

Emotional salience modulates the forward-flow of memory

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As we navigate our day to day lives, we regularly adapt our behaviour according to what we predict may happen next in a given context. When an unexpected event occurs our predictions about the world are disrupted and must be updated. Unexpected, isolated events, particularly with high emotionality, are also better recalled. In the present work, we investigated how oddballs affect recall dynamics. Seventy young, healthy participants encoded word lists containing either emotional or perceptual oddballs at varying stimulus onset asynchronies followed by free recall. It is well established that after recalling an item, we have a higher probability of recalling items encoded nearby, particularly those that were encoded after the item recalled, a phenomenon known as forward contiguity of recall. The present results provide empirical evidence of forward contiguity modulation selectively by emotional salience and suggest that recall patterns after presenting emotional and perceptual oddballs are mediated by different mechanisms.

Keywords: salience, recall, emotion, episodic memory

Introduction

As we navigate our day to day lives, we continuously adapt behavior to what we believe will happen next in a specific context (Kurby & Zacks, 2008). However, what if something unexpected and emotional, like witnessing a robbery, occurs? These isolated events tend to be better recalled than neutral ones in a continuous stream and are also known to affect memory for nearby events. Research has focused on understanding how these emotional unexpected events affect memory. However, less is known about how emotion may constitute shifts in context, affecting nearby events.

Salient, oddball stimuli that deviate from the prevailing context typically show a mnemonic enhancement (Hunt, 1995) which has been reported across item modalities (Frank & Kafkas, 2021), and at different deviance attributes (Strange, Henson, Friston, & Dolan, 2000). In the case of emotionally salient items, the mnemonic enhancement can be accompanied by an anterograde (Angelini, Capozzoli, Lepore, Grossi, & Orsini, 1994) and/or retrograde (Strange, Hurlmann, & Dolan, 2003) amnesic effect for neutral stimuli presented immediately after (Hurlmann et al., 2005; Sakaki, Fryer, & Mather, 2014) or before the emotional oddball. However, there have been mixed-findings regarding these properties (Schmidt & Schmidt, 2016) as they are modulated by task (Anderson, Wais, & Gabrieli, 2006), stimulus onset asynchrony (SOA) (Schmidt & Schmidt, 2018), retention intervals and arousal characteristics of the items (Mather & Sutherland, 2011; Schmidt & Schmidt, 2016), as well as priority of the to-be-encoded stimuli (Mather & Sutherland, 2011). Furthermore, peri-oddball effects have been proposed to occur as an encoding disruption of the item preceding the emotional stimulus at the synaptic and/or systems level (Strange et al., 2003; Strange & Galarza-Vallejo, 2016). Others, however, have proposed that retrograde amnesic effects in free recall could be due to item inaccessibility at retrieval, which can disappear by cueing recall (Detterman, 1976). This recall failure for items presented before the oddball at encoding could arise due to the likely recall of the oddball and subsequent recall transitions occurring in the forward direction (i.e., of items presented after the oddball at encoding).

In a real-world environment, as we experience continuous events on a long timescale, we tend to segment them into shorter occurrences. The point where an event changes, known as an event boundary, which could arise due to the presentation of an oddball, is used to update our predictions of the world and to what may occur next. These boundaries are also better remembered than middle events, as attention is drawn to the boundaries (Radvansky & Zacks, 2017). Thus, unexpected emotional events may disrupt the way we segment our

continuous daily activity. Likewise, people are less likely to recognize items they had seen before an event boundary occurrence (Radvansky & Zacks, 2017; Swallow et al., 2011) and have worse temporal-order memory across episodes than within episodes (Sols, DuBrow, Davachi, & Fuentemilla, 2017). In the present study, we investigated how the presentation of unexpected emotional and perceptual oddballs affect recall dynamics, which is, therefore, potentially relevant to mnemonic effects of event boundaries.

Free recall dynamics, and, particularly, inter-item organization, can be studied using the quantitative method of conditional response probability (CRP) (Kahana, 1996). CRP quantifies, under the condition that item x is immediately followed by item y during encoding, the probability of recalling item y if x is recalled (Kahana, 1996). CRP in free recall is characterized by the generalizable findings that 1) recall transitions are more likely to be amongst items contiguous at encoding and 2) to occur in the forward direction (Kahana, 1996), which could be due to the strengthening of inter-item associations and their shared context. At retrieval, a recalled item serves as a contextual cue for the recall of related items (Howard & Kahana, 1999). These findings have served to develop computational models of memory (Polyn, Norman, & Kahana, 2009) in which temporal context (items encoded nearby) and source context (source item's encoding features and characteristics resulting, for example, from encoding operations performed during a given task) influence item encoding and recall dynamics. More recent computational models have included an emotionality factor (Talmi, Lohnas, & Daw, 2019) and developed computational models to better model memory effects in emotional disorders (Cohen & Kahana, 2022).

A strong contextual change produced, for example, by the presentation of an unexpected, oddball stimulus, is predicted to evoke a contextual item association shift from the oddball's appearance onwards, and, therefore, for upcoming items to be encoded in an updated or modulated context. Brain correlates of this context-updating are considered to be reflected by the P300 event-related potential component in electroencephalography (EEG) studies; if a new, or unexpected, stimulus is detected in a stream of stimuli it evokes a P300 potential (Polich, 2007).

In the present study, we tested the hypothesis that recall of emotional (aversive in content) and perceptual (presented in a different font) oddballs prompts an update in source context, thereby promoting a contextual update and, thus, a stronger contextual binding with the updated context for items encoded after the oddballs. We predicted this would result in increased forward-contiguity for items encoded after oddballs. Lastly, we hypothesized that oddballs would be recalled early on and that transitions from emotional oddballs would be

enhanced which would correlate with an oddball-induced retrograde amnesic effect. However, we acknowledge that some studies have reported a weaker memory for items presented after emotional oddballs (Hurlemann et al., 2005; Sakaki et al., 2014), but this has not been observed in the task employed here (Strange et al., 2003; Strange, Kroes, Roiser, Tan, & Dolan, 2008). Strange et al. (2003) showed that oddballs elicited a retrograde amnesic effect that spanned for 2 items preceding oddballs. Therefore, next, we aimed at investigating whether the induced retrograde amnesia spanned to 2 items or 6 seconds (as items in the original paradigm were presented every 3 seconds) by varying SOAs between stimuli.

Methods

Subjects

70 healthy right-handed native Spanish-speaking subjects took part in this study [35 male, 35 female (age range, 18–32 yr; mean age, 22.5)]. All subjects gave informed consent and did not have neurological or psychiatric history.

Task

Lists from Strange et al. (2003) were translated to Spanish (Table S6, S7). Subjects were presented 40 lists of 14 nouns with the words “New List” presented between lists. To control semantic effects, 13 of the nouns were of the same semantic category (*e.g.* animals, occupations), emotionally neutral, and were presented in the same font (referred to as standard nouns). To set the context, the first five nouns in each list were always standard nouns (*i.e.* not oddballs). 20 lists contained an emotional oddball, aversive in content, but of the same semantic category and perceptually identical to control nouns. Control nouns were pre-selected items within each list to be later used as a recall reference of a given list *i.e.* to calculate recall of the oddballs with respect to a pre-selected non-oddball item. The remaining 20 lists contained a perceptual oddball. Oddballs were randomly allocated to the 7, 8, 9, 11 or 12th serial position, to maximise list position distance between oddballs and control nouns, permitting at least two serial positions following an oddball (if presented at serial position 12). All nouns were presented in Times font, except for perceptual oddballs, which were presented in 20 different fonts. The order of oddball list type was random. Nouns were presented visually in lowercase for 800ms. Subjects made push-button responses to indicate whether the first letter in each noun contained an enclosed space (shallow encoding task). The rate of stimulus presentation was randomly varied at a SOA of 1, 2, 3, 4 or 6s. This

selection was conducted to investigate how the presentation rate of items affected peri-oddball amnesic effects. In Tulving's (1969) original paradigm, retrograde amnesic effects were reported for words presented at a rate of 1 but not 2s and Anderson, Wais, & Gabrieli (2006) reported memory enhancement for items preceding emotionally arousing images at a presentation rate of 4s. Lastly, to determine whether the retrograde amnesic effect reported by Strange et al. (2003) spanned to 2 items or 6 s, and whether SOA influenced oddball effects on CRP, SOAs of 3 and 4s were included in the experimental design. Thus, for each of the 20 lists for each oddball type, 4 of these lists were presented at a given SOA. Subjects were informed of the presentation rate in each forthcoming list, by presenting the SOA under the “New List” marker (Fig.1a). Control nouns, like the oddballs, could not occur within the first five nouns of each list and were at least 3 serial positions apart from oddball nouns to control for peri-oddball effects.

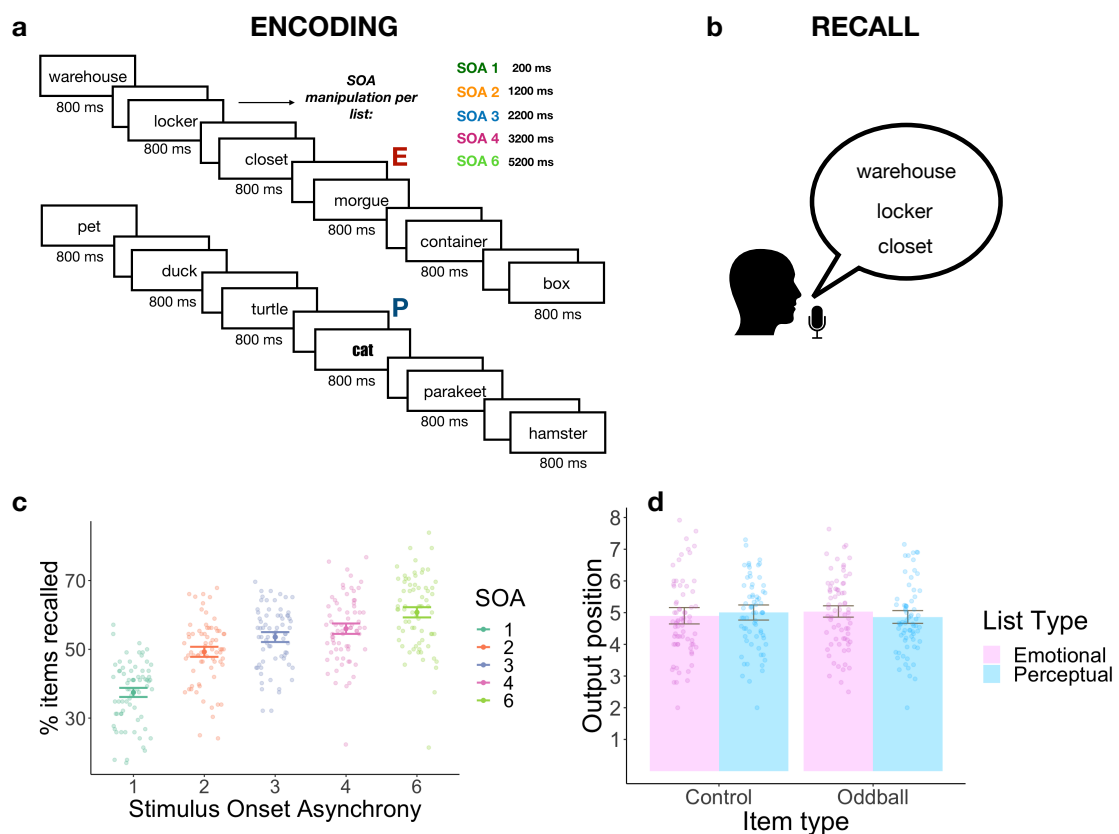


Figure 1. Memory task and total recall performance for list types. (a) Example of items used in the task where E and P are the Emotional and Perceptual oddballs. Each word was presented for 800ms followed by a blank screen where presentation timings varied depending on the SOA, which was kept constant within a list. (b) Example of forward-

contiguity in recall where items nearby each other are more likely to be recalled and more so in the forwards direction. (c) The number of items recalled increased as SOA augmented. Percent of items recalled per list is plotted for each SOA, bars show subjects mean \pm 95% confidence intervals. Jittered points show single subject mean recall. (d) Output position of both oddballs for each SOA and controls, matched by input position. Bars show subjects mean \pm 95% confidence intervals. Jittered points show single subject mean output position.

The presentation of each list was followed immediately by a 30s distractor task, during which subjects were instructed to count backwards in steps of 3 (out loud) from a number presented on the screen followed by instructions to recall the words presented in the preceding list.

Statistical analyses

Analyses were conducted using MATLAB (R2019b, The MathWorks, Inc). Statistical analyses and figures were conducted in Rstudio (version 1.3.1093) and JASP (Jasp Team, 2021). Post-hoc t-tests were FDR-corrected and effect sizes were calculated with partial eta squared (η_p^2) or Cohen's d.

CRP analyses were conducted using original and modified versions of the Behavioral Toolbox for MATLAB R2019b (http://memory.psych.upenn.edu/Behavioral_toolbox). *Lag* refers to the word-distance to an item at encoding; all analyses and visualization were performed on lags \pm 5 as previously reported (Kahana, 1996). *Backwards vs. forwards* refer to words presented before or after a specific item at encoding, analogous to negative and positive lags, respectively.

Results

Recall performance improved with increasing SOA (Fig. 1c). There was an oddball recall enhancement compared to selected control items (Fig.S1a). However, the current, Spanish version of this task did not elicit an emotion-induced retrograde amnesic effect as previously reported which was confirmed by strong evidence for a null effect of peri-oddball amnesic effects using Bayesian statistics (See Supplementary Results and Fig.S1b). Due to the lack of retrograde amnesic effects, we conducted further ratings tasks, which confirmed

emotional negative valence but also showed a decrease in semantic relatedness in emotional lists compared to perceptual ones (Table S6, S7).

CRPs showed an enhanced forward contiguity effect after recalling emotional oddballs

To comprehensively evaluate recall properties, we first evaluated oddball recall position, hypothesizing that oddballs would be recalled early in the serial recall order. A repeated measures (RM) ANOVA with salience [control, oddball] and list type [emotional, perceptual] as factors showed that this was not, however, the case (Fig. 1d). Neither emotional nor perceptual oddballs were recalled early compared to input-matched control items (Fig. 1d, no significant main effect (m.e.) of list type [emotional, perceptual] $F(1,68) = 0.006$, $p=0.94$, $\eta_p^2 = 0.00$, m.e. of item recall position [control, oddball] $F(1,68)=0.78$, $p=0.78$, $\eta_p^2 = 0.00$, nor a significant interaction $F(1,68) = 2.07$, $p=0.155$ $\eta_p^2 = 0.00$).

Next, we tested whether the presentation of an oddball would provoke a shift in the encoding context which would lead to items encoded after the oddballs to be studied in an updated context and to be more strongly bound to the oddballs. To do so we investigated, with CRP curves, whether the presence of an oddball affects forward recall transitions: hypothesizing that there would be an enhancement in transitions, particularly from emotional oddballs, which would, in turn, explain a potential retrograde amnesic effect. Indeed, the present results showed an enhancement in forward transitions from emotional oddballs (Fig. 2d, e).

Forward transitions, with list type [emotional, perceptual] and salience [oddball, controls] showed a significant oddball list type x salience interaction ($F(1,69)=12.21$, $p<0.001$, $\eta_p^2 = 0.15$). Transitions from emotional oddballs were enhanced compared to transitions from pre-selected control items in emotional lists (Fig. 2d,e, $t(69) = -3.23$, $p<0.005$, *Cohen's d* = -0.386) whilst transitions from perceptual oddballs did not differ from pre-selected control items in perceptual lists ($t(69) = 1.73$, $p=0.09$, *Cohen's d* = 0.206). There was no significant m.e. of list type [emotional, perceptual] ($F(1,69)=2.675$, $p=0.11$, $\eta_p^2 = 0.037$) or salience [oddball, control] ($F(1,69)=1.36$, $p=0.25$, $\eta_p^2 = 0.019$). For completion, we tested that this enhancement was not present in backwards transitions. A 2-way RM-ANOVA, in backwards transitions, between oddball list type [emotional, perceptual] and salience [oddball, control noun] showed a significant m.e. of oddball list type ($F(1,69) = 3.992$,

$p=0.050$, $\eta_p^2 = 0.055$) and salience ($F(1,69) = 4.65$, $p=0.035$, $\eta_p^2 = 0.06$) but no significant oddball list type x salience interaction ($F(1,69)=0.98$, $p=0.33$, $\eta_p^2 = 0.014$).

These results indicate that CRP values in backwards transitions (negative lags) were higher for emotional than perceptual lists as well as higher for transitions from oddball items compared to transitions from controls in the same lists. However, forward transitions (positive lags) showed an enhancement in CRP values from emotional oddballs relative to control items and perceptual oddballs. Although we did not observe a retrograde amnesic effect in the present task (Fig.S1b), for completeness, we evaluated whether lag +1 CRP values from emotional oddballs correlated with recall of items preceding emotional oddballs and we did not find this to be the case (Fig.S3). Lastly, across all stimuli in both types of lists, recall transitions preserved forward-contiguity overall (Fig.2b) and across SOAs (Fig. S2) as typically reported in free recall tasks.

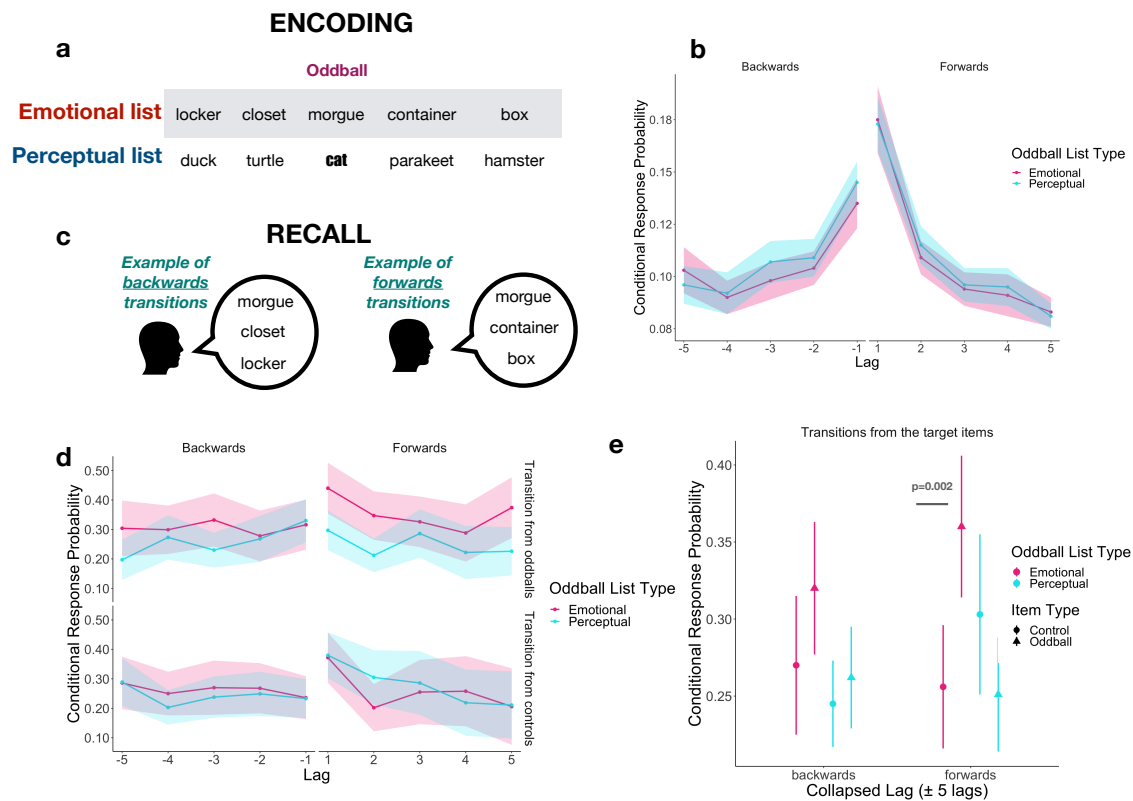


Figure 2. Transitions from emotional oddballs are enhanced compared to controls. (a) Example of encoding emotional and perceptual lists. (b) Preserved forward contiguity across both list types. (c) Example of *backwards* transitions where the oddball would be recalled and followed by the recall of items preceding it at encoding and *forward* transitions whereby the oddball would be recalled and followed by items encoded after the oddball. (d) CRP curves showing enhanced forward transitions from emotional oddballs

compared to pre-selected control items (mean \pm confidence intervals). (e) CRP values (mean \pm 5 lags) showing increased CRP in forward transitions from emotional oddballs compared to control items.

Discussion

We used a word oddball paradigm containing emotional and perceptual oddballs to investigate recall organization after unexpected events. Overall, both emotional and perceptual oddballs were better recalled than all other items. Previous research using similar paradigms had reported peri-oddball amnesic effects often resulting in anterograde and/or retrograde amnesia for items presented after/before the oddballs (Schmidt & Schmidt, 2016). However, such effects were not observed in the current version of the paradigm.

We calculated CRP curves on recalled items from an oddball paradigm that employed word lists containing either an emotional or perceptual oddball. Considering all words presented at encoding, forward-contiguity, a key property of free recall (Kahana, 1996), was preserved. We further looked at transitions to and from the oddballs to evaluate whether these core properties remained present. Interestingly, while we found that contiguity was maintained for both oddball types and transitions to and from oddballs, there were enhanced CRP forward transitions from emotional oddballs – relative to control nouns– which were not present in transitions from perceptual oddballs. These effects could represent an underlying stronger binding of temporal order between emotional items and succeeding items due to a contextual update.

We did not find support for the hypothesis that oddballs are recalled earlier than matched input position control items (Talmi et al., 2019) (Fig.1d). We speculate that this may be due to different recall strategies: whilst some participants may start recalling the items presented first in the list and move forwards in recall, others may adopt a strategy of recalling the oddball first. Our current empirical findings suggest that emotional and perceptual oddballs modulate memory-related CRP differently, and these differences could inform future development of computational models of memory. The neurobiological processes underlying emotional and perceptual salience have also been dissociated in studies with pharmacological manipulations; while recall in the former was modulated by the adrenergic system and focal amygdala lesions, the latter was not (Strange et al., 2003). The present task in combination with pharmacological manipulations of the beta-adrenergic system could

provide insight into the biological mechanisms behind the CRP lag contiguity property of memory recall and its modulation by emotional salience.

Previous studies using oddball paradigms found a mnemonic enhancement for oddballs accompanied by a retrograde amnesic effect (Hurlemann et al., 2005, 2007; Schmidt & Schmidt, 2016; Strange et al., 2003). Given that we found a forward-flow enhancement in transitions from emotional oddballs, we hypothesized that it would serve as an anchor to move forwards in recall and thus, explain the retrograde amnesic effect. However, we did not find such significant correlation, most likely because retrograde amnesia in the present task was not reliable across subjects. A potential explanation for this could be that the translated items used in the current paradigm did not elicit the same levels of arousal as items in previous experiments (Sutherland & Mather, 2018) or, that in this paradigm, the peri-oddball amnesic effects were modulated by the inclusion of a distractor task as previously shown (Detterman, 1975; Schmidt & Schmidt, 2016; Strange, Hurlemann, & Dolan, 2003). In the present task we found that emotional lists had decreased semantic relatedness compared to perceptual lists, however, if decreased semantic associations within emotional lists was strongly influencing the present results, we would have expected to see diminished CRP curves in emotional lists. This, however, was not the case as we observed an enhancement CRP values from emotional oddballs. In the present study, we applied CRP curve analysis on a free recall paradigm to investigate emotional and perceptual salience. Oddballs were not retrieved earlier than control words. We found an enhancement in recall transitions from emotional oddballs which was not present in transitions from perceptual oddballs. These results show a dissociation in emotional and perceptual salience at recall and provide empirical evidence that could be used to update computational models of emotional memory and the von Restorff effect.

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Declarations of interest

Authors have no conflicts of interest to disclose.

Data availability and code

Raw data is available here: <https://osf.io/4rbeq/> as well as here (with analysis code): <https://github.com/albaperis/PerisYague2023>

CRedit contributions

	APY	DF	RH	BAS
Conceptualization	X	X	X	X
Data curation	X			X
Formal analysis	X			X
Funding acquisition				X
Investigation				X
Methodology	X	X	X	X
Project administration				X
Resources				X
Software	X			X
Supervision		X	X	X
Visualization	X			
Writing-original draft	X			
Writing- review & editing	X	X	X	X

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