Emotional salience modulates the forward flow of memory

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ABSTRACT

Conditional response probability (CRP) analyses applied to free recall data indicate that recall occurs for contiguous items with forward-directionality, thought to reflect the shared encoding context of nearby items. We hypothesized that a context disruption, produced by presenting infrequent oddballs, would modulate CRP curves, increasing the forward-flow of recall due to strong binding of items presented after these oddballs to the new encoding context. Seventy young, healthy male and female participants encoded word lists containing either emotional or perceptual oddballs at varying stimulus onset asynchronies (SOA) followed by free recall. Serial recall transitions from emotional, but not perceptual, oddballs were enhanced in the forward direction except at the shortest SOA (1s). The present results provide empirical evidence of CRP modulation selectively by emotional salience and suggest that recall patterns after presenting emotional and perceptual oddballs are mediated by different mechanisms.

STATEMENT OF RELEVANCE

When we remember, we usually recall events or items that we encoded close to each other in time. We also tend to move forwards in recall: if we remember one event, we are more likely to remember the subsequent events over the preceding ones. However, what would happen to our recall if we experienced something unexpected? In this study, we evaluated how this forward-contiguity property of recall is modulated by the presence of emotional and perceptual oddballs, that is, items that are unexpected because of their aversive emotional content or for being perceptually different. We found that after recalling emotional, but not perceptual oddballs, there was a stronger tendency to move forwards in recall, but only if the time separating items during encoding exceeded 1 second. These findings provide a better understanding of emotional memory and could inform future work into clinical manifestations of emotional memory retrieval, such as Post Traumatic Stress Disorder.

INTRODUCTION

Free recall dynamics, and in particular 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 *x* if *y* is recalled (Kahana, 1996). CRP in free recall data 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). These *lag contiguity* properties can be explained as a strengthening of inter-item associations and their shared context when they are present in short-term storage (Raaijmakers & Shiffrin, 1980). At recall, recollection of an item serves as a contextual cue for the recollection of related items (Howard & Kahana, 1999). These findings have served to develop computational models of memory, such as the Context Maintenance and Retrieval (CMR) model (Polyn, Norman, & Kahana, 2009) in which temporal context (items encoded nearby) and source context (source item's encoding features and characteristics) influence item encoding and recall dynamics.

Data from human intracranial electrophysiological recordings during free recall support these interpretations of CRP effects in free recall data, by providing neural evidence of context reinstatement. Patterns of neural activity when recalling an item are similar to those when studying the item itself, as well as neighboring items, with similarity decreasing the further away two items are from each other (Folkerts, Rutishauser, & Howard, 2018; Manning, Polyn, Baltuch, Litt, & Kahana, 2011). Furthermore, neural evidence of the behavioral lag contiguity effect, as a recovery of temporal context during retrieval, is present in single-unit recordings from both the hippocampus and amygdala (Folkerts et al., 2018).

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, promote recall of items that shared the oddball's new context. Salient, oddball stimuli that deviate from the prevailing context typically show a mnemonic enhancement (Von Restorff, 1933). Different oddball modalities are associated with this phenomenon, including words, objects, scenes and faces (Frank & Kafkas, 2021), as well as with different deviance attributes, such as perceptual, emotional and semantic (Strange, Henson, Friston, & Dolan, 2000). To computationally model enhanced memory for emotional items and peri-oddball effects for surrounding items in oddball tasks, Talmi et al. (2019) developed a variation of the CMR model: the emotional CMR (eCMR). Since oddballs have a different source context than the rest of the items in a study list, there is a decrease in source and semantic similarity between the oddball and the rest of items, which predicts diminished recall of the oddballs (Talmi et al., 2019). However, in the eCMR model, they counterbalanced the previous prediction by showing that increased attention to the oddball at encoding increased its link to the temporal context, thereby promoting its recall (Talmi et al., 2019) as previously reported in behavioral oddball paradigms (Strange, Hurlemann, & Dolan, 2003). Although the eCMR model has provided a framework to expand the CMR model to emotional settings, this model remains to be studied empirically in oddball paradigms which contrast different salience types, to provide a better understanding of recall properties under contextual novelty.

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, Hurlemann, & Dolan, 2003; Tulving, 1968) amnesic effect for neutral stimuli presented immediately after or before the emotional oddball, respectively. These peri-oddball effects are modulated by task (Anderson, Wais, & Gabrieli, 2006), stimulus onset asynchrony (SOA) (Schmidt & Schmidt, 2016; Tulving, 1968), retention intervals and arousal characteristics of the items (Mather & Sutherland, 2011; Schmidt & Schmidt, 2016). 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 unavailability at retrieval, and can be reversed 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 the present study, we tested the hypothesis that oddball recall prompts an update in temporal context, thereby promoting recall of items that were encoded after the oddballs. Given an oddball-evoked shift in source context, we predicted that items studied after the oddball at encoding would be strongly coupled with the oddballs at retrieval, and therefore, for items following the oddball to show enhanced conditional response probability. To test this hypothesis, we presented word lists containing one of two oddball types, emotional and perceptual, to healthy young participants (N=70).

The order in which nouns were recalled was recorded to test for oddball-evoked forward-contiguity recall enhancement and how this influences the recall of the words preceding the oddball. To explore whether salience contiguity modulation is time-dependent we also introduced 5 different SOAs (1, 2, 3, 4 and 6 seconds) which were fixed within a list.

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. Sample size was calculated using original data from (Strange et al., 2003) and G*Power software (Erdfelder, Faul, Buchner, & Lang, 2009; Faul, Erdfelder, Lang, & Buchner, 2007) using an a priori power analysis for t-tests (means difference between matched pairs) with an effect size dz=1.84, α=0.05 and power set at 0.95. Effect size calculation returned a total sample size of 7 which we then multiplied by 5 SOA groups (n=35) and doubled because in the present task there were about half the number of trials compared to the original 2003 paper (because only one oddball type is presented in each list, as described below).

Stimuli. Lists were based on those used in Strange et al. (2003), translated from English to Spanish, and normed for emotional valence and semantic relatedness by a separate group of 11 native Spanish-speaking subjects [5 male, 6 female (age range: 25-34; mean age: 30.2)].

Task. Subjects were presented with 40 lists of 14 nouns with the words ‘‘New List’’ presented between lists. For each list, 13 of the nouns were of the same semantic category (*e.g.* animals, occupations), emotionally neutral, and were all presented in the same font. These are referred to as control nouns. To set the context, the first five nouns in each list were always control nouns (*i.e.* not oddballs). Twenty lists contained an emotional oddball, aversive in content, but of the same category and perceptually identical to control nouns. The remaining 20 lists contained a perceptual oddball. All oddballs were randomly allocated to the 7th, 8th, 9th, 11th or 12th serial position, thereby maximising 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 800 ms. Subjects made a push-button response 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 stimulus onset asynchrony (SOA) of 1, 2, 3, 4 or 6 s, to determine whether the retrograde amnesic effect reported by Strange et al. (2003) spanned to two stimuli or 6 s. Thus, for each of the 20 lists for each oddball type, four 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).

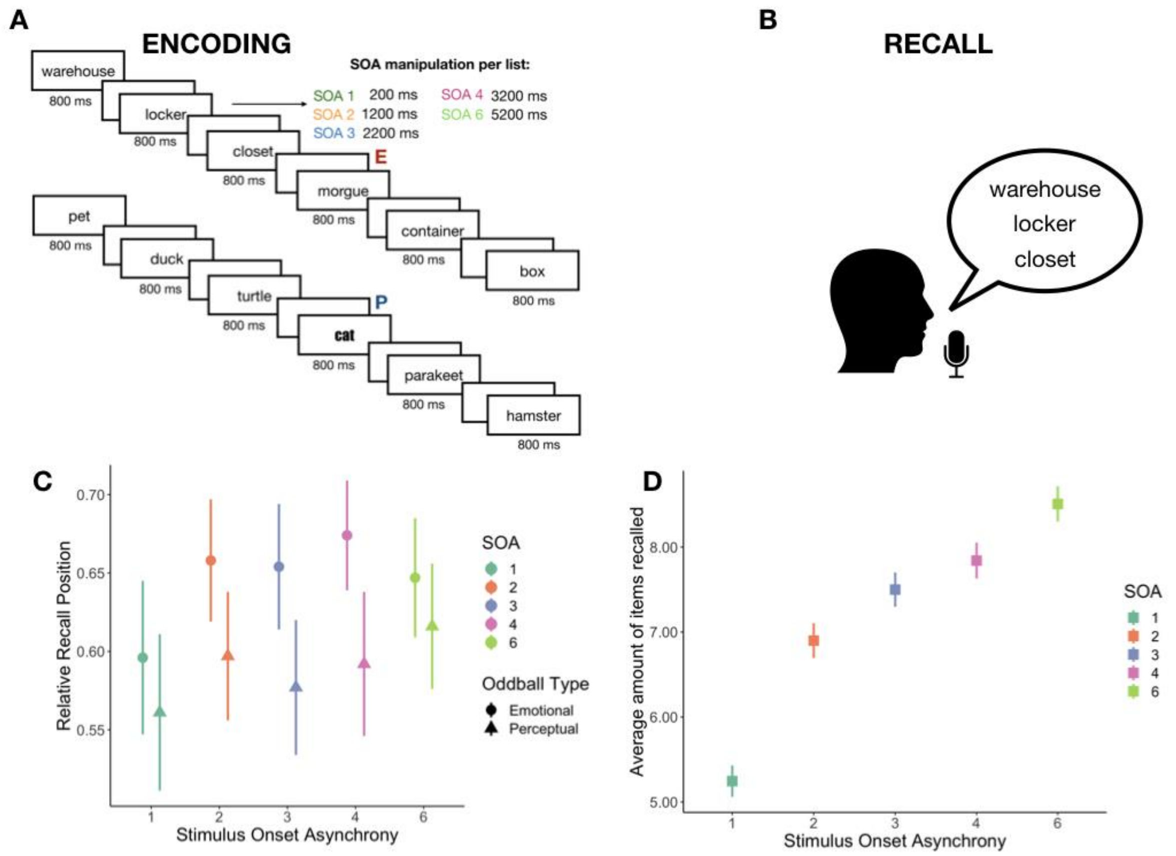

Figure 1. Memory task and total recall performance for list types. A) Example of items used in the task where E and P are the Emotional and Perceptual oddballs, respectively. Each word was presented for 800 ms followed by a blank screen where presentation timings varied depending on the stimulus onset asynchrony (SOA) for that list. SOA was kept constant within the same 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 relative recall position of both oddballs for each SOA. There was a trend for items to be recalled later on as SOA increased. Emotional oddballs were recalled later than perceptual ones across SOAs. Bars show mean $\pm$ 95% confidence intervals. D) The number of items recalled increased as SOA augmented. The average number of items recalled per list is plotted for each SOA, bars show mean $\pm$ 95% confidence intervals.

The presentation of each 14-word list was followed immediately by a 30 s distractor task, during which subjects were instructed to count backwards in threes (out loud) from a number presented on the screen. The distractor task was followed by instructions to free-recall the words presented in the preceding list. Recall performance in the experiment is expressed relative to one randomly selected control noun in each list. The chosen control nouns, like the oddballs, could not occur within the first five nouns of each list and were at least three serial positions apart from oddball nouns.

Statistical analysis. Lists that contained data collection errors (*e.g,* missing data, coding errors) were excluded from all analyses across all subjects (11 emotional lists, 6 perceptual lists out of a total of 1400 emotional and 1400 perceptual lists across subjects). All analyses were conducted using MATLAB (R2019b, The MathWorks, Inc). Statistical analyses and figure creation were conducted in Rstudio (version 1.3.1093), JASP (Jasp Team, 2021) and GraphPad Prism version 9 for Macintosh, GraphPad Software, San Diego, California USA, www.graphpad.com. All data were tested for normality using QQ plots; Greenhouse-Geisser sphericity correction was applied when appropriate and non-parametric tests were used if needed. Post-hoc t-tests were FDR-corrected unless stated otherwise. Effect sizes were calculated with Cohen's d or by calculating the r statistic in Wilcoxon's tests (Kassambara, 2013).

Conditional response probability analyses were conducted using the Behavioral Toolbox for MATLAB R2019b (http://memory.psych.upenn.edu/Behavioral_toolbox) with modified scripts where the CRPs were investigated for the words recalled one serial position before or after the oddball. *Lag* refers to the word-distance to an item at encoding; all analyses and visualization were performed on lags ± 5 as previously reported (Healey, Long, & Kahana, 2019; Kahana, 1996). *Backwards vs. forwards* refer to words presented before or after a specific item at encoding. Accordingly, *backwards* and *forwards* are analogous to negative and positive lags, respectively. In analyses investigating CRP curves with respect to oddball recall, *to* refers to transitions to the oddballs whereas *from* refers to transitions from the oddballs at recall.

RESULTS

Emotional and perceptual oddballs are remembered late during free recall

While some have reported that oddballs are recalled early in the recall order (Elhalal, Davelaar, & Usher, 2014; Siddiqui & Unsworth, 2011; Talmi et al., 2019), other computational models predict that optimal recall occurs when recall begins with items from the beginning of an encoded list and there is a strong forward-contiguity (Zhang, Griffiths, & Norman, 2021). We therefore expected oddballs to be recalled early in the serial recall order. This was not, however, the case. Oddball recall position was calculated relative to the total number of words recalled in each list across all lists in which the oddball was recalled. For example, if an oddball was recalled in the 6th recalled position out of a total of 6 items recalled, this would translate to a relative recall position of 1, whereas an oddball recalled in the 1st position, would have a relative recall of 0.167. Emotional and perceptual oddballs were remembered late in the serial recall order, both at a relative recall position of approximately 0.6 [emotional oddballs (0.65); perceptual oddballs (0.59)]. A mixed-effects model with SOA [1, 2, 3, 4, 6] and oddball type [emotional, perceptual] as factors, showed a significant main effect of oddball type ($F(1,69)=8.91$, $p<0.005$) indicating that emotional oddballs were recalled later than perceptual ones. There was a trend of a main effect of SOA ($F(4,276)=2.38$, $p=0.06$) indexing a general trend for both E and P oddballs to be recalled slightly later as SOA increased. There was no significant SOA x oddball interaction ($F(4,244)=0.62$, $p=0.64$). This occurred against a background increase of memory performance for all list items with increasing SOA for both emotional and perceptual lists ($F(3.35, 231.4)=136.9$, $p<0.0001$; Fig. 1D).

Conditional response probability curves preserve a contiguity effect during recall of lists containing oddballs

We next evaluated CRP curves considering all recalled items in both emotional and perceptual oddball lists. Overall, CRP curves showed a preserved forward-contiguity effect, i.e. words near each other were more likely to be recalled, and more so in the forwards direction. This effect was observed regardless of whether the oddball was recalled or not (Fig. S1).

CRPs were analyzed with a three-way RM ANOVA (oddball list type [emotional, perceptual] x lag [1-5] x direction [backwards, forwards]) where lag refers to the encoding position of words, with respect to a specific recalled item, and direction indicates whether words were presented before (backwards) or after (forwards) an item. There was a significant main effect of oddball list type ($F(1,69)=4.07$, $p=0.048$), lag ($F(2.95,203.77)=105.11$, $p<0.001$) and a lag x direction interaction ($F(3.06, 210.95)=13.58$, $p<0.001$). However, the main effect of direction ($F(1,69)=1.61$, $p=0.21$), oddball list type x lag ($F(4, 276)=0.93$, $p=0.47$), oddball list type x direction ($F(1,69)=0.252$, $p=0.62$) and 3-way interaction ($F(4,276)=0.54$, $p=0.71$) did not reach significance. Post-hoc t-tests, following up on the lag x direction interaction, confirmed contiguity as transitions at lag 1 were significantly different from those at other lags both in the backwards ($p<0.001$) and forwards directions ($p<0.001$). Forward contiguity was further confirmed as CRP values in the forwards direction at lag 2 were also significantly different than at all other lags ($p<0.005$) (Table S1). Forward contiguity was present across all SOAs (Fig. 2B), but, interestingly, increased with increasing time between stimuli at encoding. We ran a one-way ANOVA with SOA as a factor, collapsing across all 5 lags in the forwards direction which confirmed a significant main effect of SOA ($F(4,276)=31.17$, $p<0.0001$). Follow up post-hoc t-tests confirmed that CRP values in the forwards direction were overall lower at SOA 1 compared to all other SOAs (p<0.0001) as well as CRP values were lower at SOAs 2, 3 and 4 than at SOA 6 (p<0.001) (Table S2).

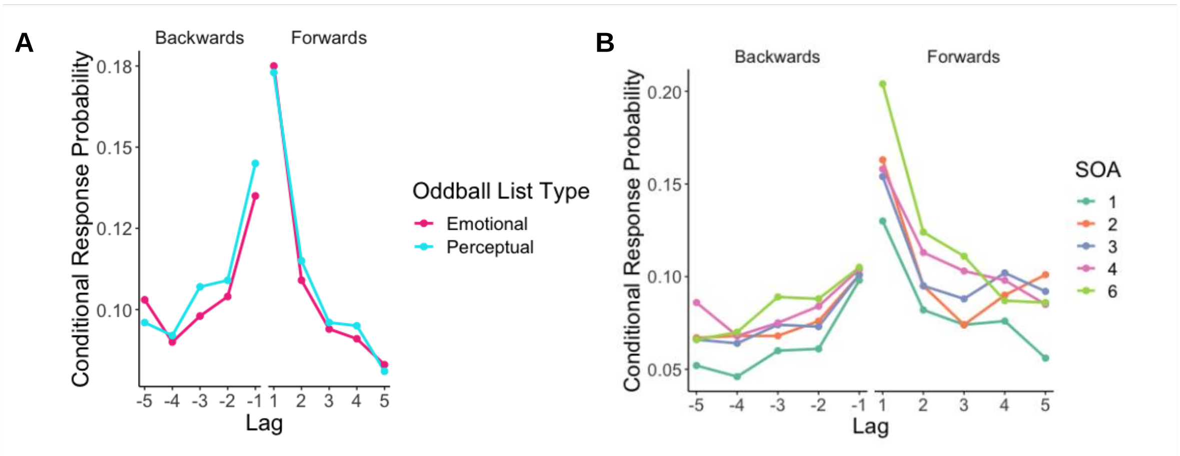

Figure 2. Conditional response probability (CRP) curves show a preserved forward-contiguity effect for both emotional and perceptual oddball lists across stimulus onset asynchronies (SOA). A) CRP curves by oddball lists, showing forward-contiguity. B) CRP curves by SOA (1, 2, 3, 4, or 6 seconds) show higher CRP for longer SOAs.

Transitions from emotional oddballs show enhanced conditional response probability curves

We hypothesized that recall transitions from the oddballs (i.e. the item recalled right after the oddball was recalled) would show enhanced CRP due to a strong contextual change which would serve as an anchor to move forwards in recall.

We calculated CRP curves for items recalled immediately before the oddballs (to evaluate transitions *to* the oddballs) and for items recalled immediately after the oddballs (to evaluate transitions *from* the oddballs) (Fig.3A, 3B). To avoid an increase in missing values, which arises from splitting the data into transitions to and from oddballs, we averaged the CRP values across all 5 positive and negative lags, separately, only including the lags that contained a CRP value. We conducted a 3-way

RM-ANOVA with oddball type [emotional, perceptual], direction [forwards, backwards] and transition [to vs. from] as factors. This analysis showed that transitions *from* emotional oddballs were enhanced compared to perceptual ones, with transitions from emotional oddballs showing an enhanced forward contiguity effect (Fig. 3C). That is, we found a significant main effect of oddball ($F(1,69)=12.45$, $p<0.001$), showing that emotional oddball lists had overall enhanced CRPs compared to perceptual oddball lists. Furthermore, transitions *from* oddballs were enhanced compared to transitions *to* oddballs (main effect of transition ($F(1,69)=6.87$, $p=0.01$). A significant oddball type x transition interaction ($F(1,69)=15.39$, $p<0.001$) indicated that transitions *from* emotional oddballs were significantly increased compared to transitions *to* emotional oddballs ($t(69)=4.41$, $p<0.001$, *Cohen's d*=0.52) whilst transitions *from* perceptual oddballs did not differ from transitions *to* perceptual oddballs ($t(69)=-0.73$, $p=0.47$, *Cohen's d*=-0.09). Lastly, there was a significant direction x transition interaction ($F(1,69)=7.47$, $p=0.008$) whereby transitions *from* oddballs were significantly different to transitions *to* oddballs in the forwards direction ($t(69)=4.21$, $p<0.001$, *Cohen's d*=0.50) but not in the backwards direction ($t(69)=-0.17$, $p=0.87$, *Cohen's d*=-0.02). There were no significant main effects of direction ($F(1,69)=2.46$, $p=0.122$), or oddball type x direction interaction ($F(1,69)=1.12$, $p=0.29$), or a three-way interaction ($F(1,69)=0.64$, $p=0.43$).

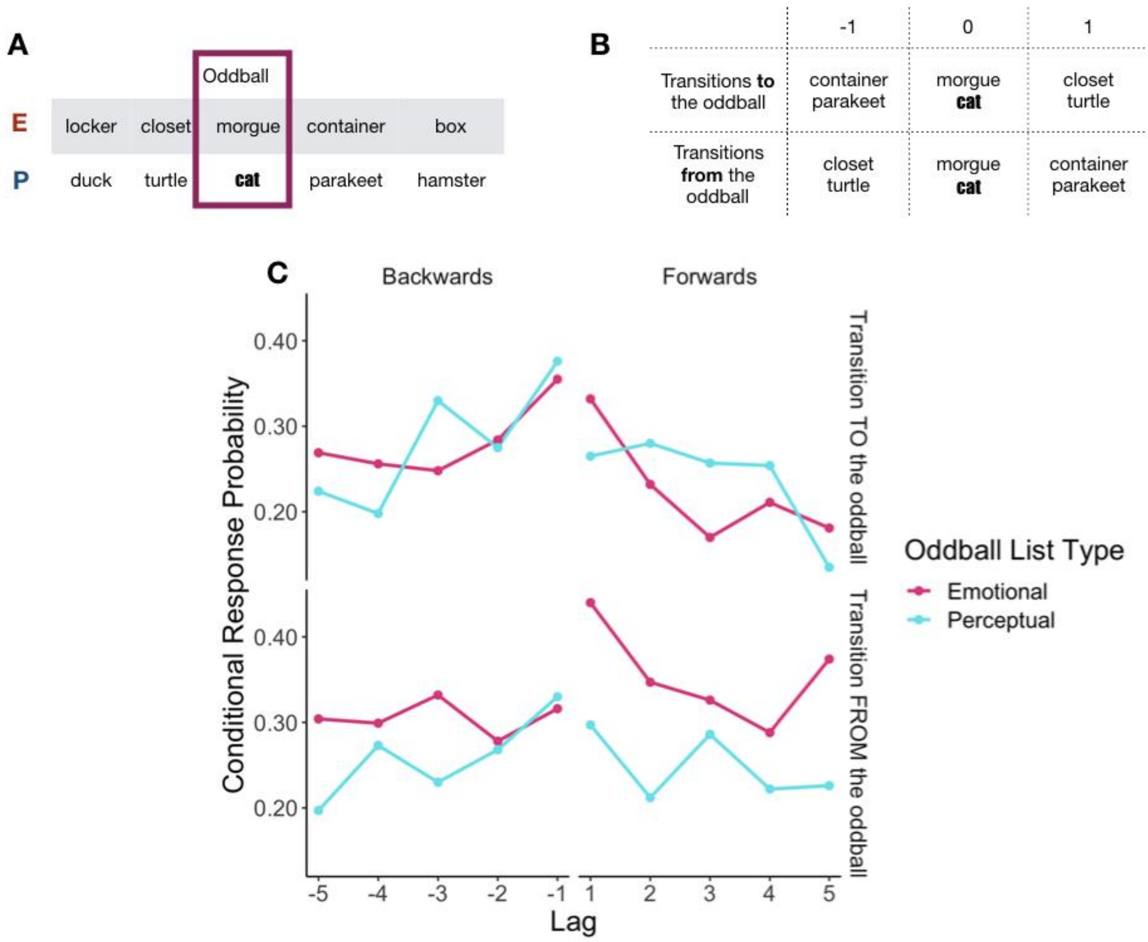

Figure 3. Transitions from emotional oddballs show enhanced conditional response probabilities in the forwards direction compared to perceptual lists. A) Example items presented at encoding in emotional (E) and perceptual (P) lists. B) Schematic of item transitions during recall of items with encoding order shown in A (in relation to lag values, shown here from -1 to 1) depending on whether transitions were *to* or *from* oddballs. In the first of the 4 examples, the subject has recalled “container”, “morgue” and “closet” in that specific order. C) Conditional response probability curves in transitions *to* and *from* emotional and perceptual oddballs.

To investigate whether this emotional salience forward enhancement was dependent on temporal proximity of stimuli at encoding, we further analyzed how transitions to and from emotional oddballs were modulated by SOA (Fig. 4). Overall, there was an enhancement in CRP across SOAs in transitions from emotional oddballs compared to transitions to these oddballs ($W=1965$, $p<0.0001$, $r=0.51$). We further analyzed whether forward transitions from the oddballs differed across SOAs, which was not the case (Friedman test; $X^2(4)=2.39$, $p=0.67$). Friedman testing was used as a non-parametric alternative to a repeated measures three-way ANOVA. A considerable limitation of the present approach is that, when splitting the data in forward transitions from emotional oddballs, only 23 subjects, on which the Friedman test was run, contained data values for all SOAs. However, visual inspection of the whole dataset showed that CRP of forward transitions at SOA 1 were the opposite of those observed at longer SOAs. That is, at 1s SOA, transitions to the emotional oddball were more probable in the forward vs backward direction, and the opposite is observed for transitions from the emotional oddball.

Overall, lists containing an emotional oddball showed increased CRP compared to perceptual oddball lists. As we hypothesized, transitions from emotional oddballs showed an enhanced forward-flow of recall which was particularly consistent when temporal proximity was larger than a second, although this effect was not statistically significant.

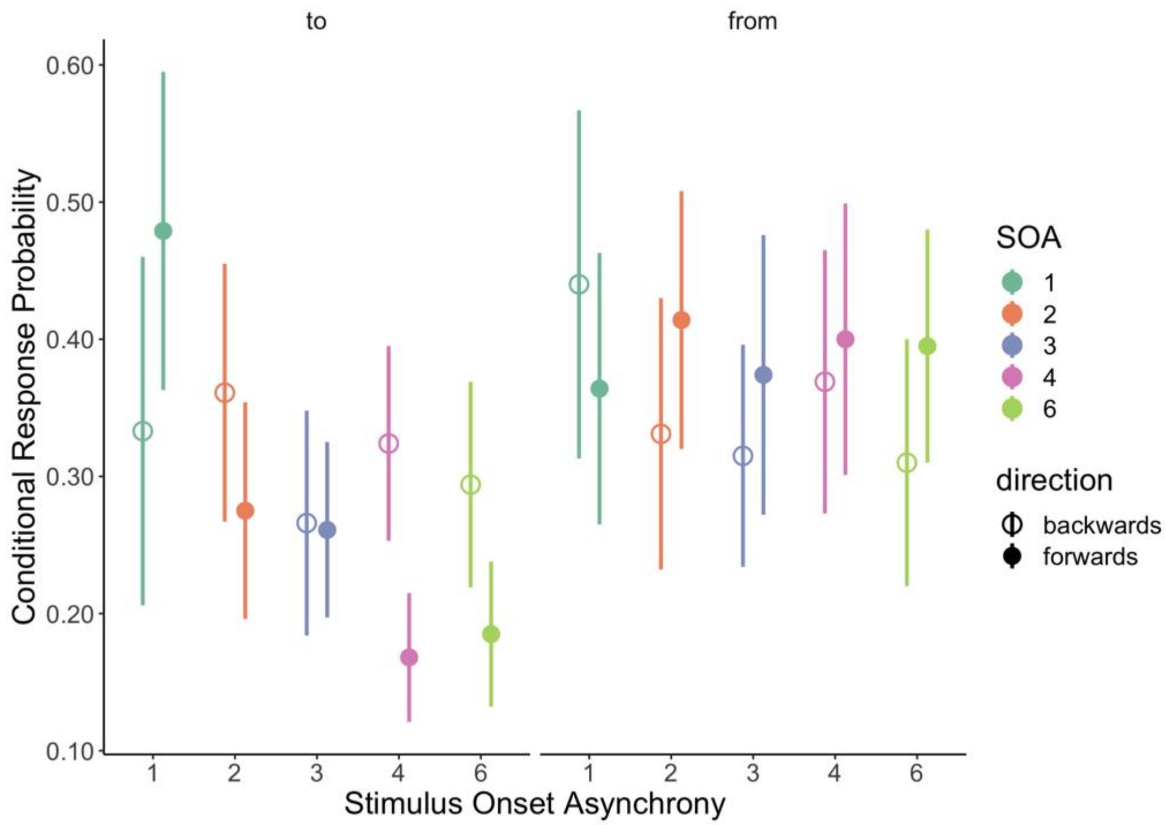

Figure 4. Conditional response probabilities (CRP) show an enhancement in transitions from emotional oddballs in the forwards direction. CRP mean ± 95% confidence intervals of emotional oddball lists across stimulus onset asynchronies (SOA). CRP curves were collapsed across 5 lags; therefore, forwards direction indicates positive lags whereas backwards refers to negative lags. Left panel included transitions to emotional oddballs whereas right panel shows transitions from emotional oddballs.

Enhanced forward contiguity in emotional oddball lists cannot explain retrograde amnesia

In lists containing emotional and perceptual oddballs we found that while transitions to both types of oddballs preserved a contiguity effect, transitions from emotional oddballs showed a forward-enhancement (Fig. 3C). Transitions *from* emotional oddballs showed an enhancement in the CRP curves which was not present in transitions *from* perceptual oddballs. We next tested whether this CRP enhancement in transitions from emotional oddballs (especially at lag +1) could contribute to emotion-induced retrograde amnesia – observed in previous experiments employing the current task – for the items presented just before emotional oddballs ("E-1" items). That is, if the emotional oddball is likely to be recalled, and this evokes a forward bias to recall items presented after the E item at encoding, this could potentially lead to a reduced recall for items preceding the E oddball. However, in the current Spanish version of this task, no retrograde odbball-1 effects were observed (Fig. S2). That is, E-1 item recall performance was not different from that of control items (Fig. S2). There was no between-subject correlation between E-1 normalized recall and lag +1 values transitions *from* emotional oddball (Spearman's rho=-0.04, p=0.76) (Fig. S3).

DISCUSSION

We calculated CRP curves on recalled items from an oddball paradigm that employed word lists containing either an emotional oddball (aversive in content) or a perceptual oddball (presented in a different font). Overall, analysis of CRP curves showed preserved key properties of free recall, in which items contiguous at encoding are more likely to be recalled together and more so in the forwards direction (Kahana, 1996). 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 which were not present in transitions *from* perceptual oddballs. This forward enhancement could be time dependent as it was present at SOAs greater than 1 second, (on visual inspection of the data).

Oddball recall occurred at a serial recall position later than predicted (Elhalal et al., 2014; Siddiqui & Unsworth, 2011; Talmi et al., 2019) (Fig. 1C). The eCMR model also predicted that the presentation of an emotional item would decrease the CRP of items encoded following the oddball (Talmi et al., 2019). This approach, however, modeled emotion as an all-or-none phenomenon where emotional oddballs increased arousal (Cohen & Kahana, 2019; Talmi et al., 2019). Whilst the eCMR's simulations do not fit the present CRP curve results from emotional lists, their results were aligned with the present results from perceptual oddball lists. 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. For example, a more recent computational model, the CMR3, aimed to model memory in emotional and mood disorders. Instead of operationalizing emotionality as a binary factor, it was represented it in terms of both valence (positive or negative) and arousal (Cohen & Kahana, 2019). 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, the latter was not (Strange et al., 2003). Using the present task to investigate how pharmacological manipulations of the beta-adrenergic system modulate CRP in oddball-lists could provide insight into the biological mechanisms behind the lag contiguity property of memory recall.

We further investigated timing effects on CRP curves by modulating SOAs. We found that at high temporal proximity, *i.e.,* SOA 1 s, items presented before the oddball were more strongly paired with the oddball, as transitions to the emotional oddballs were enhanced in the forwards direction. However, at longer SOAs (*i.e.,* > 1 s), transitions from emotional oddballs were stronger in the forwards direction, suggesting that forward-enhancement is time-dependent. These observations must be interpreted with caution, as due to a large presence of missing values, they did not reach statistical significance. Nevertheless, these are relevant when extrapolating the present results to real-world settings, where emotion plays a key role, such as when investigating recall in post-traumatic stress disorders (PTSD) (Brewin & Holmes, 2003; van der Kolk & Fisler, 1995). Particularly, at short SOAs, the present findings show that transitions to emotional oddballs tended to occur in the forwards direction (i.e. from items encoded before the oddballs), and that transitions from emotional oddballs occurred more so in the backwards direction (i.e. items encoded before the oddball presentation). These could mimic aspects of intrusive memories in PTSD, where temporal context preceding the traumatic event serves as a cue for its recollection and recalling a memory reactivates its encoding context, thus reinstating it (Cohen & Kahana, 2019).

Previous studies using oddball paradigms found a mnemonic enhancement for oddballs accompanied by a strong retrograde amnesic effect (Schmidt & Schmidt, 2016; Strange et al., 2003; Tulving, 1968). 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. We did not find a strong retrograde amnesic effects as previously described (Strange et al., 2003) even though the present items used were translated from Strange et al. (2003) and normed for emotional content and semantic relatedness.

In the present study, we applied CRP curve analysis on a free recall paradigm to investigate emotional and perceptual salience (via oddball presentations). Oddballs were retrieved relatively late in the recall order. Memory performance increased with increasing SOA at encoding, as did forward asymmetry of the CRP curves. We found an enhancement in transitions from emotional oddballs which was not present in transitions from perceptual oddballs. The enhanced forward transitions from emotional oddballs were not, however, evident if encoded stimuli were presented at an interval of 1 s. The current 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.

AUTHOR CONTRIBUTION

B.S designed the experiment. A.P.Y analyzed the data and wrote the manuscript with input from B.S and D.F.

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ETHICAL CONSIDERATIONS

The present work had ethical approval from the Universidad Politécnica de Madrid under the project ‘Estudio de los efectos de la emoción sobre la cognición humana’.

REFERENCES

Anderson, A. K., Wais, P. E., & Gabrieli, J. D. E. (2006). Emotion enhances remembrance of neutral events past. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(5), 1599–1604. https://doi.org/10.1073/pnas.0506308103

Angelini, R., Capozzoli, F., Lepore, P., Grossi, D., & Orsini, A. (1994). “Experimental amnesia” induced by emotional items. *Perceptual and Motor Skills*, *78*(1), 19–28. https://doi.org/10.2466/pms.1994.78.1.19

Brewin, C. R., & Holmes, E. A. (2003). Psychological theories of posttraumatic stress disorder. *Clinical Psychology Review*, *23*(3), 339–376. https://doi.org/10.1016/S0272-7358(03)00033-3

Cohen, R. t., & Kahana, M. J. (2019). Retrieved-context theory of memory in emotional disorders. *BioRxiv*.

Detterman, D. K. (1976). The retrieval hypothesis as an explanation of induced retrograde amnesia. *The Quarterly Journal of Experimental Psychology*, *28*(4), 623–632. https://doi.org/10.1080/14640747608400588

Elhalal, A., Davelaar, E. J., & Usher, M. (2014). The role of the frontal cortex in memory: An investigation of the Von Restorff effect. *Frontiers in Human Neuroscience*, *8*(JUNE), 1–20. https://doi.org/10.3389/fnhum.2014.00410

Erdfelder, E., Faul, F., Buchner, A., & Lang, A. G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Folkerts, S., Rutishauser, U., & Howard, M. W. (2018). Human episodic memory retrieval is accompanied by a neural contiguity effect. *Journal of Neuroscience*, *38*(17), 4200–4211. https://doi.org/10.1523/JNEUROSCI.2312-17.2018

Frank, D., & Kafkas, A. (2021). Expectation-driven novelty effects in episodic memory. *Neurobiology of Learning and Memory*, *183*(December 2020), 107466. https://doi.org/10.1016/j.nlm.2021.107466

Healey, M. K., Long, N. M., & Kahana, M. J. (2019). Contiguity in episodic memory. *Psychonomic Bulletin and Review*, 699–720. https://doi.org/10.3758/s13423-018-1537-3

Howard, M. W., & Kahana, M. J. (1999). Contextual Variability and Serial Position Effects in Free Recall. *Journal of Experimental Psychology: Learning Memory and Cognition*, *25*(4), 923–941. https://doi.org/10.1037/0278-7393.25.4.923

Kahana, M. J. (1996). Associative retrieval processes in free recall. *Memory & Cognition*, *24*(1), 103–109. https://doi.org/https://doi.org/10.3758/BF03197276

Kassambara, A. (2013). wilcox_effsize: Wilcoxon Effect Size.

Manning, J. R., Polyn, S. M., Baltuch, G. H., Litt, B., & Kahana, M. J. (2011). Oscillatory patterns in temporal lobe reveal context reinstatement during memory search. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(31), 12893–12897. https://doi.org/10.1073/pnas.1015174108

Mather, M., & Sutherland, M. R. (2011). Arousal-biased competition in perception and memory. *Perspectives on Psychological Science*, *6*(2), 114–133. https://doi.org/10.1177/1745691611400234

Polyn, S. M., Norman, K. A., & Kahana, M. J. (2009). A Context Maintenance and Retrieval Model of Organizational Processes in Free Recall. *Psychological Review*, *116*(1), 129–156. https://doi.org/10.1037/a0014420

Raaijmakers, J. G., & Shiffrin, R. M. (1980). SAM: A theory of probabilistic search of associative memory. *The Psychology of Learning and Motivation*, *14*. https://doi.org/https://doi.org/10.1016/S0079-7421(08)60162-0

Schmidt, S. R., & Schmidt, C. R. (2016). The emotional carryover effect in memory for words. *Memory*, *24*(7), 916–938. https://doi.org/10.1080/09658211.2015.1059859

Siddiqui, A. P., & Unsworth, N. (2011). Investigating the role of emotion during the search process in free recall. *Memory and Cognition*, *39*(8), 1387–1400. https://doi.org/10.3758/s13421-011-0125-9

Strange, B. A., Henson, R. N. A., Friston, K. J., & Dolan, R. J. (2000). Brain mechanisms for detecting perceptual, semantic, and emotional deviance. *NeuroImage*, *12*(4), 425–433. https://doi.org/10.1006/nimg.2000.0637

Strange, B.A., Hurlemann, R., & Dolan, R. J. (2003). An emotion-induced retrograde amnesia in humans is amygdala- and β-adrenergic-dependent. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(23), 13626–13631. https://doi.org/10.1073/pnas.1635116100

Strange, Bryan A, & Galarza-Vallejo, A. (2016). Bidirectional synaptic plasticity can explain bidirectional retrograde effects of emotion on memory. https://doi.org/10.1017/S0140525X15001958

Talmi, D., Lohnas, L. J., & Daw, N. D. (2019). A retrieved context model of the emotional modulation of memory. *Psychological Review*, *126*(4), 455–485. https://doi.org/10.1037/rev0000132

Tulving, E. (1969). Retrograde Amnesia in Free Recall. *Science*, *164*.

van der Kolk, B. A., & Fisler, R. (1995). Dissociation and the Fragmentary Nature of Traumatic memories: Overview and Exploratory Study. *Journal of Traumatic Stress*, *505*(525), 1–20. https://doi.org/10.1007/BF02102887

Von Restorff, H. (1933). Über die Wirkung von Bereichsbildungen im Spurenfeld. *Psychologische Forschung*, *18*, 299–342. https://doi.org/https://doi.org/10.1007/BF02409636

Zhang, Q., Griffiths, T. L., & Norman, K. A. (2021). Optimal policies for free recall. *PsyArxiv*. https://doi.org/10.31234/osf.io/sgepb