for representations presented at perceptual boundaries, these boundaries resulted in a decrease in temporal order memory for items studied in adjacent events (Figure 3a). The reduction in temporal order memory observed is consistent with previous work showing event boundary-related reductions in cued recall for narrative stimuli (Ezzyat & Davachi, 2011), as well as an influence of boundaries on temporal memory for visual images (Dubrow & Davachi, 2013; Ezzyat & Davachi, 2014). Interestingly, our temporal order memory effects emerged using a simple color manipulation, demonstrating that boundary-related temporal memory disruptions can result from simple changes in a perceptual feature of an event. Moreover, we found that slower boundary encoding response times were associated with worse temporal order memory for objects spanning those boundaries. In other words, the larger the magnitude of the "boundary effect" (as indexed by response

time), the worse the temporal order memory for pairs of objects that spanned the boundary. The current data supports previous work by replicating the boundary-related reduction of across-event temporal order memory and importantly extends it to suggest a trade-off between boundary processing itself and across-event order memory. In other words, this data highlights the idea that orienting to something salient in the environment comes at the cost of the ongoing maintenance of items over time. Our finding of relatively better temporal order memory for within-event items as compared to across-event items is also consistent with buffer models of episodic memory (Atkinson & Shiffrin, 1968; Lehman & Malmberg, 2009, 2013; Raaijmakers & Shiffrin, 1981). Lehman and Malmberg (2013) buffer model hypothesizes that during encoding, a buffer process exists that can maintain or drop information depending upon the goals of the subject or the demands of the task. Items and contexts that are maintained in the buffer become associatively linked, while information experienced in different buffers does not become as strongly associated. In our task, we hypothesize that items encountered in the same color are maintained in the same buffer whereas a switch in color (i.e. perceptual event boundary) may serve as a cue for the brain to flush the contents of the current buffer, thus creating an associative disconnect between items studied in different contexts. Thus, one possible explanation for our observed difference between within and across event temporal order memory is that items encountered within the same event occupy the same buffer and thus are more strongly bound to each other than items encountered in different events (i.e. distinct buffers). Buffer models of episodic memory have been quite successful at accounting for patterns in episodic memory, particularly in studies with an intentional forgetting component (Lehman & Malmberg, 2013). Typically in these studies, at the end of an encoding list, subjects are instructed on whether or not to forget the previously studied list. The model predicts that the cue to forget causes a flushing of the previously studied items from the buffer (a buffer operation the authors call "compartmentalization"). One major difference between our study and these prior studies is that we do not explicitly instruct participants to forget between events. In fact, we encourage participants to bind together items irrespective of the background color. Thus, a possible interpretation of our findings is that perceptual event boundaries serve as a bottom-up cue that triggers the brain to remove the contents of the current buffer. Thus, compartmentalization may occur spontaneously if there is sufficient perceptual change in the environment. Future work should be conducted to characterize whether the nature of the task (i.e. top-down vs. bottom-up compartmentalization) has differential consequences for the organization of events in episodic memory. Finally, the memory "trade-offs" reported here can be contrasted with a body of literature investigating block-level or instruction-level trade-offs in item vs. associative in formation in memory (Einstein & Reed, 1980; Gronlund & Ratcliff, 1989; Hockley & Cristi, 1996; Hunt & Einstein, 1981; Sharps & Tindall, 1992). In this literature, the overarching theme is that when item encoding is prioritized over associative or relational encoding, item memory benefits and associative memory suffers. In contrast, when associative memory is prioritized, there is a benefit for associative memory but interestingly, item memory remains intact. In the current work, we show that at event boundaries, when attention is presumably redirected from item-item associative processing to more local item-context processing, across-event temporal order memory suffers, while boundary item-context memory is enhanced. To coalesce these findings, it appears that regardless of whether the manipulation is top-down

and extended in time (such as an instructional manipulation) or bottom-up and dynamic (such as a perceptual event boundary in the current design), attention to "in-the-moment" representations trades off with more temporally extended relational encoding (i.e. focusing on item-item relationships). Thus, in contrast to previous work, the results reported in the current study highlight the temporally dynamic nature of item and relational tradeoffs during episodic memory encoding.

Experiment 3: Perceptual boundaries impose structure on verbal free recall

So far, we've provided evidence that perceptual boundaries enhance boundary-related associative memory, while simultaneously reducing across-event temporal order memory, and that the magnitude of the boundary effect is predictive of the cost in temporal order memory. One intuitive explanation for this pattern of results is that when encountering a perceptual boundary, there is a shift in attention to the processing of the novel color information, which trades off with the integration of the previous item representation (i.e. the pre-boundary trial) and the current (boundary) trial. We reasoned that if within-event item representations are more strongly integrated than items that span a boundary, then one might expect within-event items may be represented more similarly in memory. If asked to recall the items, this could lead to a greater likelihood of sequentially recalling within-event items relative to across event items. Thus, in Experiment 3, we tested the hypothesis that the likelihood of making a local forward transition (e.g. n+1, n+2, n+3) from boundary items to other within-event items would be greater than the likelihood of a local forward transition from pre-boundary items, where forward transitions would be to items in a new event. To test this hypothesis, we employed a modified version of the encoding paradigm used in Experiments 1 and 2 that was optimized to test memory using verbal free recall (see Design for details). In this experiment, participants encoded lists of visual objects embedded in a colored frame with an accompanying verbal label, and after a short distractor task were instructed to verbally recall as many items as possible. Critically, like the previous experiments, the studied objects were embedded on a colored frame that periodically changed in color.

Methods

Participants—Participants were 24 individuals (ages 18–35) recruited from New York University and the greater New York Metropolitan Area. All participants gave informed written consent in accordance with the University Committee on Activities Involving Human Subjects (ACAIHS) and participated in exchange for monetary compensation. One person was excluded for not completing the experiment, leaving 23 participants for all analyses.

Materials—For this experiment, we used a subset of the objects (totaling 384 grey-scale objects) used in Experiments 1 and 2. We also included a written label displayed below each presented object to encourage participants to use the same label during verbal recall. Each list was designed to have minimal conceptual overlap, to minimize confusion during free recall scoring as well as semantic clustering at retrieval.

Design—In this experiment, participants studied lists of 24 objects (along with a written label) embedded in a colored frame that changed to a new color after every 4 trials. Like the previous experiments, there were 6 'events' and 5 'event boundaries' per list. We chose to present 24 items per list rather than 36 (as in Experiment 1 and 2) due to pilot data suggesting poor free recall performance when longer study lists were used. Additionally, we reduced event length from 6 to 4 items to ensure adequate power for the free recall analyses (i.e. to have sufficient boundary trials). Like Experiments 1 and 2, trials that were studied concurrently with a color change are considered "boundary" trials and objects studied in the other event positions (2–4) are called "non-boundary" trials.

Procedure—For each list (12 total), participants encoded 24 object-color pairs. Participants were instructed to imagine the object in the color of the frame and make a pleasantness judgment on the object/color combination. After each study list, participants completed a distractor task in which they were asked to indicate whether arithmetic problems were correct or incorrect (e.g. "5+4+2=11?"). The numbers 1–6 were used for the arithmetic problems, and the probability of the answer being correct was 50%. Each problem was presented for 3 seconds for a total of 10 problems during each distractor period (30 seconds). They were also given immediate feedback to encourage engagement. Following the distractor task, participants were presented with a screen prompting them to say "Next Block" and then verbally recall as many words as they could. They were given a minimum of 90 seconds and told to use more time if they felt they could recall more words. A schematic of a block of the experiment is displayed in Figure 4a.

Audio was recorded throughout the entire session. Unclear responses were excluded from the analysis. Synonyms to words that were actually studied were not considered correct responses. For example, if the correct response was "panther" and the subject reported "leopard", this would not be considered a correct response. However, partial answers were counted as correct. For example, if the correct response was "toy train" and the subject responded "train", it would be marked as correct. The total number of excluded trials (combining across synonyms, unclear responses and prior list intrusions) was small (3.7%). Analysis of the free recall audio files was performed by one author and one research assistant using Penn TotalRecall (http://memory.psych.upenn.edu/TotalRecall). Using this program, the onset and serial recall order of each retrieved object was recorded. Crucially, scorers were blind to the encoding condition to which each object belonged.

After each free recall period, participants were given an object-color memory task following the same protocol as Experiments 1 and 2. The object-color memory test was self-paced. For this experiment, we tested color memory for all 24 studied items in the list. Across the entire experiment, there were a total of 36 color memory test trials for each condition (event positions: 1–4).

Results

Overall Free Recall Performance—Participants recalled an average of 31.30% (SD=12.6%) of the items presented for each list (or 7.51 out of 24 items per list). As expected, free recall varied as a function of serial position of the list [F(23,506)=6.82, p<.

001, η^2 =.237, Figure 4a], where items at the beginning and the end of the list were more likely to be recalled than items in the middle of the list (Murdock, 1962). We also computed free recall performance as a function of event position within an event, but did not observe an effect [F(3,66)=.96, p>.1], meaning that all event positions 1–4 were equally likely to be recalled. We discuss the implication of this finding in more detail in the general discussion.

Then, we computed the mean lag-conditional response probability (lag-CRP) curve (Figure 4b; see Kahana (1996)) which showed that, given free recall of an item, participants were most likely to make free recall transitions to items in neighboring list positions, consistent with previous reports (Howard & Kahana, 2002; Kahana, 1996).

Local Transition Probabilities in Free Recall—To measure the influence of perceptual event boundaries on free recall, our next analysis focused on local transition probabilities. That is, given the recall of item n, what is the likelihood of the next item recalled being locally forward (i.e. n+1, n+2, or n+3) or locally backward (i.e. n-1, n-2, or n-3)?. First, we focused on local forward transitions up to a lag of three because for boundary items, local forward transitions would be to other within-event items whereas for pre-boundary items (i.e. position 4 items), local forward transitions would be to items in the next event. We predicted that there would be a greater likelihood of local forward transitions from boundary items as compared to pre-boundary items due to the fact that local forward transitions from boundary items would be to other within-event items. To test this prediction, for each within-event position, we computed the likelihood of a local forward transition (i.e. the sum of the number of transitions from n to n+1, n+2, and n+3) divided by the number of transitions to all other items. This resulted in a measure representing the proportion of the time participants made a local forward transition relative to all other transitions to items elsewhere in the list. Critically, there were no differences in the total number of items recalled for each within-event position (see Free Recall Performance Section) and thus, the above analysis is only sensitive to the order of free recall, rather than the total number of items recalled. The results of this analysis are plotted in Figure 5a. Consistent with our hypothesis, relatively more local forward transitions were made from boundary items than pre-boundary items [t(22)=1.88, p= .07, Cohen's d = .71]. This data is consistent with the idea that perceptual event boundaries influence the structure of free recall behavior.

Next, we tested the idea that local backward transitions from pre-boundary items might be relatively more likely than local backwards transitions from boundary items because for pre-boundary items, local backwards transitions were to other within-event items. We performed the same analysis as described above, but now for only local backwards transitions as a function of within-event position (Figure 5b). Interestingly, we did not observe the predicted effect that local backward transitions would be relatively more likely for pre-boundary items as compared to boundary items [t(22)=.10, p>.9]. To summarize, while local forward transitions were more likely from boundary relative to pre-boundary items, there was no difference in the likelihood of backward transitions.

Distal Transition Probabilities in Free Recall—The intriguing result that there were no differences in backward transition probabilities led us to the follow question: If participants are not transitioning from pre-boundary items to other within-event items (i.e.

local backward transitions), to which items are they are more likely to transition? We reasoned that if local forward transitions from pre-boundary items are relatively unlikely (as compared to boundary items) and there were no differences in local backward transitions, then transitions from pre-boundary items must be to more distal items in the list. To quantify this, we computed the average transition distance as a function of position (Figure 5c). That is, given the recall of item n, what is the average lag of the next recalled item? For this analysis, our hypothesis was that transitions from pre-boundary items would be to more distal items relative to all other within-event positions. Put another way, when one recalls the last item in an event, we predicted that they would be relatively more likely to transition to a distal item. To test this hypothesis, we computed a contrast of the average transition distance from pre-boundary items relative to the other within-event positions. The analysis revealed that the average transition distance from pre-boundary items was significantly more distal than the average transition distance from other within-event positions [t(22)=2.63, p<.05, Cohen's d=.48]. Furthermore, the direct comparison of average transition distance from preboundary and boundary items revealed that pre-boundary transitions are significantly more distal than boundary transitions [t(22)=2.55, p<.05, Cohen's d=.39]. Thus, compared to other within-event positions, free recall transitions from pre-boundary trials are to relatively more distal items providing further support for the idea that perceptual event boundaries influence the structure of free recall behavior.

Transitions from Pre-boundary Items—Our last free recall analysis was designed to test the idea that transitions from pre-boundary items would be disproportionately more likely to boundary items relative to items in other within-event positions. We predicted that given the recall of the last item in an event (and thus terminating the recall of a particular episode), one might initiate a memory search process in an attempt to recall additional items. If boundary items somehow 'stand out' in memory (Radvansky, 2012; Zacks et al., 2007), then the likelihood of transitioning to a boundary item given the recall of a pre-boundary item may be relatively higher than transitioning to other within-event positions. In this way, boundary items may serve as a 'gateway' into an episodic event. To test this prediction, we computed the conditional likelihood of transitioning to each within-event position given the recall of a pre-boundary item (Figure 5d). A contrast of pre-boundary transitions to boundary items relative to items in other positions suggests that following the recall of a preboundary item, there is a trending effect for boundary items to be recalled next [t(22)=1.89, p<.10, Cohen's d=.79]. One potential issue with the analysis described above is that the effect could be driven solely by local forward transitions (i.e. a temporal contiguity effect). To rule out this explanation, we performed the analysis again, now removing all local transitions (n +/-1, 2 or 3). When analyzing only transitions from pre-boundary items to other distal items (greater than 3 positions away), the trend remained [t(22)=1.73, p<.10, Cohen's d=.60]. Thus consistent with our prediction (albeit a trend), following the recall of the last item in an event, distal boundary items are more likely to be recalled next (as compared to other within event positions). Together with the free recall analyses described above, these data support the idea that perceptual boundaries introduce structure into free recall behavior.

Color Memory Performance—Analysis of variance revealed a trend for color memory to vary as a function of within-event position $[F(3,66)=2.57, p=.06, \eta^2=.11]$. A planned contrast demonstrated object-color memory was better for boundary trials than non-boundary trials [t(22)=2.67, p=.01, Cohen's d=.80]. Post-hoc pairwise t-tests revealed that memory was significantly better for boundary trials than all non-boundary trials [1 vs. 2: t(23)=2.1, p<.05, Cohen's d=.24; 1 vs. 3: t(23)=2.84, p<.05, Cohen's d=.31; 1 vs. 4: t(23)=2.1, p<.05, Cohen's d=.22]. The interaction between confidence and condition was not significant. Note that in this experiment, we replicate Experiments 1 and 2 by showing that boundary object-color memory accuracy was better than non-boundary memory. While the effect was modest in this version of the paradigm, together with the color memory enhancements observed in both Experiments 1 and 2, these results provide consistent evidence for boundary-related memory enhancements.

Response times for correct color memory retrieval trials also varied as a function of within-event position [F(3,66)=10.29, p<.001, η^2 =.319]. A planned contrast between boundary and non-boundary color retrieval RTs revealed that boundary RTs were significantly faster than non-boundary RTs [t(22)=-4.24, p<.001, Cohen's d=1.26]. Post-hoc tests showed that color retrieval RTs were significantly faster for boundary trials compared to all non-boundary trials [1 vs. 2: t(23)=4.71, p<.001, Cohen's d=.48; 1 vs. 3: t(23)=2.47, p<.05, Cohen's d=.29; 1 vs. 4: t(23)=4.08, p<.001, Cohen's d=.5]. There was no significant interaction between condition and confidence, so these analyses were performed on data collapsed across condition.

Encoding Response Times—There was a significant effect of event position on encoding response times $[F(3,66)=28.90, p<.001, \eta^2=.57]$. A planned contrast reveals that boundary response times were significantly slower than non-boundary [t(22)=6.72, p<.001, Cohen's d=2.04]. Pairwise t-tests revealed that boundary encoding response times were significantly slower than all non-boundary trials [1 vs. 2: t(23)=7.08, p<.001, Cohen's d=.55; 1 vs. 3: t(23)=5.21, p<.001, Cohen's d=.54; 1 vs. 4: t(23)=7.11, p<.001, Cohen's d=.55] and there were no other differences. This finding replicates Experiments 1 and 2 and extends it to include shorter events (four as compared with six items in Experiments 1 and 2).

Math Accuracy—Accuracy on the math task was high (mean=.89, SD=.08) and all participants performed statistically above chance.

Discussion

In the current experiment, we aimed to examine whether and how free recall organization was influenced by perceptual event boundaries. Overall, we found that transition likelihoods varied as a function of within-event position (Figure 5). First, our results suggest that local forward transitions were significantly more likely from boundary items as compared to preboundary items whereas there were no differences between conditions for local backward transitions (Figure 5a, b). Second, we found that transitions from pre-boundary were on average to more distal items than transitions from other within-event positions. Lastly, transitions from pre-boundary items were most likely to be to boundary items as compared

to other within-event positions. These findings argue that perceptual event boundaries influence the structure of free recall behavior.

Our finding that local forward transitions (n+1, n+2, n+3) were more likely from boundary items than from pre-boundary items is consistent with the idea that items encountered in the same event are more strongly associated to each other than items in distinct events. For boundary items, forward local transitions were all to other within event items, whereas for pre-boundary items local forward transitions were all to items in the neighboring event. This result is in line with temporal context models of memory (Howard & Kahana, 2002; Manning, Polyn, Baltuch, Litt, & Kahana, 2011; Polyn, Natu, Cohen, & Norman, 2005; Polyn et al., 2009a), that propose that during the study of a list of stimuli, items are bound to a slowly-changing representation of context. Although the particular features (e.g. semantic, source, temporal) that are included in the context representation vary according to the specific model, all retrieved context models propose that when an item is recalled from memory, the context representation is reinstated and used to guide the retrieval process. Because the context representations of neighboring items are most similar, this leads to free recall transitions between neighboring items, and the overall lag-CRP pattern. Our data are in line with such a retrieval interpretation to the extent that the perceptual details associated with each item are also reinstated during recall. Thus, reinstatement of the color associated with an object may make it more likely that participants will recall other objects encoded with the same color.

In a previous study, Polyn et al. (2009b) found that when freely recalling a short list of 12 words that included one task switch at the halfway point in the list, participants tended to cluster their recall responses by items that shared an encoding task. That is, more free recall transitions were made between words that were encoded using the same task as compared to words encoded under two different tasks. Our results are consistent with that result and extend it to suggest that the change in a perceptual feature during experience is sufficient to impose structure in the free recall of events. While Polyn and colleagues focused their analyses on the effect of task boundaries on the likelihood of within- vs. across-event transitions (irrespective of the list position of the item), we specifically asked whether items that flanked a perceptual boundary would show a within-event bias. This analytic approach allowed us to determine precisely how boundaries modulate the likelihood of within-event recall transitions.

Interestingly, while we found that local forward transitions are significantly more likely from boundary items relative to pre-boundary items, we found no difference between the two conditions in local backwards transitions. If shared context results in stronger associative binding between items in the same event, one might expect local backwards transitions to be relatively greater for pre-boundary items compared to other within-event positions, since local backwards transitions would be to other within-event items. While we note that the aforementioned result is a null finding (and therefore not directly interpretable), we can offer a few speculations as to why we might not expect to see an effect. Previous studies suggest that free recall is reliably bias in the forward direction (Howard & Kahana, 2002; Kahana, 1996) and backwards transitions are relatively more rare. We see this pattern in our data as well (Figure 4b, 5a, b). Thus, it's possible that perceptual boundaries exert a substantially

stronger effect on forward transition probabilities. An alternative explanation is that our experimental design was not sensitive enough to detect the effect of boundaries on backward transitions (e.g., lists too long, events too short or boundaries not strong enough). Nonetheless, the fact that that we do observe a greater likelihood of local forward transitions from boundary items as compared to pre-boundary items is evidence that perceptual boundaries do indeed shape free recall behavior.

A second notable observation from this experiment was that the average transition distance from pre-boundary items was significantly further than from boundary items. On other words, given the successful recall of a pre-boundary item, participants were more likely to next recall a more distal item in the list. One possible explanation for this finding is that perceptual event boundaries result in a weak associative link between a pre-boundary item and its neighboring boundary item (Dubrow & Davachi, 2013; Ezzyat & Davachi, 2011). Because of this weak associative link, after the successful recall of a pre-boundary item, a memory search process might be initiated and as a consequence, more distal item may be subsequently recalled. This finding is consistent with the idea that event boundaries disrupt associative binding between items and suggest that transitions following the recall of the last item in an event are on average more distal than transitions fro other within-event positions.

Another interesting finding from this experiment was that following the successful recall of a pre-boundary item, the next item recalled is most likely to be a boundary item. Given that pre-boundary items are neighbored by boundary items and that participants generally tend to transition forward in free recall, this may not seem entirely surprising. However, this effect remains significant after removing local items from the analysis, suggesting that when one transitions from a pre-boundary item to a more distal item, it tends to be a boundary item. An intriguing interpretation of this finding is that event boundaries may serve as a 'gateway' into an episodic event. In other words, after successfully recalling the end of a previous event and during a mnemonic search for more items, boundary items might stand out as entry points into other mnemonic episodes. Consistent with this interpretation, we found that on average transitions from pre-boundary items were more distal than from other positions and out of those distal transitions, transitions to boundary items were most probable. While the 'gateway' idea is certainly attractive, future studies will be necessary to determine if this is the most likely explanation for this pattern of results.

Finally, event segmentation theory suggests that items encountered at event boundaries may be more memorable than items encountered elsewhere in an event, possibly due to increased attention at boundaries (Radvansky, 2012; Zacks et al., 2007). All three experiments are consistent with this idea by showing that object-color memory is better at event boundaries than at other within-event positions. Interestingly, however, in Experiment 3 we did not observe an overall increase in free recall of boundary items, as one might have predicted from EST. While we hesitate to over interpret this null finding, we can offer some speculation to why we observed this effect. Rather than boundaries generally boosting memory for boundary information, boundaries may selectively increase associative binding between a boundary item and its context. A mechanism of this nature would predict greater object-color associative memory, but not necessarily better encoding of boundary items alone. Alternatively, perceptual boundaries may generally enhance encoding, but our study

may not have been sensitive enough to detect it. Future work will be necessary to disentangle whether event boundaries differentially influence item memory vs. item-context associative binding.

General Discussion

The studies presented here demonstrate that perceptual boundaries influence the organization of events stored in long-term memory. In Experiment 1, we found that perceptual boundaries enhanced associative binding between an object and a color background. In Experiment 2, we show that while boundary-related associative memory was enhanced, temporal order memory for pairs of items that span a perceptual boundary was disrupted relative to order memory for within-event item pairs. Furthermore, the magnitude of the boundary effect (i.e. the response time to the boundary) predicted the cost in temporal order memory suggesting a trade-off between boundary processing and across-event temporal order memory. Finally, in Experiment 3, we found that participants exhibited recall behavior that was structured by perceptual event boundaries. Taken together, this work provides compelling evidence that perceptual boundaries have a lasting influence on the structure of our memories. These results add to a growing body of literature characterizing the influence of event segmentation on long-term memory (Boltz, 1992; Dubrow & Davachi, 2013; Ezzyat & Davachi, 2011, 2014; Newtson & Engquist, 1976; Schwan & Garsoffky, 2004; Zacks, Speer, Vettel, & Jacoby, 2006). Previous studies using naturalistic stimuli have provided data consistent with the idea that information experienced at event boundaries is better encoded in memory (Boltz, 1992; Newtson & Engquist, 1976; Schwan & Garsoffky, 2004). However, there is some concern that these effects could be explained by differences in the amount of diagnostic information between conditions; that is, if boundary test items provide a better 'summary' of a particular event than non-boundary test items, one might expect higher boundary memory that is not driven by event segmentation processes, per se. By contrast, in the current study, we carefully matched the boundary and non-boundary conditions during retrieval, such that the only difference between the two was their position within an event during encoding. Thus, the best explanation for the boundary-related memory enhancement in our study is an influence during encoding of the perceptual boundary on associative binding (between the object and color). This effect, which we see across three experiments is consistent with previous research demonstrating boundaryrelated memory enhancements, and confirms that segmentation processes during encoding lead to better memory for information encoded at event boundaries.

These results are also consistent with studies of contextual novelty that find that items that are in someway deviant from the local surroundings show a boost in memory (Cimbalo, 1978; Fabiani & Donchin, 1995; Lin, Pype, Murray, & Boynton, 2010; Swallow & Jiang, 2011, 2013; Wallace, 1965). Typically, these studies have observed differences in item memory based on deviance status. The present study is novel in that we find enhanced item-context associative binding for contextually novel trials (i.e. object-color pairs encoded at perceptual event boundaries). While this distinction may seem subtle, it does not follow that better item encoding should necessarily entail better item-context associative memory. For instance, compared to neutral stimuli, emotionally arousing stimuli show better item memory and worse item-context associative memory (Bisby & Burgess, 2014; Madan,

Caplan, Lau, & Fujiwara, 2012). Furthermore, it is now well established that different neural structures support the encoding of item information vs. the binding of an item to its context (Davachi, 2006; Davachi, Mitchell, & Wagner, 2003; Ranganath et al., 2004). Therefore, it is conceivable that item memory and item-context associative memory are dissociable memory representations. Future work should test the relationship between item memory and item-context associative memory at perceptual boundaries.

In Experiment 2, we found that temporal order memory was relatively worse for acrossevent trial pairs relative to within-event trial pairs. This is consistent with previous results that show that cued recall (Ezzyat & Davachi, 2011) and temporal order memory decisions (Dubrow & Davachi, 2013) are more accurate for test items that were from the same 'event' compared to those from adjacent 'events' - even though the actual temporal lag was the same in both conditions. The current study complements these previous results that used more complex boundaries (e.g. task/stimulus class switches, narrative temporal boundaries) by demonstrating that simple perceptual boundaries are sufficient to induce event segmentation processes that result in better within-event versus across-event associative memory. It's worthwhile to note that some theories of recency memory might predict the opposite pattern of results (see Friedman (1993) for review). For instance, if participants were using an item-strength or contextual overlap retrieval strategy to recover recency information, a change in context between items could be beneficial for performance. On the other hand, if participants are performing recency discrimination by recovering associative information among a set of items, one might predict that within-event temporal order memory would be greater than across-event temporal order memory since shared contextual features can help to bind items across time. The latter prediction is consistent with our results, suggesting that rather than a distance-based retrieval strategy, participants may be relying on retrieving the associative links between a series of items. Further evidence for this type of retrieval mechanism comes from a study that found that during a recency discrimination test, the speed of retrieval for items that intervened the recency test pair during encoding is facilitated relative to items that did not intervene the test pair (DuBrow & Davachi, 2014). Furthermore, in a related fMRI experiment, the category of items that intervened the recency test probes during encoding was "reactivated" during successful recency discrimination (DuBrow & Davachi, 2014). Together, these findings suggest that in at least some cases (i.e. when the lag between the tested items is short), recency discrimination can be successfully performed by recovering the items that intervened the test pair.

Finally, the results from our free recall data (Experiment 3) underscore the influence of perceptual event boundaries on memory organization. Namely, we found that perceptual boundaries modulated free recall transition probabilities: local forward transitions from boundary items were more likely as compared to local forward transitions from preboundary items (Figure 5). This is likely due to the fact that for boundary items, local forward transitions were to other within-event items where as local forward transitions from pre-boundary items were to items in a different event. This result is consistent with previous studies that find evidence for recall organization according to the source of the stimuli (Frost, 1971; Hintzman et al., 1972; Murdock & Walker, 1969; Nilsson, 1974; Polyn et al., 2009b). Interestingly, however, we did not find that local backwards transitions we more

likely for pre-boundary items, as one might expect if recall organization is strongly influenced by source information. However, since this was a null finding, its interpretation is not entirely straight-forward as many factors could have influenced the lack of a finding. Nonetheless, the fact that we see a larger proportion of local forward transitions from boundary items compared to pre-boundary items is evidence that perceptual event boundaries structure memory recall behavior. We also found that transitions from preboundary items were more likely to be to distal items (as compared to transitions from boundary items). One interpretation of this result is that when a participant recalls an item that occurred just prior to an event boundary, the associative link to the next item was severed by the perceptual boundary, thus prompting a memory search to recall other items in the list. A mechanism of this nature could lead to selectively more distal transitions for preboundary items relative to other within-event positions. Lastly, we found that following the successful recall of a pre-boundary item, there was a trend for boundary items to be recalled next. This was evident for local transitions as well as distal transitions. One explanation for this pattern of results is that following the recall of the end of an event, participants may initiate a memory search process in an effort to recover additional list items. If boundary items 'stand out' in memory due to better overall encoding or better item-context binding, then the likely of a boundary transition would be greater than the likelihood of transitioning to other list positions. This last preliminary data point is consistent with the idea that event boundaries may act as 'gateways' into an episodic events. That is, during free recall, boundaries may stand out as entry points into an episodic memory and facilitate the retrieval of additional within-event information.

Conclusions

Together, Experiments 1 and 2 suggest that while perceptual boundaries may enhance some forms of memory (i.e. object-color associative memory), this comes at the cost of reduced across-event associative memory (temporal order memory). In other words, shifting one's attention to a novel stimulus in the environment trades off with the ongoing maintenance and integration of representations into an event model, and this causes a disruption in the associative binding of items encountered across time. Finally, Experiment 3 highlights that perceptual boundaries influence natural recall behavior and suggests the possibility of a mechanism where event boundaries may serve as a 'gateway' into an episodic memory. In summary, the findings from all three studies highlight that organizational processes during encoding influence the structure of later episodic memories.

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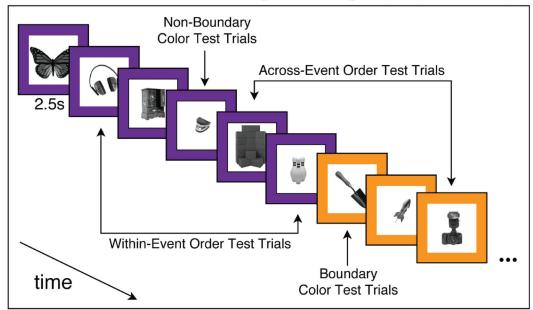
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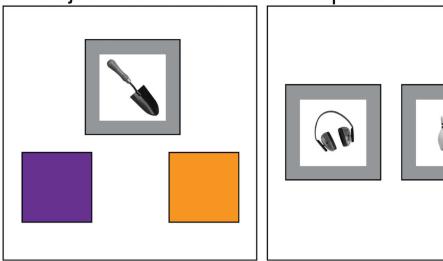
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Schematic of Encoding Paradigm (Exp. 1 and 2)



Object-Color Test

Temporal Order Test



Which color was studied with the object?

Which object appeared first?

Figure 1. Schematic of the Task

Participants made pleasant/unpleasant judgments on object-color pairs. Critically, the color switched every 6 trials. Object-color associative memory test. (Bottom, left) After encoding, participants performed a two alternative forced choice object-color memory test. The object-color test was in both Experiment 1 and 2. Temporal order memory test. (Bottom, right) After the color test, temporal order memory was tested using a two alternative forced choice task. Participants indicated which of two studied objects appeared first in the list. The temporal order test was only in Experiment 2.

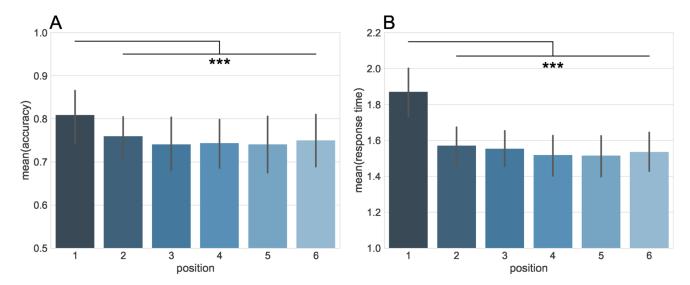


Figure 2. Experiment 1 Results

Object-color associative memory accuracy (A) and response times are shown as a function of within-event position (B). Error bars represent 95% confidence intervals. *p < .05, **p < .005, ***p < .001.

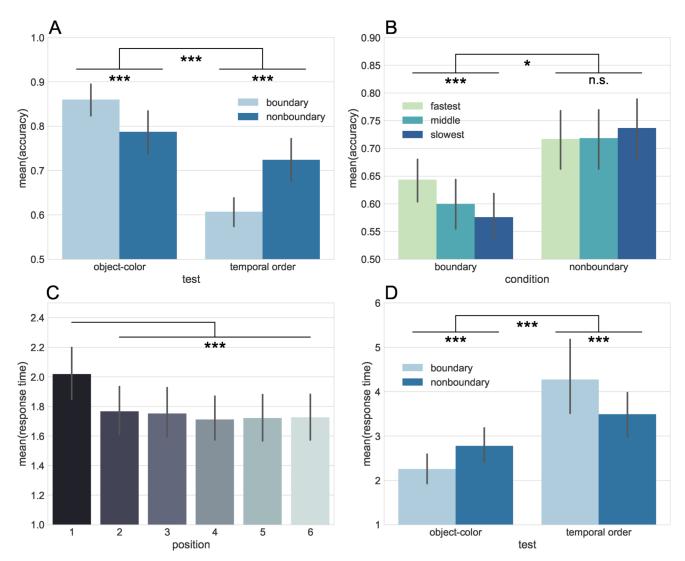


Figure 3. Experiment 2 Results

(A) Memory accuracy is shown as a function of test and condition. (B) Temporal order memory accuracy split into terciles by encoding response time of intervening boundary (for across-event) or non-boundary (for within-event) trial. (C) Task response times during encoding as a function of event position. (D) Retrieval response times for correct trials as a function of condition and memory test. All error bars represent 95% confidence intervals. *p<.05, **p<.005, ***p<.001.

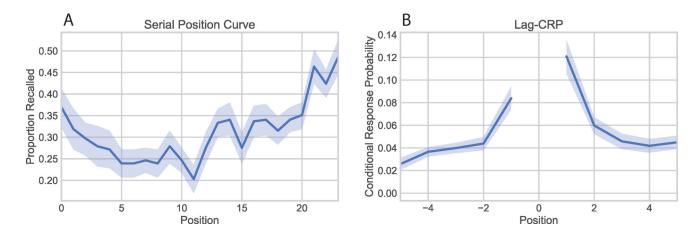


Figure 4. Experiment 3: Serial Position Curve and Lag-CRP (A) Memory accuracy broken down by list position. (B) Given the recall of an item in position n, this graph plots the probability of recalling a neighboring items next in the recall sequence (+/-5).

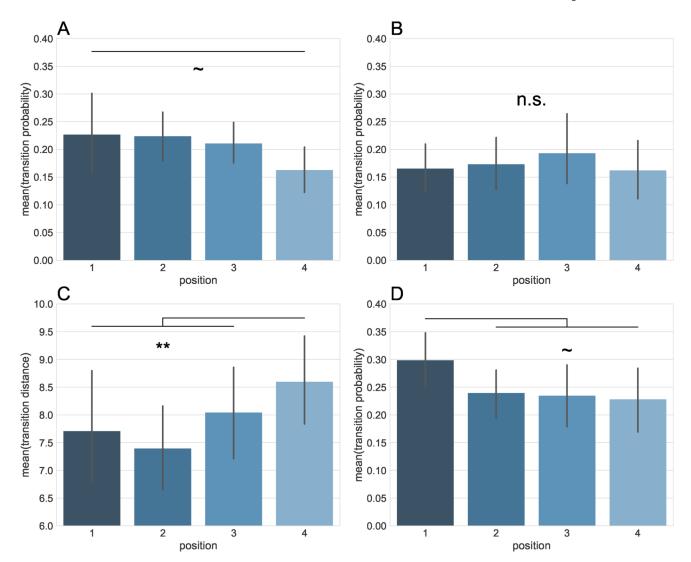


Figure 5. Experiment 3 Results

(A) Local forward (sum of n+1, n+2, n+3) transition likelihood as a function of within-event position. (B) Local backward (sum of n-1, n-2, n-3) transition likelihood as a function of within-event position. (C) Average transition distance as a function of within-event position. (D) Likelihood of transition from pre-boundary items as a function of within-event position. Error bars represent 95% confidence intervals. p<.10, *p<.05, **p<.005.