Emotional salience enhances the forward flow of memory

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ABSTRACT

Conditional response probability (CRP) curves applied to memory tests of free recall show that recall occurs for contiguous items with forward-directionality given that nearby items share an encoding context. We hypothesized that a context disruption by presenting emotional oddballs would modulate CRP curves, increasing the forward-flow of memory in free-recall emotional oddball tasks due to items presented after an emotional oddball being strongly bound to the new emotional encoding context. Seventy young, healthy male and female participants encoded word lists containing either emotional or perceptual oddballs at varying stimulus onset asynchronies followed by free recall. Serial recall transitions from emotional, but not perceptual, oddballs were enhanced in the forward direction. Thus, the present results provide the first 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.

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STATEMENT OF RELEVANCE

We applied a quantitative analysis, conditional response probability, to free recall of word lists containing perceptual or emotional oddballs. In conclusion, whilst both oddball types showed forward contiguity effects, we found stronger forward contiguity effects in transitions from the emotional oddballs i.e an enhanced memory forward-flow after emotional oddballs compared to perceptual ones. Overall, these results shed light on potentially distinct mechanisms underlying conditional response probability curve modulation by different types of salience and could inform future work into clinical manifestations of emotional memory.

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The aim of the Statement of Relevance is to broaden the impact of the science reported in the journal and make it easier for interested readers to appreciate and understand our efforts. It should make clear why the questions that motivated the study and the findings that bear on them matter beyond psychology laboratories and college and university campuses.

INTRODUCTION

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Free recall dynamics, and in particular inter-item organization, can be studied and analyzed using the quantitative method of conditional response probability (CRP) Kahana (1996). CRP quantifies, under the condition that x is immediately followed by y, the probability of recalling item x, if y is recalled (Kahana, 1996) and is characterized by the generalizable findings that 1) recall transitions are more likely to be amongst contiguous items and 2) to occur in the forward direction (Kahana, 1996). These *lag contiguity* properties can be accounted for by considering a strengthening of inter-item associations and their shared context when they spend more time together in the short-term storage (Raaijmakers & Shiffrin, 1980). At time of recall, recollection of an item serves as a contextual cue for the recollection of related items (Howard & Kahana, 1999). More recently Polyn et al (2009) developed the Context Maintenance and Retrieval (CMR) model to distinguish between different types of contexts that affect item encoding and recall dynamics.

Electrophysiological studies lend further support for these theories and computational models, 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 and this similarity decreases the further away two items are from each other (Folkerts, Rutishauser, & Howard, 2018; Manning, Polyn, Baltuch, Litt, & Kahana, 2011). 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 by an oddball, is predicted to evoke a contextual item association shift from the oddball presentation onwards, with the further prediction that oddballs are recalled early in recall order (Elhalal, Davelaar, &

Usher, 2014; Talmi, Lohnas, & Daw, 2019). Furthermore, computational models have shown that optimal recall occurs when recall begins at the beginning of a list and there is a strong forward-contiguity (Zhang, Griffiths, & Norman, 2021).

Salient "oddball" stimuli that deviate from the prevailing context typically show mnemonic enhancement (Von Restorff, 1933). To address 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). Their simulations showed that increasing attention to the oddball at encoding increased its link to the temporal context, thereby promoting its recall. However, due to the fact that the oddball has a different source context than the rest of the items in a study list, there was a decrease in source and semantic similarity between the oddball and the rest of items (Talmi et al., 2019). Although the eCMR model has provided a framework to expand the CMR model to emotional settings, this model remains to be investigated empirically in oddball paradigms. Given an oddball-evoked shift in source context, we hypothesized that items studied after the oddball at encoding are strongly coupled with the oddballs at retrieval, and therefore, for items following the oddball to show enhanced CRPs.

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 amnesic effect for neutral stimuli presented immediately before or after the emotional oddball (Strange, Hurlemann, & Dolan, 2003; Tulving, 1968). These peri-oddball effects are modulated by stimulus onset asynchrony (SOA) (Schmidt & Schmidt, 2016; B.A. Strange et al., 2003; Tulving, 1968), retention intervals and arousal characteristics of the items (Mather & Sutherland, 2011; Schmidt & Schmidt, 2016) and 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). In the context of the present study, we hypothesized that given that there was an enhancement in CRP from oddballs onwards this could explain the widely reported retrograde amnesic effects in oddball paradigms.

In the present study, we investigated oddball effects on CRP curves, by presenting two oddball types, emotional and perceptual, to healthy young participants (N=70), on a Spanish version of the oddball free recall paradigm reported in Strange et al. (2003). The order in which nouns were recalled was recorded in order to test for oddball-evoked forward-contiguity recall enhancement and how this influences the recall of the words preceding the oddball. We also investigated whether salience contiguity modulation is time-constrained by introducing 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 were free of 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 due to the fact that in the present task there were about half of number

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of trials compared to the original 2003 paper (as only one oddball type is presented in each list, as described below).

Stimuli. Lists were based on those presented 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 yr; 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 7^{th}, 8^{th}, 9^{th}, 11^{th} or 12^{th} serial position. 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. 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.

	E-2	**E-1**	**E**	**E+1**	
warehouse	locker	closet	morgue	container	box
	P-2	**P-1**	**P**	**P+1**	
pet	duck	turtle	cat	parakeet	hamster
	E-2	**E-1**	**E**	**E+1**	
creativity	head	neuron	tumor	thought	cranium
	P-2	**P-1**	**P**	**P+1**	
ball	football	coliseum	goalkeeper	fan	grandstand

Figure 1. Example of items used in the task where E and P are the emotional and perceptual oddballs respectively. -2, -1 or +1 indicate the two (or one) items preceding the oddballs and +1 indicates the item following the oddball.

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 3 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 (10 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). All data were tested for normality using Shapiro-Wilk or QQ plots;

Greenhouse-Geisser sphericity correction was applied when appropriate. Post-hoc t-tests were FDR-corrected.

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. All analyses and visualization were on lags ± 5 as previously reported (Healey, Long, & Kahana, 2019; Kahana, 1996).

RESULTS

The influence of emotional and perceptual oddballs on Conditional Response Probability Curves

Analyses were focused on lags ± 5 for both statistical analyses as well as visualization purposes.

Conditional response probability curves preserve a forward-contiguity effect

We first evaluated CRP curves taking all recalled words in both emotional and perceptual oddball lists. Overall, CRP curves showed a preserved forward-contiguity effect, i.e words nearby each other were more likely to be recalled and more so in the forwards direction. This effect was preserved both in lists when oddballs were recalled as well as when they were forgotten (Fig. S1).

A three-way RM ANOVA (oddball list type [emotional, perceptual] x lag [1-5] x direction [backwards, forwards]) did not show a significant 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 ($F(1,69)=0.252$, $p=0.62$) nor a significant 3-way interaction $F(4,276)=0.54$, $p=0.71$). However, 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 lag x direction interaction ($F(3.06, 210.95)=13.58$, $p<0.001$). Post-hoc t-tests showed enhanced CRP for contiguous lags, specifically lags 1 and 2 as well as a significant forward enhancement for lag 1 (t(139)=-5.11, p<0.001, *Cohen's d*=-0.43) and a backwards enhancement for lag 5 (t(139)=4.15, p<0.001, *Cohen's d*=0.35) (Fig. 2A).

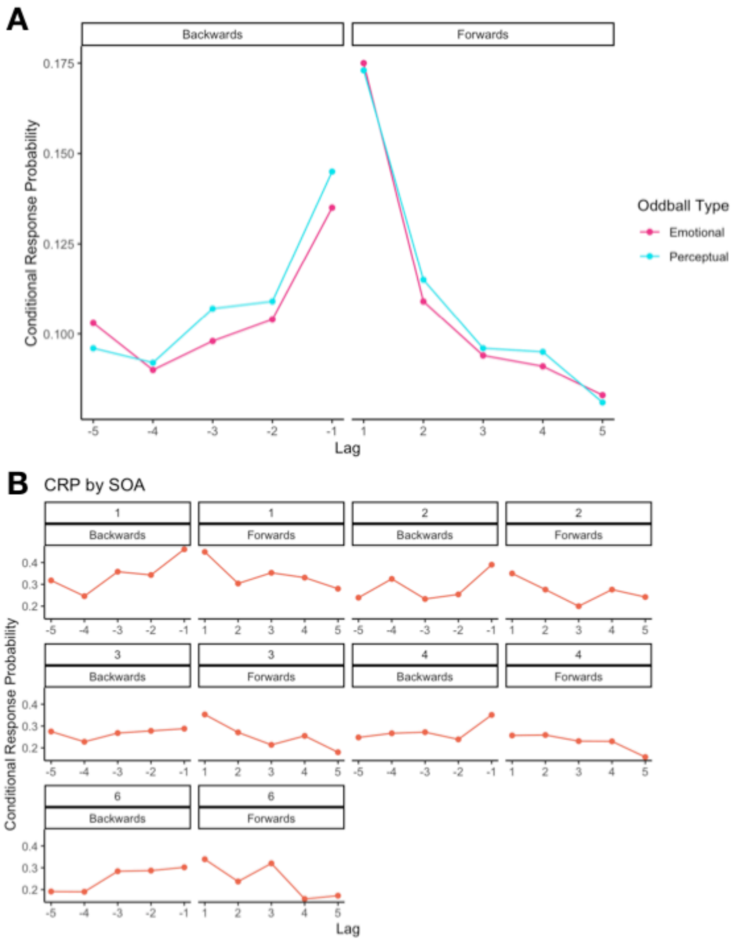

Figure 2. CRP curves show a preserved forward-contiguity effect for both emotional and perceptual oddball lists and CRP are modulated by temporal contiguity (SOA). A) CRP curves by emotional-oddball lists show forward-contiguity. B) CRP curves by SOA (1, 2, 3, 4, or 6 seconds) show higher CRP for shorter SOAs and a preserved contiguity effect.

Next, we evaluated temporal contiguity by variating SOAs. In order to maintain statistical power, we grouped together both oddball list types and fit a linear mixed effects model which revealed a significant main effect of word position ($X^2(4)=9.74$, $p=0.0451$) showing enhanced CRP at lag 1 vs. all other lags ($p<0.005$) as well as a significant difference between lag 2 vs. 5 ($p=0.018$). Furthermore, there was a main effect of SOA ($X^2(4)=11.38$, $p=0.023$) which showed that CRP were enhanced at SOA 1 vs. SOA 4 ($p=0.002$) and vs. SOA 6 ($p=0.006$), confirming temporal contiguity, i.e that shorter SOAs had enhanced CRP curves (Fig 2. B). However, we did not find a significant main effect of direction [backwards vs. forwards] ($X^2(1)=0.035$, $p=0.851$) nor a significant interaction of lag x direction ($X^2(4)=1.94$, $p=0.747$), lag x SOA ($X^2(16)=17.186$, $p=0.374$), direction x SOA ($X^2(4)=6.56$, $p=0.161$), nor a significant three way interaction of lag x direction x SOA ($X^2(16)=13.49$, $p=0.637$).

Transitions to and from oddballs modulate conditional response probability curves

Our hypothesis was that recall transitions from the oddballs (i.e. the item recalled after the oddball was recalled) would show enhanced CRP curves due to a strong contextual change which would serve as an anchor to strongly move forwards in recall, thereby, contributing to a retrograde amnesic effect.

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). Again, we found a significant main effect of lag ($F(4, 36)=3.50$, $p=0.02$), which showed a contiguity effect for lag 1 (vs. 2, $t(506)=3.44$, $p=0.002$, *Cohen's* d=0.15); vs. 3, $t(493)=3.75$, $p<0.001$, *Cohen's* d=0.17; vs.4, $t(479)=4.29$, $p<0.001$, *Cohen's* d=0.20; vs. 5, $t(482)=4.63$, $p<0.001$, *Cohen's* d=0.21) a trend of direction [forwards, backwards] (F(1,9)=4.63, p=0.06) and, importantly, a significant oddball [emotional, perceptual] x transition [to vs. from oddballs] interaction (F(1,9)=14.34, p=0.004). This interaction reflected an enhancement in CRP in transitions from emotional oddballs compared to perceptual oddballs (t(573)=4.47, p<0.001, *Cohen's d*=0.19) as well as a significant difference in transitions to emotional oddballs vs. transitions from emotional oddballs (t(584)=4.18, p<0.001, *Cohen's d*=0.17) (Fig. 3C), indicating that transitions from emotional oddballs onwards were enhanced compared to transitions from perceptual oddballs. None of the other effects reached significance levels.

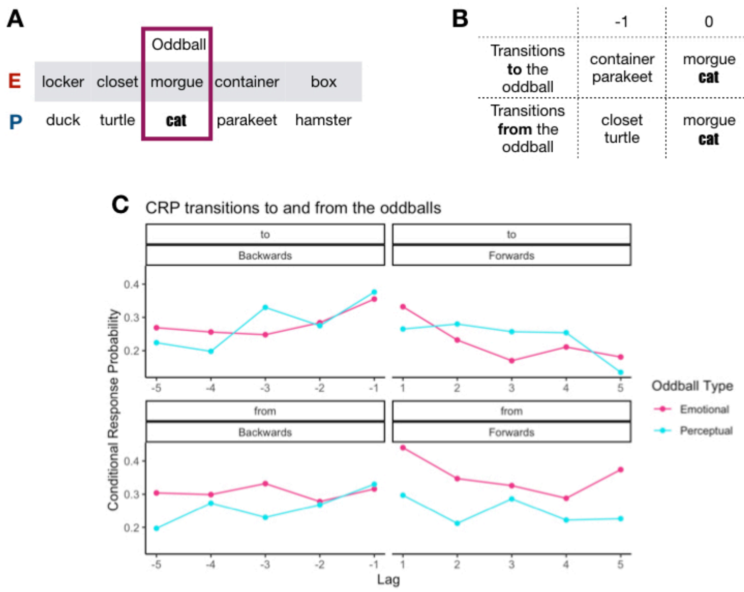

Figure 3. Transitions from emotional oddballs show enhanced conditional response probabilities compared to perceptual lists. A) Examples of a subset of items presented at encoding in emotional (E) and perceptual (P) lists. B) Example of item transitions (in relation to lag values) depending on whether transitions were to or from oddballs. In the first example, the subject has recalled "container", "morgue" and "closet" in that specific order. C) CRP curves in transitions to and from emotional and perceptual oddballs.

In order to investigate whether this emotional salience forward-enhancement was time-constrained we further analyzed how transitions to and from emotional oddballs were modulated by SOA (Fig. S4). We ran a linear mixed-effects model with the factors direction [forwards vs. backwards], transition [to vs. from oddballs] and SOA [1,2,3,4,6] and there was a significant three-way interaction between direction x transition x SOA ($X^2(1)=10.058$, $p=0.39$). Post-hoc tests grouping by SOA showed a significant difference in transitions to and from oddballs at SOA 2 ($t(110)=2.06$, $p=0.042$) and SOA 6 ($t(199)=2.72$, $p=0.007$) as well as a trend at SOA 4 ($t(179)=1.94$, $p=0.054$) (see complete results in supplementary material).

Emotional and perceptual oddballs are remembered late during free recall

Following predictions from the eCMR model, we expected oddball recall to occur early in recall order which was not the case. To further investigate whether the oddballs were recalled early-on we calculated the relative recall position of the oddballs to all the words recalled in each list across all trials in which the oddball was recalled. If, say, an item was recalled on the 6th position out of a total of 6 items recalled, this would translate to a relative recall position of 1, whereas an item recalled on the 1st position, would have a relative recall of 0.167. Contrary to prediction, both emotional and perceptual oddballs were remembered later on in recall; at a relative recall position of approximately 0.6 [emotional oddballs (0.65); perceptual oddballs (0.59)]. An unpaired Wilcoxon rank sum test showed that emotional oddballs were recalled significantly later than perceptual oddballs ($W=395538$; $p<0.001$) (Fig. 4).

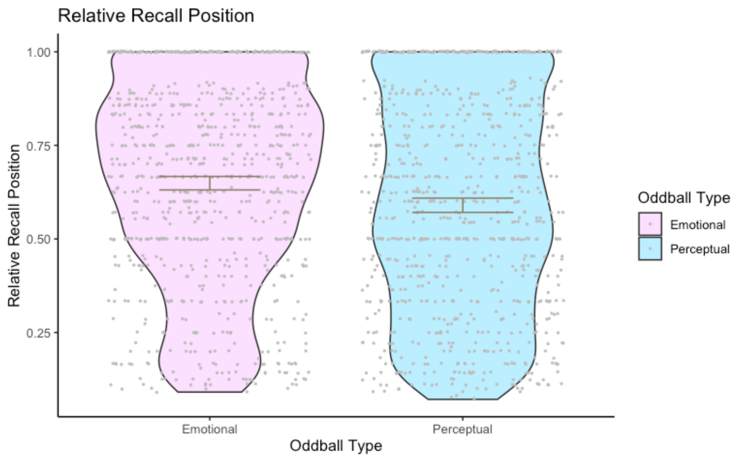

Figure 4. Oddballs are recalled late in serial recall order. Bars show mean $\pm$ 95% confidence intervals. Emotional items were recalled slightly later than perceptual oddballs (p<0.001).

Enhanced forward contiguity in emotional oddball lists cannot explain retrograde amnesia

In lists containing emotional and perceptual oddballs we found that while transitions to the oddballs preserved a contiguity effect, the forward effect was modulated (Fig. 3C). As hypothesized, transitions from emotional oddballs showed an enhancement in the CRP curves which was not present in transitions from perceptual oddballs. We next sought to test whether this CRP enhancement in transitions from emotional oddballs (specially at lag +1) explained retrograde amnesia for the items presented just before emotional oddballs (E-1 items). Despite the weak retrograde effect observed in the current experiment, we wondered whether the between-subject variability in E-1 memory could be related to a Spearman's rank correlation, however, it did not show a significant relationship between the two variables [E-1 normalized recall and lag +1 values transitions *from* emotional oddball], (rho=-0.04, p=0.76) (Fig. S5).

Items preceding and following emotional and perceptual oddballs are less well-remembered than the oddballs

Due to the fact that we did not find a significant relationship between the forward-memory enhancement and the retrograde amnesic effects in emotional lists, we next tested overall recall of the oddballs and the items nearby to determine whether the previously-reported retrograde (Strange et al., 2003) amnesic effects in the words near the oddball were present in the current Spanish version of the task. We found an overall mnemonic enhancement of both emotional and perceptual oddballs accompanied with an anterograde and retrograde amnesia for items preceding and following the oddballs at encoding, although less pronounced than the effects observed for the English and German versions of this task (Strange et al., 2003). Item recall was normalized with respect to a pre-selected control noun within the list. Normalized recall, therefore, was calculated by subtracting the proportion of recalled control items to the proportion of recalled items of interest separately for emotional and perceptual lists for each subject.

A repeated measures two-way ANOVA (word position [odd-2, odd-1, odd, odd+1] x oddball type [emotional, perceptual]) showed a significant interaction between the two factors ($F(3, 207)=3.61$, $p=0.01$), a significant main effect of word position ($F(3,207)=55.19$, $p<0.001$) and a trend towards significance in oddball type ($F(1, 69)=3.44$, $p=0.07$). Post-hoc t-tests showed a significant enhancement in oddball recall compared to its nearby items (vs. odd-1 $t(139)=-10.75$, $p<0.001$, *Cohen's d*=-0.91; vs. odd-2 $t(139)=-9.5$, $p<0.001$, *Cohen's d*= -0.80; vs. odd+1 $t(139)=10.41$, $p<0.001$, *Cohen's d*=0.88). Furthermore, emotional oddballs were significantly better recalled than perceptual oddballs ($t(69)=3.93$, $p<0.001$, *Cohen's d*=0.47) (Fig. 5).

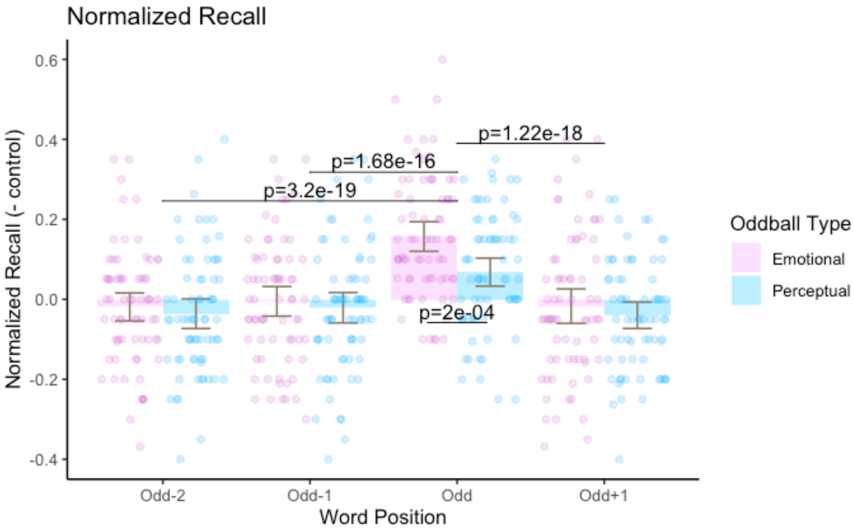

Figure 5. Oddballs were better recalled than their surrounding items. The proportion of normalized recalled words (minus control) items across word positions i.e -2 (item presented two serial positions preceding the oddball at encoding), -1 (item presented one serial position preceding the oddball at encoding), +1 (item presented one serial position after the oddball at encoding) was lower than for oddballs (odd). Bars show mean ± 95% confidence intervals.

Recall patterns in an oddball task are modulated by SOA

Previous studies indicate that retrograde and anterograde amnesia effects may also be modulated by timing effects. Recall performance indicated increased overall memory at longer SOAs compared to shorter ones (Fig. 6).

A three-way RM ANOVA (oddball type [emotional, perceptual] x SOA [1, 2, 3, 4, 6] x word position [odd-2, odd-1, odd, odd+1]) did not reveal significant interactions between oddball type x SOA ($F(4,276)=1.50$, $p=0.20$), SOA x word position ($F(12,828)=1.21$, $p=0.27$) nor a significant three-way interaction between oddball type x SOA x word position ($F(12,828)=1.14$, $p=0.33$). There was a trend towards a significant main effect of oddball type ($F(1,69)=3.33$, $p=0.07$), indicating, at a trend level, that overall emotional lists were better remembered than perceptual ones. There was a significant main effect of SOA ($F(4, 276)=3.87$, $p=0.004$) which we further explored by plotting the overall item recall per list by SOA which showed that recall improved as SOA increased (Fig. 4B). The results showed a main effect of word position ($F(3,207)=55.87$, $p<0.001$) in which the oddball, regardless of oddball type and SOA, was always better remembered than its surrounding items (vs. odd-2 $t(699)=-9.44$, $p<0.001$, *Cohen's d*=-0.36; vs. odd-1 $t(699)=-10.99$, $p<0.001$, *Cohen's d*=-0.42; vs. odd+1 $t(699)=10.77$, p,0.0001, *Cohen's d*=0.41). Furthermore, there was a significant interaction between oddball type x word position ($F(3,207)=3.55$, $p=0.02$); showing that emotional oddballs were better recalled than perceptual ones ($t(349)=3.34$, $p<0.001$, *Cohen's d*=0.18).

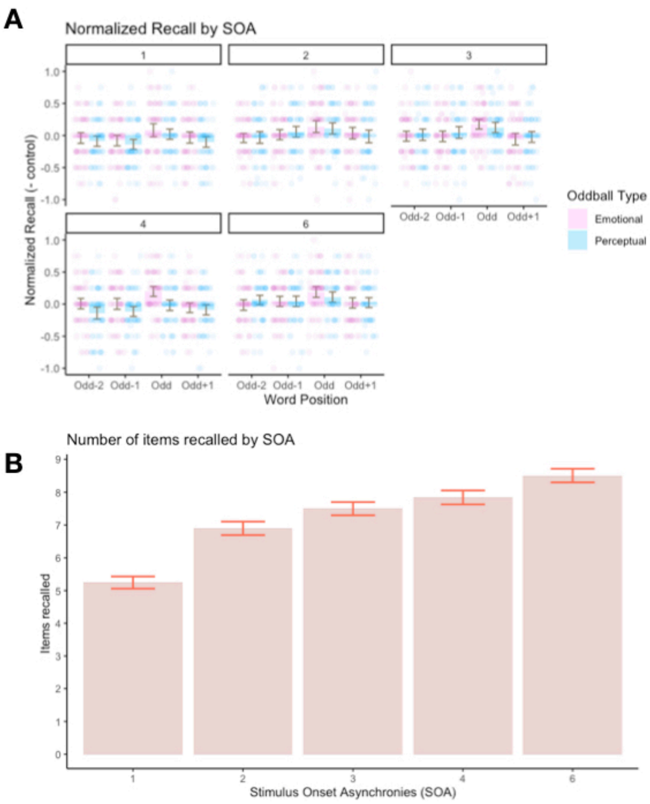

Figure 6. The amount of items recalled increased as SOA augmented. A) Modulation of normalized recall as a function of SOA. Bars show normalized recall (- control) with mean ± 95% confidence intervals by SOA. B) Total amount of items recalled per list across SOAs, bars show mean ± 95% confidence intervals.

DISCUSSION

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We calculated CRP curves on recalled items from an oddball paradigm that presented word-item lists which contained either an emotional oddball (aversive in content) or a perceptual oddball (presented in a different font). Overall CRP curves showed preserved key properties of free recall in which contiguous items are better recalled 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 a significant main effect of lag which showed that contiguity was maintained throughout, in perceptual oddballs, the forward transitions effect was reduced; however, it was enhanced in transitions from emotional oddballs.

Although the current version of the oddball paradigm showed that overall recall was worse at short SOAs, we did not find as strong retrograde amnesic effects as previously described (Strange et al., 2003). The present items used were translated from Strange et al. (2003) and normed for emotional content and semantic relatedness, therefore, the differences in the current task with previous studies are not attributable to differences in word valence. On the other hand, differences in experimental design and choice of control words could explain the hindered retrograde amnesic effect. For instance, the paradigm in Strange et al. (2003) consisted of 16-item lists which contained both an emotional and a perceptual oddball as well as a semantic oddball and two control nouns. In our current task, recall improved as SOA increases. It remains possible that in previous experimental designs the presentation of emotional oddballs increased salience for perceptual oddballs, and therefore, contributed to their increased recall (Sutherland & Mather, 2012) which did not occur in the present task.

The present findings provide empirical data to the eCMR computational model; we found a later-than-expected oddball recall and an enhancement in forward transitions from emotional oddballs but transitions from perceptual oddballs show a diminished forward transition effect, in line with the predictions of the eCMR (Talmi et al., 2019).

The idea of increased attention to the oddballs has been the basis for the development the eCMR (Talmi et al., 2019) where, by calculating CRP curves, they simulated that increased recall of an emotional oddball hindered recall of its nearby items. Increased attention due to increased arousal produced by item presentation can occur due to a variety of interacting factors. Behavioral studies investigated the influence of emotional modulations on attention and perception by presenting fearful faces followed by an orientation-decision task on Gabor stimuli; Phelps et al. (2006) provided evidence that emotion modulates attention i.e how we ‘‘see’’ upcoming stimuli as well as it enhanced perceptual processing. Emotionality is gradually incorporated into item context at encoding; whereby attention could be interacting with context setting, and is used during retrieval for item recollection (Long, Danoff, & Kahana, 2015). Thereby, we propose that while the presentation of emotional oddballs induces an interaction between emotional and attentional processes to gradually change context (Long et al., 2015), perceptual oddballs (and possibly, mainly increased attention) disrupt source contexts which in turn, disturb temporal context (Talmi et al., 2019) thus, decreasing CRP from perceptual oddballs in the forward direction.

Pharmacological approaches have shown that the beta-adrenergic blocker, propranolol, blocks memory for emotional but not perceptual oddballs (Strange et al., 2003). It is possible that carry-over effects after exposure to emotional oddballs (Schmidt & Schmidt, 2016) induce a bias, mediated by the adrenergic system, which underlies the forward-recall enhancement. If this were the case, we would expect propranolol to diminish the forward-transitions enhancement.

Previous studies using oddball paradigms had found a mnemonic enhancement for oddballs accompanied by a strong retrograde amnesic effect (Schmidt & Schmidt, 2016; Strange et al., 2003; Tulving, 1968), however, the precise timing effects on the retrograde amnesic effects remained to be further investigated. A key manipulation of the present paradigm was that items were presented at varied SOAs to investigate temporal contiguity and to unravel how timing affected memory. Whilst overall we found a mnemonic enhancement for oddballs accompanied by a decline in recall for items preceding oddballs, this effect was less strong than previously reported at SOA of 3 seconds (Strange et al., 2003). We found a significant main effect of SOA which showed that overall, the shortest SOA demonstrated worse recall than longer SOAs. Due to the fact that we found a forward-flow enhancement in transitions from emotional oddballs we evaluated whether it explained the retrograde amnesic effect, however, we did not find such significant correlation. This could be explained by the fact that the retrograde amnesia in the present task was not strong, thereby not allowing us to investigate this relationship.

This was the first study to apply CRP curve analysis on a free-recall paradigm to investigate emotional and perceptual salience (via oddball presentations). We found that whilst transitions from emotional oddballs were enhanced in the forwards direction, transitions from perceptual oddballs were reduced. We further hypothesized that this enhancement in transitions from emotional oddballs would explain the widely reported retrograde amnesic effect in these paradigms, however, it did not seem to be the case. This could be because the present version of the task did not induce as strong retrograde amnesic effects as previously reported. The current results, which indicate a dissociation in emotional and perceptual salience, provide empirical evidence that could be used to update the emotionality component in the eCMR. Future work could re-evaluate this approach in tasks which induce a stronger retrograde-amnesic effect such as in the English and German versions conducted by Strange et al. (2003).

The present findings could help the study of memory in disorders where strong emotion plays a key role, such as posttraumatic stress disorder as retrograde amnesia and dissociative experiences are present in the disorder (Brewin & Holmes, 2003; van der Kolk & Fisler, 1995). Applying quantitative approaches such as done in the present study to investigate memory recollection would help elucidate the underlying mechanisms of memory recall underlying the disorder.

AUTHOR CONTRIBUTION

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

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OPEN PRACTICES STATEMENT

The experiments were not pre-registered. Raw data, analysis pipelines and code used in the present paper can be found here: https://github.com/TheStrangeLab/Odd_SOA_CRP

Commented [BS7]: Or better https://osf.io/aw4e8/

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'.

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