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

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# **ABSTRACT**

Memory enhancement for emotional and perceptual oddballs in free-recall paradigms has been widely reported. This mnemonic enhancement for oddballs has been reported alongside with retrograde and anterograde amnesia for the words preceding and following the oddballs, however the precise mechanisms driving these recall patterns remain unknown. Conditional response probability (CRP) curves provide a quantitative approach to evaluate free recall upon availability of recalling two items. CRP curves consistently show that recall tends to occur for contiguous items and with a strong forward directionality. We hypothesized that the presentation of emotional oddballs would increase CRP curves, thereby, increasing the forward-flow of memory from emotional oddballs and that it would be related to the retrograde amnesic effect. A total of 70 participants (35 females) were presented 40 lists of 13 neutral words and 1 oddball (either emotional or perceptual; 20 lists each) at varying stimulus onset asynchronies (SOA: 1, 2, 3, 4 or 6 seconds) followed by a distractor task (counting backwards) before free recalling the items. In line with previous findings, we found enhanced recall of both oddball types accompanied by a mild retrograde and anterograde amnesic effect. Forward-contiguity was present in both oddball type lists (p<0.0001). We then investigated transitions to and from oddballs. In line with our predictions, we found a significant oddball x transition type interaction (p=0.004). Transitions from emotional oddballs were enhanced whereas transitions from perceptual oddballs showed contiguity in recall but no forwards-directionality. Lastly, we did not find a significant correlation with this enhancement and retrograde amnesia (p=0.76). Thus, the present results provide the first empirical evidence of CRP curve modulation by different types of salience and suggest that recall patterns upon the presentation of emotional and perceptual oddballs are mediated by different mechanisms.

# **INTRODUCTION**

Novel unexpected item presentation induces a mnemonic enhancement of salient items among lists of related items which is known as the Von Restorff effect (Von Restorff, 1933). Precisely, in the presence of an emotionally salient item the mnemonic enhancement is often accompanied by an anterograde (Angelini et al., 1994) and retrograde amnesic effect (Strange et al., 2003; Tulving, 1968). Memory enhancement for emotional words has been widely reported (Schmidt and Schmidt, 2016; Strange et al., 2003), however there have been mixed findings regarding the mnemonic effects on the words preceding and following the oddballs which has been shown to be modulated by stimulus onset asynchrony (SOA), retention intervals and arousal characteristics of the items (Mather and Sutherland, 2011; Schmidt and Schmidt, 2016). While some suggest that amnesic effects on items surrounding an oddball occur at very short SOAs (< 2 seconds) (Schmidt and Schmidt, 2016; Tulving, 1968) others have found this effect in longer SOAs (3 seconds) (Strange et al., 2003). These timing effects on oddball memory and its amnesic effects for surrounding items remain to be studied in oddball paradigms where the only manipulation is timing.

The presentation of salient items at encoding leads to increased arousal and attention to these items via amygdalar-frontoparietal interactions (Mather and Sutherland, 2011) and to enhanced memory of emotional items via amygdala-hippocampal coupling via the -adrenergic system (Richardson et al., 2004; Strange and Dolan, 2004) shortly after encoding. This memory enhancement they suggest often comes at the cost of lower memory for surrounding items that are not as relevant as the target (Mather and Sutherland, 2011; Strange et al., 2003), therefore, providing a framework by which arousal could explain the amnesic effects in oddball paradigms in items surrounding the oddball. Besides these behavioral theories, neurobiological approaches to explain the retrograde amnesic effects have centered around arousal, valence and the noradrenergic system as this effect is modulated by noradrenaline, specifically, it appears absent upon administration of a 12-adrenergic antagonist (Hurlemann et al., 2005; Strange et al., 2003). This has been proposed to occur as an encoding disruption at the synaptic and/or systems level (Strange et al., 2003; Strange and Galarza-Vallejo, 2016). Others, however, have proposed that the amnesic effects, specifically retrograde amnesic effects in free recall, could be due to item unavailability at retrieval and can be reversed by cueing recall (Detterman, 1976). Furthermore, it remains possible that pharmacological influences were still present at the time of retrieval (Hurlemann et al., 2005), complicating untangling encoding vs. retrieval effects on emotion-induced retrograde amnesia.

To provide more insight on free recall and interitem organization Kahana (1996) developed a quantitative method to analyze free recall data termed conditional response probability (CRP). CRP quantifies, under the fact that x is immediately followed by y, the probability of recalling item x, given that item 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 and Shiffrin, 1980). At time of recall, recollection of an item serves as a contextual cue for the recollection of related items explained by the *temporal context model* (Howard and Kahana, 1999)*.* More recently Polyn et al (2009) expanded this work, by developing the Context Maintenance and Retrieval (CMR) model, to distinguish between different types of contexts that affect item encoding and recall dynamics: temporal context refers to items that were studied close in time, source context which refers to the source commonalities among items and, lastly, semantic relatedness (Polyn et al., 2009).

Electrophysiological studies have further confirmed these theories and computational models by providing neural evidence of context reinstatement; specifically, 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 et al., 2018; Manning et al., 2011). Neural evidence of the behavioral lag contiguity effect as a recovery of temporal context during retrieval is present in both recordings from the hippocampus and amygdala (Folkerts et al., 2018).

To address enhanced memory for emotional items and an amnesic effect for its surrounding items in oddball tasks in the context of the CMR computational model, Talmi et al. (2019) developed a variation of the model: the emotional CMR (eCMR). Talmi et al. (2019) showed in simulated data, that increasing attention to the oddball at encoding would increase its link to temporal context and help promote its recall. However, due to the fact that the oddball has a different source context than the rest of items in a study list, there would be a decrease in source and semantic similarity between the oddball and the rest of items (Talmi et al., 2019).

At first glance, the core features of the lag contiguity effect are conflicting with the findings that recall of words nearby an oddball are less well-remembered (Strange et al., 2003). However, the eCMR model explained these effects by positing that the oddball presentation produced a source context switch which disrupts temporal context therefore, hindering the recall of the items near the oddball (Talmi et al., 2019). This was further explained by applying the model to simulated recall data in which they reported decreased CRP of items following the oddball i.e a decreased likelihood of retrieving items presented right after the oddball (Talmi et al., 2019). Although the eCMR model has provided a framework to expand the CMR model to the recall of lists containing an emotional oddball, this has yet to be investigated empirically.

In the context of the computational models of recall abovementioned, a strong contextual change, produced by an oddball presentation, would predict a contextual item association shift from the oddball presentation onwards. We would expect oddballs to be recalled early in recall order (Elhalal et al., 2014; Talmi et al., 2019). Given the shift in source context, we would anticipate for items studied after the oddball at encoding to be strongly coupled with the oddballs at retrieval, and therefore, for items following the oddball to show enhanced CRP. Specifically, we hypothesize this forward lag contiguity enhancement to account for the retrograde amnesic effect. That is, if an oddball is well remembered and involves a forward progression of recall, it will be less likely that preceding items (i.e oddball-1) will be recalled.

All in all, in the present study we aim to investigate oddball effects, using emotional and perceptual oddballs, in a sample of 70 healthy young participants, on a Spanish version of the oddball free recall paradigm originally reported in Strange et al. (2003). Previously reported retrograde amnesia effects (Angelini et al., 1994; Schmidt and Schmidt, 2016; Tulving, 1968) were limited in temporal duration, spanning to the order of 1 second. Therefore, in the present task we aim at 1) investigating how recall patterns are modulated by timing (SOA) by introducing 5 different SOAs (1, 2, 3, 4 and 6 seconds) which were fixed within a list. Furthermore, we recorded the order in which nouns were recalled and studied in order to 2) apply computational models to empirical data to evaluate how the presentation of an oddball modulates recall and 3) investigate whether there is a forward-contiguity enhancement and how it influences the recall of the words preceding the oddball.

# **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. The study had full ethical approval from the Universidad Politécnica de Madrid ethics committee.

**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, 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. 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.

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| **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 immediately 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.

**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)].

**Analyses.** Lists that contained data collecting errors (e.g missing data, repeats) were excluded from all analyses across all subjects (11 emotional lists, 6 perceptual lists out of a total of 20 emotional and 20 perceptual lists per subject). All analyses were conducted using MATLAB (R2019b, The MathWorks, Inc). Statistical analyses and figures were conducted on Rstudio (version 1.3.1093). All data was tested for normal distribution using Shapiro-Wilk or QQ plots, Greenhouse-Geisser sphericity correction was applied when appropriate.

Conditional 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 et al., 2019; Kahana, 1996).

# **RESULTS**

## **Emotional and perceptual oddballs are remembered rather late during recall and primacy effects are preserved**

We assessed the overall probability of first recall in our dataset, including the first two recalled items. We conducted a three-way RM ANOVA (serial position [1-14] x recall [oddball recalled, oddball forgotten] x oddball type [emotional, perceptual]). We aimed to investigate not only the effects of oddball type and serial position but also to assess whether recalling an oddball produced a change in the probability of first recall curves. The counting backwards distractor task correctly abolished recency effects in all conditions.

There was not a significant three-way interaction between oddball type x recall x serial position (F(8.44, 582.31)=0.802, p=0.607, nor a significant two-way interaction between oddball type x recall (F(1, 69)=0.184, p=0.670) nor oddball type x serial position (F(8.54, 589.06)=0.988, p=0.447). However, there was a significant recall x serial position interaction (F(8.82, 608.52)=5.527, p<0.0001) indicating that the probability of first recall of the word in the 1st serial position was higher when oddballs were recalled vs. when they were not (t(139)=-3.25, p=0.001) as well as in the 7th position (t(139)=-3.70, p<0.001). However, items in the 3rd (t(139)=2.30, p=0.02), 12th (t(139)=-3.74, p<0.005) or 13th position (t(139)=3.73, p<0.005) had a higher probability of first recall in lists in which the oddball was forgotten vs. recalled. Furthermore, there was a significant main effect of recall (F(1, 69)=7.15, p=0.009), which showed that lists in which an oddball was recalled (mean=0.071) had a higher probability of first recall than when oddballs were not (mean=0.07). Lastly, there was also a significant main effect of serial position (F(3.82, 263.26)=61.183, p<0.0001), consistent with the primacy effect (Fig. 2).

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| **Figure 2.** Graphs show probability of first recall; bars represent mean. Both graphs show a strong primacy effect in emotional and perceptual lists which is enhanced in trials in which the oddball was recalled. |

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. A Wilcoxon rank sum test showed that emotional oddballs were recalled significantly later than perceptual oddballs (W=395538; p<0.0001) (Fig. 3).

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| **Figure 3**. Bars show mean SEM. Graph shows the relative recall position of the emotional oddball and the perceptual oddball. Emotional items were recalled slightly later than perceptual oddballs (p<0.0001). |

We confirmed a primacy effect was maintained and enhanced in trials in which the oddball was recalled. However, contrary to what we expected, 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)]. If, say, an item was recalled on the 6th position out of a total of 6 items recalled; that would produce a relative recall position of 1; whereas an item recalled on the 1st position, would have a relative recall of 0.167.

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

We next sought to investigate overall recall of the oddballs and the items nearby to investigate whether the previously-reported retrograde and anterograde (Strange et al., 2003) amnesic effects in the words near the oddball were present in the present 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.

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<0.0001) and a trend towards significance in oddball type (F(1, 69)=3.44, p=0.07). Uncorrected post-hoc t-tests showed a significant enhancement in oddball recall compared to its nearby items (vs. odd-1 t(139)=-10.75, p<0.0001; vs. odd-2 t(139)=-9.5, p<0.0001; vs. odd+1 t(139)=10.41, p<0.0001). Furthermore, emotional oddballs were significantly better recalled than perceptual oddballs (t(69)=3.93, p<0.001) (Fig. 4). For completeness, we conducted contingency analyses on the oddballs and odd-1 items which showed that recalling the oddballs did not come at cost of recalling its items preceding them (Fig. S1).

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| **Figure 4.** All graphs show mean SEM.Graph showing the proportion of normalized recalled words (minus control) items across word positions, oddball (odd), -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). Oddballs were better recalled than its surrounding items. |

## **Recall patterns in an oddball task are modulated by SOA**

Previous literature has shown conflicting results regarding SOA manipulations and their effect on retrograde and anterograde amnesia. In the present study we modulated item presentation by varying SOAs to 1, 2, 3, 4 and 6 seconds. These results indicate that longer SOAs show a trend to increased memory compared to shorter ones (Fig. 5), however, since we found no significant interactions between SOA and oddball type or word position, we did not further investigate the issue with follow-up post-hoc tests.

We ran 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 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). 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 also a significant main effect of SOA (F(4, 276)=3.87, p=0.004) which showed, that at SOA 1 all words were less well remembered than at SOAs 2, 3 and 6 (vs. 2 t(559)=-3.78, p<0.0001; vs. 3 t(559)=-3.76, p<0.0001; vs. 6 t(559)=-5.11, p<0.0001). Furthermore, words shown at SOA 4 were less well remembered than at SOAs 2 (t(559)=2.90, p<0.05), 3 (t(559)=2.81, p<0.05) and 6 (t(559)=-4.03, p<0.0001). 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 (p<0.001 vs. all items). 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). We further conducted contingency analyses on the oddballs and oddball-1 items. Emotional lists showed a significant co-dependency whilst perceptual lists did not (Fig. S2).

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| **Figure 5.** Modulation of normalized recall as a function of SOA. Bars show normalized recall (- control) with mean SEM by SOA. All contingency tables are shown to compare memory for oddballs and items at oddball-1 serial positions. |

## **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.

### **Do conditional response probability curves preserve a forward-contiguity effect?**

Firstly, taking all recalled words, we evaluated CRP curves 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 when oddballs were recalled as well as when they were forgotten (Fig. S3).

A three-way RM ANOVA (oddball 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 type x lag (F(4, 276)=0.93, p=0.47), oddball 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 type (F(1,69)=4.07, p=0.048), lag (F(2.95,203.77)=105.11, p<0.0001) and lag x direction interaction (F(3.06, 210.95)=13.58, p<0.0001). Uncorrected post-hoc t-tests showed enhanced CRP for contiguous lags, specifically lags 1 and 2 as well as a significant forward effect for lags 1 (t(139)=-5.11, p<0.0001) and 5 (t(139)=4.15, p<0.0001).

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| **Figure 6.** CRP curves show a preserved forward-contiguity effect for both emotional and perceptual oddball lists. |

### **Do transitions to and from oddballs modulate conditional response probability curves?**

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

We calculated CRP curves for items recalled right before the oddballs (to evaluate transitions to the oddballs) and for items recalled right after the oddballs (to evaluate transitions from the oddballs). Again, we found a significant main effect of lag (F(4, 36)=0.02), which showed a contiguity effect for lag 1 (p<0.001), a trend of direction (F(1,9)=4.63, p=0.06) and, importantly, a significant oddball x transition interaction (F(1,9)=14.34, p=0.004) that revealed an enhancement in CRP in transitions from emotional oddballs compared to perceptual oddballs (t(573)=4.47, p<0.0001) as well as a significant difference in transitions to emotional oddballs vs. transitions from emotional oddballs (t(584)=4.18, p<0.0001) (Fig. 7). None of the other effects reached significance levels.

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| **Figure 7.** CRP curves in transitions to and from emotional and perceptual oddballs. Transitions from emotional oddballs show enhanced CRP compared to perceptual oddball lists. |

## **Does enhanced forward contiguity in emotional oddball lists 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. 7). As hypothesized, transitions from emotional oddballs showed an enhancement in the CRP curves which was not present in transitions from perceptual oddballs. We next ought to test whether this CRP enhancement in transitions from emotional oddballs (specially at lag +1) explained retrograde amnesia for E-1 items. A Spearman’s rank correlation, however, did not show a significant relationship between the two variables [E-1 normalized recall and lag +1 values], (rho=-0.04, p=0.76) (Fig 8).

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| **Figure 8.** Spearman’s correlation between normalized recall values of E-1 items and CRP values at lag +1 in transitions from emotional oddballs. |

Considering that, on average, contrary to what we expected, the relative recall positions of the oddballs was rather late (Fig. 3) we investigated whether E-1 recall position changed depending on the recall position of emotional oddballs. Indeed, we found that when emotional oddballs were recalled at late positions, recall moved in the forwards direction from E-1 items to emotional oddballs. However, when oddballs were recalled early on, recall moved in the backwards direction (from emotional oddballs to E-1 oddballs) (Fig. 9).

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| **Figure 9.** Plot shows the recall pattern relationship between emotional oddballs and E-1 oddballs. X axis shows the recall position of emotional oddballs whilst y axis shows the recall position of emotional oddballs minus the recall position of E-1 items. Therefore, negative values show a *forwards recall* (E-1 to E) whilst positive values show a *backwards recall* (E to E-1). |

# **DISCUSSION**

In the present study, 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 the task in 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 used in Strange et al. (2003) consisted on 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 improves as SOA increases with the exception of perceptual lists at SOA 4 is most likely driven by the fact that the chosen control words are recalled even better than the perceptual oddballs. It remains possible that in previous experimental designs the presentation of emotional oddballs were increasing salience for perceptual oddballs, and therefore, contributing to their increased recall (Sutherland and Mather, 2012) which did not occur in the present task. Furthermore, when emotional oddballs were recalled at late serial positions, recall moved forwards i.e from E-1 to E, however, when oddballs were recalled early on, recall went backwards from E to E-1. Indicating that when emotional oddballs are recalled early-on, E-1 items are recalled later-on

Arousal-biased competition theory suggests that memory for items with increased priority (due to increased arousal and attention to that item) is increased, whereas items with low priority (e.g neutral items vs. oddballs) are less well remembered (Mather and Sutherland, 2011). The idea of increased attention to the oddballs has been the basis for the development of a variation of the computational model CMR; the eCMR (Talmi et al., 2019) where, by calculating CRP curves, they showed that increased recall of an emotional oddball hindered recall of its nearby items. Specifically, contrary to the present findings, Talmi et al. (2019) report a decreased forward-transitioning effect from emotional oddballs after a temporal context disruption (i.e a simulated presentation of an emotional oddball). While the present empirical findings find the opposite effects that eCMR model predicts and a later-than-expected oddball recall, as we report an enhancement in forward transitions from emotional oddballs, transitions from perceptual oddballs show a diminished forward transition effect, in line with the predictions of the computational model eCMR model. These results indicate that modeling increased attention to oddballs alone, does not explain CRP curves in emotional oddball paradigms but it does in perceptual oddball paradigms.

Increased attention due to increased arousal produced by item presentation can occur due to a variety of interacting factors. Perceptual salience is mainly modulated by bottom-up processes whereby, in the present study, the presentation of an item in a different font evokes perceptual salience for that item. On the other hand, emotional salience, is modulated by an interaction of top-down and bottom-up processes (Mather and Sutherland, 2011). Furthermore, behavioral studies investigated the influence of emotional modulations on attention and perception via the presentation of 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. Considering that emotion and attention interact to modulate perception, we propose that, in the context CRP curves from free-recall oddball paradigms, the eCMR model explains perceptual oddball salience. However, it still requires fine-tunning to model an *emotional factor* to interact with the increased attention to the oddball in order to account for the present empirical results of emotional oddball modulations of CRP curves. Alternatively, this could also be explained by the fact that emotionality in the current version of the eCMR model is an all-or-none phenomenon (Talmi, 2020), which could account for perceptual salience (as in the present results) but may not be suitable to model emotional salience.

This is analogous to the role of the -adrenergic system, which plays a key part in emotional processing. In this line, previous work showed that propranolol, a -antagonist, blocked memory for emotional but not perceptual oddballs (Strange et al., 2003). It is possible that carry-over effects after exposure to emotional oddballs (Schmidt and Schmidt, 2016) induces 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.

Further research of emotion on context representation in free recall tasks comes from Long et al. (2015) who presented lists of several items including neutral as well as emotional (positive and negative) and investigated free recall patterns for which they found emotional item clustering. They concluded that 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 et al., 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.

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 hypothesized that this enhancement in transitions from emotional oddballs would explain the widely reported retrograde amnesic effect in these types of paradigms, however, it did not seem to be the case. This, however, could be due to the fact that the present version of the task did not induce as strong retrograde amnesic effects as previously reported work. Future work could re-evaluate this approach in tasks which induce a stronger retrograde-amnesic effect. Furthermore, the current results provide empirical evidence that could be used to update the eCMR model. Previous studies using oddball paradigms had found a mnemonic enhancement for oddballs accompanied by a strong retrograde amnesic effect (Schmidt and 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 in order 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 3 seconds (Strange et al., 2003). We found a significant main effect of SOA which showed that overall, the shortest SOA (1 second) demonstrated worse recall than longer SOAs except at SOA 4 seconds. We next decided to focus on emotional oddballs and evaluated whether the CRP enhancement in transitions from emotional oddballs explained the retrograde amnesic effect, however, we did not find such significant correlation which could be explained by the fact that the retrograde amnesia in the present task was not strong.

The present results could help the study of memory in disorders where strong emotion plays a key role such as posttraumatic stress disorder (PTSD). Although, in the context of PTSD, research conducted in a laboratory setting highly differs from a real-world setting, research with functional magnetic resonance imaging has shown similar brain activity in trauma-unrelated settings which involve negative emotions such as sadness and anxiety as trauma-involving settings (Lanius et al., 2010). PTSD research has shown that recollection of traumatic events differs from natural, neutral events and, that retrograde amnesia and dissociative experiences are also present in the disorder (Brewin and Holmes, 2003; van der Kolk and Fisler, 1995). Applying quantitative approaches such as done in the present study to investigate memory recollection in PTSD would help elucidate the underlying mechanisms of memory recall underlying the disorder.

**CODE AVAILABILITY**

Raw data, analysis pipelines, statistical results and figures can be found here: <https://github.com/TheStrangeLab/Odd_SOA_CRP>

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