# **Emotional salience enhances the forward flow of memory**

Alba Peris-Yague1,2, Darya Frank1, Bryan Strange1,3

1 Laboratory for Clinical Neuroscience, Centro de Tecnología Biomédica, Universidad Politécnica de Madrid, Madrid, Spain

2 PhD Program in Neuroscience, Autonoma de Madrid University, Madrid, Spain, 28029

3 Department of Neuroimaging, Alzheimer’s Disease Research Centre, Reina Sofia–CIEN Foundation, Madrid, Spain.

# **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.

# **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.

# **INTRODUCTION**

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) (Fig. 1C). 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 the presentation of an oddball, is predicted to evoke a contextual item association shift from the oddball’s appearance onwards, with the additional prediction that oddballs are recalled early in recall order (Elhalal, Davelaar, & Usher, 2014; Talmi, Lohnas, & Daw, 2019). 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 a mnemonic enhancement (Von Restorff, 1933); there are different oddball types which have been paired with this phenomenon such as words, objects, scenes and faces (Frank & Kafkas, 2021) as well as with different deviance attributes for example perception, emotion and semantics (Strange, Henson, Friston, & Dolan, 2000). To computationally address and 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). 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).

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; 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). There are, nonetheless, neurobiological differences amongst several deviance types. Whilst there has been reported to be a general ‘deviance detection system’ there are deviance-specific processing areas such as the amygdala in the context of emotional salience and the bilateral fusiform cortices in perceptual oddball processing (Strange et al., 2000). The molecular mechanisms of salience processing and memory involvement highlight a major role of the dopaminergic and cholinergic systems (Frank & Kafkas, 2021) which varies amongst different salience types, for example, pharmacological approaches have shown that the beta-adrenergic blocker, propranolol, blocks memory for emotional but not perceptual oddballs (Strange et al., 2003) upon administration of the drug before encoding.

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 as well as it remains to be tested on various salience types in order to provide a better understanding of recall properties under contextual novelty. 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.

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, =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 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 yr)].

**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. 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 (Fig. 1A).

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| **Figure 1.** A) Example of items used in the task where E and P are the emotional and perceptual oddballs, respectively. Each word was presented for 800ms followed by a blank screen where presentation timings varied depending on each SOA manipulation. SOA was kept constant within the same list, in the image above they vary for illustration purposes. B) The relative recall position of both oddball types did not vary as a function of SOA. Bars show mean CI. C) Example of forward-contiguity in recall where items nearby each other are more likely to be recalled and more so in the forwards direction. |

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**

### **Conditional response probability curves preserve a 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 regardless of oddball recall (Fig. S1).

A three-way RM ANOVA (oddball list type [emotional, perceptual] x lag [1-5] x direction [backwards, forwards]) showed 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 confirmed 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). However, there was not 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).

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| **Figure 2.** CRP curves show a preserved forward-contiguity effect for both emotional and perceptual oddball lists. 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. C) The amount of items recalled increased as SOA augmented. Total amount of items recalled per list across SOAs, bars show mean 95% confidence intervals. |

Next, we evaluated temporal contiguity by variating SOAs. In order to maintain statistical power, to account for missing values, we grouped together both oddball list types and fit a generalized linear mixed effects model with lag [1-5], SOA [1-4;6] and direction [forwards, backwards] as factors. SOA manipulation confirmed forward-contiguity as well as a CRP enhancement for shorter SOAs. There was a main effect of SOA (X2(4)=11.38, p=0.023) which showed that CRP were enhanced at SOA 1 vs. SOA 4 (t(369)=3.8, p=0.002, *Cohen’s d*=0.20) and vs. SOA 6 (t(408)=3.25, p=0.006, *Cohen’s d*=0.16), confirming temporal contiguity, i.e that shorter SOAs had enhanced CRP curves (Fig. 2B). Furthermore, there was a significant main effect of lag (X2(4)=9.74, p=0.0451) showing enhanced CRP at lag 1 vs. all other lags (vs. 2, t(798)=4.03, p<0.001, *Cohen’s d=*0.14; vs. 3 t(691)=3.29, p=0.003, *Cohen’s* d=0.13; vs. 4 t(665)=3.76, p<0.001, *Cohen’s d=*0.15; vs. 5 t(669)=4.38, p<0.001, *Cohen’s d*=0.17) as well as a significant difference between lag 2 vs. 5 (t(693)=2.62, p=0.018, *Cohen’s d*=0.099). We did not find a significant main effect of direction [backwards vs. forwards] (X2(1)=0.035, p=0.851) nor a significant two-way or three way interaction.

Previous studies indicate that retrograde and anterograde oddball-induced amnesic effects may be modulated by timing. In the present task, although CRP curves were increased at SOA 1 (Fig. 2B), recall performance was diminished (Fig. 2C). Data was analyzed with 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]). 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 recalled than perceptual ones. There was, also, 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 that showed that recall improved as SOA increased (Fig. 6). 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). There were no 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).

All in all, the well described forward-contiguity effect was present in lists containing both emotional and perceptual oddballs as items at lag 1 were better recalled than items at other serial positions, and more so in the forwards direction. Also, as items studied at a closer temporal interval (i.e shorter SOAs) were better recalled than those encoded spaced out in time. Lastly, recall improved as temporal contiguity (i.e SOA) increased.

### **Transitions to and from oddballs modulate conditional response probability curves**

We hypothesized 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.

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). To avoid an increase in missing values as a result of grouping the data into transitions to and from oddballs, we averaged the CRP values across the 5 lags 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. The present results showed that transitions from emotional oddballs were enhanced compared to perceptual ones as well as transitions from emotional oddballs showed an enhanced forward contiguity effect (Fig.3C). We found a significant main effect of oddball (F(1,69)=12.45, p=0.0008), showing that emotional oddballs had overall enhanced CRPs compared to perceptual oddballs (t(279)=2.85, p=0.005, *Cohen’s d =*0.17), furthermore, transitions from oddballs were enhanced compared to transitions to oddballs (main effect of transition (F(1,69)=6.87, p=0.01); t(279)=2.44, 0.015, *Cohen’s d =0.15*). 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(139)=3.99, p<0.001, *Cohen’s d=*0.34) whilst transitions from perceptual oddballs did not differ from transitions to perceptual oddballs (t(139)=-0.66, p=0.51). Lastly, there was a significant direction x transition (F(1,69)=7.47, p=0.008) interaction where transitions from oddballs were significantly different to transitions to oddballs in the forwards direction (t(140)=p<0.001, *Cohen’s d*=0.35) but not in the backwards direction (t(140)=-0.17, p=0.87). There were no significant main effects of direction (F(1,69)=2.46, p=0.122) nor an oddball type x direction interaction (F(1,69)=1.12, p=0.29).

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| **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-dependent we further analyzed how transitions to and from emotional oddballs were modulated by SOA (Fig. 4). We ran a generalized linear mixed-effects model with the factors direction [forwards, backwards], transition [to vs. from oddballs] and SOA [1- 4; 6] on emotional oddball lists. We did not find a significant main effect of direction (X2(1)=1.21, p=0.27), transition (X2(1)=2.16, p=0.14), SOA (X2(4)=5.31, p=0.26) nor a significant direction x SOA interaction (X2(4)=3.95, p=0.41) or transition x SOA (X2(4)=2.28, p=0.69). There was, however, a significant three-way interaction between direction x transition x SOA (X2(4)=13.38, p=0.01) as well as a significant direction x transition interaction (X2(1)=4.88, p=0.03). Post-hoc t-tests confirmed that an enhanced-forward flow was present as there was a significant enhancement in transitions from vs. to emotional oddballs in the forwards direction (t(1053)=4.21, p<0.001, *Cohen’s d=*0.36)as well as a significant difference in transitions from oddballs in the backwards direction vs. transitions to oddballs in the forwards direction (t(1058)=2.88, p=0.012, *Cohen’s d=* 0.24) and a significant difference between forwards transitions from oddballs vs. backwards transitions to oddballs (t(1059)=2.63, p=0.018, *Cohen’s d*=0.23). All other comparisons were not significant (Table S1). We next conducted post-hoc tests to evaluate how direction, transition and SOA affected CRP. At SOA 1, transitions to the oddballs were enhanced in the forwards-direction compared to all other SOAs (forwards to SOA 1 vs. SOA 2 t(1066.37)=3.13, p=0.02, *Cohen’s d=* 0.63*;* vs. SOA 3 t(1062.33)=3.40, p=0.01, *Cohen’s d=* 0.67; vs. SOA 4 t(1060.71)=4.89, p<0.001, *Cohen’s d=* 0.96*;* vs. SOA 6 (t(1064.12)=4.58, p<0.001, *Cohen’s d=*0.90)*.* Overall transitions in the forwards direction were enhanced when transitioning from oddballs compared to transitioning to oddballs (except at SOA 1). This effect was significantly different at larger SOAs. At SOA 4, transitions from emotional oddballs in the forwards direction were significantly different than transitions to oddballs in the forwards direction (t(1045.543)=3.95, p=0.002, *Cohen’s d=*0.73) as well as at SOA 6 (t(1039.76)=3.62, p=0.006, *Cohen’s d*=0.64). See full table of significant comparisons in Table S2. These differences in the forward-backward contiguity effects were not due to changes in oddball recall order as the relative recall position of both emotional and perceptual oddballs did not change depending on oddball type (X2(1)=0.98, p=0.322), SOA (X2(4)=3.99, p=0.41) nor there was an interaction between the two factors (X2(4)=1.51, p=0.83) (Fig 1B).

Lists containing an emotional oddball showed overall increased CRP curves compared to perceptual oddball lists. As we hypothesized, transitions from emotional oddballs showed an enhanced forward-flow of recall which was particularly present when temporal proximity was larger than 1 second.

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| **Figure 4.** Conditional response probability (CRP) mean 95% confidence intervals of emotional oddball lists across SOAs. CRPs 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 one shows transitions from 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 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 (Fig. S3), 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. S4).

# **DISCUSSION**

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, there was an enhancement in CRP in transitions from emotional oddballs which was not present in transitions from perceptual oddballs. This forward enhancement was time-dependent as it was present at SOAs greater than 1 second and was not influenced by the relative recall position of the oddballs across SOAs. Lastly, we tested the hypothesis that this forward enhancement from emotional oddballs would explain the previously reported oddball-induced retrograde amnesic effect, however, our hypothesis was rejected.

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). 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. 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). Future lines of research should investigate how the beta-adrenergic system regulates forward-recall in the context of emotional salience.

We further investigated timing effects on CRP curves by modulating SOAs. We found that at very high temporal proximity, i.e SOA 1s, 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 > 1s, transitions from emotional oddballs were stronger in the forwards direction. These indicate that this forward-enhancement may be time-constrained and further research should consider these findings, specially, when extrapolating the present results to real-world settings such as when investigating recall in post-traumatic stress disorders (PTSD). Whilst the abovementioned results are not explained by the relative recall position of the oddballs across SOAs, they could be potentially influenced by the number of items recalled; since recall improved as SOA increased. Therefore, it remains possible that the current findings were underpowered at shorter SOAs

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). Due to the fact that we found a forward-flow enhancement in transitions from emotional oddballs we hypothesized 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. 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. We did not find as 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. Differences in experimental design and choice of control words could explain the hindered retrograde amnesic effect as 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. 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).

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 an enhancement in transitions from emotional oddballs which was not present in transitions from perceptual oddballs and did not explain the widely reported retrograde amnesic effect in these paradigms potentially because the present version of the task did not induce as strong retrograde amnesia as previously reported. 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*.* 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 PTSD 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. A.P.Y analyzed the data and wrote the manuscript with input from B.S and D.F.

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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>

# **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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