# Event Segmentation Promotes the Reorganization of Emotional Memory

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## Abstract

■ Event boundaries help structure the content of episodic memories by segmenting continuous experiences into discrete events. Event boundaries may also serve to preserve meaningful information within an event, thereby actively separating important memories from interfering representations imposed by past and future events. Here, we tested the hypothesis that event boundaries organize emotional memory based on changing dynamics as events unfold. We developed a novel threat-reversal learning task whereby participants encoded trial-unique exemplars from two semantic categories across three phases: preconditioning, fear acquisition, and reversal. Shock contingencies were established for one category during acquisition (CS+) and then switched to the other during reversal (CS−). Importantly, reversal either was separated by a perceptible event boundary (Experiment 1) or occurred immediately after acquisition, with no perceptible context shift (Experiment 2). In a surprise recognition memory test the next day, memory performance tracked the learning contingencies from encoding in Experiment 1, such that participants selectively recognized more threat-associated CS+ exemplars from before (retroactive) and during acquisition, but this pattern reversed toward CS− exemplars encoded during reversal. By contrast, participants with continuous encoding—without a boundary between conditioning and reversal—exhibited undifferentiated memory for exemplars from both categories encoded before acquisition and after reversal. Further analyses highlight nuanced effects of event boundaries on reversing conditioned fear, updating mnemonic generalization, and emotional biasing of temporal source memory. These findings suggest that event boundaries provide anchor points to organize memory for distinctly meaningful information, thereby adaptively structuring memory based on the content of our experiences. ■




## INTRODUCTION

The intricate process of recalling emotional experiences from our past is more complex than it appears, especially amidst the ongoing accumulation of new events that continuously compete for space in memory. Segmenting ongoing experiences into discrete episodes aids in structuring memory, creating organized units of time that later facilitate retrieval. Perceptible boundaries between events can act as natural cues for anchoring memories to a specific time or place. Organizing memory in this way might optimize retrieval by narrowing the search space to information from the most relevant time and place. For example, if you were trying to recall how you had injured yourself with a new kitchen tool, it is beneficial to remember experiences that occurred in the kitchen, rather than sifting through the entire day's events. There is considerable research on how event boundaries can segment our experiences and shape the content and temporal order of episodic memory. Evidence from the wider episodic memory literature demonstrates how event segmentation can shield memories encoded earlier in time from new experiences that might contradict them, when these subsequent episodes are demarcated by an event boundary, such as a temporal gap or spatial change (Clewett & Davachi, 2017; Ezzyat & Davachi, 2014; DuBrow & Davachi, 2013; Kurby & Zacks, 2008; Speer & Zacks, 2005).

This segmentation mechanism could prove an indispensable component in the updating of negative emotional episodes, which can become deeply entrenched and resistant to change in the face of contradictory experiences. For example, an intense experience of narrowly avoiding a snake bite while on a hike will likely be remembered far longer than the subsequent memory of safely viewing snakes at a zoo later that day. Likewise, the memory of encountering a vicious dog on your way to the zoo is likely to dominate memory beyond the experience of passing by a calm dog on the hike. Event boundaries might serve as anchor points to organize these types of discrete experiences into distinct memory traces, leading us to prioritize meaningful information extracted across events (e.g., the dangerous snake on a hike, the dangerous dog near the zoo) despite closely related episodes that might contradict our emotional experiences (e.g., snakes were safe at the zoo; dogs were safe on your hike).

The capacity to flexibly update threat appraisals in line with an ever-changing external environment serves as an indispensable adaptive mechanism, with clear

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implications for long-term well-being (Grasser & Jovanovic, 2021; Laing et al., 2021; Odriozola & Gee, 2021; van Rooij & Jovanovic, 2019; Gazendam, Kamphuis, & Kindt, 2013; Holt, Coombs, Zeidan, Goff, & Milad, 2012). This active learning and relearning of fears is modeled by Pavlovian fear conditioning experiments, where neutral cues (conditioned stimuli [CS]) acquire associations with the occurrence (CS+) or nonoccurrence (CS−) of threat outcomes (e.g., shock). Threat reversal learning refers to the process of updating conditioned fear associations when contingencies are switched (Atlas, Dildine, et al., 2022; Atlas, Sandman, & Phelps, 2022; Savage, Davey, Fullana, & Harrison, 2020a; Schiller, Levy, Niv, LeDoux, & Phelps, 2008), which is seen to be disrupted in fear-related psychiatric disorders (Savage, Davey, Fullana, & Harrison, 2020b; Homan et al., 2019; Apergis-Schoute et al., 2017). Unlike the related process of fear extinction, where a single threat association is diminished (CS+), reversal demands concurrent reevaluation of threat cues as safe and vice versa, and the efficient adjustment of learned threat responses. For fear reversal to occur, initial emotional learning needs to be contradicted effectively by subsequent events. Although fear extinction and reversal rely on overlapping neural mechanisms and both involve flexible reevaluation of fears (Battaglia, Harrison, & Fullana, 2022; Laing, Felmingham, Davey, & Harrison, 2022; Atlas, 2019; Delgado et al., 2016), the latter is rarely investigated in terms of its lasting memory trace. Episodic memory research indicates that event boundaries provide a transition between periods of encoding and consolidation, providing a safeguard from immediate interference (Nolden, Turan, Güler, & Günseli, 2024; Flores, Bailey, Eisenberg, & Zacks, 2017; Zacks & Swallow, 2007). In the threat context, separating acquisition from reversal with a clear boundary (such as in the hike/zoo example above) could render a clear temporal or spatial distinction that facilitates organization of emotional value, protecting consolidation of initial learning at the expense of reversal learning (Dunsmoor et al., 2018; Ezzyat & Davachi, 2010, 2014; Herry et al., 2008). If learned without such a boundary, the contradictory experience of reversal may disrupt consolidation of initial learning, delaying updating and distorting retrieval. However, relatively few studies have combined episodic memory with Pavlovian conditioning (Dunsmoor & Kroes, 2019), leaving the role of event segmentation in long-term fear memories unclear.

Several studies have demonstrated selective and retroactive enhancement of emotional memory by integrating category conditioning and episodic memory tasks. In these experiments, CS+/CS− are represented by numerous unique items from higher-order categories, subsequently presented at ~24 hr after conditioning to examine what was explicitly remembered from learning. Threat conditioning produces a distinct memory advantage for CS+ category items that had appeared outside (before or after) the threat conditioning phase itself (Hennings, Lewis-Peacock, & Dunsmoor, 2021; Dunsmoor, Murty, Davachi, & Phelps, 2015). Beyond general memory accuracy, recent studies also suggest that "precision" can distinguish how fear and safety are configured in episodic memory, with fear memories becoming widely generalized (Starita, Kroes, Davachi, Phelps, & Dunsmoor, 2019) and extinction (safety) memories being highly specific (Laing & Dunsmoor, 2023)—despite equivalent memory accuracy. These approaches can track how changes in learning scenarios (e.g., fear extinction, reversal) affect the strength (accuracy) and precision of memories formed during conditioning. One such study demonstrated how the segmentation of extinction from conditioning decisively protects fear memory from the intervening effects of safety learning (extinction), finding a reliable decline in memory for CS+ items encoded immediately after a brief conditioning–extinction break (Dunsmoor et al., 2018), which replicated across both enhanced (novelty-facilitated) and delayed extinction iterations. Whereas extinction provides a ready-made demarcation between aversive and safe periods, threat reversal evokes a more demanding learning situation, with bidirectional updating (safe-to-threat and threat-to-safe). It is therefore unclear whether segmentation would exclusively bias memory in favor of initial learning, newer threat contingencies, or some combination thereof.

Exploring event segmentation's role in fear reversal may shed light on its broader implications for emotional learning. First, event segmentation appears to share neurobiological pathways with fear extinction and reversal, involving structures like the ventromedial pFC (vmPFC) and hippocampus, which encode safety signals and reevaluate threats (Battaglia et al., 2022; Laing, Felmingham, et al., 2022; Laing, Steward, et al., 2022; Savage et al., 2020a; Fullana et al., 2015). Deficient safety processing, indicated by failures to adjust prior threat expectations, has been specifically linked with alterations in vmPFC and hippocampal responses (Via et al., 2018; Apergis-Schoute et al., 2017; Garfinkel et al., 2014). Episodic memory studies highlight the temporally dynamic roles of these regions in processing event boundaries and their benefits on memory performance. Neural activity, in regions like the hippocampus, synchronizes with event boundaries and reactivates patterns from prior learning periods, influencing memory for items encoded during those events (Hahamy, Dubossarsky, & Behrens, 2023; Ezzyat & Davachi, 2021; Silva, Baldassano, & Fuentemilla, 2019; Sols, DuBrow, Davachi, & Fuentemilla, 2017). Hippocampal–vmPFC activation, integral in fear extinction, is also critical for integrating episodic memories into coherent representational structures (Cowan et al., 2020; Morton, Sherrill, & Preston, 2017; Schlichting, Mumford, & Preston, 2015; Schlichting & Preston, 2015; Davachi, 2006). Thus, connecting fear reversal and event segmentation mechanisms at a behavioral level could provide a useful bridge between conditioning and episodic memory frameworks, exploring how important mechanisms of explicit memory organize information about threat and safety. These factors also have compelling relevance to fear-related disorders, including obsessive-compulsive disorder and posttraumatic stress disorder. For instance, anxiety-related failures to encode and express safety information, prompting the return of fear (Apergis-Schoute et al., 2017; Jovanovic, Kazama, Bachevalier, & Davis, 2012), might be determined by the organization of conflicting emotional events in episodic memory (Dunsmoor, Cisler, Fonzo, Creech, & Nemeroff, 2022; Bisby, Burgess, & Brewin, 2020).

In the current study, we examined selective memory enhancements ~24 hr after threat reversal learning. In Experiment 1 (event boundary), participants encoded nonrepeating exemplars from two higher-order categories (CS+/CS−) spanning three phases that were separated by distinct event boundaries: preconditioning (neutral encoding), threat acquisition, and threat reversal. In acquisition, the CS+ category underwent threat learning via shock pairings while CS− were unpaired, which then switched during threat reversal (CS+ unpaired, CS− shock-paired). Experiment 2 (no boundary) featured an identical sequence, except that threat reversal begun immediately after acquisition, with no pause between phases. Memory was assessed via a specialized mnemonic similarity test (MST), with items that were exact repeats from encoding (memory "accuracy"), similar yet distinct from conditioning (testing memory "generalization"), or entirely novel (controlling for false alarms). Each item from Day 1 was further assessed for temporal source memory ("When did you see this image?"), to examine emotional biases upon temporal context retrieval. We hypothesized that event boundaries between acquisition and reversal would organize selective memory enhancements that flowed in synchrony with changes in threat contingencies during learning: better recognition for CS+ items encoded before reversal (including retroactive enhancement, items before acquisition) and CS− items encoded after reversal. The absence of a boundary was expected to generate poor differentiation of CS+/CS− memory, particularly those encoded during the unsignaled changing of threat contingencies. Additional analyses explored how these memory outcomes were influenced by autonomic arousal during encoding (skin conductance response [SCR]) and individual differences in negative mood.

## METHODS

### Participants

Sixty-nine healthy adult volunteers were recruited for the 2-day within-participant study at the University of Texas at Austin, earning course credit or $40 reimbursement for their participation. Upon arrival, participants provided written informed consent and confirmed that they had fluency in English; normal or corrected-to-normal vision; no current major illnesses, including psychiatric or neurological disorders; and no hearing impairments. Participants completed computerized self-report measures, including the "DSM-5 cross-cutting symptom measure" (Gibbons, Farmer, Shaw, & Chung, 2023); the Beck Anxiety Inventory (Beck, Epstein, Brown, & Steer, 1993); and the short-form Depression, Anxiety, and Stress Scale (DASS-21; Lovibond & Lovibond, 1995). Participants were excluded for technical problems (7), discontinuing the experiment (1), and disclosing failure to meet inclusion/exclusion criteria after enrollment had completed (1). This resulted in final samples of $n$ = 34 (Experiment 1: 62% female, mean age = 20.27 ± 3.36 years, age range = 18–34 years) and $n$ = 26 (Experiment 2: 76.9% female, mean age = 20.88 ± 3.82 years, age range = 18–34 years). Sample sizes were determined based on prior studies using the same experimental designs, ranging between 25 and 35 participants (Laing & Dunsmoor, 2023; Keller, Hennings, Leiker, Lewis-Peacock, & Dunsmoor, 2022; Hennings et al., 2021; Hennings, McClay, Lewis-Peacock, & Dunsmoor, 2020; Keller & Dunsmoor, 2020; Starita et al., 2019; Dunsmoor et al., 2018; Patil, Murty, Dunsmoor, Phelps, & Davachi, 2017; Dunsmoor, Kragel, Martin, & LaBar, 2014; Dunsmoor & Murphy, 2014). This study was approved by the University of Texas at Austin Institutional Review Board (IRB: 2020020157-MOD08).

### Experiment Tasks

The experiment used a hybrid category conditioning and episodic memory paradigm, adapted from a previous fear extinction study (Laing & Dunsmoor, 2023). Participants attended two sessions on consecutive days, approximately 24 hr apart, with category conditioning on Day 1, followed by episodic memory (MST) on Day 2.

#### *Fear Reversal (Day 1)*

Day 1 featured a category conditioning paradigm (Figure 1) with three phases: preconditioning (Pre-Con), threat acquisition (ACQ), and reversal learning (REV). Participants viewed a series of nonrepeated items, which were unique exemplars from two superordinate semantic categories (animals/tools) displayed on a white background. The category items served as CS (CS+/CS−), with a brief electric shock (50 msec) serving as the unconditioned stimulus, which coincided with CS offset for reinforced trials and was delivered through electrodes fixed to the participants' right wrist. After Pre-Con, but before threat acquisition, shocks were calibrated to a level deemed "highly annoying and unpleasant, but not painful." For each trial, the CS image appeared in the center of the screen for a 5-sec duration. Intertrial intervals were randomly jittered between 5 and 7 sec (mean = 6 sec). CSs were presented in pseudorandomized order, ensuring that there were never three or more items from the same category (CS+/CS−) presented in a row. The experiments were counterbalanced such that approximately

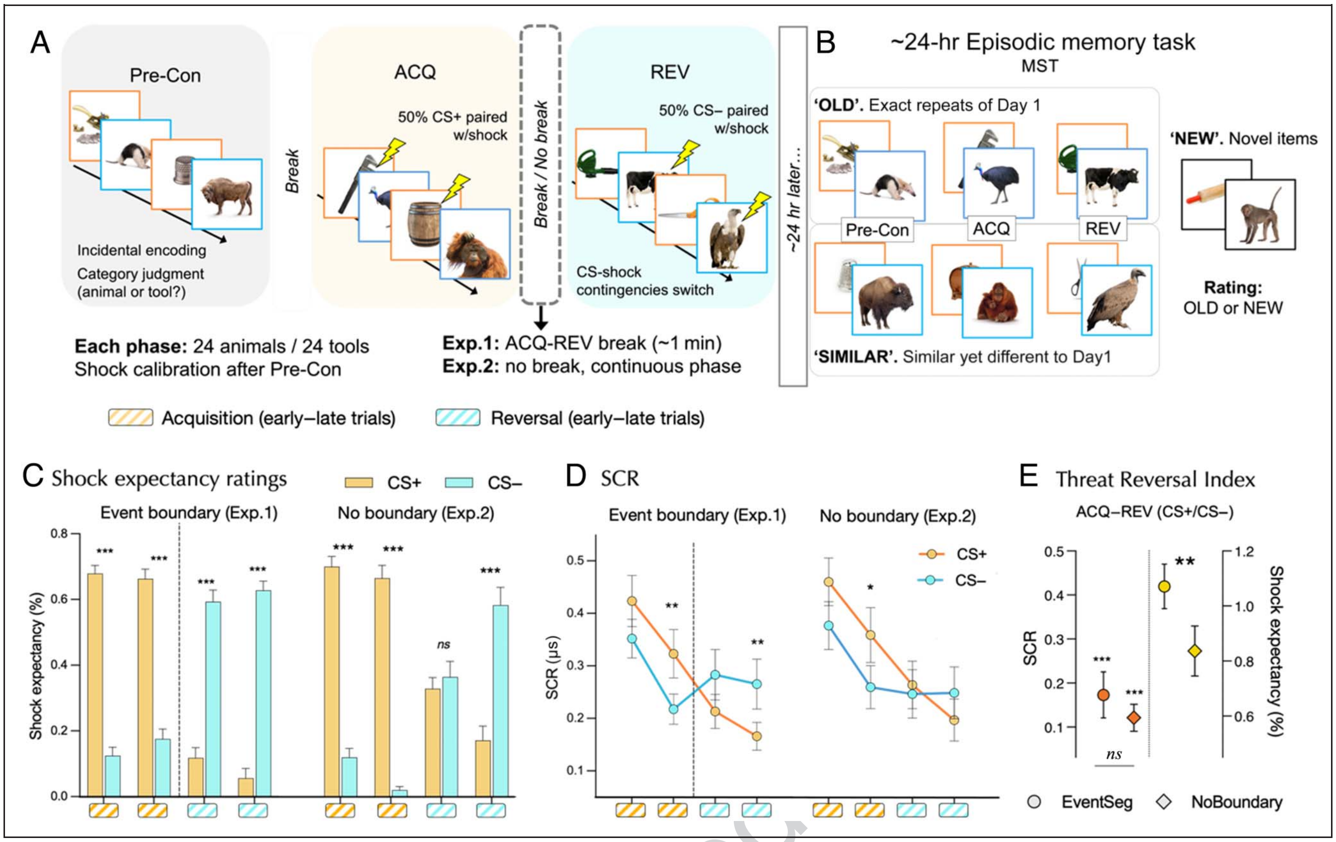


**Figure 1.** Experiment paradigm and conditioned fear responses. (A) Day 1: threat acquisition (ACQ) involved items from one category paired with shock (CS+), whereas the other was unpaired (CS−). Contingencies were then switched from CS+ to CS− items in the reversal phase (REV). Experiment 1 featured a brief break period (~1–2 min) between each phase, whereas Experiment 2 had no ACQ–REV break. (B) Episodic memory was assessed the next day via an MST procedure, with items rated "old" or "new." Ratings were made for three conditions: "old" (repeats), "similar" (resembled Day 1), and "new" (novel). Responses were used to calculate recognition (old rated old minus false alarms) and generalization (similar rated old minus false alarms). (C) Shock expectancy ratings and (D) SCRs indicated successful fear acquisition and reversal but that conscious reversal learning was delayed when the event boundary was removed (Experiment 2). (E) A threat reversal index revealed that differential CS+/CS− responses were reversed for SCR (red) and ratings (yellow) and that shock expectancy reversal was elevated in Experiment 1, $t(58) = 2.80$, $d = 0.73$, $p = .003$. Error bars reflect *SEM*. Exp. = Experiment; *ns* = nonsignificant ($p > .05$). *$p < .05$. **$p < .01$. ***$p < .001$.



50% of the sample had animal images as CS+ and tool images as CS−, and vice versa.

In total, the encoding phases included 144 unique category items, with 48 items per phase (Pre-Con/ACQ/REV) and each phase containing 24 CS+ and 24 CS− (animals/tools). Exactly half of the items from each phase, for each CS type, were treated as "old targets" that would appear as exact repeats during the memory task on Day 2. The other half were replaced with "similar lures" during the memory test (different but similar items; see details below). Before Pre-Con, participants had skin conductance electrodes (but not shock electrodes) attached and were instructed that no shocks were to occur in the first phase. During Pre-Con, participants judged the category of each item (animal/tool) while the image was onscreen (2AFC). After Pre-Con, shock electrodes were attached and a shock calibration procedure was performed, to ensure the shock was tailored to a level that was intense, annoying, and unpleasant, but not painful. During threat acquisition (ACQ), 50% of CS+ items were reinforced (12/12 shocked/unpaired), whereas CS− items were never reinforced. During reversal (REV), this contingency switched (CS−, 50% shocked; CS+, 0% shocked). Shock expectancy ratings were acquired throughout ACQ and REV on a trial-by-trial basis, during the CS's onscreen duration, with rating options (3AFC: 1 = yes, 2 = unsure, 3 = no) remaining onscreen throughout the task. At the conclusion of the REV phase, participants completed a computerized survey, judging the intensity of the shock and the number of shocks delivered during the tasks as well as describing how they felt when anticipating a shock. The only difference between experiments was that during Experiment 1, the experiment program was closed, the next phase was opened, and instructions were repeated to the participant (reminder of same instructions as acquisition), lasting between 1 and 2 min. In Experiment 2, the first trials of reversal began immediately after the final intertrial interval of acquisition, such that emotional learning acted as one continuous phase, with no additional instructions.

*Episodic Memory (Day 2)*

Memory retrieval at 24 hr after learning was assessed with a specialized iteration of the MST (Stark, Kirwan, & Stark, 2019; Stark, Yassa, Lacy, & Stark, 2013), adjusted to fit the requirements of the fear extinction task (Laing & Dunsmoor, 2023). These procedures feature a battery of items including "old targets" (exact repeats of items from encoding), "similar lures" (similar, but not identical to, items from encoding), or "new foils" (novel items that never appeared during encoding). Our specialized MST consisted of 216 items in total (108/108, CS+/CS−), with equal parts "old," "similar," and "new" (72 each, 36 CS+/36 CS− per condition), and with old/similar items drawn equivalently from the three conditioning phases. Because of 50% reinforcement, old and similar CS+ ACQ and CS− REV items were balanced to have equal sets of shocked/nonshocked exemplars. Items appeared on a white background in the center of the screen and rated "OLD" or "NEW" (2AFC), by pressing "1" and "2" on the keyboard. The task was self-paced, with the text of the chosen response option briefly changing color from white to orange, followed by the item terminating from the screen, and a randomly jittered intertrial interval between 2 and 3 sec (mean = 2.5 sec). Given the high number of trials, the MST was split into two separate parts to allow a brief rest period (<1 min).

*Temporal Source Memory*

Temporal source memory was examined using a self-paced experiment, which included a current assessment of "stimulus typicality," based on the methods of prior studies (Laing & Dunsmoor, 2023; Hennings et al., 2021). In this task, participants were presented with all 144 of the unique category exemplar items that had appeared across the three phases of Day 1 and were tasked with making two ratings per item. Participants were reminded that three separate phases had occurred on Day 1 and prompted as to what each one involved (e.g., "Phase 1 was at the beginning when you classified each item as being an animal or a tool…." For source memory, 3AFC ratings were made, with options of "Phase 1," "Phase 2," and "Phase 3"), which were presented onscreen below where the images would appear (Figure 4). Participants were instructed to judge the phase that each item had originally occurred in on Day 1. When participants were being introduced to the task, they were reminded—and asked to confirm their agreement—that the prior day's session involved three specific phases. Both the event boundary and no boundary experiments involved the same description of Phase 1 (Pre-Con: "You classified images as animals or tools and no shocks occurred") but differing descriptions of Phases 2 and 3. For the event boundary group, they were reminded that Phase 2 featured shocks after certain images, and rating expectations of shock, and that Phase 3 followed similarly, except that the kind of image being shocked (animals or tools) was switched from one to the other. The no-boundary group was instructed that Phase 2 was described as the phase where originally one category had been shocked early on, with the shocks switching to the other category approximately halfway through the phase. Participants were asked to verbally confirm that they recalled this having occurred, after which they were instructed that the early portion of Phase 2 would be referred to as Phase 2 and the latter half (when contingencies changed) would be referred to as Phase 3. After the rating was made, the item remained onscreen, and ratings of "typicality" were made, this time on a 7-point scale (1 = *not at all typical*, 7 = *very typical*). Before the task, participants were given an example of typicality with an analogy to an unrelated category (not tools or animals): "For example, an apple is a typical fruit, it is representative of the entire fruit category. On the other hand, a dragon fruit is not a typical fruit, at least in American grocery stores." Typicality results are included in the intertrial intervals that were randomly jittered between 500 and 800 msec.

*Conditioned Threat Responses*

Physiological threat learning was assessed via electrodermal activity, acquired via electrodes attached to participants' left palms, with conductive gel (0.5% saline) applied to the skin surface. Electrodermal activity signal was continuously sampled at 200 Hz throughout the experimental procedures of Day 1 using snap electrodes (BIOPAC EL509) routed through the BIOPAC MP150 System. Trial-wise SCR data were considered valid conditioned responses if they were > 0.02 μs, occurred between 0.5 and 5 sec after CS onset, and lasted a maximum of 5 sec. SCRs were preprocessed using an automated script in MATLAB (Green, Kragel, Fecteau, & LaBar, 2014). To normalize distributions, data were square root transformed before analyses. Shock expectancy ratings were made during CS item presentation, on a 3AFC scale (1 = yes, 2 = unsure, 3 = no), with responses recorded as 0 (no), 0.5 (unsure), and 1 (yes) for each trial.

## Statistical Analyses

Shock expectancy and SCR (Day 1) and memory performance (Day 2) were analyzed via two-way repeated-measures ANOVAs, which included Greenhouse–Geisser correction. Partial eta-squared ($\eta_p^2$) and Cohen's $d$ served as effect sizes (for main effects and post hoc tests, respectively), with Bonferroni correction for multiple comparison performed on all post hoc tests. Bonferroni-adjusted significance thresholds were calculated as the standard alpha level of $\alpha = .05$ divided by the number of tests. For threat acquisition and reversal analyses (SCR and ratings), this significance threshold was $\alpha = .0125$ (four tests), comparing CS+ versus CS− responses between early and late trials for within a phase. For episodic memory analyses (recognition, generalization), the threshold was $\alpha = .01$ (five tests), including a within-phase stimulus comparison (CS+ > CS−) for items of each phase (PreCon, acquisition, reversal) and an additional two between-phase (acquisition–reversal) comparisons for CS+/CS−. For memory scores, a series of one-sample *t* tests confirmed significant difference from a mean of zero, to indicate that recognition and generalization did occur when correcting for false alarms (e.g., subtracting proportion of "old" ratings to "new" items at test; see Appendix). The distribution of raw old/new ratings for each stimulus condition (old/similar/new) is reported in the Appendix. Source memory biases and accuracies were defined as significantly above 0.33, with 33% representing a chance rating when three options are available (3AFC: Phase 1/2/3). All correlational analyses were conducted starting with zero-order Pearson correlations and hierarchical regression models. One participant had instances of outlier data in SCR and recognition memory, identified via visual inspection of scatter plots. For SCR/memory correlational analyses, this outlier was removed, although the outlier neither caused nor negated the statistical significance of the correlations reported here (e.g., $p < .05$ with or without the outlier). Statistical analyses were conducted using MATLAB (Version 23.2, The MathWorks) and JASP software (JASP Team, 2021).

Change-point analyses (CPAs) were conducted to identify significant changes in episodic memory according to the original order of items during encoding. Our approach was similar to prior studies (Dunsmoor et al., 2018; Herry et al., 2008) based on methods by Taylor (2000). Memory scores (recognition, generalization) were averaged across three trial bins, creating eight trial blocks corresponding to the order of stimuli during encoding, from acquisition to reversal. CPA was performed separately for "old-target" MST items (recognition memory) and "similar-lure" MST items (memory generalization). The data were transformed into a smoothed time series by calculating the moving average. CPA employs "cumulative sum" (CUSUM) scores, reflecting the absolute magnitude of change at each time point. The initial value ($S_0$) is set at zero, and the CUSUM for the current time point ($S_i$) is calculated according to Equation 1.

$$S_i = S_{i-1} + (X_i - \bar{X}) \tag{1}$$

Here, $X_i$ is the memory score for the current trial bin, and $\bar{X}$ is the average memory score for all trial bins. The CUSUM line trends positively when a time point is above the total average and declines when below average (Taylor, 2000). Steps for identifying significant change points are described in Equations 2 and 3. First, the difference between maximum and minimum CUSUMs in the time series is calculated (Equation 2). Next, bootstrapping is performed by randomly reordering the original data points ($X_n$) and calculating 10,000 new CUSUM lines for each new bootstrapped order. For each iteration, a bootstrapped CUSUM difference (max–min) is calculated. The number of bootstrapped CUSUM differences lower than the original CUSUM difference (max–min) is divided by the overall number of bootstrap iterations to derive the confidence level. Each time point with a confidence level >95% is defined as a significant change point, where changes in the time series of memory data could be considered more than a random fluctuation. If a trial bin had a greater value than the prior trial bin, the change point was registered as a significant increase in memory or a decrease if the value was beneath the preceding trial bin. In-house MATLAB scripts were developed to perform these procedures.

$$S_{\text{diff}} = S_{\text{max}} - S_{\text{min}} \tag{2}$$

$$\text{Confidence Level\%} = \frac{100 \times (\text{bootstr. } S_{\text{diff}} < \text{orig. } S_{\text{diff}})}{\text{N bootstr.iterations}} \tag{3}$$

## RESULTS

### Event Boundaries Facilitate Threat Reversal Learning

First, we established learning effects by examining SCRs and shock expectancy ratings across the acquisition reversal phases. Threat reversal learning was examined by comparing responses for each CS type across four blocks of 12 trials, split into early and late trials of ACQ and REV (Figure 1). In Experiment 1 (event boundary), shock expectancy ratings showed a main effect of trials (early ACQ/late ACQ/early REV/late REV), $F(1, 33) = 9.31$, $p < .001$, $\eta_p^2 = .22$, and a CS × Trials interaction, $F(1, 33) = 148.12$, $p < .001$, $\eta_p^2 = .82$. Post hoc tests ($\alpha = .0125$) showed CS+ > CS− discrimination was maintained across early ($t = 10.99$, $d = 1.88$, $p < .001$, 95% CI [0.51, 0.67]) and late ($t = 14.35$, $d = 2.46$, $p < .001$, 95% CI [0.51, 0.67]) acquisition and reversed (CS− > CS+) across early ($t = 8.53$, $d = 1.46$, $p < .001$, 95% CI [0.36, 0.59]) and late ($t = 12.27$, $d = 2.11$, $p < .001$, 95% CI [0.48, 0.67]) reversal trials. SCRs showed a main effect of trials, $F(1, 33) = 26.30$, $p < .001$, $\eta_p^2 = .44$, and a CS × Trials interaction, $F(1, 33) = 8.86$, $p = .001$, $\eta_p^2 = .21$. CS+ > CS− discrimination in early acquisition was nonsignificant after Bonferroni correction ($t = 2.37$, $p = .024$, 95% CI [0.05, 0.15]) but significant in late acquisition ($t = 3.56$, $d = 0.61$, $p = .001$, 95% CI [0.05, 0.17]). SCRs showed no CS−/CS+ discrimination in early reversal but a significant CS− > CS+ effect in late reversal ($t = 2.92$, $d = 0.50$, $p = .006$, 95% CI [0.03, 0.17]).

For Experiment 2 (no break between acquisition and reversal), shock expectancy showed main effects of CS, $F(1, 25) = 31.40$, $p < .001$, $\eta_p^2 = .56$, and trials, $F(1, 25) = 4.40$, $p = .007$, $\eta_p^2 = .15$, and an interaction, $F(1, 25) = 68.91$, $p < .001$, $\eta_p^2 = .73$. CS+ > CS− discrimination persisted across early ($t$ = 11.21, $d$ = 2.20, $p$ < .001, 95% CI [0.47, 0.68]) and late ($t$ = 16.85, $d$ = 3.21, $p$ < .001, 95% CI [0.56, 0.72]) acquisition. No CS+/CS− difference occurred in early reversal ($t$ = 0.50, $p$ = .62), but a notable CS− > CS+ difference occurred in late reversal ($t$ = 4.94, $d$ = 0.97, $p$ < .001, 95% CI [0.24, 0.58]), indicative of slower yet eventual contingency reversal. SCRs showed main effects of CS, $F(1, 25) = 6.46$, $p = .018$, $\eta_p^2 = .21$, and trials, $F(1, 25) = 21.20$, $p < .001$, $\eta_p^2 = .46$, and a significant interaction, $F(1, 25) = 5.31$, $p = .005$, $\eta_p^2 = .18$. CS+ > CS− differences were significant in early ACQ ($t$ = 3.05, $d$ = 0.60, $p$ = .005, 95% CI [0.03, 0.14]), but late ACQ trials did not survive correction for multiple comparisons ($t$ = 2.34, $p$ = .028). As with expectancy ratings, SCRs showed no differences across early reversal ($t$ = 0.67, $p$ = .51) but a significant CS− > CS+ difference in late reversal ($t$ = 2.82, $d$ = 0.55, $p$ = .009, 95% CI [0.01, 0.09]). There were no direct differences between experiments in terms of differential SCR (CS+ > CS−) within phase for acquisition, $t(2, 58) = 0.006$, $d = 0.002$, $p = .99$, or reversal, $t(2, 58) = 0.83$, $d = 0.216$, $p = .41$.

A "threat reversal index" was calculated by subtracting the CS+ > CS− difference during reversal from CS+ > CS− discrimination in acquisition (ACQ − REV), for SCR and threat expectancy data (Homan et al., 2019). Across all participants, the reversal index was significantly above zero for SCRs, $t(1, 59) = 4.64$, $d = 0.60$, $p < .001$, and shock expectancy ratings, $t(1, 59) = 15.683$, $d = 2.03$, $p < .001$. When compared directly between experiments, the reversal index for expectancy ratings was significantly higher for the event boundary group, $t(2, 58) = 2.80$, $d = 0.73$, $p = .003$, but equivalent between groups in terms of SCRs, $t(2, 58) = 1.06$, $d = 0.27$, $p = .15$. Analyses of within-session threat learning indicate that although threat reversal learning can occur with and without event segmentation, the presence of an event boundary facilitates faster reversal of threat associations.



### Event Segmentation Facilitates Memory Reversal and Retroactive Enhancement

Next, we investigated effects of emotional learning on 24-hr memory accuracy and how this fluctuated over the course of learning. Recognition memory was calculated as the proportion of "hits" ("old" items rated old) subtracting "false alarms" ("new" items rated old) as follows: $p(\text{old} \mid \text{old}) - p(\text{new} \mid \text{old})$. Memory for the event boundary experiment showed a main effect of CS type, $F(1, 33) = 5.43$, $p = .026$, $\eta_p^2 = .141$, no significant effect of phase, $F(1, 33) = 0.613$, $p = .54$, $\eta_p^2 = .018$, and a significant Phase × CS Type interaction, $F(1, 33) = 15.51$, $p < .001$, $\eta_p^2 = .32$. CS+ items were selectively remembered better than CS− items encoded during the Pre-Con ($t$ = 2.98, $d$ = 0.51, $p$ = .005, 95% CI [0.15, 0.86]) and acquisition ($t$ = 4.10, $d$ = 0.70, $p$ < .001, 95% CI [0.32, 1.08]) phases. Notably this replicates prior findings, showing selective and retroactive memory enhancement via emotional learning (Figure 2A). Memory for reversal items extended this pattern, observing the emotional advantage switching from CS+ to CS− for exemplars encoded during the reversal phase ($t$ = 2.52, $d$ = 0.43, $p$ = .017, 95% CI [0.08, 0.78]).

Experiment 2 replicated the conventional CS+ > CS− memory enhancement for acquisition items but found no retroactive enhancement for Pre-Con items, nor significant memory reversal from CS+ to CS− (Figure 2A). ANOVA showed no main effects except for a significant CS Type × Phase interaction, $F(1, 26) = 8.11$, $p < .001$, $\eta_p^2 = .24$. The sole similarity with Experiment 1 was the selective CS+ > CS− memory enhancement for acquisition items ($t$ = 3.99, $d$ = 0.94, $p$ = .002, 95% CI [0.05, 0.35]), with no within-phase CS+/CS− differences for the other phases. To unpack this, cross-phase comparisons suggested that although memory appeared to "increase" for CS− from acquisition to reversal ($t$ = 3.68, $d$ = 0.85, $p$ = .005, 95% CI [0.03, 0.33]), there was no corresponding significant "decrease" for CS+ ($p$ = .28). To compare experiment outcomes more directly, an analysis of the combined sample ($n$ = 60) was run with "Experiment" (Experiment 1, Experiment 2) as a between-participant effect, which was found to be nonsignificant as a main effect, $F(1, 58) = 0.137$, $p = .713$, $\eta_p^2 = .002$. Significant main effects of CS type, $F(1, 58) = 7.795$, $p = .007$, $\eta_p^2 = .118$, and a Phase × CS interaction, $F(2, 116) = 21.090$, $p < .001$, $\eta_p^2 = .267$, persisted similar to within-experiment outcomes. There were no Experiment × CS and Experiment × Phase interactions. Deviations between experiments were unpacked by looking at simple main effects, especially the factor of phase with moderators of CS type and experiment group. Indeed, despite significant Phase × CS− effects for both experiments (Experiment 1: $F(2, 58) = 4.997$, $p = .010$; Experiment 2: $F(2, 58) = 8.027$, $p < .001$), a significant Phase × CS+ effect occurred selectively for Experiment 1, $F(2, 58) = 10.79$, $p < .001$, but not Experiment 2, $F(2, 58) = 1.108$, $p = .338$.

These outcomes suggest that the no boundary experiment (Experiment 2) had successful reversal of CS− (safe-to-threat) memory but delayed reversal of CS+ memory (threat-to-safe). To clarify the specificity of reversal "within stimulus," a reversal index was calculated for recognition memory scores, subtracting reversal memory scores from acquisition for CS+/CS− separately (Figure 2C). Consistent with main effects analyses, Experiment 1 indicated significant reversal for both CS+ ($t$ = 4.19, $d$ = 0.73, $p$ < .001, 95% CI [0.09, 0.25]) and CS− memory ($t$ = 2.99, $d$ = 0.51, $p$ = .005, 95% CI [0.04, 0.19]), whereas Experiment 2 only showed reversal of CS − ($t$ = 3.46, $d$ = 0.68, $p$ = .002, 95% CI [0.07, 0.29]) but not CS+ memory ($t$ = 1.74, $p$ = .095). These indicate that the absence of an acquisition–reversal event boundary may have prevent the unreinforced CS+ category exemplars

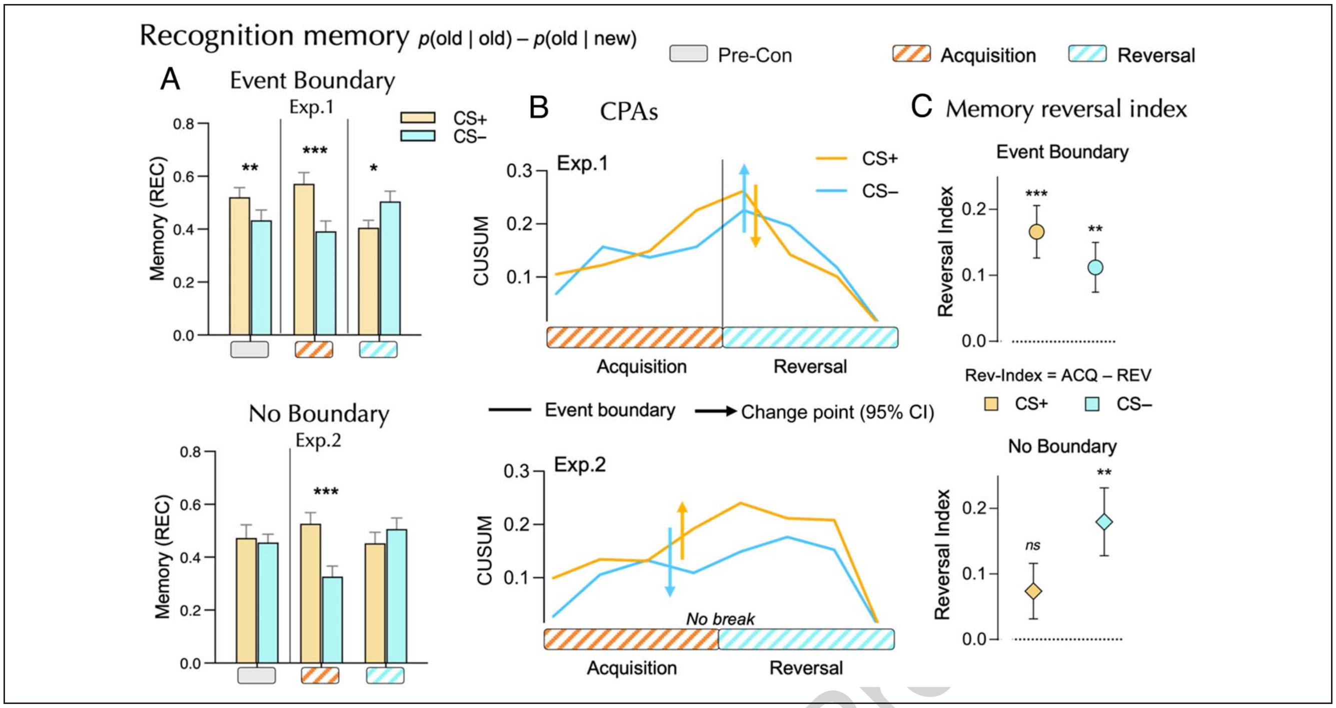


**Figure 2.** Temporal dynamics of selective and retroactive memory enhancement. (A) In Experiment 1 (event boundary), threat learning resulted in memory enhancement for CS+ > CS− items from acquisition (selective enhancement) and Pre-Con (retroactive enhancement), as well as the reversal of memory in favor of CS− for reversal items. Absence of an event boundary (Experiment 2) maintained the selective memory for acquisition (CS+ > CS−) without selective retroactive enhancement or reversal effects. (B) Examining item memory over time, CPA revealed significant points of memory increase (CS−) and decrease (CS+) immediately after the event boundary in Experiment 1 (Trial Bin 4), but no significant change points of memory decline for CS+ in Experiment 2. Arrows on the CUSUM line demarcate positive or negative direction of change points (95% confidence, 10,000 bootstraps). (C) A memory reversal index confirmed that, in Experiment 2, CS− memory reversed from ACQ to REV, whereas CS+ memory remained elevated, indicating specificity to safety encoding of previous threat cues. Error bars represent *SEM*. *$p < .05$. **$p < .01$. ***$p < .001$. *ns* = nonsignificant ($p > .05$).

from losing the emotional memory enhancement that was accrued during threat acquisition.

To elucidate the trajectory of memory changes across learning, CPA was applied to unpack retrieval of CS+/CS− exemplars according to their original order during encoding (Dunsmoor et al., 2018; Herry et al., 2008; Taylor, 2000), treating memory performance as a continuous time series running from acquisition to reversal. This CPA method tested significance with 10,000 bootstrap iterations, reordering trial bins and calculating CUSUM scores to assess if the original data fell above a 95% confidence level (>95% of bootstrapped iterations; see Methods). In Experiment 1, CPA indicated that CS+ memory had significantly increased by the final period of acquisition (Trial Bin 3), followed by a steep decline immediately after the event boundary (Time Point 4), for items encoded at the earliest period of reversal (Figure 2B). Changes in CS− memory showed the inverse effect, "increasing" sharply after the event boundary, at the same time point where CS+ memory declined. Thus, event segmentation seemed to signal an effective temporal marker, delineating the moment at which certain inputs would be prioritized over others because of changing threat contingencies. This was clarified further by Experiment 2, wherein CPA indicated significant CS+ memory increase during acquisition, but no corresponding points of decline during reversal. CS− memory also showed a significant decline during acquisition, but—in contrast to the overall mean differences—no significant points of increase were identified via CPAs. Experiment 2 outcomes are consistent with the interpretation that the observed lack of CS+/CS− memory reversal is because of the "persistence" of CS+ memory, which fails to markedly decline when no external boundaries occur (Figure 2B). Notably, in Experiment 2, both categories exhibited change points during late acquisition, thereby preceding the significant change points for memory adjustment identified in Experiment 1 (occurring right after the boundary). These support the hypothesis that event segmentation facilitates updating memory prioritization when external contingencies change.

In summary, these outcomes indicate that a lack of an event boundary did not prevent updating memory advantages to newly aversive stimuli (CS−) but failed to enact the typical drop-off in CS+ memory seen after discrete boundaries (Dunsmoor et al., 2018). Similarly, the absence of selective CS+ > CS− retroactive enhancement for Pre-Con items was not purely because of poorer memory, but globally elevated memory for both CS categories. Because the only boundary in Experiment 2 was between the Pre-Con phase and a combined acquisition–reversal phase, this may have allowed the two periods to be segmented into "emotional" (acquisition–reversal) and "nonemotional" (Pre-Con) events, thus facilitating consolidation of items encoded before the event boundary—irrespective of their semantic relatedness to subsequent items.

### Memory Generalization Synchronizes with Threat Reversal

The above results illustrate effects of reversal and event segmentation on selective memory "enhancement." Next, we examined how participants shifted memory in terms of generalization, which can be dissociable from recognition memory in distinguishing the properties of fear and extinction (safety) memories (Laing & Dunsmoor, 2023). "Mnemonic generalization" refers to how items that resembled initially encoded (Day 1) stimuli are appraised as old (generalized) compared to new (discriminated; Bernstein, Brühl, Kley, Heinrichs, & McNally, 2020; Dohm-Hansen & Johansson, 2020; Stark et al., 2019). Here, generalization (also known as "behavioral pattern completion") was calculated as the rate of "similar" items appraised as old minus the false alarm rate: $p(\text{old} \mid \text{sim}) - p(\text{old} \mid \text{new}$; Laing & Dunsmoor, 2023; Granger et al., 2021; Starita et al., 2019; Ally, Hussey, Ko, & Molitor, 2013; Yassa, Lacy, et al., 2011; Yassa, Mattfeld, Stark, & Stark, 2011).

In Experiment 1, mnemonic generalization appeared to update considerably, switching from CS+ to CS− in sync with reversal learning, immediately after an event boundary, the day prior. Generalization scores showed main effects of phase, $F(1, 33) = 26.03$, $p < .001$, $\eta_p^2 = .44$, and a Phase × CS Type interaction, $F(1, 33) = 14.69$, $p < .001$, $\eta_p^2 = .31$. Acquisition CS+ > CS− differences failed to meet the Bonferroni-corrected significance threshold ($\alpha = .01$) but were significant at a two-tailed uncorrected ($p < .05$) threshold ($t = 2.60$, $d = 0.45$, $p = .014$, 95% CI [0.02, 0.20]). By contrast, CS− > CS+ differences for reversal items were significant after correcting for multiple comparisons ($t = 3.90$, $d = 0.67$, $p < .001$, 95% CI [0.08, 24]). Between-phase comparisons revealed that generalization significantly decreased for CS+ ($t = 4.38$, $d = 0.75$, $p < .001$, 95% CI [0.09, 0.24]) and increased for CS− ($t = 3.05$, $d = 0.52$, $p = .004$, 95% CI [0.03, 0.18]) from acquisition to reversal. Experiment 2 broadly replicated this pattern of changes in mnemonic generalization, with a main effect of phase, $F(1, 25) = 6.48$, $p = .003$, $\eta_p^2 = .21$, and a Phase × CS Type interaction, $F(1, 25) = 14.26$, $p < .001$, $\eta_p^2 = .36$. Generalization was selectively elevated for ACQ CS+ > CS− ($t = 3.26$, $d = 0.64$, $p = .003$, 95% CI [0.06, 0.28]) and reversal CS− > CS+, although the latter did not meet significance after correcting for multiple comparisons ($t = 2.52$, $p = .019$, 95% CI [0.02, 0.21]). Between-phase comparisons showed significant increases (CS+: $t = 3.74$, $d = 0.73$, $p < .001$, 95% CI [0.06, 0.22]) and decreases (CS−: $t = 3.88$, $d = 0.76$, $p < .001$, 95% CI [0.07, 0.22]) for CS+ and CS− items, in the same fashion as the event boundary experiment.

A reversal index was used to quantify these changes in mnemonic generalization directly. One-sample $t$ tests supported that effective reversal of generalization was seen for Experiment 1 concerning CS+ ($t = 4.38$, $d = 0.75$, $p < .001$, 95% CI [0.09, 0.24]) and CS− memory ($t = 3.05$, $d = 0.52$, $p = .004$, 95% CI [0.03, 0.17]) after the event boundary, as well as for Experiment 2, to an equivalent extent (CS+: $t = 3.74$, $d = 0.73$, $p < .001$, 95% CI [0.06, 0.22]; CS−: $t = 3.88$, $d = 0.76$, $p < .001$, 95% CI [0.07, 0.22]). These outcomes suggest that the fidelity of emotional memories is effectively changed after threat reversal learning and, furthermore, that this updating of precision is robust to the presence or absence of discrete event boundaries.

To clarify these patterns, CPA was applied to mnemonic generalization in the same fashion as recognition memory (see above). Interestingly, although both experiments showed equivalent changes in CS+/CS− memory generalization across the phases, the no boundary data (Experiment 2) appeared to undergo substantial fluctuations in both positive and negative directions across learning. By contrast, Experiment 1 indicated only two major change points, falling on either side of the event boundary (Figure 3C). Interestingly, as with recognition memory (Figure 2B), Experiment 1 saw memory generalization changes synchronized nearby the event boundary, with generalization showing an increase for CS− encoded just before the boundary, and a decrease for CS+ encoded in the next trial bin after the boundary. As with recognition memory, these represent two distinct change points of significance. However, Experiment 2 showed numerous change points for CS+ and CS−, which were not as closely linked to the points at which contingencies changed. This may correspond with the inherent uncertainty about stimulus–outcome associations incurred by the lack of a clear event boundary. Although the overall reversal of memory generalization occurred irrespective of event segmentation, event boundaries indicated a more stable trajectory over trials, whereas lack of boundary may create an aversive yet ambiguous situation, with greater variation in perceptions of when and where contingencies changed.

Prior work indicates that recognition memory, under conditions of event segmentation, are dissociated from levels of autonomic arousal (i.e., SCR) evoked during encoding (Dunsmoor et al., 2018). A recent study of explicit memory "generalization" observed a robust correlation between fear conditioning SCRs and selective memory generalization ~24 hr later as well as an additional association between SCR and negative mood traits (Starita et al., 2019). Here, we examined individual differences in arousal and negative mood that may influence whether emotional memories become generalized or precise after reversal. Experiment 1 showed a robust positive correlation between mean SCRs for

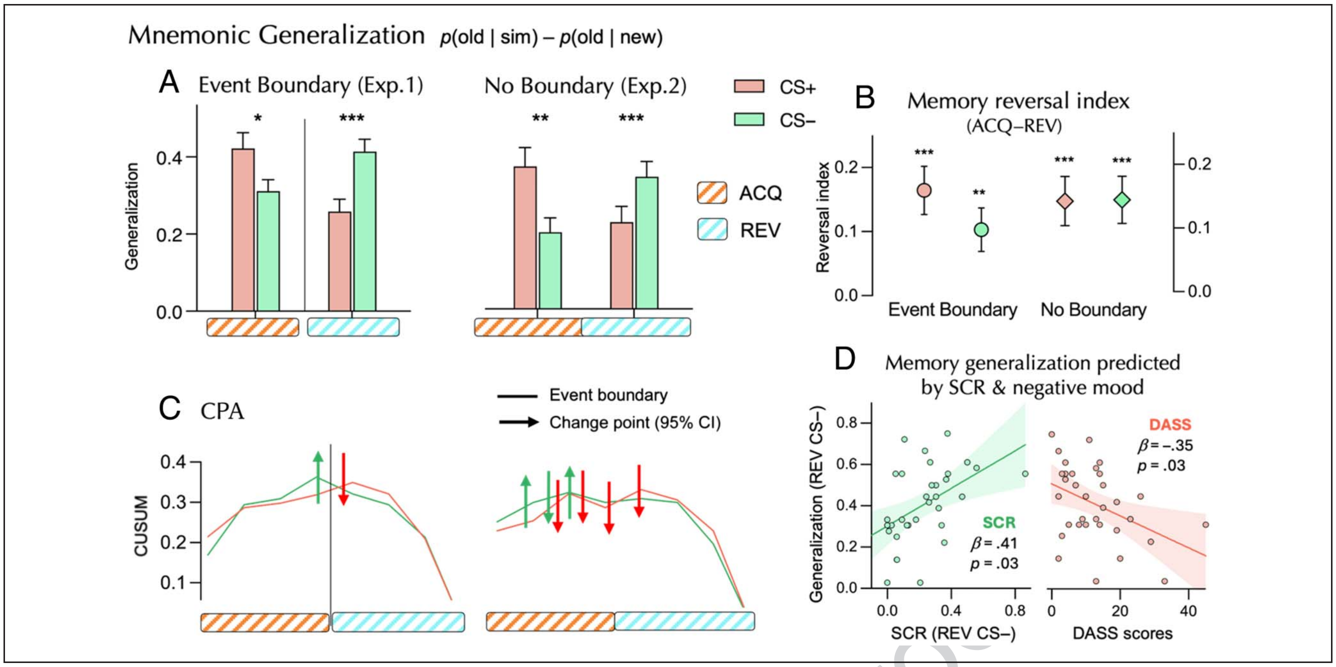


**Figure 3.** Reversal of mnemonic generalization. (A) For both experiments, memory generalization selectively synchronized with threat contingency, with generalized memory for CS+ from acquisition and CS− from reversal. (B) Similarly, a reversal index showed significant updating of generalization for both groups, for both CS categories. (C) However, whereas Experiment 1 suggested these changes were anchored to either side of the event boundary (late acquisition/early reversal), Experiment 2 revealed multiple time points of fluctuating changes in positive and negative directions across the continuous emotional learning phase. (D) For Experiment 1, the overall magnitude of generalization for recent threat cues (CS−) was positively correlated with the magnitude of autonomic arousal (SCR) stimuli evoked during reversal learning and negatively correlated with negative mood scores (DASS). Error bars represent *SEM*. *$p < .05$. **$p < .01$. ***$p < .001$.

reversal CS− (shock-paired) during encoding and memory generalization for reversal CS− (Figure 3D; $r = .48$, $p = .005$, 95% CI [0.16, 0.70]), which did not occur for recognition memory ($r = .279$, $p = .115$, 95% CI [−0.07, 0.57]). Negative mood scores (DASS-21) were negatively correlated with generalization for reversal CS− ($r = -.428$, $p = .013$, 95% CI [0.10, 0.67]).

Multiple regression analysis was conducted to evaluate the relative contributions of within-session arousal and negative mood to predicting memory generalization. Independent variables included age and sex (to account for demographics), with the predictors of interest being negative mood (DASS-21 scores) and mean SCRs evoked by CS− during the reversal phase. The results of the regression analysis are summarized in Table 1, and bootstrapped coefficients are detailed in Table 2. The intercept-only model (Model 1) provided no meaningful information and is omitted from detailed reporting. Model 2 included SCR as a predictor (β = 0.476), $t(1, 31) = 3.01$, $p = .004$, and was significant, explaining 22.6% of the variance ($R^2 = .226$), $F(1, 31) = 9.07$, $p = .005$. Model 3 added negative mood (β = −0.346), $t(2, 30) = 2.28$, $p = .036$, retaining the significant positive coefficient of SCR (β = 0.406), $t(2, 30) = 2.68$, $p = .009$, and improving overall model fit with 34.1% explained variance in memory generalization ($R^2 = .341$), $F(2, 30) = 7.76$, $p = .002$, reflecting a significant increase from Model 2 ($R^2 = .115$, $F = 5.22$, $p = .03$). Part and partial correlations support that negative mood (part = −.339, partial = −.385) and SCR (part = .398, partial = .44) were significant contributors to the model. Neither age nor sex was a significant coefficient and therefore not included in the final models. Collinearity diagnostics indicated no multicollinearity issues among the predictors, with variance inflation factor (VIF) values close to 1 (tolerance = 0.959, VIF = 1.043). These results support SCR and negative mood as predictors of memory generalization at 24 hr after encoding—specifically the generalization of episodic memory for recent threat exemplars (reversal CS−). Generalization is associated

**Table 1.** Regression Models—Mnemonic Generalization (Reversal CS−)

| *Model* | $R^2$ | *df* | *Mean Square* | *F* | *p Value* |
|---|---|---|---|---|---|
| 2. GEN ~ REV-SCR | .226 | 1, 31 | 0.249 | 9.07 | .005 |
| 3. GEN ~ REV-SCR + DASS | .341 | 2, 30 | 0.187 | 7.76 | .002 |

GEN = generalization.

**Table 2.** Bootstrapped Regression Coefficients (Mnemonic Generalization)

| *Model* | *Coefficient* | *SE* | β | *t Value* | *p Value** | *95% CI* |
|---|---|---|---|---|---|---|
| 1 | (Intercept) | 0.031 | – | 12.633 | <.001 | [0.34, 0.47] |
| 2 | REV-SCR (CS−) | 0.142 | 0.476 | 3.012 | .004 | [0.22, 0.77] |
| 3 | REV-SCR (CS−) | 0.142 | 0.406 | 2.682 | .009 | [0.12, 0.67] |
| | DASS | 0.003 | −0.346 | −2.284 | .036 | [$-0.01$, $-5.24 \times 10^{-4}$] |

Bootstrapping based on 5000 replicates. Coefficient estimate is based on the median of the bootstrap distribution. *SE* = standard error; β = standardized beta.

* Bias corrected accelerated.

with higher SCRs evoked by these stimuli during encoding, as well as lower scores on negative mood, encompassing depressive, anxiety, and tension stress domains (DASS).

In summary, these result support the notion the storage and retrieval of explicit threat and safety memories can be distinguished in terms of their generalizability (threat) and precision (safety), beyond general accuracy (Laing & Dunsmoor, 2023). The current experiments further clarify the trajectory of memory updating over the course of reversal learning as well as how conditioned fear responses during learning might influence

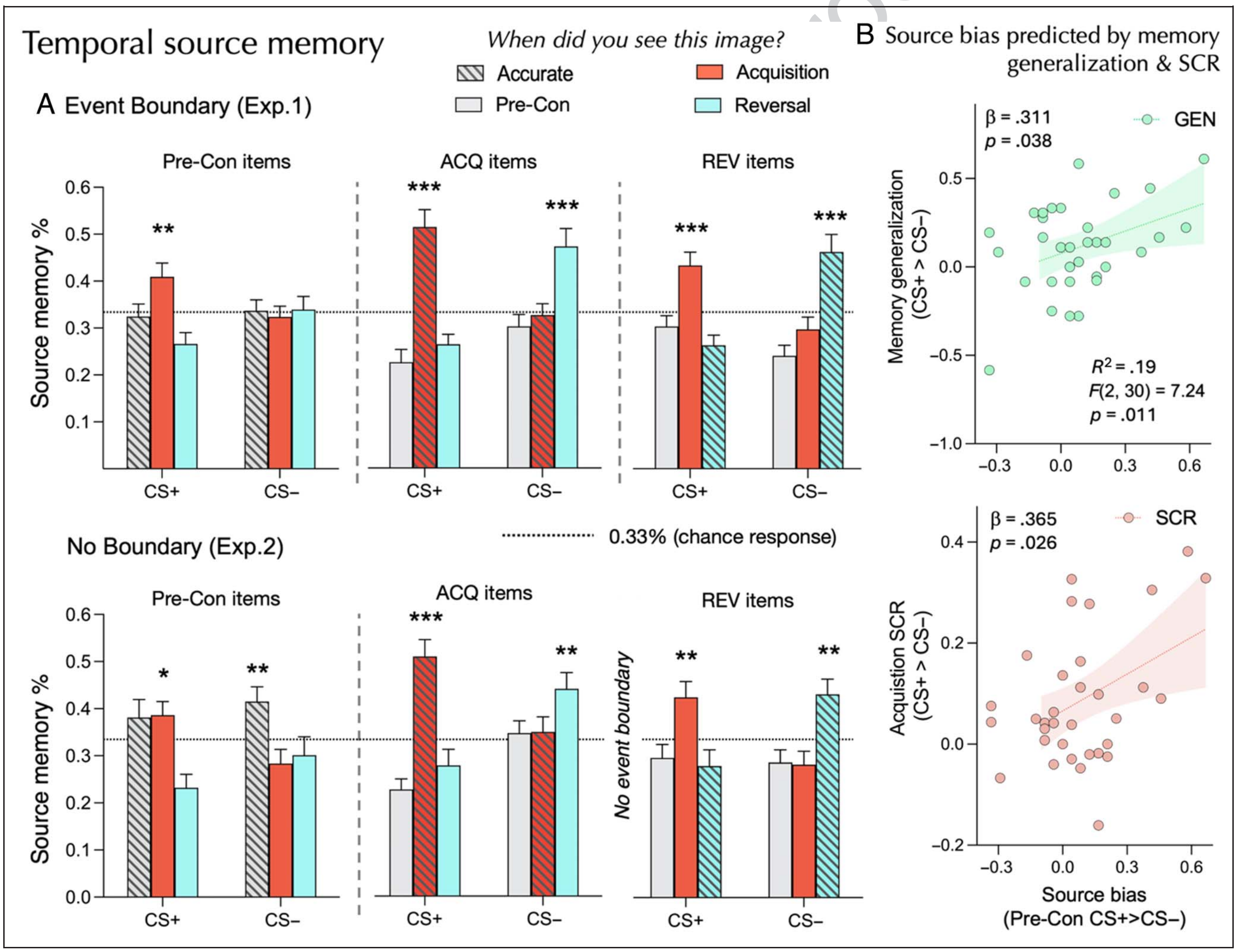


**Figure 4.** Enhanced and distorted temporal source memory. (A) Significant emotional biases were incurred by threat conditioning (ACQ), with CS+ category items attributed to the ACQ phase even if they had originated before or after (Pre-Con/REV). (B) For Experiment 1, selective retroactive threat biases (Pre-Con items rated acquisition, CS+ > CS−) were predicted by autonomic threat responses during threat acquisition (SCRs, ACQ CS+ > CS−) and selective generalization of memory for those same items (ACQ CS+ > CS−). Error bars represent *SEM*. *$p < .05$. **$p < .01$. ***$p < .001$.

the fidelity of long-term memory (LTM) for those stimuli. Negative mood domains may also be associated with diminished generalization of memory for recently learned threat stimuli, which could be considered an adaptive process, indicative of a role for mnemonic precision as a process of relevance to psychopathology.

## Enhancement and Distortion of Temporal Source Memory

Our final analyses examined emotional biases on temporal source memory, wherein participants were tasked with judging which phase (Pre-Con, acquisition, reversal) each item had originally appeared in. Results were organized based on the proportion of those items attributed to each phase (e.g., proportion of CS+ from Pre-Con attributed to Pre-Con, acquisition, or reversal). Significant (above-chance) judgments were defined as those with means above 0.33 (random guess out of three options). Both experiments replicated prior findings, insofar as CS+ items were highly attributed to the acquisition phase, even if they had been encoded before (Pre-Con) or after (reversal) that phase (Figure 4). The threat selectivity (CS+ > CS−) of this bias effect was significant for Pre-Con and reversal items from both experiments (Table 1). Beyond replicating prior findings, the current experiments also demonstrate a selective source memory advantage for reversal CS− items, which showed substantial accuracy (assigned to the reversal phase; Experiment 1: $t = 3.54, p < .001$; Experiment 2: $t = 3.12, p = .002$). It appears that emotional learning toward reversal CS− evoked an emotional bias similar to acquisition CS+, yet this bias only affected CS− items from acquisition, such that Pre-Con CS− were not misattributed to the reversal phase (Table 2). Thus, despite the lack of any outwardly observable transition point between acquisition and reversal, participants in Experiment 2 nevertheless showed the same selective accuracies and biases as in Experiment 1.

To expand on these outcomes, we examined whether individual differences in memory and threat learning influenced emotional source memory biases. One prior study showed that accuracy of item-level recognition memory for acquisition CS+ > CS− predicted selective (CS+ > CS−) source bias (e.g., Pre-Con items misattributed to acquisition; Hennings et al., 2021). Another suggested that source memory accuracy for extinction items correlated with mnemonic discrimination (behavioral pattern separation) for those items (Laing & Dunsmoor, 2023). As such, we examined differential conditioning (ACQ SCR CS+ > CS−) during acquisition (SCRs) and mnemonic generalization of acquisition items (ACQ GEN CS+ > CS−) as predictors. Both variables positively correlated with threat-induced source memory biases (SCR: $r = .435$, $p = .011$, 95% CI [0.11, 0.68]; generalization: $r = .394$, $p = .023$, 95% CI [0.06, 0.65]). Regression analyses were run to clarify the contributions of SCR and generalization as predictors, using the same approach applied to above (see Tables 1 and 2). The results of these regression analyses are summarized in Table 4. An intercept-only model (Model 1) provided no meaningful information and is omitted from detailed reporting. Model 2 (ACQ-SCR: $\beta = 0.435, t(1, 31) = 2.69, p = .024$) was significant ($R^2 = .189$), $F(1, 31) = 7.24$, $p = .011$. Model 3 added ACQ

**Table 3.** Emotional Learning Selectively Biases Temporal Source Memory

| *Source Judgment* | *t* | *p* | *Cohen's d* |
|---|---|---|---|
| *Experiment 1* | | | |
| Pre-Con CS+ rated ACQ (bias)** | 2.702 | .005 | 0.463 |
| Acq. CS+ rated ACQ (accurate)*** | 4.974 | <.001 | 0.853 |
| Acq. CS− items rated REV (bias)*** | 3.700 | <.001 | 0.635 |
| Rev. CS+ items rated ACQ (bias)*** | 3.590 | <.001 | 0.616 |
| Rev. CS− items rated REV (accurate)*** | 3.552 | <.001 | 0.609 |
| *Experiment 2* | | | |
| Pre-Con CS− rated Pre-Con (accurate)** | 2.695 | .006 | 0.529 |
| Pre-Con CS+ rated ACQ (bias)* | 1.950 | .031 | 0.382 |
| Acq. CS+ rated ACQ (accurate)*** | 5.034 | <.001 | 0.987 |
| Acq. CS− rated REV (bias)** | 3.273 | .002 | 0.642 |
| Rev. rated ACQ CS+ (bias)** | 2.807 | .005 | 0.550 |
| Rev. rated REV CS− (accurate)** | 3.117 | .002 | 0.611 |

Alternative hypothesis specifies the mean is > 0.33.

**Table 4.** Regression Models–Source Memory Bias

| *Model* | $R^2$ | *df* | *Mean Square* | *F* | *p Value* |
|---|---|---|---|---|---|
| 2. SourceBias ~ ACQ-SCR | .189 | 1, 31 | 0.332 | 7.241 | .011 |
| 3. SourceBias ~ ACQ-SCR + ACQ-GEN | .281 | 2, 30 | 0.247 | 5.87 | .007 |

generalization (SCR: $\beta = 0.365$, $t(2, 30) = 2.30$, $p = .026$; generalization: $\beta = 0.311$, $t(2, 30) = 1.96$, $p = .038$), improving the fit, with 28.1% explained variance ($R^2 = .281$), $F(2, 30) = 5.87$, $p = .007$. Despite the overall Model 3 having robust explained variance and significance, the 9.2% increase in explained variance caused by generalization scores was not a statistically significant increase ($R^2 = .092$, $F = 3.83$, $p = .06$). Similarly, the generalization coefficient alone was subthreshold significance, before bootstrapping ($p = .06$). Bootstrapped coefficients are detailed in Table 5. Part and partial correlations further indicated that SCR (partial = .387, part = .355) and memory generalization (partial = .337, part = .303) were significant contributors to the model. Collinearity diagnostics indicated no multicollinearity issues among the predictors for the final analysis (tolerance = 0.949, VIF = 1.054).

Together, these suggest the magnitude of physiological fear during learning and generalization of the resulting memory trace influence the magnetic pull of temporal source misattributions toward the threat learning phase. This combination of strongly encoded yet imprecise fear memories may distort contextual recollections for related events (CS+ exemplars) encoded in temporal proximity (Clewett, Dunsmoor, Bachman, Phelps, & Davachi, 2022; Dunsmoor, Murty, Clewett, Phelps, & Davachi, 2022; Dunsmoor et al., 2015).

### *Segmenting Neutral and Emotional Phases Enhances Neutral Source Memory*

Event segmentation has compelling relevance to source memory performance, given the emphasis on discrete temporal learning periods. As seen in Figure 4A, Experiment 2 showed above-chance accuracy in source memory for Pre-Con CS− items ($t = 2.69$, $p = .006$), which did not occur for Experiment 1 ($t = 0.30$, $p = .38$), which is reflected by a significant between-experiment difference ($t = 2.04$, $d = 0.53$, $p = .023$). To elucidate this effect, a combined regression model was run including recognition memory for Pre-Con CS− as a predictor and experiment as a random effect. The intercept-only model (Model H ) provided no meaningful information and is omitted from detailed reporting. The full model was significant ($R^2 = .228$), $F(2, 57) = 8.429$, $p < .001$. Bootstrapped coefficients (Table 6) supported higher source accuracy for Pre-Con CS− items predicted by experiment (Experiment 2 > Experiment 1: $\beta = 0.237$, $t(2, 57) = 2.04$, $p = .046$, 95% CI [0.001, 0.14]) and "recognition memory accuracy" for the same items ($\beta = 0.402$, $t(2, 57) = 3.45$, $p < .001$, 95% CI [0.13, 0.48]). Part and partial correlations support Pre-Con CS− memory (partial = .416, part = .401) and experiment (partial = .261, part = .237) as significant model contributors. No variables in this model were affected by multicollinearity (tolerance = 0.997, VIF = 1.003). Because the within-experiment associations between recognition and source memory were only significant for Experiment 1 ($r = .51$, $p = .023$), it is possible individuals with greater memory for individual events may likewise acquire more accurate source memory, with less emotional interference.

In summary, the presence of a single boundary between neutral and emotional learning phases facilitated neutral source memory (Experiment 2), but this accuracy was decreased when emotional learning phases were chunked into more than one discrete period (Experiment 1). Having a single boundary may accentuate the protective effects of segmentation on temporal memory consolidation. Of note, this example illustrates distinct effects of event segmentation on memory for temporal context, separable from item memory performance (i.e., Figure 2B).

**Table 5.** Bootstrapped Regression Coefficients (Source Memory Bias)

| *Model* | *Coefficient* | *SE* | β | *t Value** | *p Value** | *95% CI** |
|---|---|---|---|---|---|---|
| 1. | (Intercept) | 0.041 | – | 2.013 | .028 | [0.01, 0.17] |
| 2. | ACQ-SCR | 0.343 | 0.435 | 2.691 | .024 | [0.10, 1.44] |
| 3. | ACQ-SCR | 0.301 | 0.365 | 2.296 | .026 | [0.08, 1.28] |
| | ACQ-GEN | 0.137 | 0.311 | 1.958 | .038 | [0.02, 0.54] |

Bootstrapping based on 5000 replicates. Coefficient estimate is based on the median of the bootstrap distribution.

* Bias corrected accelerated.

## DISCUSSION

In a changing environment, emotional memories must be strong enough to be well remembered yet plastic enough to be updated in the face of new information. Recalling prior threat cues can facilitate adaptive survival responses but, in excess, can produce overgeneralized fears, emblematic of debilitating anxiety-related disorders. Segmenting competing experiences of emotional learning into separate event periods can influence the longevity of these memories over time (Dunsmoor et al., 2018; Ezzyat & Davachi, 2010; Kurby & Zacks, 2008). In this study, we examined the organization of episodic memories formed during threat reversal learning—where conditioned fear is acquired, and then switched, across stimulus categories. We investigated the nature of memory updating when threat reversal was marked by an event boundary (Experiment 1) and when it occurred seamlessly, without any break (Experiment 2).

Our findings underscore the role event segmentation can have upon the changes in recognition memory observed ~24 hr after reversal learning. In Experiment 1, participants effectively reversed conditioned fear responses during encoding, as measured by SCRs and shock expectancy ratings. Memory was preferentially heightened for stimuli associated with threat both before (CS+, acquisition) and after (CS−, reversal) the event boundary, and neutral items from the Pre-Con phase showed a selective retroactive enhancement (CS+ > CS−). These outcomes replicate prior patterns of memory advantages for items encoded before and during threat learning (Hennings et al., 2021; Dunsmoor et al., 2015), further showing how these threat-induced benefits can be reversed across categories, which has not been examined previously. Experiment 2 showed that the lack of a clear break during emotional learning hindered the immediate reversal of conditioned responses and did not produce the selective memory effects observed in Experiment 1. Rather than reflecting diminished memory, this pattern suggests a "global" retroactive memory enhancement that is not exclusive to CS+ items. Reversal memory was also undifferentiated, but this was instead because of sustained memorization of reversed threat exemplars (unpaired CS+) combined with increased memory for "new threat" exemplars (shocked CS−). CPAs indicated that significant shifts in memory—strengthening for new threat cues (CS−) and weakening for old ones (CS+)—occurred immediately after the event boundary in Experiment 1, whereas Experiment 2 exhibited no significant period of negative change in CS+ memory during continuous learning.

Here, we interpret the above results by considering the interaction of two episodic memory frameworks: event segmentation theory and the "behavioral tagging" model (Figure 6A). The latter offers a compelling account of retroactive memory enhancement. Neutral stimuli encoded during Pre-Con produce a weak "tag" and are liable to fade from LTM if no salient events occur in temporal proximity. However, if soon after tagging, related stimuli undergo salient learning (e.g., threat acquisition), they effectively "capture" the initial weak memory trace, stabilizing it within LTM. Our principal findings suggest that such a memory consolidation process may be modulated by the way weak and salient learning bouts are segmented. Here, we refer to the arrangement of Experiment 1 as "three-way segmentation" (Figure 6B), where two clear boundaries divide the learning into three distinct phases: neutral encoding (Pre-Con), threat acquisition (CS+ shocked), and threat reversal (CS− shocked). Experiment 2 could be described as "two-way segmentation," where the single boundary in the task creates a clearer segmentation between neutral learning beforehand and continuous emotional learning afterward.

In Experiment 1, retroactive enhancement remained selective, with Pre-Con CS− items poorly remembered, despite CS− undergoing as many shocked trials as CS+ over the course of the task. When the same contingencies were subject to two-way segmentation, selectivity was ablated, and retroactive memory was achieved for both stimulus categories. Thus, removing the intervening acquisition–reversal boundary seen in Experiment 1 may have facilitated emotional learning for CS− to reach backward in time and "capture" the tagged memories of Pre-Con with greater ease (Figure 6C). One might argue that, despite continuous learning, CS− were shocked at a much later part of the phase than CS+. However, event segmentation theories suggest that encapsulating both emotional learning events (acquisition and reversal) within a seamless period leads them to consolidate in the same time window. Various evidence show that continually segmenting events with further and further additional boundaries produces overestimated temporal duration across experiences (Jeunehomme & D'Argembeau, 2020; Bonasia, Blommesteyn, & Moscovitch, 2016; Lositsky et al., 2016; Faber & Gennari, 2015; Poynter, 1983). Thus, in Experiment 2, the psychological distance separating neutral CS− (Pre-Con) from shocked CS− (reversal) could be reduced, meaning that the salience of the later salient learning only needs to traverse a single event boundary to stimulate memory capture for neutral events (Figure 6C). In other words, two-way segmentation would allow later shocked trials of CS− to be treated as "salient events encoded close in time" to the event boundary, leveraging the temporal proximity aspect of behavioral tagging to facilitate retroactive carryover for both categories, leading to a global (rather than CS+ selective) retroactive memory enhancement (Dunsmoor, Murty, et al., 2022; Redondo & Morris, 2011; Moncada & Viola, 2007). By splitting emotional learning into multiple separate consolidation periods, three-way segmentation widens the psychological distance between neutral encoding and shocked CS− trials, diluting the capacity of these experiences to exert retroactive potentiation.

Alternatively, differences between "selective" (Experiment 1) and "global" (Experiment 2) retroactive memory enhancement can be explained by the arousal-based competition model and its neurobiological counterpart, the glutamate amplifies noradrenergic effects model. These models suggest that arousal enhances or impairs memory by contrasting high- and low-priority representations (Mather, Clewett, Sakaki, & Harley, 2016; Mather & Sutherland, 2011). Arousal triggers localized norepinephrine release, which boosts high-priority memories and inhibits low-priority ones, directing resources toward relevant information. If shocked trials of CS+ and CS− are consolidated in separate periods (three-way segmentation), the initial shocked category (acquisition CS+) becomes high priority, with arousal-induced norepinephrine localized to preconditioned nonshocked CS+ sites. This retroactively enhances memory for these items while inhibiting low-priority CS− traces (Dunsmoor, Murty, et al., 2022; Mather et al., 2016). This event boundary allows this category differentiation to consolidate without contradictory experiences (reversal). In contrast, when acquisition and reversal are consolidated within a single period (Experiment 2, two-way segmentation), shocked CS+ trials lack event segmentation, leading to simultaneous consolidation of CS+ and contradictory shocked CS− experiences. This prevents a clean high–low priority distinction, blocking arousal-based benefits to one category over the other. From a behavioral tagging or synaptic tag-and-capture perspective, the absence of Pre-Con CS+/CS− differences results from nonspecific elevations in both categories (global retroactive memory). Meanwhile, the arousal-based competition or glutamate amplifies noradrenergic effects models attribute this to a loss of selective prioritization (inhibiting irrelevant CS− and exciting CS+).

Synthesizing insights from event segmentation and behavioral tagging theories illuminates a possible contradiction. Behavioral tagging explains how neutral stimuli encoded after emotional learning also accrue a "proactive" memory enhancement (Dunsmoor, Murty, et al., 2022; Hennings et al., 2021; Patil et al., 2017; Dunsmoor et al., 2015), which may seem at odds with the "decline" in memory predicted by event segmentation, for related items encoded soon after a boundary. Current evidence from reversal, and prior evidence from extinction, support the decline of memory for nonreinforced CS+ after the event boundary (Dunsmoor et al., 2018), in sync with event segmentation theory. Yet at an overall level, unpaired CS+ (encoded during reversal) exemplars continue to maintain better memory performance relative to neutral (also nonreinforced) CS− exemplars (Laing & Dunsmoor, 2023; Hennings et al., 2021; Dunsmoor et al., 2018). In other words, extinguished CS+ are less well remembered than threat-conditioned CS+ when separated by an event boundary yet still substantially better remembered than neutral stimuli that never undergo salient learning (CS−).

These findings have implications for understanding the shared neural substrates underpinning event segmentation of emotional learning. Human fear conditioning studies reveal a broad involvement of the hippocampus and vmPFC in processing threat and safety signals. This is particularly evident through their synchronized activity during the reassessment of threats, as seen in fear extinction and reversal (Battaglia et al., 2022; Laing, Felmingham, et al., 2022; Laing, Steward, et al., 2022; Savage et al., 2020a; Fullana et al., 2015, 2018; Harrison et al., 2017). The exact temporal dynamics of these regions in terms of shaping emotional memories, however, remains unclear. A great variety of nonemotional memory paradigms have verified brain activations corresponding to event segmentation, notably in the hippocampus, default mode network, and vmPFC. These areas are selectivity activated by event boundaries, corresponding with perceived segmentation between event periods, and predict the quality of memory retrieval for information encapsulated within those periods (Wang, Adcock, & Egner, 2024; Hahamy et al., 2023; Ben-Yakov & Henson, 2018; Sols et al., 2017; Ben-Yakov, Eshel, & Dudai, 2013; Ben-Yakov & Dudai, 2011). Immediately after an event boundary, these neural systems—particularly the hippocampus—appear to recapitulate or replay the preceding events, facilitating the integration of the segmented information into a cohesive memory (Clewett & Davachi, 2017; Sols et al., 2017; DuBrow & Davachi, 2014; Ezzyat & Davachi, 2014; Swallow et al., 2011).

Recent work indicates that reinstatement of fear and safety memories is guided by patterns of hippocampal activity with similarities to those implicated in event segmentation. Using a similar task to the current study, Hennings and colleagues found that reinstatement of fear memories via the dACC (dorsal–posterior hippocampus), or safety memories via the vmPFC (ventral–anterior hippocampus), was differentially determined by dorsal–posterior and ventral–anterior hippocampal subregions, respectively (Hennings, McClay, Drew, Lewis-Peacock, & Dunsmoor, 2022). Put differently, similarity in multivariate patterns of hippocampal activity between learning and test influenced how threat- and safety-selective regions reinstated temporal contexts of fear conditioning (dACC) or extinction (vmPFC) during memory retrieval. Our findings hint that event segmentation might shape the hippocampal structuring of fear and safety memories. Without clear segmentation, the hippocampus may lack the cues needed to replay initial threat learning and segregate it from later, nonthreatening experiences (e.g., CS+ reversal). In addition, event segmentation might engage associative learning processes, such as prediction error or surprise, facilitating the encoding of new emotional associations (Rouhani, Niv, Frank, & Schwabe, 2023; Rouhani, Norman, Niv, & Bornstein, 2020; Rouhani & Niv, 2019). By letting initial learning consolidate briefly, boundaries may boost the salience evoked by incoming changes to learned associations. When subsequent events contradict established cue–outcome relationships, these may trigger strong expectation–outcome mismatches, promoting LTM reallocation through dopamine-mediated prediction errors (Rouhani et al., 2020, 2023; Lee et al., 2021; Rouhani & Niv, 2021; Abraham, Neve, & Lattal, 2014; Ben-Yakov et al., 2013). For instance, the experiment context may become consolidated as a context where CS+ and CS− are paired and unpaired with shocks, respectively, leading altered contingencies after the boundary to contradict expectations and evoke more rapid learning and memory updating. With no segmentation, the experiment context is experienced as containing all iterations of CS–shock relations, attenuating experiences of surprise and prediction error (Kim, Lewis-Peacock, Norman, & Turk-Browne, 2014), thereby preventing the nonemotional CS+ items from losing priority in memory (e.g., Figure 2B).

Our findings indicate that event segmentation's relevance to source memory (judging when an item was encoded) could be selective to influencing source attribution accuracy for neutral events (e.g., Pre-Con CS−; Figure 5A), while leaving emotional biases unaltered (e.g., CS+ assigned to ACQ; Figure 4A). As outlined above, Experiment 2 involved "two-way event segmentation" (Figure 6), rendering a clean separation between neutral (Pre-Con) and emotional encoding periods (ACQ–REV, no boundary). This single separation saw accurate source attribution for a Pre-Con CS− item, which was absent for Experiment 1, as well as in prior studies of emotional source memory (Laing & Dunsmoor, 2023; Hennings et al., 2021). Observations of heterogeneous accuracy in Experiment 1 could be explained by the difficulty imposed by participants having to distinguish between three discrete phases, wherein two phases share emotional salience and can both exert biasing effects. Furthermore, individual differences in source memory for these items in Experiment 1 correlated with their recognition memory, suggesting that interferences imposed by competing event segmentations could be compensated for if earlier neutral events were individually well remembered. Overall, the presence of a single neutral–emotional boundary may increase the salience of the neutral phase, facilitating item–context binding. This is consistent with evidence for the enhancement of source memory across other learning modalities (Wang et al., 2024; Clewett, DuBrow, & Davachi, 2019; Clewett & Davachi, 2017).

Interestingly, threat-related biases in neutral source memory (Pre-Con CS+ > CS−) were predicted by within-session arousal (SCR) and mnemonic generalization for threat-conditioned items (acquisition CS+ > CS−). Specifically, heightened SCRs during threat learning and a more generalized retrieval of these events were associated with the misattribution of neutral CS+ items to the threat learning period. Consistent with earlier studies, Pre-Con CS+ were disproportionately misattributed toward the acquisition phase (Laing & Dunsmoor, 2023; Hennings et al., 2021). Our results also found that reversing shocks to CS− resulted in source memory accuracy for those items (reversal CS− judged correctly) and biased memory acquisition CS− (misattributed to reversal). This pattern occurred in both experiments, suggesting that emotional source memory distortion aligns with the threat status of CS, irrespective of whether contingency changes are signaled by an event marker. Thus, even when participants did not directly experience the transition point between acquisition and reversal (Experiment 2), they were able to enact the same threat-induced accuracies and misattributions seen when phases were segmented (Figure 4). Moreover, the generalization associated with actual threat memories appears to play a role in the misattribution of related stimuli to the threat learning period. This sheds light on a new aspect of the relationship between the generalization of fear memories and distortions in temporal source memory. In summary, although item-level recognition memory may safeguard source memory accuracy, the generalization of item-level memory seems to drive source memory biases.



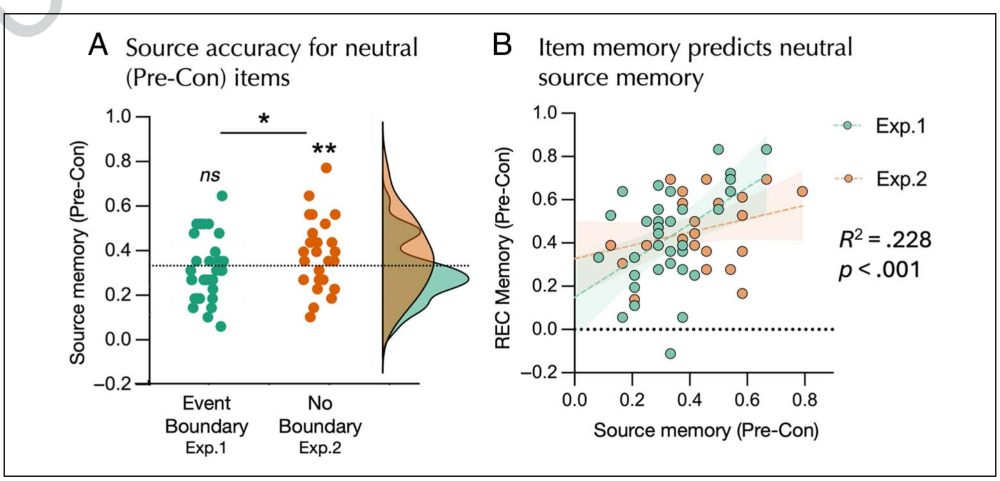


**Figure 5.** Impact of event segmentation on neutral source memory accuracy. When the only boundary in the task was between Pre-Con and continuous emotional learning (Experiment 2), source memory for Pre-Con neutral items (CS−) was accurate above chance ($p$ = .006), but not when emotional learning was segmented (ACQ/REV, Experiment 1). Individual differences in recognition memory correlated with Pre-Con source accuracy for the latter group ($r$ = .51, $p$ = .001). Separating neutral and emotional phases with a single boundary may enhance neutral source memory consolidation, which may also be elevated when neutral stimuli are strongly encoded at the individual item level. Error bars indicate *SEM*. *$p$ < .05. **$p$ < .01. ***$p$ < .001.

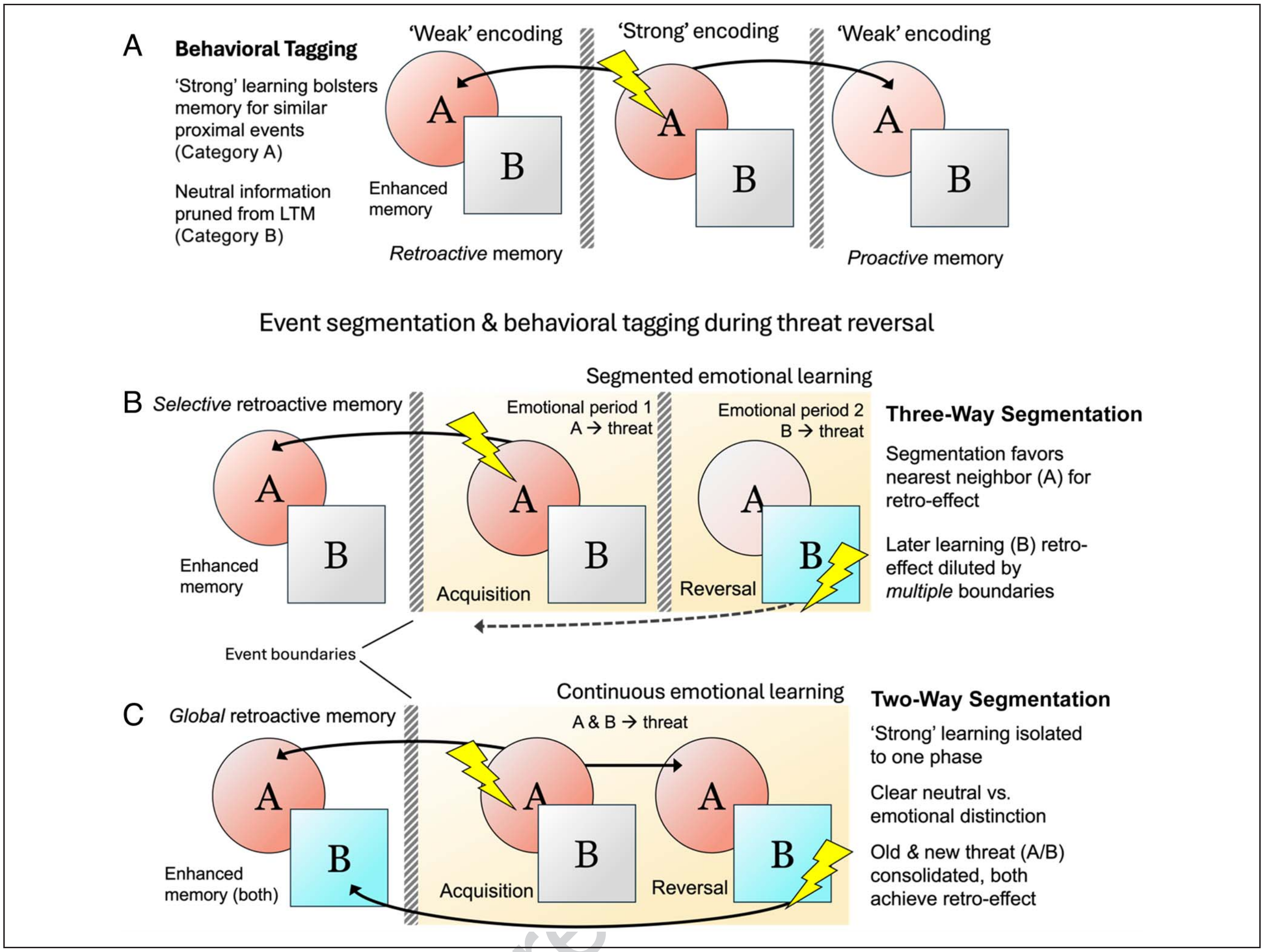


**Figure 6.** Hypothesized mechanism of event segmentation and behavioral tagging. Current results are interpreted via behavioral tagging hypothesis. Panel A illustrates the application of the behavioral tagging framework of LTM in the context of generic threat learning. Red/blue indicates enhanced memory retrieval; gray reflects poor memory. "Weakly encoded" events can be strengthened when similar events undergo salient learning soon afterward. Category A items undergo threat conditioning, causing selective retroactive enhancement of related events encoded beforehand (A > B). The weak "tag" assigned to Category A during weak learning is then "captured" in LTM, when those items undergo salient learning (shock). Panel B applies this framework to the findings of Experiment 1, where selective retroactive effects persisted despite both categories undergoing threat conditioning later. Threat learning (category B) cannot overcome two boundaries (three-way segmentation), leaving retroactive memory selective to Category A, which benefits from temporal proximity. Panel C interprets lack of selective memory after continuous emotional learning ("two-way event segmentation"). Chunking all emotional encoding (A and B) into a single uninterrupted period accentuates neutral versus salient encoding distinctions (Pre-Con vs. ACQ-REV phases). Removing this barrier allows reversal-B items to be consolidated in the same periodic window as acquisition-A. This pulls threat-conditioned B items into closer temporal proximity to weakly encoded B items, facilitating retroactive memory. Consolidation of emotional learning is shielded within (but not across) event boundaries, explaining the perseverance of reversal-A memory across the uninterrupted phase (Experiment 2).

Beyond general memory performance, our results indicate novel effects of threat reversal on the generalization of episodic memories. Including measures of memory generalization and precision (similar items appraised as "old" or "new") allows us to simultaneously examine whether an item is remembered (recognition) as well as how it was remembered. Previous research demonstrated that although fear-conditioned and extinguished CS+ items display comparable recognition accuracy, they exhibit significant differences in generalization and discriminability (Laing & Dunsmoor, 2023). Specifically, items resembling the CS+ exemplars encoded during conditioning were often generalized as "old," whereas those resembling CS+ exemplars from extinction were likely to be discerned as "new." This study replicated this distinction, emphasizing that memory precision synchronizes with shifts in threat–safety learning, regardless of event boundaries (Figure 3A). Such differences may correspond with established episodic memory constructs, with aversive learning biasing representations toward mnemonic integration or pattern completion-like processes, and retrieval of safety-associated stimuli showing effects consistent with constructs like behavioral pattern separation, differentiation, or fragmentation (Loetscher & Goldfarb, 2024; Morton et al., 2017; Rolls, 2016; Schlichting et al., 2015; Schlichting & Preston, 2015; Norman & O'Reilly, 2003; O'Reilly & McClelland, 1994). These mnemonic processes, well established outside emotional domains, rely heavily on neural systems that are likewise indispensable to Pavlovian fear and safety learning, such as the hippocampus, amygdala, and vmPFC (Concina et al., 2024; Zuniga et al., 2024; Amer & Davachi, 2023; Laing, Felmingham, et al., 2022; Corcoran & Quirk, 2007; Kensinger & Schacter, 2006).

Emotional memory research indicates that although aversive memories are robustly retained, they can often possess a low fidelity, retaining only the "gist" of the original content, or entail other subtle aspects of misremembering (Kensinger & Ford, 2020; Leal, Tighe, & Yassa, 2014; Kensinger, 2009). When a new stimulus partially matches a threat-encoded item, it may trigger this generalized representation, eliciting behaviors suited to a perceived threat. Conversely, memories from safety learning are precise and distinct, engaged by stimuli that closely match the original safe event, emphasizing the potential difficulty for fear extinction memories to generalize compared to established fear memories (Vervliet, Baeyens, Van den Bergh, & Hermans, 2013; Bouton & Moody, 2004; Bouton, 1993, 1994, 2002). Considering that fear extinction is often gauged via physiological responses in human studies (Ney et al., 2020; Marin et al., 2017), the integration of episodic memory paradigms could provide richer insights into mnemonic precision, including how safety memories might be augmented to better compete with maladaptive fear (Keller et al., 2022; Esser, Korn, Ganzer, & Haaker, 2021; Keller, Hennings, & Dunsmoor, 2020; Papalini, Beckers, & Vervliet, 2020; Kalisch, Gerlicher, & Duvarci, 2019; Gerlicher, Tüscher, & Kalisch, 2018; Haaker et al., 2013).

Finally, the field of emotional memory research has often focused on how conditions at the encoding stage—particularly physiological arousal—affect later retrieval (Madore & Wagner, 2022; Goldfarb, Tompary, Davachi, & Phelps, 2019; Goldfarb & Phelps, 2017; McGaugh, 2015). In addition, such work often refers to an enduring conceptual paradox between the "enhancement" and "distortion" incurred by emotion upon LTM. Our research sheds light on this issue, demonstrating that mnemonic generalization for newly aversive stimuli is not influenced by event segmentation in the same manner as memory accuracy and that conditioned arousal responses (indexed by SCRs during reversal) can predict memory generalization 24 hr later. In addition, individual variances in negative mood symptoms correlate with reduced memory generalization for these stimuli. The tendency to generalize fearful associations, often linked to anxiety disorders, can also represent an adaptive mechanism for updating memories in response to changing conditions. For instance, modifying the memory of an object that shifts from safe to harmful supports appropriate defensive responses, whereas failing to adjust may reflect a cognitive inflexibility or an overemphasis on original threat cues, hindering the adoption of new, safe associations. The concept of mnemonic discrimination is relatively new in the context of fear and anxiety, with few studies directly exploring its role in associative learning (Laing & Dunsmoor, 2023; Neudert et al., 2023; Starita et al., 2019; Lange et al., 2017). Further work could explore how emotional memories can be stabilized, allowing them to be sufficiently generalizable for adaptive behavior while remaining specific enough to not disrupt safety learning (Laing, Vervliet, Dunsmoor, & Harrison, 2024; Hayes et al., 2023; Laing, Steward, et al., 2022; Laing & Harrison, 2021; Bernstein et al., 2020; Dohm-Hansen & Johansson, 2020; Leal & Yassa, 2018). Crucially, physiological arousal and negative mood may be more pertinent to the quality and fidelity of emotional memories, rather than their accuracy.

## Limitations

In acknowledging the limitations of our current study, our interpretation concerning retroactive memory might have been solidified by introducing a third stimulus category during Pre-Con. For instance, if elevated Pre-Con memory is observed for both CS+ and CS− items, but not for a third category that never undergoes emotional learning, this would support the proposed interaction between mechanisms of event segmentation and behavioral tagging. Conversely, an elevation across all categories might indicate a different phenomenon, possibly related to contextual or timing effects. Future research should examine how these memory effects persist or vary over extended periods and with different emotional learning intensities. For example, it would be valuable to determine whether subtle shifts observed in reversal learning persist, wane, or reconsolidate differently over time, thereby affecting memory strength relative to original or revised threat categories (e.g., CS+ > CS− from acquisition or shifting to reversal CS−). Relatedly, these patterns could be examined in alternate domains of learning, such as associative pain or reward processing (Wimmer, Liu, McNamee, & Dolan, 2023; Atlas, Dildine, et al., 2022; Rouhani et al., 2020).

## APPENDIX

### Distribution of MST Responses

Distribution of raw old/new ratings is illustrated in Appendix Figure A1.

#### *Responses to Old Targets*

Participants rated old-target items "old" significantly more than rating them "new," for both stimulus categories (CS+: $M = 0.364$, $t = 9.235$, $p < .001$; CS−: $M = 0.275$, $t = 6.11$, $p < .001$). Old items from the CS+ and CS− categories were more likely to be rated old and new, respectively ($M = 0.044$, $t = 2.02$, $p = .048$).

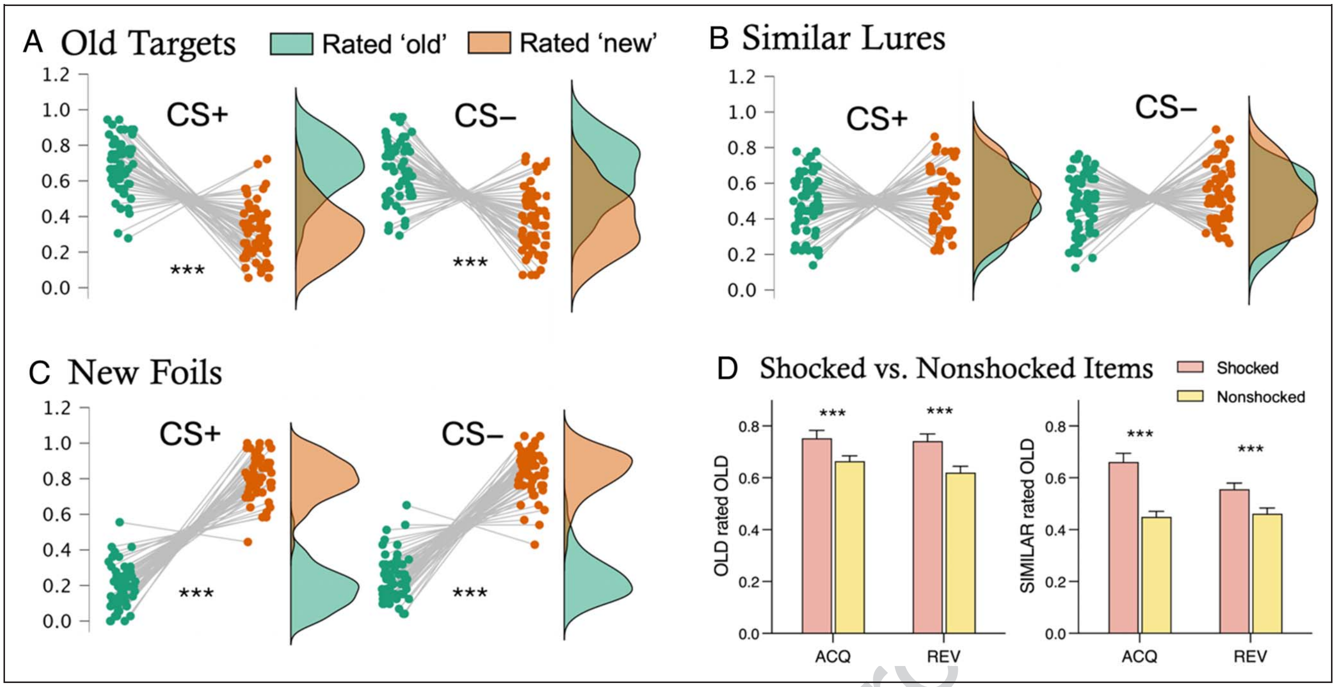


**Figure A1.** Distribution of raw memory responses (MST). Raw responses showed that participants had (A) significantly higher ratings of "old" to old-target items, (B) equivalent distributions of old/new response to similar-lure items, and (C) significantly higher ratings of "new" to new foils. (D) Participants tended to rate "old" toward items that had been shocked the day before (OLD items) as well as to items that resembled those that had been shocked (SIMILAR items). *** $p < .001$.

*Responses to Similar Lures*

There were no significant differences in the distribution of old/new ratings for similar-lure items (CS+: $M = 0.032$, $t = 0.758$, $p = .452$; CS−: $M = 0.044$, $t = 1.039$, $p = .303$). There were no differences between CS+ or CS− categories ($M = 0.006$, $t = 0.257$, $p = .798$).

*Responses to New Foils*

Participants rated new foils "new" significantly more than ratings of "old" (CS+: $M = 0.62$, $t = 20.67$, $p < .001$; CS−: $M = 0.60$, $t = 18.87$, $p < .001$). New-foil items from the CS+ and CS− categories were more likely to be rated old and new, respectively ($M = 0.011$, $t = 0.611$, $p = .543$).

*Responses to Shocked vs. Nonshocked Threat-Category Exemplars*

The experiment used partial 50% reinforcement, such that half of the CS+ in acquisition and half of the CS− in reversal were not paired with shock. Overall, participants tended to rate exemplars "old" more readily if they had been paired with shock during encoding. This was the case for rating "old-target" items during the MST task (ACQ CS+: $t = 3.29$, $d = 0.424$, $p = .002$; REV CS−: $t = 4.37$, $d = 0.564$, $p < .001$) but also for similar lures, which merely resembled items that had been shocked (ACQ: $t = 7.20$, $d = 0.929$, $p < .001$; REV: $t = 5.03$, $d = 0.65$, $p < .001$). Mean scores, and inspection of Appendix Figure A1(D), illustrate that these differences are more attributable to the markedly elevated ratings of shocked exemplars, rather than diminished ratings of nonshocked exemplars. All nonshocked old items at test were significantly rated old above chance (ACQ CS+: $t = 8.18$ $p < .001$; REV CS−: $t = 4.92$, $p < .001$, one-tailed). Nonshocked similar items, 44.9% for acquisition CS+ and 46.2% of reversal CS−, were rated old. These results suggest that overall shocked items may account for the bulk of the mnemonic generalization outcomes, where items resembling those that were shock-paired are disproportionately more likely to be rated old rather than new. Concerning recognition memory, these outcomes indicate that shocked items certainly acquire a greater memory bias than nonshocked items but that the latter nevertheless accrue some biases toward being rated old.

## Episodic Memory Scores

Memory judgments (old, similar, new) were scored as proportional responses (range = 0–1) by CS category type (CS+/CS−) and phase. "Recognition" was scored as the rate of "old" responses to old items versus new items: $p(\text{old} \mid \text{old}) - p(\text{new} \mid \text{old})$. "Pattern completion" (i.e., mnemonic generalization) was scored as the rate of "old" responses to similar versus new items: $p(\text{old} \mid \text{sim}) - p(\text{old} \mid \text{new})$. One-sample $t$ tests were used to validate whether scores for each phase and CS type significantly differed from zero (i.e., no effect). Appendix Table A1 illustrates robust significance for all memory outcomes.

**Table A1.** One-sample *t* Tests: Memory Scores

| Memory Score | *t* | *p* | Cohen's *d* | 95% Confidence Interval Lower | Upper |
|---|---|---|---|---|---|
| *Recognition* | | | | | |
| Pre-Con CS+ | 14.080 | <.001 | 0.339 | 1.739 | 3.080 |
| Pre-Con CS− | 11.235 | <.001 | 0.290 | 1.349 | 2.494 |
| ACQ CS+ | 13.661 | <.001 | 0.332 | 1.682 | 2.993 |
| ACQ CS− | 10.056 | <.001 | 0.270 | 1.186 | 2.253 |
| REV CS+ | 14.297 | <.001 | 0.343 | 1.769 | 3.125 |
| REV CS− | 12.925 | <.001 | 0.319 | 1.582 | 2.841 |
| *Generalization* | | | | | |
| Pre-Con CS+ | 8.558 | <.001 | 1.468 | 0.975 | 1.949 |
| Pre-Con CS− | 6.533 | <.001 | 1.120 | 0.684 | 1.546 |
| ACQ CS+ | 10.477 | <.001 | 1.797 | 1.244 | 2.338 |
| ACQ CS− | 10.357 | <.001 | 1.776 | 1.228 | 2.314 |
| REV CS+ | 8.068 | <.001 | 1.384 | 0.905 | 1.851 |
| REV CS− | 12.937 | <.001 | 2.219 | 1.583 | 2.844 |

Alternative hypothesis is that the mean differs from zero.

## Correlations After Outlier Removal

The presence of a notable outlier was detected for some of the main correlational analyses. The outlier in question was removed to control for its possible influence as the cause or interference with the correlational outcomes. For instance, its presence may create a false association where the entire effect is negated once the single data point is removed, or conversely, the outlier may skew or bias the correlation in an unrepresentative way. With the outlier data included, all main correlations remained significant, with minimal changes in effect sizes. Mnemonic generalization for reversal CS− remained positively correlated with reversal CS− SCR ($r$ = .475, $p$ = .005) and negatively correlated with negative mood symptom (DASS) scores ($r$ = −.42, $p$ = .013). Source memory biases, measured as the rate of preconditioning CS+ (vs. CS−) misattributed to the acquisition phase, remained positively correlated with differential scores (CS+ > CS−) for acquisition SCRs ($r$ = .385, $p$ = .024) and mnemonic generalization ($r$ = .394, $p$ = .021). Source memory accuracy, measured as the rate of correct attribution of Pre-Con CS− to the Pre-Con phase, remained significantly correlated with item-level recognition memory for the same items ($r$ = .506, $p$ = .002). In summary, inclusion/exclusion of the outlier (identified via visual inspection of scatter plots) did not influence whether the associations reported in the main article were significant at a broader level.


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## Data Availability Statement

Data from this study are available on the Open Science Framework (osf.io/vmz69/).

## Author Contributions

Patrick A. F. Laing: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Software; Validation; Visualization; Writing—Original draft; Writing—Review & editing. Joseph E. Dunsmoor: Conceptualization; Funding acquisition; Methodology; Project administration; Resources; Supervision, Writing—Original draft; Writing—Review & editing.


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## Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be M/M = .358, W/M = .3, M/W = .158, and W/W = .183.

The current article's proportion of citations by gender category is reported here, with the gender citation balance information (GCBI) in parentheses: M/M = .355 (−.146), W/M = .306 (−.044), M/W = .157 (.365), and W/W = .182 (.145). GCBI values of zero denote the base rate of *JoCN* citation, whereas GCBI above/below zero denotes citations over/under the *JoCN* base rate (Fulvio, Akinnola, & Postle, 2021).

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