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# Emotional arousal lingers in time to bind discrete episodes in memory

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## ABSTRACT

Temporal stability and change in neutral contexts can transform continuous experiences into distinct and memorable events. However, less is known about how shifting emotional states influence these memory processes, despite ample evidence that emotion impacts non-temporal aspects of memory. Here, we examined if emotional stimuli influence temporal memory for recent event sequences. Participants encoded lists of neutral images while listening to auditory tones. At regular intervals within each list, participants heard emotional positive, negative, or neutral sounds, which served as “emotional event boundaries” that divided each sequence into discrete events. Temporal order memory was tested for neutral item pairs that either spanned an emotional sound or were encountered within the same auditory event. Encountering a highly arousing event boundary led to faster response times for items encoded within the next event. Critically, we found that highly arousing sounds had different effects on binding ongoing versus ensuing sequential representations in memory. Specifically, highly arousing sounds were significantly more likely to enhance temporal order memory for ensuing information compared to information that spanned those boundaries, especially for boundaries with negative valence. These findings suggest that within aversive emotional contexts, fluctuations in arousal help shape the temporal organisation of events in memory.

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Episodic memory; arousal; emotion; temporal; event segmentation


## Introduction

Our lives unfold as continuous narratives. Yet like chapters in a book, our memories of such experiences usually take the form of discrete and meaningful episodes. A rapidly growing body of work demonstrates that such memory organisation may be driven by a dynamic interplay between temporal stability and change in different contextual features across time (Brunec et al., 2018; Clewett et al., 2019; Clewett & Davachi, 2017). For example, it has been shown that following list learning, temporal order memory is impaired for item pairs that spanned a change in background colour (Heusser et al., 2018), spatial location (Horner et al., 2016), perceptual category (DuBrow & Davachi, 2013, 2014), accompanying sounds (Clewett et al., 2020; McClay et al., 2023), timing (van de Ven et al., 2021), or goals (Wen &

Egner, 2022) compared to item pairs that shared similar contextual information. Thus, while contiguities in one’s surrounding context may facilitate the binding of sequential representations in episodic memory, event boundaries (i.e. context shifts) seem to disrupt this process and lead to the formation of discrete mnemonic events.

Much of the research on event cognition to date has focused on how simple changes in the external environment, such as a change in location or local perceptual features, affect the organisation of episodic memory (Clewett et al., 2019). However, everyday experiences are also coloured by shifting emotional states and fluctuations in arousal. Emotional stimuli elicit robust effects on perception, attention, and memory (Kensinger et al., 2007; LaBar & Cabeza, 2006; Mather & Sutherland, 2011; McGaugh, 2013). While much of this work has focused on memory for

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individual items or static source information (e.g. association between item and its background colour), less work has examined how emotional arousal and valence influence the temporal aspects of episodic memory, even though this rich sequential information is a defining feature of everyday memory (Palombo & Cocquyt, 2020; Petrucci & Palombo, 2021; Wang et al., 2022). Studies on the effects of emotion on temporal memory have generally yielded inconsistent findings, whereby emotion can sometimes enhance (Dev et al., 2022; Knight & Mather, 2009; Palombo et al., 2021; Rimmele et al., 2012; Schmidt et al., 2011) and other times impair memory for the precise timing of individual items (D'Argembeau & Van der Linden, 2005) or the temporal order of emotion-related events (Huntjens et al., 2015). Likewise, emotion has been shown to disrupt temporal contiguity effects in free recall, with the output order of retrieval instead reflecting greater semantic clustering between items with negative valence (Long et al., 2015; Talmi et al., 2019). These findings suggest that emotion might in and of itself serve as a strong internal context for linking or separating memories across time.

While it is clear emotion has complex effects on memory for both the timing and temporal order of stimuli, current findings do not address how emotion shapes the episodic *structure* of memory, per se, especially for neutral details encountered in those contexts. For decades, the memory literature has been dominated by list-based paradigms that randomise and/or fully block the presentation of emotional and neutral items (Barnacle et al., 2018; D'Argembeau & Van der Linden, 2005; Long et al., 2015; Talmi et al., 2019). But this procedure results in sequences that lack the temporal stability and change in ongoing contextual features that seem to be necessary for constructing distinct episodic memories (Clewett et al., 2019; Siefke et al., 2019). Another important limitation of prior work is that it often uses aversive stimuli that elicit sustained increases in arousal or can alter an individual's mood. For instance, it has been shown that temporally extended emotional contexts, such as aversive videos (Dev et al., 2022), naturalistic environments (Cliver et al., 2023), or exposure to physiological stressors affect participants' abilities to remember when a recent event occurred (Zlomuzica et al., 2016) and to learn sequential associations (Maran et al., 2017). Prolonged elicitations of arousal and stress, however, likely obscure the transient effects of emotion on

event segmentation processes. Without discrete manipulations of arousal, it is challenging to determine if shifting emotional states also play an important role in structuring episodic memories.

Understanding the consequences of emotion on temporal memory organisation is especially important given recent evidence that even the simplest context shifts elicit increased pupil dilation, an index of physiological arousal (Clewett et al., 2020; Kahneman & Beatty, 1966). In one pupillometry study, these surges in arousal were also linked to corresponding impairments in temporal order memory, a common index of event parsing in episodic memory (Clewett et al., 2020). This finding raises the intriguing possibility that emotional stimuli may function as especially "strong" event boundaries by eliciting robust increases in arousal-related event segmentation. Supporting this idea, emotionally arousing stimuli exert strikingly similar effects on memory and attention as do event boundaries, including enhancing item recognition (Cahill & McGaugh, 1998; Dolan, 2002; Swallow et al., 2009), increasing attentional allocation (Bradley et al., 1997; Mather & Sutherland, 2011; Zacks et al., 2007), and enhancing item-source memory for concurrent contextual information (Clewett et al., 2020; Heusser et al., 2018; Kensinger et al., 2006; Rimmele et al., 2012). Recent work also shows that prediction errors, which are associated with an increase in autonomic arousal (Preuschoff et al., 2011; Raisig et al., 2010), lead to impairments in temporal order memory (Rouhani et al., 2019). Both emotional stimuli and event boundaries also elicit subjective distortions in perception and memory for the duration of recent events (Brunec et al., 2017; Droit-Volet & Gil, 2009; Ezzyat & Davachi, 2014; Faber & Gennari, 2015; Johnson & MacKay, 2019; Lake et al., 2016; Liverence & Scholl, 2012), supporting the notion that arousal mechanisms are sensitive to salient changes in the world and mediate the impact of contextual shifts on long-term memory.

While an emotional stimulus, such as a gruesome image, may be encountered only briefly, its effects on cognition do not occur in isolation. Rather, the effects of emotional items can spillover in time to influence the memorability of temporally adjacent details. A large body of work shows that embedding emotionally arousing oddball items within more mundane item sequences can enhance or impair item recognition for both preceding and ensuing neutral items (Anderson et al., 2006; Clewett et al.,

2017; Hurlemann et al., 2005; Knight & Mather, 2009; Sakaki et al., 2014; Schluter et al., 2019; Strange et al., 2003). The direction of these modulatory effects of emotional arousal on memory also seems to depend, at least in part, on the temporal proximity of nearby neutral items (Bocanegra & Zeelenberg, 2009; Schmidt & Schmidt, 2016). While these findings suggest that arousal effects may linger in time to influence the memorability of individual items, it is unknown whether and how this spillover relates to temporal encoding processes.

Alongside more general arousal effects, it is important to consider that emotional valence may also play a role in modulating the temporal structure of memory. Emotional valence has been shown to elicit opposing effects on episodic memory (Kensinger, 2004; Pierce & Kensinger, 2011). While negatively valenced stimuli tend to lead to more item-focused processing and memory, positive emotional stimuli are more likely to enhance associative memory (Clewett & Murty, 2019; Kensinger, 2009; Madan et al., 2019). Positive and negative emotions have also been shown to exert distinct effects on attention, with positive valence broadening the scope of cognitive processing and negative valence narrowing the scope of attention (Gable & Harmon-Jones, 2008, 2010; Harmon Jones et al., 2012). In parallel, it has been shown that orienting individuals to be more item-focused while encoding neutral item sequences can lead to impairments in subsequent serial recall (DuBrow & Davachi, 2013). These converging findings suggest that by recruiting greater item-focused attention, negatively valenced stimuli may elicit larger impairments in temporal order memory between information that spans them, an index of memory separation.

The goal of the current study was to examine how emotional arousal and valence influence the temporal organisation of events in memory. To this end, we adapted an existing auditory event boundary paradigm by inserting emotional sounds into a sequence of neutral object images, and then examined how these “emotional event boundaries” influenced temporal order memory for item pairs spanning those boundaries (discrete effect) as well as for item pairs appearing in the following event (carryover effect). We predicted that emotional sounds rated as being more arousing would correlate with worse temporal order memory accuracy for neutral item pairs spanning those sounds, consistent with emotion functioning as a strong event boundary during continuous

experience. In contrast, we hypothesised that the effects of highly arousing emotional sounds would carry forward in time to enhance rather than impair temporal memory binding between item pairs in the ensuing auditory event. Such benefits would be consistent with the idea that emotion tags the ensuing context as motivationally relevant, making an otherwise mundane series of neutral stimuli more memorable. With respect to valence, we predicted that emotional sounds that are perceived as being more negative would correlate with greater temporal order memory impairments more broadly, given prior evidence that negative emotional stimuli tend to enhance item-focused processing at the expense of associative memory (Bisby & Burgess, 2014).

## Methods

### Participants

Twenty-three healthy young adults were recruited from nearby community in New York City to participate in this experiment through advertisements on RecruitMe (<https://recruit.cumc.columbia.edu>). Two participants were excluded due to failure to follow instructions and one participant was excluded due to a programming error that led to one experiment block being repeated. One additional participant was excluded for not showing sensitivity to the emotion manipulation based on their subjective arousal ratings; namely, this individual rated all but two of the 32 emotional sounds as being not arousing at all and as being neutral (i.e. valence rating of 4; see Supplementary Figures 1 and 2). This left a total of nineteen participants for data analysis ( $M_{age} = 21.8$ ,  $SD_{age} = 4.65$ ; 18 F). All participants provided written informed consent approved by the Columbia University Institutional Review Board and received monetary compensation. All eligible individuals had normal or normal-to-corrected vision and hearing and were not taking beta-blockers or psychoactive drugs.

Prior to starting the experiment, we performed a power analysis in G\*Power 3.1 to estimate the appropriate sample size. The power analysis was carried out using data from three similar event boundary experiments (Clewett et al., 2020). In those studies, auditory event boundaries were shown to modulate two aspects of temporal memory: temporal order memory and temporal distance memory. The power analyses with an  $\alpha = .05$  and  $power = .80$  (pooled from the average Cohen's  $d$  values from the

three experiments) indicated we needed 40 participants to detect a large effect size ( $d = .80$ ; Cohen's criteria) to capture the weakest memory effect, temporal distance ratings. However, a separate power analysis with the same parameters on the stronger event boundary memory effect, temporal order memory, indicated that only 19 participants were needed to obtain a large effect size ( $\alpha = .05$  and power = .80,  $d = .80$ ; Cohen's criteria). Due to the COVID-19 pandemic, data collection was disrupted, and we were only able to enrol 23 participants. Accordingly, we only report the results from the temporal order memory test, which we underscore had sufficient statistical power for analysis.

### **Materials**

A total of 384 images of everyday neutral objects were selected from previous datasets (Gabrieli et al., 1997; Kensinger et al., 2006). The luminance of all object images and fixation screens was normalised using the SHINE toolbox in MATLAB. To manipulate the auditory context during the item sequences, three 1-s pure tones with sine waveforms of different frequencies (600, 700, 800 Hz,) were generated using Audacity (<https://www.audacityteam.org/>). These frequencies were chosen such that sounds were discriminable from one another and were salient enough to maintain participants' attention. A total of 20 positive (e.g. laughing, pleasant music), 20 negative (e.g. screaming, gunshots), and 24 neutral (e.g. clock ticking, ambient mumbling) stimuli were selected from the International Affective Digitized Sound system (IADS) database (Bradley & Lang, 2007) and the Internet. All auditory stimuli were edited using Audacity to be two seconds long to capture the most emotionally salient part of each clip. The volume of the audio-clips was normalised using The Levelator (<http://www.conversationsnetwork.org/levelator>).

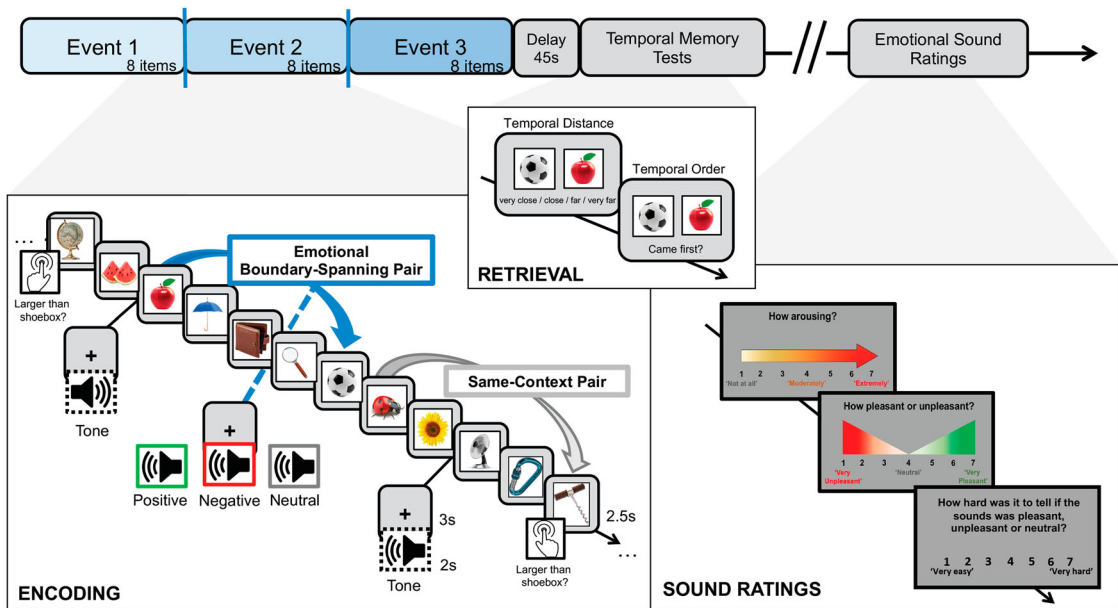
### **Event sequence encoding task**

To examine how emotion influences the temporal binding of nearby neutral items, we adapted an existing event sequence task (Clewett et al., 2020). The experiment was conducted in a quiet room at a computer. Participants viewed different sequences of 24 object images (Figure 1). Each image was displayed for 2.5s followed by a 3-s central fixation cross on a gray background. To create a stable auditory

context, or event, a 1-s pure tone with a frequency of 600, 700 or 800 Hz was played in the participant's left or right ear starting 0.5-s into each fixation period. The side of the tone cued which hand should be used to judge whether the next object was larger than a shoebox (e.g. left ear = left hand). The ear/hand remained the same for 8 sequential objects. This ear laterality manipulation was used to ensure that participants perceived a series of contextually distinct events, while the variety of within-event pure tones was used to help maintain participants' attention across the task. The same pure tone was repeated within a given list.

After participants saw the 8th object image in each auditory event, a trial-unique 2-s naturalistic audio-clip was played in the opposing ear, thereby creating a salient auditory context shift, or "event boundary". This served as the first of two event boundaries within a list. The onset of the audio-clip was 0.5-s into the fixation period between images. Each naturalistic audio-clip was emotionally positive (pleasant), negative (unpleasant), or neutral and varied in its level of arousal. After hearing a naturalistic audio-clip, participants viewed the next 8 object images, each preceded by the same neutral pure tone specific to that list (e.g. 800 Hz). After the 8th item in this second auditory event, a new naturalistic audio-clip was played in the opposite ear. This served as the second event boundary within a list. The second event boundary audio-clip was then followed by the same pure tone being played in that same new ear for the remainder of the items in the list. In total, each list contained two naturalistic audio-clips, or event boundaries, which served to parse each 24-item sequence into 3 discrete auditory events with 8 object images each. The type (i.e. pitch) of each pure tone used as same-context sounds was randomised across lists, and the ear that the tones first played in (left or right) was counterbalanced across lists. Participants viewed a total of 16 lists/sequences.

To reduce potential interactions between sound valences and boundary positions within a list (1st or 2nd), we constructed two types of lists: mixed-valence lists (one emotional and one neutral) and pure-valence lists (only negative, neutral, or positive). In the mixed lists, a positive or negative sound served as either the first or second event boundary, while the other event boundary sound was always neutral. These emotion-neutral combinations were chosen to reduce cross-contamination between positive and



**Figure 1.** Schematic of the emotional auditory event boundary paradigm. Participants studied lists of 24 everyday objects and indicated whether each item would fit in a shoebox. The surrounding auditory context was manipulated by playing a pure tone in either participants' left or right ear prior to viewing each image. The laterality of the tone also cued which hand participants should use to make their object size judgements. After viewing 8 successive items, participants heard an emotional negative (e.g. scream), neutral (e.g. clock ticking), or positive (e.g. baby giggling) audio-clip in their other ear. Participants then heard the pure tone again in that same (new) ear prior to the next 7 items. Next, a new naturalistic audio-clip played in their original ear and was then followed by a new pure tone for the next 7 items. The two naturalistic audio-clips served as event boundaries that divided each sequence into three discrete auditory events. After a short arrow distractor task, participants performed two different temporal memory tests. First, they had to rate the temporal distance between a pair of items from the prior sequence, ranging from "very close" to "very far" apart in the event sequence. Second, they had to indicate which of the two presented items had appeared first in the prior event sequence. The key memory comparison was between to-be-tested pairs that had spanned an emotional sound ("boundary-spanning pair"; blue) during encoding or were encountered within the same auditory event ("same-context pair"; grey). Following the event boundary task, participants re-listened to all naturalistic audio-clips from the experiment and provided subjective ratings of arousal, valence, and ambiguity.

negative sounds within a given sequence. In pure-valence lists, both emotional event boundaries had the same valence. Based on the two event boundary positions (after the 8th and 16th item in a sequence), the lists were broken down as follows: 8 pure lists total (three positive-positive, three negative-negative, two neutral-neutral) and 8 mixed lists (two neutral-positive, two positive-neutral, two negative-neutral and two neutral-negative). The order of the different event boundary list types was randomised across participants, and the trial-unique naturalistic audio-clips were pseudorandomized across event boundary positions and across lists.

### Delay distractor task

To reduce potential recency effects in memory, participants performed a 45-s arrow distracter task after studying each list. Participants viewed a rapid stream of either left-facing (<) or right-facing (>)

arrow symbols. The arrows appeared in the middle of the screen for 0.5s and were separated by a 0.5-s fixation cross. Participants simply had to indicate the direction of each arrow via button press.

### Temporal memory tests

Following the distracter task, participants viewed pairs of items from the prior list and had to provide a temporal distance rating and judge their correct order. First, participants rated the subjective temporal distance between two items using the following response options: "very close", "close", "far" or "very far" apart in the prior sequence (Figure 1). Second, participants indicated which of the two probe items had appeared first (temporal order memory; Figure 1). Crucially, each item pair had always been presented with three intervening items during encoding and were thereby always encountered the same



objective distance apart. Each tested item only appeared once during the temporal memory tests. To examine how emotional sounds influence temporal memory, we tested memory for two types of item pairs: (1) items that had appeared within the same auditory event and (2) items that had spanned an intervening positive, negative, or neutral audio-clip.

The structure of the event sequences as well as the specific item positions that were tested are displayed in Supplementary Figure 3. Of note, there were two item pairs spanning each naturalistic audio-clip (event boundary) and two same-context item pairs per auditory event. The specific positions of these pairs were spread out in time, enabling us to examine temporally dynamic effects of emotion on temporal memory. That is, determine whether temporal memory differed according to an item pair's proximity to a preceding emotional event boundary. Because we were interested in the discrete (e.g. boundary) and forward carryover effects of emotion on memory, data analyses did not include same-context item pairs from the first event of each list (i.e. the 8 items encountered before the first naturalistic audio-clip). This resulted in a total of 64 same-context pairs and 64 boundary-spanning pairs (4 of each type per list).

### ***Emotional sound ratings***

After the entire event boundary experiment was completed, participants listened to all emotional sounds again and provided separate ratings for arousal (from 1 = "not at all" to 7 = "extremely"), valence (from 1 = "very unpleasant" to 7 = "very pleasant"), and ambiguity (from 1 = "very easy to discriminate" to 7 = "very hard to discriminate"). Ambiguity ratings were collected as a covariate to account for variability in whether participants had trouble deciding whether a sound was positive, negative, or neutral. The three sound rating scales are depicted in the rightmost panel of [Figure 1](#).

### ***Testing trial-level associations between emotion ratings and encoding response times***

To examine how emotion influences attention dynamics during encoding, we conducted linear mixed modelling relating sound-level emotion ratings to both object categorisation accuracy and response times using the lme4 package in R ([\[cran.r-project.org/web/packages/lme4/\]\(http://cran.r-project.org/web/packages/lme4/\)\). Object size judgements were first categorised as being accurate or inaccurate based on consensus responses across participants. This approach was chosen to account for variable perceptions of the size of some of the objects across participants. For example, some participants may have tried to imagine the object as being true to its size in the real world, whereas others may have based their judgements on more literal perceptual information \(e.g. a very large image of a baseball on the screen would be judged larger than a shoebox\). Additionally, some objects could be manipulated mentally to fit inside a shoebox \(e.g. a baseball glove could hypothetically be folded up to fit into a shoebox\).](http://</a></p></div><div data-bbox=)

To examine attention dynamics during encoding, we performed a generalised linear mixed effects model for categorisation accuracy and a linear mixed effects model for response times. For both models, continuous subjective ratings for each boundary sound's arousal, valence, and ambiguity were first mean-centered and then modelled as fixed-effect predictors. Boundary items, or the objects encountered immediately after participants heard a naturalistic audio-clip, were assigned the emotion rating provided during the post-encoding sound ratings task. Same-context items, or objects that appeared in item positions 2–8 within each 8-item auditory event, were assigned the subjective ratings of the emotional boundary sounds that immediately preceded them. This enabled us to examine the proactive, or carryover, effects of emotional boundaries on attention and encoding processes in the subsequent event. The first item in each list was excluded from all analyses, because it may be construed as an event boundary of no-interest (i.e. was not a boundary that was explicitly manipulated and does not involve emotional sounds). Condition was entered as a fixed-effect predictor (1 = boundary item; -1 = same-context item) of the two encoding performance measures. In addition, we included two-way interaction terms between subjective arousal and valence ratings, both of their individual interactions with Condition, as well as a three-way arousal-by-condition-by-valence interaction term.

Model testing was performed to identify random effects that accounted for significant variance in temporal order memory performance. The effects of List Type (e.g. positive-positive, neutral-positive etc.), Event Number (event 2 or event 3), and Block Number (1 through 16) were entered as covariates

in each model to account for potential differences in the time-course of arousal and valence effects. The best fitting model included random intercepts for Block Number and Participant, so they were included in all remaining mixed models. We did not include random slopes for these terms, because we expected the effects of emotion and block order to be consistent across individuals.

In the first encoding model, object categorisation accuracy, as defined by the consensus size judgement across participants, was coded as a binary variable (1 = correct, 0 = incorrect) and modelled as the dependent measure in a generalised linear mixed effects model. Altogether, the following formula was used to assess the effects of subjective emotional experience on judgement accuracy:

```
glmer(Judgement Accuracy ~ Arousal Ratings
      + Ambiguity Ratings + Valence Ratings
      + Condition*Arousal + Condition*Valence
      + Condition*Valence*Arousal + (1|Block)
      + (1|Participant), family
      = binomial(link = 'logit'))
```

In the second mixed effects encoding model, we examined the relationship between emotion ratings and size judgement response times. Notably, we only analysed trials in which participants made an accurate judgement based on the study sample's consensus response. The following formula was used for this analysis:

```
lmer(Judgment Response Times ~ Arousal Ratings
      + Ambiguity Ratings + Valence Ratings
      + Condition*Arousal + Condition*Valence
      + Condition*Valence*Arousal + (1|Block)
      + (1|Participant))
```

### ***Generalised linear mixed modelling analyses between emotional arousal, valence, and temporal memory***

To test our key hypotheses that emotional arousal and valence influence the temporal structure of memory, we performed generalised linear mixed modelling analyses. As in the prior analyses, trial-level subjective ratings for the arousal, valence, and ambiguity for each emotional event boundary sound were mean-centered and entered into the model as fixed-effect predictors. Boundary-spanning item pairs were assigned the

subjective ratings of their intervening emotional boundary sounds. Same-context item pairs were assigned the subjective ratings of the emotional boundary sounds that immediately preceded them. Again, Participant was specified as a random effect with a random intercept, enabling us to account for individual differences in emotion-memory relationships.

Notably, we designed this study to use a linear mixed modelling approach for several reasons. This statistical method differs somewhat from the common approach of dividing and binning emotional stimuli or ratings into distinct valence categories (e.g. defining a range of valence ratings as belonging to a single “negative”, “positive” or “neutral” valence bin). However, defining these bins also relies on subjective and arbitrary definitions of category cut-offs. For example, it is equally reasonable to define “negative valence” as ratings of 1–3 or ratings of 1–2. These differing cut-offs could clearly lead to differences in the results, and running linear mixed models obviates the need to make a subjective decision. Subdividing the ratings into distinct bins also creates empty data bins, especially when arousal and valence categories are taken into consideration in the same Analysis of Variance (ANOVA). This is problematic for running statistical analyses, and avoiding category definitions again avoids this issue. Critically, we also had very direction-specific predictions about the effects of valence on temporal memory. Specifically, we predicted that valence exerts different memory effects according to a linear spectrum, ranging from narrowing or order memory impairment at the most negative emotional moments to a gradual broadening, or enhancement of temporal memory, as positive emotional moments reach their highest point. Our hypothesis therefore strongly motivates the use of a linear mixed modelling approach.

We have made our data publicly available so that individuals interested in testing categorical or inverted-U predictions about emotion-memory interactions (e.g. treating “positive” and “negative” valence as one “emotion” bin) may do so. We also note that the results of our analyses were similar regardless of whether the data were analysed using distinct valence and arousal categories or continuous emotion ratings.

### ***Effects of emotional boundaries on temporal binding within and across events***

To determine if emotional boundaries exert different effects on temporal binding for boundary-spanning



pairs compared with same-context pairs, Condition was modelled as a fixed-effect predictor (1 = boundary-spanning pair; -1 = same-context pair). We also included two-way interaction terms between subjective arousal and valence ratings, both of their individual interactions with Condition, as well as a three-way arousal-by-condition-by-valence interaction term. Temporal order memory accuracy for the item pairs was coded as a binary variable (1 = correct, 0 = incorrect) and modelled as the dependent measure, resulting in the following formula:

```
glmer(Order Memory ~ Arousal Ratings
+ Ambiguity Ratings + Valence Ratings
+ Condition*Arousal + Condition*Valence
+ Condition*Valence*Arousal + (1|Block)
+ (1|Participant), family = binomial(link = 'logit'))
```

Like the encoding analyses, we excluded the first to-be-tested item pair in each list, because it contained the very first item in the lists. As such, this pair could be construed as a task-related boundary effect that is different from the explicit auditory context manipulation. For all analyses, the statistical significance of the regression models was determined using model comparisons, which resulted in  $\chi^2$  values and corresponding  $p$  values. Statistical assumptions of the two main generalised linear mixed models for temporal order memory were tested using the “DHARMA” package in R (Hartig, 2022). These diagnostics were performed for the model examining the condition-related interaction effects of emotion ratings on temporal order memory. For the condition model, we did not find significant evidence of an incorrect distribution (tested using Kolmogorov–Smirnov, or KS test;  $p = .83$ ), over- or under-dispersion ( $p = 1.0$ ), or outlier datapoints ( $p = .65$ ). Using the “car” package in R (Fox et al., 2012), we verified that all VIFs were below 1.23, indicating low collinearity between the fixed-effects predictors. The “performance” package in R was also used to verify normality of all random effects (Lüdtke et al., 2021).

### ***Carryover of emotional boundaries on temporal encoding earlier versus later within a stable event***

In a separate generalised linear mixed modelling analysis, we also tested if potential carryover effects of emotional boundaries influence temporal encoding in a time-dependent manner. That is, we examined if

emotion had a larger impact on memory for same-context pairs encountered earlier compared to later in the next event. Here, we used the same generalised linear mixed modelling approach as before, except this time we modelled the Pair Position (1 = early, -1 = late) of same-context item pairs as a fixed-effect predictor of temporal memory instead of Condition (see Supplementary Figure 3 for an illustration of which pairs were examined). Random intercepts were modelled for Participant and Block Number, resulting in the following formula:

```
glmer(Order Memory ~ Arousal Ratings
+ Ambiguity Ratings + Valence Ratings
+ Condition*Arousal + Condition*Valence
+ Condition*Valence*Arousal + (1|Block)
+ (1|Participant), family = binomial(link = 'logit'))
```

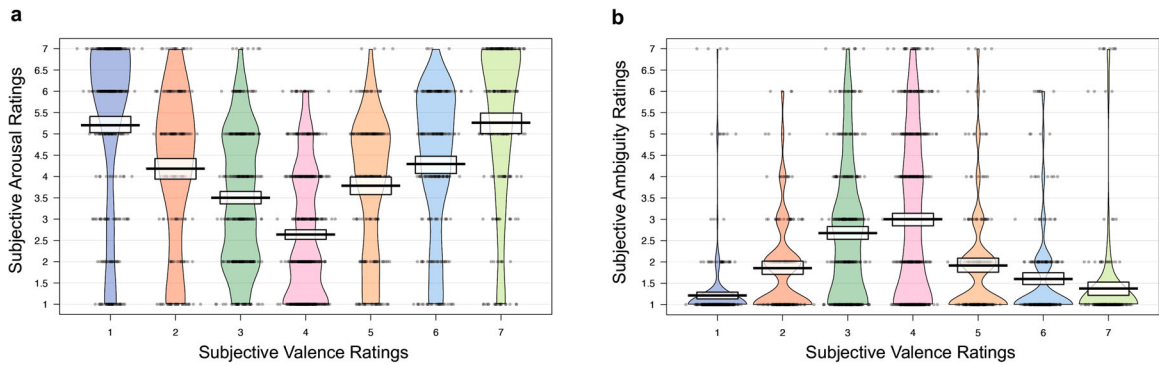
We verified this model met the main statistical assumptions of a generalised linear mixed effects model. Specifically, we did not find significant evidence of an incorrect distribution (tested using Kolmogorov–Smirnov, or KS test;  $p = .96$ ), evidence of over- or under-dispersion ( $p = 0.98$ ), or outlier datapoints ( $p = 1$ ). All VIFs were below 1.19 and we verified the normality of all random effects.

Finally, to disentangle the effects of arousal and valence on temporal memory, we also performed simple slopes analyses following any significant interaction effects. Here, we examined whether the linear relationship between arousal ratings and temporal order memory differed at low, moderate, and high levels of emotional valence. Fitted regression lines were plotted at low (-1 SD; negative) and moderate (average; neutral) and high (+1 SD; positive) levels of emotional sound valence ratings using estimates from the relevant generalised linear mixed effects model.

## **Results**

### ***Emotional sound ratings***

First, we examined if participants' arousal and ambiguity ratings significantly differ by valence based on participants' own post-task ratings (see Figure 2). For each participant, positive, neutral, and negative valence categories were defined in the following way: a valence rating  $\geq 5$  was defined a “positive”; a rating = 4 was defined as “neutral”; and a rating  $\leq 3$  was defined as “negative”. Planned paired samples  $t$ -



**Figure 2.** Participants' post-task emotional sound ratings broken down by participants' subjective valence ratings. (A) Participants' subjective arousal ratings were highest for positive (valence ratings 5–7) and negative (valence ratings 1–3) sounds. (B) Participants' subjective ratings of ambiguity (i.e. how difficult it was to discern how pleasant a sound was) were highest for neutral (valence rating of 4) and then for negative (ratings 1–3) sounds. The pirate plots show the raw datapoints across all participants as individual dots. They also include smoothed density distributions (violin plots) of ratings across all participants. Bold, horizontal lines signify mean ratings for each of the three valence categories and the boxes represent 95% confidence intervals.

tests indicated that participants rated negative sounds ( $M = 4.31$ ,  $SD = 1.51$ ) and positive sounds ( $M = 4.34$ ,  $SD = 1.34$ ) as being significantly more arousing than neutral sounds ( $M = 2.76$ ,  $SD = 0.98$ ); negative:  $t(18) = 5.03$ ,  $p < .001$ ; positive:  $t(18) = 6.86$ ,  $p < .001$ . However, positive and negative sounds did not significantly differ in arousal ( $t(18) = 0.14$ ,  $p = .89$ ).

With respect to the ambiguity of the valence of different naturalistic sounds, neutral sounds ( $M = 2.86$ ,  $SD = 1.11$ ) were rated as being significantly more ambiguous than positive ( $M = 1.60$ ,  $SD = 0.63$ ;  $t(18) = 5.76$ ,  $p < .001$ ) and negative sounds ( $M = 1.91$ ,  $SD = 0.65$ ;  $t(18) = 4.39$ ,  $p < .001$ ). Negative sounds were also rated as being more ambiguous than positive sounds ( $t(18) = 2.31$ ,  $p = 0.033$ ).

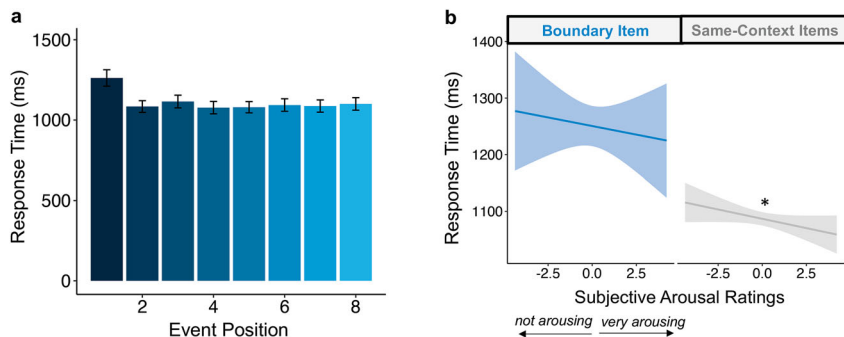
### Object categorisation accuracy and encoding response times

During item sequence encoding, participants were less accurate at categorising the size of boundary objects (i.e. after naturalistic audio-clip;  $M = 0.84$ ,  $SD = .36$ ) compared to other objects in the sequences (i.e. after repeated pure tone;  $M = 0.88$ ;  $SD = .32$ ;  $\chi^2(1) = 5.92$ ,  $p = .015$ ). However, we did not observe any statistically significant main or interaction effects of arousal, valence, or ambiguity ratings on categorisation accuracy.

Regarding response times, participants were slower to judge items appearing just after a boundary sound (i.e. item in event position 1;  $M = 1250$  ms,  $SD$

$= 409$  ms) compared to objects appearing within the same auditory context (i.e. items in event positions 2–8;  $M = 1088$  ms,  $SD = 366$  ms;  $\chi^2(1) = 106.57$ ,  $p < .001$ ; see Figure 3A for an illustration of event position effects). We also observed a significant main effect of sound ambiguity ratings on response times, such that participants were faster at judging the size of objects if they perceived sounds as being more ambiguous ( $\chi^2(1) = 4.63$ ,  $p = .031$ ). Further, arousal ratings were marginally significantly negatively correlated response times ( $\chi^2(1) = 3.32$ ,  $p = .069$ ), and there was a marginally significant arousal-by-valence-by-condition interaction effect on response times ( $\chi^2(1) = 3.52$ ,  $p = .061$ ).

When examining objects from the two conditions separately, we found that sound arousal ratings were significantly negatively correlated with response times for same-context items, indicating that participants were faster at responding to items from auditory events that followed highly arousing boundaries (i.e. in event positions 2–8;  $\chi^2(1) = 5.09$ ,  $p = .024$ ; see Figure 3B). A similar pattern was observed following for same-context items that followed more ambiguous sounds, but this effect was only marginally significant ( $\chi^2(1) = 3.69$ ,  $p = .055$ ). There were no significant main or interaction effects of the emotion ratings on response times for boundary items specifically (all  $p$ 's  $> .05$ ). Together these findings suggest that hearing ambiguous and arousing sounds impacts attention dynamics during sequence encoding, primarily by modulating attentional processes within an otherwise stable perceptual event.

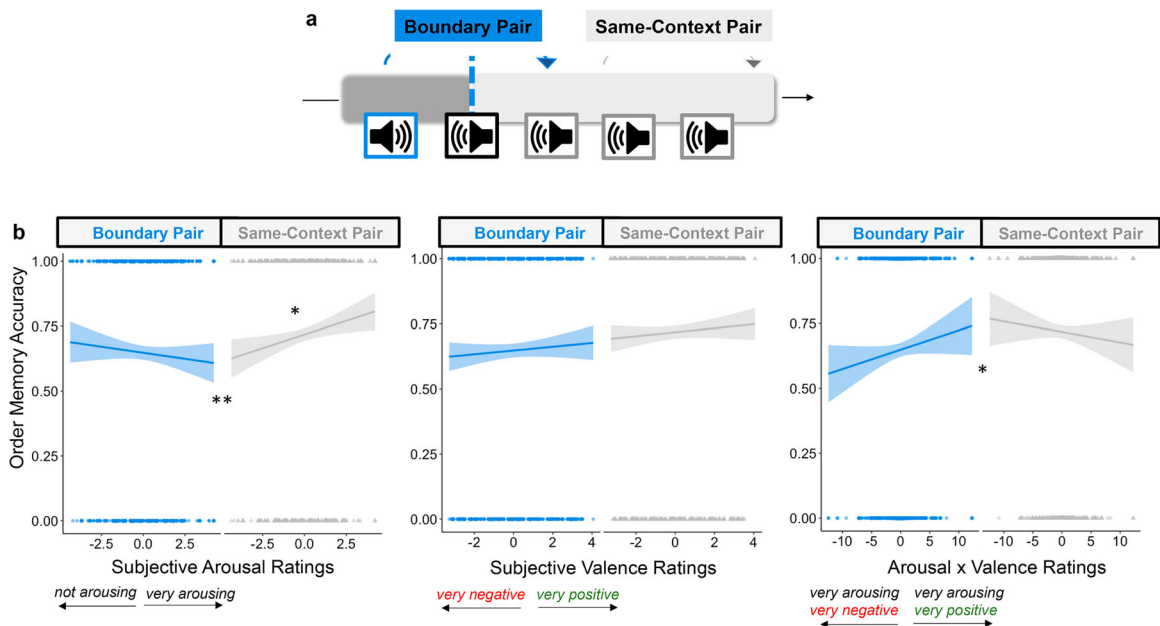


**Figure 3.** Effects of emotional event boundaries on response times during item encoding. (A) During encoding of event sequences, participants judged whether each object could fit in a shoebox. Size judgements for the objects were significantly slower for the object encountered immediately after participants heard a naturalistic audio-clip, or event boundary (i.e. item position 1 in an event). Objects in positions 2 through 8 within an auditory event, or same-context items, followed a repeated neutral tone in participants’ left or right ear. Bars represent mean response times broken down by the object’s position within the 8-item auditory events. Error bars represent standard error of the means. (B) The relationship between trial-level subjective arousal ratings for the emotional sounds and response times to boundary items and same-context items, separately. Highly arousing event boundaries led to faster response times for same-context items encountered in the next auditory event. Shaded bars represent 95% confidence intervals. \* $p < .05$ .

### Trial-level effects of emotional event boundaries on temporal order memory

To test our key hypothesis that emotional context influences the temporal structure of memory, we

performed generalised linear mixed modelling analyses using participants’ trial-level subjective arousal, valence, and ambiguity ratings for each emotional sound (Figure 4A). We first found a main effect of Condition, such that that temporal order memory was



**Figure 4.** Generalised linear mixed modelling analyses of the relationship between subjective emotional ratings and temporal order memory. (A) Schematic of the two types of item pairs that were tested for temporal order memory after sequence encoding. The direction of the audio icons represents the ear that participants heard the sounds in. Gray-bordered icons represent pure tones, whereas the black-framed icon and blue dashed line represent the emotional sound, or event boundary. Some item pairs spanned an intervening emotional sound (“boundary-spanning pair”; blue). The other item pairs were encountered within the same auditory context. That is, they were preceded by a pure tone (“same-context pair”; grey). (B) Generalised linear mixed modelling results between trial-level temporal order memory and emotional sound ratings for arousal (left panel), valence (middle panel), and their interaction (right panel). Dots represent individual datapoints across all participants. \* $p < .05$ ; \*\* $p < .01$ .

significantly better for same-context item pairs compared to boundary-spanning item pairs ( $\chi^2(1) = 14.04$ ,  $p = .00018$ , odds ratio = 0.84). This result replicates longstanding work on event cognition and supports the notion that temporal memory integration is supported by context stability while memory separation is driven by context shifts (Clewett et al., 2019; Clewett & Davachi, 2017).

Critically, we also identified a significant arousal-by-condition interaction effect on temporal memory. Highly arousing event boundaries were significantly more likely to impair temporal order memory for boundary-spanning pairs compared to same-context pairs ( $\chi^2(1) = 6.74$ ,  $p = .0094$ , odds ratio = 0.93; Figure 4B, left panel). There was no main effect of valence or valence-by-arousal interaction effect on temporal order memory (all  $p$ 's  $> .05$ ; Figure 4B, middle panel).

To determine which factors drove the arousal-by-condition interaction effect on order memory, we performed separate generalised linear mixed modelling analyses for boundary-spanning and same-context pairs (Figure 4B, left panel). We found that higher arousal ratings for boundary sounds were significantly correlated with better temporal order memory for same-context item pairs encountered within the next auditory event ( $\chi^2(1) = 3.93$ ,  $p = .047$ , odds ratio = 1.09). However, there was no statistically significant association between higher arousal ratings for boundary sounds and temporal order memory for those same boundary-spanning pairs ( $\chi^2(1) = 2.20$ ,  $p = .14$ , odds ratio = 0.94).

The full model results with both conditions also revealed a significant three-way interaction between arousal, valence, and condition on temporal memory ( $\chi^2(1) = 3.98$ ,  $p = .046$ , odds ratio = 1.03; Figure 4B, right panel). Finally, the full model results also revealed that sounds that were later rated as more ambiguous in valence were related to worse temporal order memory irrespective of condition ( $\chi^2(1) = 4.82$ ,  $p = .028$ , odds ratio = 0.93).

### ***Valence-specific effects of arousing event boundaries on temporal order memory***

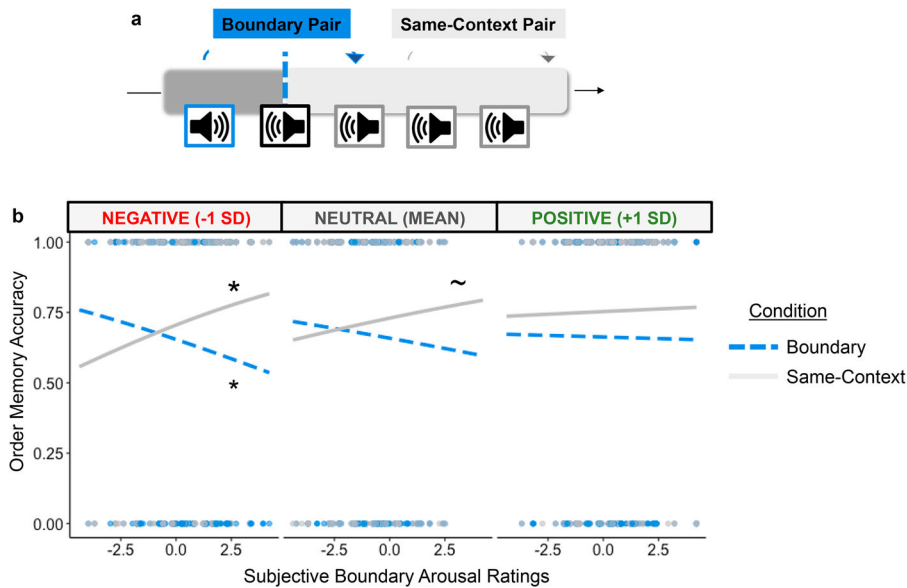
Next, we performed a simple slopes analysis to dissociate the effects of arousal on memory at different levels of pleasantness, or valence. We adopted this approach, because it allows us to disentangle arousal-by-valence interactions that may otherwise

be obscured by treating valence as a continuous variable. These analyses were performed separately for the two conditions (Figure 5A).

For same-context pairs, we found that emotional event boundary sounds rated as arousing and more negative led to better temporal order memory (valence rating  $-1$  SD below the mean;  $z = 2.45$ ,  $p = .01$ ; Figure 5B, left panel). That is, naturalistic sounds that were perceived as highly negative and arousing led to better temporal binding between item pairs that were encountered several seconds later. A similar but marginally significant arousal-memory correlation was observed for sounds rated as neutral (mean valence rating;  $z = 1.99$ ,  $p = .05$ ; Figure 5B, middle panel). By contrast, there was no significant association between arousal and temporal order memory when the preceding emotional event boundary sounds were rated as more positive (valence rating  $+1$  SD above the mean;  $z = 0.32$ ,  $p = .75$ ; Figure 5B, right panel).

For boundary-spanning pairs, we observed an event segmentation pattern that was consistent with our prediction that negative, arousing boundaries would impair temporal memory. Emotional sounds that were rated as more negative showed a significant negative association between arousal and temporal order memory (valence rating  $-1$  SD below the mean;  $z = -2.05$ ,  $p = .04$ ; Figure 5B, left panel). There were no significant associations between emotional arousal and temporal memory for sounds that were rated as neutral (mean valence rating;  $z = -1.59$ ;  $p = .11$ ; Figure 5B, middle panel) or more positive (valence rating  $+1$  SD above the mean;  $z = -0.17$ ,  $p = .87$ ; Figure 5B, right panel).

Taken together, these findings suggest that the divergent effects of emotionally arousing event boundaries on temporal order memory emerge under increasingly aversive contexts. On the one hand, negative and arousing emotional moments facilitated the segmentation of adjacent experiences in memory. On the other hand, negative emotional boundary-induced arousal carried forward in time to promote temporal binding between information within the next auditory event. These results underscore the temporally dynamic and complex effects of arousal on the temporal integration of negative memories, with associative binding differing according to the timing to of an emotional shift during sequence encoding.



**Figure 5.** Temporal order memory accuracy as a function condition and the arousal and valence of emotional event boundaries. (A) Schematic of the two types of item pairs that were tested for temporal order memory after sequence encoding. The direction of the audio icons represents the ear in which participants heard the sound in each trial. Grey-bordered icons represent pure tones, whereas the black-framed icon and blue-dashed line represent the naturalistic sounds, or event boundaries. Some item pairs spanned an intervening emotional sound (“boundary-spanning pair”; blue and dashed). Other item pairs were encountered within the same auditory context (“same-context pair”; grey and solid lines). Same-context item pairs were assigned the same arousal, valence, and ambiguity ratings as the preceding naturalistic audio-clip, or event boundary. (B) Generalised linear mixed modelling results are shown separately for boundary-spanning pairs and same-context pairs. The slopes of the lines represent the relationship between subjective arousal ratings and temporal order memory accuracy. These arousal-memory correlations are plotted separately for emotional sounds that were rated as more negative ( $-1$  SD below the mean valence), neutral (mean valence), and more positive ( $+1$  SD above the mean valence). Dots represent individual datapoints across all participants, broken down by condition in grey and blue.  $*\sim p = .05$ ;  $*p < .05$ .

### Time-dependent effects of arousing event boundaries on same-context temporal binding

The results thus far suggest that the modulatory effects of an arousing sound linger in time to influence temporal binding processes for subsequent items. Next, we tested if the strength of these arousal effects diminished or increased over time as a function of the position of different item pairs within each event. As before, we observed a significant main effect of sound arousal ratings on temporal order memory for same-context pairs, with higher arousal ratings relating to better temporal order memory, ( $\chi^2(1) = 4.02$ ,  $p = .045$ , odds ratio = 1.09). However, there were no other statistically significant main or interaction effects of emotion ratings or pair position on same-context temporal memory (all  $p$ 's  $> .05$ ).

### Testing for retroactive effects of emotional event boundaries on temporal memory

Our main results showed that arousal induced by emotional sounds can carry forward in time to

enhance memory integration. Beyond binding information in a forward manner, it is also possible that these mnemonic benefits occur retroactively. Increasing evidence suggests that, in addition to facilitating event segmentation, event boundaries may also trigger consolidation processes that reactivate and replay recent episodic information (Ben-Yakov & Dudai, 2011, 2013; Clewett et al., 2019; Lee & Chen, 2022; Sols et al., 2017). Additionally, work in rodents suggests that rewards can intensify this neural replay process, potentially leading to stronger memory consolidation (Ambrose et al., 2016). Little work, however, has investigated if emotional stimuli retroactively enhance the temporal integration of recent sequences.

To test this idea, we used the same generalised linear mixed modelling approach as before, except this time we assigned same-context pairs the valence and arousal ratings of their *ensuing* event boundary. For example, if the first emotional event boundary in a list was given an arousal rating of 4, then the two same-context pairs from the prior



auditory event (i.e. object pairs that were present in the first 8 items in the list) would be assigned an arousal rating of 4. The results revealed no significant main or interaction effects of ambiguity, valence, or arousal ratings on temporal memory binding within the prior event (all  $p$ 's > .19). Thus, the arousal induced by emotional boundaries appears to enhance encoding processes in a proactive manner but does not modulate the binding and storage of recent temporal associations.

## Discussion

Moments of emotional reactivity punctuate everyday life and lead to the formation of lasting memories. Yet, while it is commonplace to refer these memories as emotional “events”, little empirical work has examined if emotion organises continuous experiences into discrete and coherent episodes. To fill this knowledge gap, we examined how embedding emotional stimuli within otherwise neutral and continuous item sequences leads to changes in temporal order memory, a behavioural index of event formation. We also used peripheral auditory stimuli to manipulate encoding structure within these sequences, thereby creating the temporal stability and changes in contextual information that appear necessary for inducing event segmentation in perception and memory (Clewett et al., 2019; Siefke et al., 2019). Our results revealed that discrete and negative emotional moments, such as hearing screams or a gunshot, exert differential effects on temporal binding processes across time. Encountering arousing event boundaries led to transient impairments in temporal encoding processes, insofar as those boundaries were negative in valence. Our results also suggest that the arousal induced by emotional sounds lingers in time to benefit subsequent temporal encoding and sustained attention processes. Together, these findings align with the idea that negative and highly arousing stimuli support the temporal organisation of events in long-term memory.

Our most robust finding was that the arousal induced by an emotional stimulus – especially if it was negative – carries forward in time to benefit within-event binding processes. This result adds to a complex and rapidly growing literature on how emotional states influence different temporal aspects of memory. Presently, much of the work on this topic has yielded mixed findings, with emotional arousal and negative valence sometimes enhancing

different aspects of temporal memory (D'Argembeau & Van der Linden, 2005; Dev et al., 2022; Rimmelé et al., 2012; Schmidt et al., 2011) and other times impairing (Huntjens et al., 2015; for a review, see Palombo & Cocquyt, 2020) or distorting it (Hennings et al., 2021). To reconcile these seemingly contradictory findings, it is crucial to consider several factors that may differ across experiments, particularly whether evoked emotional states are highly variable or relatively tonic and sustained. Temporal memory tends to be impaired by emotional arousal when individuals must bind inter-event information in memory, such as lists of intermixed emotional and neutral stimuli (Huntjens et al., 2015; Maddock & Frein, 2009). By contrast, negative affect and arousal has been shown to improve temporal memory when participants encode and remember intra-event information; that is, items studied within “pure” negative or neutral contexts, such as a movie (Dev et al., 2022; Schmidt et al., 2011) or a continuous real-world experience, such as navigating through a haunted house (Cliver et al., 2023). These more sustained and temporally dynamic states of emotion may resemble the lingering arousal states that support within-event temporal integration in our study (also see Petrucci & Palombo, 2021).

Here, we demonstrate that emotional arousal-related enhancements and impairments in temporal memory can co-occur within the same experiment when fluctuations in emotional states are modulated in a highly structured manner. Unlike previous studies, this set-up enabled us to examine the effects of emotion on both inter- versus intra-event binding processes in memory. Prior work using sustained stressors, negative moods, or aversive events might have masked the more nuanced and dynamic effects of emotion fluctuations on temporal memory. Our finding that increased arousal enhanced intra-event binding mimics the mnemonic benefits of homogenous emotional or neutral lists manipulated on much longer timescales (e.g. Dev et al., 2022). It also supports the idea that sustained arousal and attentional states promote memory integration, insofar as arousal levels remain relatively stable for an extended period of time. Indeed, prior work has shown that greater temporal stability in pupil-linked arousal states, a probable index of sustained attention and high alertness (Regen et al., 2013; Wilhelm, 2008), predicts better temporal order memory (Clewett et al., 2020). One limitation of the current study is that we did not probe moment-to-moment arousal levels for



each item in the sequence, because we did not want to alter participants' attention at encoding. However, we speculate that within-event arousal levels likely did not vary drastically within an event due to the mundane nature of the auditory context manipulation. As a tone-defined event gradually progressed, participants repeatedly heard the same neutral sounds for seven consecutive items. Thus, there was little, if any, external stimulation to evoke additional arousal responses before the next boundary. It is also noteworthy that our study differs from most prior work in that temporal memory was not queried for emotional items themselves. Instead, we examined how moments of intense emotional arousal alters the binding of otherwise neutral details, which may be qualitatively different from retrieving explicitly emotional information.

Another critical finding was that arousal modulated an ongoing tug-of-war between memory integration and separation processes under negative emotional contexts. This valence-specific effect of arousal on memory aligns with work showing that negative affect tends to narrow the scope of attention and cognitive processing, whereas positive affect broadens them (Gable & Harmon-Jones, 2010; Harmon Jones et al., 2012). In a related manner, it is well documented that negative stimuli typically disrupt the coherence of episodic memory, leading to widespread impairments in source memory for nearby neutral items (Bisby et al., 2018; Mather, 2007). Positive emotions instead have been shown to enhance associative memory (Madan et al., 2019; Williams et al., 2022), consistent with the idea that positive affect promotes the integration of complex elements of experience into multi-faceted mental representations (Clewett & Murty, 2019; Fredrickson & Branigan, 2005). These differential effects of emotion on memory integration processes closely parallel the effects of item-focused processing on event segmentation in memory under neutral circumstances. Specifically, cognitively demanding tasks that force individuals to focus on individual items have been shown to disrupt temporal order memory (DuBrow & Davachi, 2013), thereby mimicking the effects of negative emotion and arousal on cognitive narrowing processes. Increasing evidence also indicates that boundaries enhance attention and processing of concurrently presented item representations at the expense of binding items together across those context shifts (Heusser et al., 2018). Our findings suggest that injecting arousing boundaries with

negative valence may amplify cognitive- and attention-narrowing effects even further, leading to greater memory separation between emotional and temporally adjacent neutral events.

Unfortunately, we did not collect measures of item recognition or free recall for items in the current study, so it is unclear whether certain item memory effects inform the retrieval of temporal information. Prior work on event segmentation shows that item and item-source memory tend to be enhanced for items that co-occur with a context shift (Clewett et al., 2020; Heusser et al., 2018; McClay et al., 2023; Siefke et al., 2019; Swallow et al., 2009), much like the well documented enhancing effects of emotional arousal and negative valence on memory for neighbouring neutral items (Sakaki et al., 2014; Schluter et al., 2019). Those studies raise the interesting possibility that arousing, negative event boundaries may serve to enhance individual item representations in long-term memory, which may enable individuals to use item strength-based retrieval strategies to discriminate the primacy of those items (DuBrow & Davachi, 2017). Interestingly, the potential influence of valence may manifest when arousal inductions are less intense. For example, recent work shows that positive emotions induced by music can enhance neutral item and temporal source memory after a 24-hr delay, especially if those positive emotions are arousing (McClay et al., 2023). Because music-induced arousal is presumably not as high or distressing as sounds of screaming or images of violence, it is possible that valence emerges as a key player in shaping different aspects of episodic memory under these relatively low-arousal conditions. Future research should include both item and source binding measures to examine how emotional arousal specifically influences the relationships between different features of episodic memory (e.g. Palombo et al., 2021). Moreover, future studies should explore if emotion influences the strategies individuals use to reconstruct and discriminate the order of recent events, especially if emotion functions as its own source context for binding items and facilitating their subsequent recall (Talmi et al., 2019).

Another interesting open question concerns the neural mechanisms that promote this hyper-integration of emotional episodic memories. Arousal-related activation of the noradrenergic system plays an essential role in enhancing processing of emotional information (Markovic et al., 2014; Mather et al., 2015; McGaugh, 2013; Strange et al., 2003). The

noradrenergic system has also been shown to enhance the selectivity of perception and memory under arousal, potentially leading to trade-offs between item memory and memory for peripheral contextual information (Mather et al., 2015). Accumulated evidence also shows that the noradrenergic system modulates memory processes in the hippocampus, a region that is critical for supporting representations of context and integrating memories of time and sequential events (Clewett et al., 2019; Harley, 2007; Ranganath & Hsieh, 2016; Sara, 2009; Squire, 1992). Interestingly, theories of noradrenergic system function and the neural processes that facilitate event segmentation also share considerable conceptual overlap. The release of norepinephrine is thought to facilitate a “network reset” that reorganises functional brain networks to prioritise and process salient information during a shift in environmental contingencies (Bouret & Sara, 2005). These shifts could be construed as event boundaries, which have been theorised to trigger a global neural signal that rapidly updates mental representations of the current context (Zacks et al., 2007). Given its widespread projections to most of the brain (Sara, 2009), the noradrenergic system is ideally positioned to transmit such a reset signal, while also influencing temporal encoding processes in the hippocampus.

The current findings lay important new groundwork for understanding how dynamic emotional arousal states provide a strong internal context for binding sequential representations in memory. An important open question is whether these memory-structuring effects also relate to the superior *memorability* of emotional experiences compared to neutral ones. There are some indications that event segmentation processes also lead to greater memory accuracy later on. For example, inserting event boundaries into a dynamic experience has been shown to boost free recall even up to one month later (Flores et al., 2017). Moreover, perceptual and emotional boundaries in music have been shown to enhance recognition and temporal source memory for concurrent neutral images (McClay et al., 2023). For more stressful and highly arousing situations, however, this story may be more complex. Behavioural work shows that higher rates of event segmentation during stress-inducing movies instead relates to worse item recognition memory for those films (Sherrill et al., 2019). This negative association between event segmentation performance and long-term memory was also related to greater state

anxiety across participants. In summary, further research is needed to better understand how arousal and anxiety influence event perception and its complex relationship with long-term memory, and whether such relationships differ between healthy individuals and those with affective disorders.

Insofar as event segmentation does lead to better long-term recall, our findings suggest that parsing and binding of emotionally arousing contexts may contribute to the persistence of aversive memories. This idea is supported by evidence that transitions between fear learning and extinction, which could be construed of as an event boundary, enhance recognition memory for items appearing just prior to those transitions (Dunsmoor et al., 2018). However, this result only speaks to how a coarse transition between two types of emotional learning influences memory for preceding item representations. By using temporal memory indices of event structure as well as many item sequences/trials, we demonstrate that negative emotional contexts indeed shape the temporal structure of memory as an experience unfolds. This process of negative arousal-enhanced event segmentation may bind otherwise neutral representations to an underlying emotional context, which could make items strong retrieval cues for other emotionally relevant information encountered in that event (Talmi et al., 2019). At the same time, computational models suggest that such enhancements might also disrupt the scaffolding effects of other forms of context, such as time, on memory encoding and retrieval (Talmi et al., 2019).

Several limitations in our study warrant consideration. While we had adequate statistical power to detect emotional boundary effects on temporal order memory, our study had a relatively modest sample size. Due to unforeseen disruptions in data collection during the COVID-19 pandemic, we lacked sufficient statistical power to examine how emotional boundaries affect temporal distance ratings, a subjective memory measure that is also used to operationalise event segmentation effects in memory (e.g. Ezzyat & Davachi, 2014). Examining these effects would help shed additional light on how emotional states shape episodic memory organisation as well as internal representations of time. To avoid creating inadvertent event boundaries during encoding, we also had participants re-listen to the emotional sounds and provide subjective arousal, valence, and ambiguity ratings after the entire task was completed. However, acquiring

post-experiment ratings prevented us from measuring emotional responses as they first occurred during sequence encoding. Future studies could use objective measures of physiological arousal, such as pupillometry or skin conductance, to evaluate initial emotional responses without disrupting attention during the sequence encoding task. Collecting continuous pupil measures would be especially useful for tracking the time-course of fluctuating arousal states across the course of encoding. Of relevance to our current findings, it has been shown that the temporal stability of arousal states, as indexed by variability in pupil diameter over time, relates to temporal memory integration (Clewett et al., 2020). Viewed through this lens, the current findings may reflect aversive boundaries eliciting an elevated yet stable state of arousal that transiently benefits temporal memory integration.

Unexpectedly, we also found that sounds that were perceived as being more ambiguous in valence were associated with worse temporal order memory irrespective of condition. We collected these ratings to control for variability in the emotional complexity of naturalistic sounds. However, we had no predictions about how these ratings would relate to temporal memory. We speculate that ambiguity may drive segmentation in two ways. First, the sounds that are more obscure or ambiguous might have distracted participants from the task at-hand and perhaps occupied attentional resources that were necessary for holding sequential items in working memory. Cognitive control is also thought to play a key role in updating event representations at boundaries (Wen & Egner, 2022; Zacks et al., 2007). Thus, the need to filter out these distractions may engage cognitive control processes to a larger degree, leading to greater event segmentation effects. Second, temporal binding effects in our study may have been modulated by conceptual overlap between the visual memoranda and the naturalistic sounds. The naturalistic sounds that were rated highest in ambiguity included groups of people mumbling or boring everyday sounds, such as a lawnmower or doorbell. It could be the case that rather than being distracted by these more mundane auditory inputs, participants proactively used these cues to chunk and remember event sequences in a goal-directed manner (Clewett et al., 2019). To address these possibilities, it will be important for future research to identify the unique and/

or interactive effects of different emotional, cognitive, and semantic factors on event segmentation processes in long-term memory.

Characterising how shifting emotional states organise memories is essential for understanding how prior experiences can guide both adaptive and maladaptive behaviours. Under normal circumstances, the process of event segmentation may adaptively chunk experiences to facilitate the long-term storage and retrieval of everyday memories (Flores et al., 2017; Gold et al., 2017; McGatlin et al., 2019). However, the robust memory-structuring effects of emotional arousal may become maladaptive if this makes aversive memories more resistant to updating or forgetting. For instance, failures to encode or remember the temporal order of highly emotional events are a hallmark feature of post-traumatic stress disorder (Hackmann et al., 2004; van der Kolk & Fiser, 1995). It is thought that individuals with post-traumatic stress disorder (PTSD) preferentially process perceptual information at the expense of surrounding contextual details, including the spatial or temporal context (Ehlers, 2006; Ehlers et al., 2002; Ehlers & Clark, 2000). Again, this bears a striking resemblance to the memory trade-off effects have been shown to occur during neutral context shifts, with boundaries prioritising the processing of novel incoming information at the expense of maintaining the encoding of temporal associations (Heusser et al., 2018). If successful temporal binding is a strong predictor of long-term memory, it may be the case that diminishing the arousal of emotional event boundaries helps deconstruct and reduce the durability of traumatic episodes. The current findings open several exciting avenues for identifying cognitive and neural factors that facilitate the persistent and potentially debilitating effects of emotional memories in healthy individuals and in individuals with PTSD. This knowledge can in turn be leveraged to improve therapies that treat episodic memory dysfunction in various arousal-related disorders, including PTSD, perhaps by restoring links between individual emotional details and their original temporal context.

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## Data availability

All experiment/analysis code, data, and stimuli are available on the first author's OSF page: <https://osf.io/dspqv/>

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## References

- Ambrose, R. E., Pfeiffer, B. E., & Foster, D. J. (2016). Reverse replay of hippocampal place cells is uniquely modulated by changing reward. *Neuron*, *91*(5), 1124–1136.
- Anderson, A. K., Wais, P. E., & Gabrieli, J. D. E. (2006, January). Emotion enhances remembrance of neutral events past. *Proceedings of the National Academy of Sciences*, *103*(5), 1599–1604. <https://doi.org/10.1073/pnas.0506308103>
- Barnacle, G. E., Tsivilis, D., Schaefer, A., & Talmi, D. (2018, April). Local context influences memory for emotional stimuli but not electrophysiological markers of emotion-dependent attention. *Psychophysiology*, *55*(4). <https://doi.org/10.1111/psyp.13014>
- Ben-Yakov, A., & Dudai, Y. (2011). Constructing realistic engrams: Poststimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory. *Journal of Neuroscience*, *31*(24), 9032–9042.
- Ben-Yakov, A., Eshel, N., & Dudai, Y. (2013). Hippocampal immediate poststimulus activity in the encoding of consecutive naturalistic episodes. *Journal of Experimental Psychology: General*, *142*(4), 1255.
- Bisby, J. A., & Burgess, N. (2014). Negative affect impairs associative memory but not item memory. *Learning & Memory*, *21*(1), 21–27.
- Bisby, J. A., Horner, A. J., Bush, D., & Burgess, N. (2018, February). Negative emotional content disrupts the coherence of episodic memories. *Journal of Experimental Psychology: General*, *147*(2), 243–256. <https://doi.org/10.1037/xge0000356>
- Bocanegra, B. R., & Zeelenberg, R. (2009, December). Dissociating emotion-induced blindness and hypervision. *Emotion*, *9*(6), 865–873. <https://doi.org/10.1037/a0017749>
- Bouret, S., & Sara, S. J. (2005). Network reset: A simplified overarching theory of locus coeruleus noradrenaline function. *Trends in Neurosciences*, *28*(11), 574–582. <https://doi.org/10.1016/j.tins.2005.09.002>
- Bradley, B. P., Mogg, K., Millar, N., & Bonham-Carter, C. (1997). Attentional biases for emotional faces. *Cognition & Emotion*, *11*(1), 25–42.
- Bradley, M. M., & Lang, P. J. (2007). *The international affective digitized sounds (2nd edition; IADS-2): affective ratings of sounds and instruction manual*. University of Florida.
- Brunec, I. K., Moscovitch, M., & Barense, M. D. (2018). Boundaries shape cognitive representations of spaces and events. *Trends in Cognitive Sciences*.
- Brunec, I. K., Ozubko, J. D., Barense, M. D., & Moscovitch, M. (2017). Recollection-dependent memory for event duration in large-scale spatial navigation. *Learning & Memory*, *24*(3), 104–114.
- Cahill, L., & McGaugh, J. L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*, *21*(7), 294–299.
- Clewett, D., & Davachi, L. (2017). The Ebb and flow of experience determines the temporal structure of memory. *Current Opinion in Behavioral Sciences*, *17*, 186–193.
- Clewett, D., DuBrow, S., & Davachi, L. (2019). Transcending time in the brain: How event memories are constructed from experience. *Hippocampus*, *29*(3), 162–183.
- Clewett, D., Gasser, C., & Davachi, L. (2020, August 11). Pupil-linked arousal signals track the temporal organization of events in memory. *Nature Communications*, *11*(1), 4007. <https://doi.org/10.1038/s41467-020-17851-9>
- Clewett, D., & Murty, V. P. (2019, March–April). Echoes of emotions past: How neuromodulators determine what we recollect. *eNeuro*, *6*(2). <https://doi.org/10.1523/ENEURO.0108-18.2019>
- Clewett, D., Sakaki, M., Nielsen, S., Petzinger, G., & Mather, M. (2017). Noradrenergic mechanisms of arousal's bidirectional effects on episodic memory. *Neurobiology of Learning and Memory*, *137*, 1–14.
- Cliver, K. G., Gregory, D. F., Martinez, S. A., Mitchell, W. J., Stasiak, J., Reisman, S., Helion, C., & Murty, V. P. (2023). Temporal memory for threatening events encoded in a haunted house. <https://osf.io/preprints/psyarxiv/pdcsq/>.
- D'Argembeau, A., & Van der Linden, M. (2005, December). Influence of emotion on memory for temporal information. *Emotion*, *5*(4), 503–507.
- Dev, D. K., Wardell, V., Checknita, K. J., Te, A. A., Petrucci, A. S., Le, M. L., Madan, C. R., & Palombo, D. J. (2022). Negative emotion enhances memory for the sequential unfolding of a naturalistic experience. *Journal of Applied Research in Memory and Cognition*, *11*(4), 510–521. <https://doi.org/10.1037/mac0000015>
- Dolan, R. J. (2002). Emotion, cognition, and behavior. *Science*, *298*(8), 1191–1194.
- Droit-Volet, S., & Gil, S. (2009). The time–emotion paradox. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *364*(1525), 1943–1953.
- DuBrow, S., & Davachi, L. (2013). The influence of context boundaries on memory for the sequential order of events. *Journal of Experimental Psychology: General*, *142*(4), 1277.
- DuBrow, S., & Davachi, L. (2014). Temporal memory is shaped by encoding stability and intervening item reactivation. *Journal of Neuroscience*, *34*(42), 13998–14005.
- DuBrow, S., & Davachi, L. (2017). Commentary: Distinct neural mechanisms for remembering when an event occurred. *Frontiers in Psychology*, *8*.

- Dunsmoor, J. E., Kroes, M. C. W., Moscatelli, C. M., Evans, M. D., Davachi, L., & Phelps, E. A. (2018, April). Event segmentation protects emotional memories from competing experiences encoded close in time. *Nature Human Behaviour*, 2(4), 291–299. <https://doi.org/10.1038/s41562-018-0317-4>
- Ehlers, A. (2006, June). More evidence for the role of persistent dissociation in PTSD. *American Journal of Psychiatry*, 163(6), 1112. <https://doi.org/10.1176/ajp.2006.163.6.1112>
- Ehlers, A., & Clark, D. M. (2000, April). A cognitive model of posttraumatic stress disorder. *Behaviour Research and Therapy*, 38(4), 319–345. [https://doi.org/10.1016/S0005-7967\(99\)00123-0](https://doi.org/10.1016/S0005-7967(99)00123-0)
- Ehlers, A., Hackmann, A., Steil, R., Clohessy, S., Wenninger, K., & Winter, H. (2002, September). The nature of intrusive memories after trauma: The warning signal hypothesis. *Behaviour Research and Therapy*, 40(9), 995–1002. [https://doi.org/10.1016/S0005-7967\(01\)00077-8](https://doi.org/10.1016/S0005-7967(01)00077-8)
- Ezzyat, Y., & Davachi, L. (2014). Similarity breeds proximity: Pattern similarity within and across contexts is related to later mnemonic judgments of temporal proximity. *Neuron*, 81(5), 1179–1189.
- Faber, M., & Gennari, S. P. (2015). In search of lost time: Reconstructing the unfolding of events from memory. *Cognition*, 143, 193–202.
- Flores, S., Bailey, H., Eisenberg, M., & Zacks, J. (2017). Event segmentation improves event memory up to one month later. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 43(8), 1183.
- Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., Bolker, B., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., Heiberger, R., Krivitsky, P., Laboissiere, R., Maechler, M., Monette, G., Murdoch, D., Nilsson, H., ... Zeileis, A. (2012). *Package 'car'*. Vienna: R Foundation for Statistical Computing, 16.
- Fredrickson, B. L., & Branigan, C. (2005). Positive emotions broaden the scope of attention and thought-action repertoires. *Cognition & Emotion*, 19(3), 313–332. <https://doi.org/10.1080/02699930441000238>
- Gable, P. A., & Harmon-Jones, E. (2008, May). Approach-motivated positive affect reduces breadth of attention. *Psychological Science*, 19(5), 476–482.
- Gable, P. A., & Harmon-Jones, E. (2010, February). The blues broaden, but the nasty narrows: Attentional consequences of negative affects low and high in motivational intensity. *Psychological Science*, 21(2), 211–215. <https://doi.org/10.1177/0956797609359622>
- Gabrieli, J. D. E., Brewer, J. B., Desmond, J. E., & Glover, G. H. (1997). Separate neural bases of two fundamental memory processes in the human medial temporal lobe. *Science*, 276, 264–266.
- Gold, D. A., Zacks, J. M., & Flores, S. (2017). Effects of cues to event segmentation on subsequent memory. *Cognitive Research: Principles and Implications*, 2(1), 1.
- Hackmann, A., Ehlers, A., Speckens, A., & Clark, D. M. (2004, June). Characteristics and content of intrusive memories in PTSD and their changes with treatment. *Journal of Traumatic Stress*, 17(3), 231–240. <https://doi.org/10.1023/B:JOTS.0000029266.88369.fd>
- Harley, C. W. (2007). Norepinephrine and the dentate gyrus. *Dentate Gyrus: A Comprehensive Guide to Structure, Function, and Clinical Implications*, 163, 299–318. [https://doi.org/10.1016/S0079-6123\(07\)63018-0](https://doi.org/10.1016/S0079-6123(07)63018-0)
- Harmon-Jones, E., Gable, P. A., & Price, T. F. (2012). The influence of affective states varying in motivational intensity on cognitive scope. *Frontiers in Integrative Neuroscience*, 6, 73.
- Hartig, F. (2022). *\_DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models\_*. R package version 0.4.6. <https://CRAN.R-project.org/package=DHARMA>.
- Hennings, A. C., Lewis-Peacock, J. A., & Dunsmoor, J. E. (2021). Emotional learning retroactively enhances item memory but distorts source attribution. *Learning & Memory*, 28(6), 178.
- Heusser, A. C., Ezzyat, Y., Shiff, I., & Davachi, L. (2018). Perceptual boundaries cause mnemonic trade-offs between local boundary processing and across-trial associative binding. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 44(7), 1075.
- Horner, A. J., Bisby, J. A., Wang, A., Bogus, K., & Burgess, N. (2016). The role of spatial boundaries in shaping long-term event representations. *Cognition*, 154, 151–164.
- Huntjens, R. J., Wessel, I., Postma, A., van Wees-Cieraad, R., & de Jong, P. J. (2015, July). Binding temporal context in memory: Impact of emotional arousal as a function of state anxiety and state dissociation. *Journal of Nervous & Mental Disease*, 203(7), 545–550. <https://doi.org/10.1097/NMD.0000000000000325>
- Hurlemann, R., Hawellek, B., Matusch, A., Kolsch, H., Wollersen, H., Madea, B., Vogeley, K., Maier, W., & Dolan, R. J. (2005, July 6). Noradrenergic modulation of emotion-induced forgetting and remembering. *The Journal of Neuroscience*, 25(27), 6343–6349. <https://doi.org/10.1523/JNEUROSCI.0228-05.2005>
- Johnson, L. W., & MacKay, D. G. (2019, March). Relations between emotion, memory encoding, and time perception. *Cognition and Emotion*, 33(2), 185–196. <https://doi.org/10.1080/02699931.2018.1435506>
- Kahneman, D., & Beatty, J. (1966). Pupil diameter and load on memory. *Science*, 154(3756), 1583–1585.
- Kensinger, E. A. (2004). Remembering emotional experiences: The contribution of valence and arousal. *Reviews in the Neurosciences*, 15(4), 241–251. Go to ISI>://000224545900002.
- Kensinger, E. A. (2009). Remembering the details: Effects of emotion. *Emotion Review*, 1, 99–113. <https://doi.org/10.1177/1754073908100432>
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2006, January). Memory for specific visual details can be enhanced by negative arousing content. *Journal of Memory and Language*, 54(1), 99–112. <https://doi.org/10.1016/j.jml.2005.05.005>
- Kensinger, E. A., Garoff-Eaton, R. J., & Schacter, D. L. (2007, November). How negative emotion enhances the visual specificity of a memory. *Journal of Cognitive Neuroscience*, 19(11), 1872–1887. Go to ISI>://000250669900012.
- Knight, M., & Mather, M. (2009, December). Reconciling findings of emotion-induced memory enhancement and impairment of preceding items. *Emotion*, 9(6), 763–781. <https://doi.org/10.1037/a0017281>
- LaBar, K. S., & Cabeza, R. (2006, January). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, 7(1), 54–64. <https://doi.org/10.1038/nrn1825>
- Lake, J. I., LaBar, K. S., & Meck, W. H. (2016). Emotional modulation of interval timing and time perception. *Neuroscience & Biobehavioral Reviews*, 64, 403–420.



- Lee, H., & Chen, J. (2022). Predicting memory from the network structure of naturalistic events. *Nature Communications*, 13(1), 4235.
- Liverence, B. M., & Scholl, B. J. (2012, June). Discrete events as units of perceived time. *Journal of Experimental Psychology: Human Perception and Performance*, 38(3), 549–554. <https://doi.org/10.1037/a0027228>
- Long, N. M., Danoff, M. S., & Kahana, M. J. (2015, October). Recall dynamics reveal the retrieval of emotional context. *Psychonomic Bulletin & Review*, 22(5), 1328–1333. <https://doi.org/10.3758/s13423-014-0791-2>
- Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60), 3139. <https://doi.org/10.21105/joss.03139>
- Madan, C. R., Scott, S. M. E., & Kensinger, E. A. (2019, June). Positive emotion enhances association-memory. *Emotion*, 19(4), 733–740. <https://doi.org/10.1037/emo0000465>
- Maddock, R. J., & Frein, S. T. (2009). Reduced memory for the spatial and temporal context of unpleasant words. *Cognition and Emotion*, 23(1), 96–117.
- Maran, T., Sachse, P., Martini, M., Weber, B., Pinggera, J., Zugal, S., & Furtner, M. (2017). Lost in time and space: States of high arousal disrupt implicit acquisition of spatial and sequential context information. *Frontiers in Behavioral Neuroscience*, 11, 206.
- Markovic, J., Anderson, A. K., & Todd, R. M. (2014). Tuning to the significant: Neural and genetic processes underlying affective enhancement of visual perception and memory. *Behavioural Brain Research*, 259, 229–241. <http://www.sciencedirect.com/science/article/pii/S0166432813006955>.
- Mather, M. (2007, March). Emotional arousal and memory binding: An object-based framework. *Perspectives on Psychological Science*, 2(1), 33–52. <https://doi.org/10.1111/j.1745-6916.2007.00028.x>
- Mather, M., Clewett, D., Sakaki, M., & Harley, C. W. (2015). Norepinephrine ignites local hot spots of neuronal excitation: How arousal amplifies selectivity in perception and memory. *Behavioral and Brain Sciences*, 1–100.
- Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspectives on Psychological Science*, 6, 114–133. <http://pps.sagepub.com/content/6/2/114.short>
- McClay, M., Sachs, M. E., & Clewett, D. (2023). Dynamic emotional states shape the episodic structure of memory. *Nature Communications*, 14(1), 6533.
- McGatlin, K. C., Newberry, K. M., & Bailey, H. R. (2019, January). Temporal chunking makes life's events more memorable. *Open Psychology*, 1(1), 94–105. <https://doi.org/10.1515/psych-2018-0007>
- McGaugh, J. L. (2013). Making lasting memories: Remembering the significant. *Proceedings of the National Academy of Sciences*, 110(Supplement 2), 10402–10407. [http://www.pnas.org.idpproxy.reading.ac.uk/content/110/Supplement\\_2/10402.abstract](http://www.pnas.org.idpproxy.reading.ac.uk/content/110/Supplement_2/10402.abstract)
- Palombo, D. J., & Cocquyt, C. (2020, September). Emotion in context: Remembering when. *Trends in Cognitive Sciences*, 24(9), 687–690. <https://doi.org/10.1016/j.tics.2020.05.017>
- Palombo, D. J., Te, A. A., Checknita, K. J., & Madan, C. R. (2021, July). Exploring the facets of emotional episodic memory: Remembering “what,” “when,” and “which”. *Psychological Science*, 32(7), 1104–1114. <https://doi.org/10.1177/0956797621991548>
- Petrucci, A. S., & Palombo, D. J. (2021). A matter of time: How does emotion influence temporal aspects of remembering? *Cognition and Emotion*, 35(8), 1499–1515.
- Pierce, B. H., & Kensinger, E. A. (2011, February). Effects of emotion on associative recognition: Valence and retention interval matter. *Emotion*, 11(1), 139–144. <https://doi.org/10.1037/a0021287>
- Preuschoff, K., 't Hart, B. M., & Einhäuser, W. (2011). Pupil dilation signals surprise: Evidence for noradrenaline's role in decision making. *Frontiers in Neuroscience*, 5, 115.
- Raisig, S., Welke, T., Hagendorf, H., & van der Meer, E. (2010, April). I spy with my little eye: Detection of temporal violations in event sequences and the pupillary response. *International Journal of Psychophysiology*, 76(1), 1–8. <https://doi.org/10.1016/j.ijpsycho.2010.01.006>
- Ranganath, C., & Hsieh, L. T. (2016). The hippocampus: A special place for time. *Annals of the New York Academy of Sciences*, 1369(1), 93–110.
- Regen, F., Dorn, H., & Danker-Hopfe, H. (2013). Association between pupillary unrest index and waking electroencephalogram activity in sleep-deprived healthy adults. *Sleep Medicine*, 14(9), 902–912.
- Rimmele, U., Davachi, L., & Phelps, E. A. (2012, August). Memory for time and place contributes to enhanced confidence in memories for emotional events. *Emotion*, 12(4), 834–846. <https://doi.org/10.1037/a0028003>
- Rouhani, N., Norman, K. A., Niv, Y., & Bornstein, A. M. (2019). Reward prediction errors create event boundaries in memory. *bioRxiv*, 725440.
- Sakaki, M., Fryer, K., & Mather, M. (2014). Emotion strengthens high priority memory traces but weakens low priority memory traces. *Psychological Science*, 25(387-395). <http://pss.sagepub.com/content/25/2/387.abstract>
- Sara, S. J. (2009). The locus coeruleus and noradrenergic modulation of cognition. *Nature Reviews Neuroscience*, 10(3), 211–223. <https://doi.org/10.1038/nrn2573>
- Schluter, H., Hacklander, R. P., & Bermeitinger, C. (2019, October). Emotional oddball: A review on memory effects. *Psychonomic Bulletin & Review*, 26(5), 1472–1502. <https://doi.org/10.3758/s13423-019-01658-x>
- Schmidt, K., Patnaik, P., & Kensinger, E. A. (2011). Emotion's influence on memory for spatial and temporal context. *Cognition and Emotion*, 25(2), 229–243.
- Schmidt, S. R., & Schmidt, C. R. (2016, August). The emotional carryover effect in memory for words. *Memory (Hove, England)*, 24(7), 916–938. <https://doi.org/10.1080/09658211.2015.1059859>
- Sherrill, A. M., Kurby, C. A., Lilly, M. M., & Magliano, J. P. (2019, February). The effects of state anxiety on analogue peritraumatic encoding and event memory: Introducing the stressful event segmentation paradigm. *Memory (Hove, England)*, 27(2), 124–136. <https://doi.org/10.1080/09658211.2018.1492619>
- Siefke, B. M., Smith, T. A., & Sederberg, P. B. (2019). A context-change account of temporal distinctiveness. *Memory & Cognition*, 1–15.



- Sols, I., DuBrow, S., Davachi, L., & Fuentemilla, L. (2017). Event boundaries trigger rapid memory reinstatement of the prior events to promote their representation in long-term memory. *Current Biology*, 27(22), 3499–3504.
- Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, 99, 195–231.
- Strange, B. A., Hurlmann, R., & Dolan, R. J. (2003, November). An emotion-induced retrograde amnesia in humans is amygdala- and beta-adrenergic-dependent. *Proceedings of the National Academy of Sciences*, 100(23), 13626–13631. <https://doi.org/10.1073/pnas.1635116100>
- Swallow, K. M., Zacks, J. M., & Abrams, R. A. (2009). Event boundaries in perception affect memory encoding and updating. *Journal of Experimental Psychology: General*, 138(2), 236.
- Talmi, D., Lohnas, L. J., & Daw, N. D. (2019, July). A retrieved context model of the emotional modulation of memory. *Psychological Review*, 126(4), 455–485. <https://doi.org/10.1037/rev0000132>
- van de Ven, V., Jäckels, M., & De Weerd, P. (2021). Time changes: Timing contexts support event segmentation in associative memory. *Psychonomic Bulletin & Review*, 1–13.
- van der Kolk, B. A., & Fislser, R. (1995, October). Dissociation and the fragmentary nature of traumatic memories: Overview and exploratory study. *Journal of Traumatic Stress*, 8(4), 505–525. <https://doi.org/10.1007/BF02102887>
- Wang, J., Tambini, A., & Lapate, R. C. (2022). The tie that binds: Temporal coding and adaptive emotion. *Trends in Cognitive Sciences*.
- Wen, T., & Egner, T. (2022). Retrieval context determines whether event boundaries impair or enhance temporal order memory. *Cognition*, 225, 105145.
- Wilhelm, B. J. (2008). Pupilligraphy for the assessment of driver sleepiness. *Klinische Monatsblätter für Augenheilkunde*, 225(9), 791–798.
- Williams, S. E., Ford, J. H., & Kensinger, E. A. (2022). The power of negative and positive episodic memories. *Cognitive, Affective, & Behavioral Neuroscience*, 22(5), 869–903.
- Zacks, J. M., Speer, N. K., Swallow, K. M., Braver, T. S., & Reynolds, J. R. (2007). Event perception: A mind- brain perspective. *Psychological Bulletin*, 133(2), 273.
- Zlomuzica, A., Preusser, F., Totzeck, C., Dere, E., & Margraf, J. (2016). The impact of different emotional states on the memory for what, where and when features of specific events. *Behavioural Brain Research*, 298, 181–187.