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Abstract

Emotion enhances episodic memory, an effect thought to be an adaptation to prioritise the memories that

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best serve evolutionary fitness. But viewing this effect largely in terms of prioritising what to encode or

consolidate neglects broader rational considerations about what sorts of associations should be formed at

encoding, and which should be retrieved later. Although neurobiological investigations have provided many

mechanistic clues about how emotional arousal modulates item memory, these effects have not been wholly

integrated with the cognitive and computational neuroscience of memory more generally.

Here we apply the Context Maintenance and Retrieval Model (CMR, Polyn, Norman & Kahana, 2009) to this

problem by extending it to describe the way people may represent and process emotional information. A

number of ways to operationalise the effect of emotion were tested. The winning emotional CMR (eCMR)

model reconceptualises emotional memory effects as arising from the modulation of a process by which

memories become bound to ever-changing temporal and emotional contexts. We show that eCMR provides

a good qualitative fit for the emotional list composition effect and the emotional oddball effect, illuminating

how these effects are jointly determined by the interplay of encoding and retrieval processes, and discuss

the prediction of the model to delayed memory tests.

By leveraging the rich tradition of temporal context models, eCMR helps integrate existing effects of emotion

and provides a powerful tool to test mechanisms by which emotion affects memory in a broad range of

paradigms.

Key words: Memory, Emotion, Arousal, Retrieved context models, Free recall.

1. Introduction

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There is tremendous interest in the effect of emotional arousal on episodic memory. The literature generally agrees that moderate emotional arousal enhances item memory (Cahill & McGaugh, 1998; LaBar & Cabeza, 2006; Yonelinas & Ritchey, 2015). However, the circumstances in which it does so, and the mechanisms and models by which these effects are understood, might look unusual to a student of memory more generally. The mainstream human memory literature has traditionally tested memory within minutes of encoding because most functional manipulations do not dissociate immediate and delayed memory performance. By contrast, the research focus for emotional memory is on factors that influence delayed memory, and those are interpreted mostly in terms of prioritised storage of memory. Furthermore, the emotional memory literature has so far marginalised the influence of the retrieval test, which the mainstream memory literature cares a great deal about. One reason the focus of the emotional memory literature on long-term storage of memory traces and their delayed retrieval seems appealing is that it suggests an interpretation in terms of the broader purpose of memory in guiding behaviour, and connections to an emerging set of rational, decision-theoretic accounts of the allocation of limited cognitive resources. In particular, emotionally charged memories may be most relevant to fitness-relevant decisions later (Boureau, Sokol-Hessner, & Daw, 2015; Gershman & Daw, 2017), and therefore should enjoy priority for encoding and maintenance in the face of limited memory capacity. However, we argue this view is incomplete from both an empirical and a normative perspective.

Empirically, current models of emotional memory fail to predict when enhancement would be exhibited and when it would not. In particular, a simple prioritization explanation fails to account for situations in which emotion does *not* benefit memory, such as in free recall tests for pure lists of emotional and neutral stimuli (the emotional list-composition effect, described below); in recognition tests for mixed lists of emotional and neutral stimuli (Dougal & Rotello, 2007; Sharot & Yonelinas, 2008); and in tests of associative memory (Bisby, Horner, Hørlyck, & Burgess, 2016; Madan, Caplan, Lau, & Fujiwara, 2012). Moreover, existing models of emotional memory concentrate on maintenance, and to a lesser degree, encoding. Yet outside the

emotional memory sphere, there has been a recent emphasis on retrieved context models of memory, which

stress associations between items and context during study and the way these interact with retrieval

processes (Howard & Kahana, 2002a; Lohnas, Polyn, & Kahana, 2015; Polyn, Norman, & Kahana, 2009;

Sederberg, Howard, & Kahana, 2008). Here we reinterpret emotional memory effects in the framework of

retrieved context models with the aim to explain how emotion enhances episodic memory through their

already-established mechanisms, thus bringing the emotional memory literature more closely into the fold

of the mainstream memory literature. In so doing, we can clarify the relation of emotional memory effects to

other established memory effects.

Apart from addressing these empirical considerations, retrieved context models suggest a more nuanced

normative interpretation. Instead of simply ranking which individual items should be prioritized in isolation,

the retrieved context models speak to what sorts of memory structures should be built by encoding

associations among these items. Indeed, these associations themselves have a clear normative

interpretation in that the item-context associations at the heart of retrieved context models mathematically

correspond to a particular sort of world model for guiding utility maximizing future choices (Gershman,

Moore, Todd, Norman, & Sederberg, 2012). Retrieved context models also shed light on the distinct question

of how memories will be prioritized for retrieval in a test context. In decision making, such modulation of

retrieval will promote consideration of particular (emotionally charged) outcomes of candidate actions, and

are reminiscent of mechanisms independently proposed in the decision-making literature for rationally

prioritized evaluation (Cushman & Morris, 2015; Huys et al., 2012).

Our aims are, first, to consider systematically the different ways in which emotion can be operationalised

within retrieved context models, specifically the Context Maintenance and Retrieval Model (CMR); and

second, to identify which constellation of mechanisms allow the extended model, emotional CMR (eCMR), to

capture qualitatively key effects of episodic memory for emotionally arousing items.

1.1 Existing models of emotional memory

The focus of the literature on emotional memory on delayed effects stems partly from the social value of

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understanding memory for key life events, that is, memories for experiences that define us as people

(graduating from school, winning a competition) and as community members (birthdays, weddings, flash-

bulb memories for culturally important events). Another contributing factor for the focus on delayed

memory is that the dominant model for emotional memory, the modulated-consolidation model (Cahill &

McGaugh, 1998; McGaugh et al., 2000), is concerned with effects that manifest themselves after a few

hours, but not before.

Related to this, much of the theory-building work on human emotional memory has been conducted at the

level of the neurobiological mechanism, contributing to an emphasis on consolidation processes and testing

memory post-consolidation. In addition to the modulated-consolidation model (Cahill & McGaugh, 1998;

McGaugh et al., 2000), other models include the Emotional-Binding Account (Yonelinas & Ritchey, 2015), and

GANE (Mather et al., 2015). It remains much less clear how emotional memory enhancement relate to the

processes associated with the cognitive and computational neuroscience of memory. This is because factors

that have traditionally interested human memory researchers, such as the level of processing at encoding, or

the nature of the memory test, are not central to these frameworks; and none of these frameworks have

been implemented quantitatively in a formal model. Talmi's multi-factor mediation mode (Talmi, 2013)

discusses a number of known cognitive processes that allow emotion to influence encoding and retrieval, but

like all other existing models of enhanced emotional memory, this model, too, did not yield quantitative

predictions.

In addition, these models also are not able to relate to current memory effects because they neglect the

retrieval stage. Both the Modulated-consolidation model and the emotional binding account attribute all of

the explanatory power to processes that occur after stimulus encoding is completed. The former suggests

that emotional arousal directly modulates the consolidation of memory traces, a process that can be

triggered when emotional stimuli are encoded but equally when arousal is experienced after neutral stimuli

are encoded. The latter suggests that the arousal experienced at encoding results in attenuated forgetting

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because of reduced interference from less-common emotional experiences, without influencing

consolidation. Arousal-Biased Competition (ABC) theory (Mather & Sutherland, 2011) dissects the influence

that arousal has on competitive attention allocation at encoding, while GANE (Mather, Clewett, Sakaki, &

Harley, 2015) also proposes a neurobiological mechanisms for the effect of arousal and arousal-attention

interactions on protein synthesis after encoding is completed. Less central to ABC and GANE are non-

attentional factors that can influence performance on subsequent memory tests memory tests, such as the

nature of the test itself (recall, recollection, familiarity) or its timing (prioritised encoding should enhance

both immediate and delayed memory).

This neglect of the retrieval stage in these frameworks looks odd when compared to the mainstream human

memory literature, where the consensus has long been that the conditions of retrieval often determine

memory performance, as in the encoding specificity principle (Tulving & Thomson, 1973) and transfer-

appropriate processing (Graf & Ryan, 1990) as well as their neural concomitant, instantiation (Danker &

Anderson, 2010). Specifically in relation to emotion, the literature on mood congruency established that the

retrieval context matters for emotional memory, with memory performance increases when the mood at

encoding and retrieval is consistent (Blaney, 1986). A study where participants encoded and retrieved stimuli

with an emotional or a neutral context showed that this effect is not due solely to an emotional context at

encoding or at retrieval, but to their match (Xie & Zhang, n.d.)

1.2 The potential of retrieved context models in research of emotional memory

Generally, memory is better when the similarity between the mental context of the test and the context that

prevailed when a particular item was encoded is greater. Some have attributed the recency effect to such

contextual similarity (Glenberg & Swanson, 1986; Neath, 1993). A "brain state" (Tambini, Rimmele, Phelps, &

Davachi, 2017) is a term that is employed currently to describe mental context that evolves and changes

gradually with time (Bower, 1967; Estes, 1955). By moving from random fluctuations in mental context to encoding-dependent changes in context, where context changes as a result of experiencing individual episodes or experimental stimuli, temporal context models that have had much success in accounting for free recall dynamics (Howard & Kahana, 2002a; Sederberg et al., 2008), including not only recency effects but also, famously, the contiguity effect - the propensity to recall contiguously items that have been encoded close in time to each other. The contiguity effect correlates highly with memory success (Sederberg, Miller, Howard, & Kahana, 2010).

While the temporal context model (Howard & Kahana, 2002a) based memory solely off of temporal associations, it has been clear for some time that semantic associations also contribute to retrieval success (Howard & Kahana, 2002b). CMR (Polyn et al., 2009) formally includes the non-temporal context of encoding. CMR is a computational model that makes predictions about memory dynamics in free recall and recognition. Built on the notion that the content of a memory is intimately tied to its associated (internal) context, CMR assumes that each presented item is associated with a context state, and that the brain's maintained state of context is updated by each presented or retrieved item. In this way, context changes slowly over time, as a recency-weighted sum of prior context states. During memory retrieval, the current context state is used to cue recall or recognition. CMR includes two dimensions of items' non-temporal context. Semantic context refers to the pre-experimental associations between studied items. Source context refers to any specific encoding operations performed during the study of some items but not others; in Polyn's et al.'s first simulation this referred to judging the size of half of the items in the list and the animacy of the other half. CMR also assumed that a switch between these two source contexts triggers an extra 'drift' in the temporal context. Although this assumption was necessary for CMR to account for the effects of encoding tasks, it is not clear exactly when this assumption is entirely necessary, a point we return to in section 3. The model was supported by evidence of clustering around the source context, concomitant with reduced reliance on temporal context (Polyn, Erlikhman, & Kahana, 2011; Polyn et al., 2009). Because similarity between the study and test contexts on any dimension can help retrieve a studied item, this

generalisation enables CMR to explain the increased tendency to recall contiguously items that are similar to

each other on non-temporal dimensions.

The fact that CMR considers the memory consequences of the similarity between encoded experiences beyond temporal context alone is important for the purpose of accounting for the effects of emotion on memory, not only to represent the emotional dimension of presented stimuli, but also because emotional stimuli are often more similar to each other than randomly selected neutral stimuli, as discussed below. Indeed, if one only assumes that emotional items have a higher degree of similarity to one another, CMR would predict that participants will cluster their recall around the dimension of emotionality. There is, in fact, empirical evidence for emotional clustering of free recall. In one study participants encoded three pure lists of emotional, random-neutral and related-neutral items, and received a single, surprise final free recall test after all three lists were encoded (Talmi, Luk, McGarry, & Moscovitch, 2007). Participants who clustered their recall around list categories exhibited a larger emotion-enhanced memory . In that study, temporal and emotional context effects were confounded because the three categories were studied in three separate lists, but emotional clustering appears also in free recall of mixed lists that contain both emotional and neutral items. For example, Barnacle et al. (Barnacle, Montaldi, Talmi, & Sommer, 2016) presented participants with mixed lists of emotional and neutral pictures which were equally semantically related, and found clustering around the emotional/neutral category; the degree of clustering predicted memory performance. Long and colleagues (Long, Danoff, & Kahana, 2015) presented participants with mixed lists of words, some of which were negative and some positive, and found that participants tended to retrieve positive items after other positive items, and similarly for negative and neutral items. In another study the transition probability from pleasant items to pleasant items, and from unpleasant items to other unpleasant items, was higher than the transition from neutral to neutral items (Siddiqui & Unsworth, 2011). These findings suggest that participants retrieve the valence, which updates the context and becomes part of the next retrieval cue. Importantly, Long et al (2015) found that emotional clustering was observed even when pre-experimental semantic associations between words (obtained through latent semantic analysis scores) were taken into account.

1.3. The emotional Context-Maintenance and Retrieval (eCMR) model

capture the empirical emotional list composition effect.

Although CMR did not consider emotion, by putting together a general scheme to consider multidimensional similarity between stimuli CMR provides an infrastructure that we exploit here to examine hypotheses about the loci where emotion influences memory. In this section, we consider systematically which aspect of CMR may be influenced by emotion. This results in 3 possible variants of our extended model, eCMR, which are described formally in the appendix. The baseline model simply represents certain items as belonging to an emotional category, and others as belonging to an emotional category. The next variant allows emotional items to attract more attention than neutral items during encoding. In the final variant we remove an assumption that was included in the first two variants, that alternating between emotional and neutral items causes context drift. In the next section, we describe the list composition

1.3.1 The baseline variant of eCMR: Emotional items are represented as belonging to an emotional item

pattern resulting from each of these variants, and show that the third model variant emerges as best able to

category

In CMR each item is represented with three types of features: temporal, semantic, and source. Semantic features – essentially, the identity of the item - are implicitly represented in a matrix that codes the pre-existing associations between items. Temporal features, dating back to the original temporal context model, are unique to each presented item. Each item also has a 'source' feature corresponding to aspects of the stimulus that are common to a number of stimuli in the study set. This was introduced in CMR to represent the orienting task that alternated during encoding. For example, when participants judged the size of some items and the animacy of the rest, the orienting task was represented as a source feature. Polyn and colleagues also recognized that source features could be internal – unique operations that participants may engage in during the encoding of certain stimulus types. In CMR, the semantic item features determine the

semantic context of items, and semantic similarity increases an item's chances of retrieval, but does not further influence encoding. By contrast, items update their temporal and source context during the experiment itself (see appendix), such that items that are encoded close to each other in time, or through the same orienting task, share a more similar temporal or source context, respectively, a similarity that also boosts retrieval success.

Consider the emotional items that are prevalent in emotional memory experiments, such as a picture depicting a train crash (Figure 1). The baseline eCMR variant replaces the 'source' item feature with an 'emotional' item feature, which defines certain items as 'emotional' and others as 'neutral' (graded coding is entirely feasible but was not necessary for the purpose of the simulations we present here). The emotional features of items update the emotional context, such that it changes more when the first emotional item is presented, and less when subsequently presented items are emotional (Eldar et al., 2016). Just as in CMR items that share source context promote each other's recall, in eCMR items that share emotional context will also promote each other's recall.

The temporal and semantic features are represented in exactly the same way in eCMR as in CMR, but the meaning of the semantic item features is a little different. It is known that randomly selected emotional pictures are rated as more similar to each other than randomly selected neutral pictures (Talmi & Moscovitch, 2004). This is because even when experiments equate emotional and neutral stimuli for some similarities, such as the increased abstractness of emotional words (Vigliocco et al., 2014), emotional stimuli are likely to be perceived as more similar to each other semantically; for example, the words 'bomb' and 'starvation' may be thematically linked within a story of war. Many items used in research may be construed as socially more 'distant' (Trope & Liberman, 2003). Emotional pictures, a prevalent stimulus in emotional memory research, may share affordances such as approach (towards positive content) and avoidance (away from negative content), rendering them more similar to each other (Greene, Baldassano, Esteva, Beck, & Fei-Fei, 2016). Emotional stimuli are also similar because they trigger unique operations when they are encoded, such as feelings, embodied in a myriad of peripheral physiological processes (Bradley, Lang, & Cuthbert,

1993), cognitions, and behaviours, all of which could increase their rated similarity to other emotional items. These differences between emotional and neutral stimuli increase the cohesiveness of emotional stimuli, compared to that of randomly selected neutral stimuli, resulting in increased ratings of similarity of emotional stimuli. The increased similarity between emotional stimuli has memory consequences, and it explains part of the recall advantage of emotional items (Talmi, Luk, et al., 2007; Talmi & Moscovitch, 2004). In eCMR the semantic associations of items encompass both semantic and emotional similarity. It is important to note that some experiments go to great lengths to equate the pre-experimental similarity of emotional and neutral stimuli (Kensinger, 2009b; Schmidt & Saari, 2007; Sommer, Gläscher, Moritz, & Büchel, 2008), including the key experiment we simulate in section 2 (Talmi et al., 2007). However, even when pre-experimental similarity is controlled, however, emotional items will still end up, in effect, more similar to each other in eCMR because on study they will be bound to a shared emotional context.

Lastly, a critical aspect of CMR is the assumption that the temporal context drifts whenever the orienting task alternates during encoding (Polyn et al., 2009). While the task Polyn and colleagues used is akin to task-switching paradigms, mixed lists of emotional and neutral items more closely resemble cue-shift paradigms, where the task remains the same, but cued by several different cues (for example, an animacy-judgment task could be cued by both a circle and a square, while a size judgment task could be cued by both a triangle and a rectangle). Importantly, both task-switches and cue-switches slow reaction times in the post-shift trials (Schneider & Logan, 2006), a result that may indicate that both type of switches could be modelled as causing the temporal context to drift. The baseline variant of eCMR assumes that the temporal context drifts whenever emotional and neutral items alternate, in keeping with CMR, but it is not clear that this assumption is warranted here. In summary, the baseline variant of eCMR is very similar to CMR but uses emotionality as an internal source feature of items.

1.3.2 The attention variant of eCMR: Emotional items are represented as belonging to an emotional item category and as attracting extra attention

Emotional stimuli attract more attention than neutral stimuli. Empirically, it is known that when participants are presented with stimuli that trigger emotional arousal, the arousal enhances attentional selection, modulation and vigilance (Golomb, Turk-Browne, & Chun, 2010). For example, autonomic arousal or visual attention to objects that have been previously presented on emotional backgrounds is enhanced even when those emotional backgrounds are no longer there (Ventura-Bort et al., 2016). The amygdala is thought to drive these effects by appraising stimuli as goal-relevant (Sander, Grafman, & Zalla, 2003) and enhancing the processing of these stimuli in downstream sensory processing regions. The amygdala-driven allocation of attention to emotional stimuli is distinct from (direct) stimulus-driven effects or strategic top-down effects (Pourtois, Schettino, & Vuilleumier, 2013). The mechanism involves amygdala-dependent activation of the locus coeruleus, where noradrenergic neurons increase the neural gain throughout the brain through their wide-ranging projections (Mather et al., 2015). The general consensus in the emotional memory literature is that the attentional effects are driven by emotional arousal, rather than valence (Bradley, Greenwald, Petry, & Lang, 1992; Hamann, 2009, Mather & Sutherland, 2009; Schimmack & Derryberry, 2005; but see Kensinger, 2009a) or other aspects of the emotional experience. We do not take a stance on this here eCMR only assumes, based on the consensus in the literature, that stimuli high on the 'emotional' item feature attract attention preferentially.

In retrieved context models such as CMR, CMR2 and TCM-A (Lohnas et al., 2015; Polyn et al., 2009; Sederberg et al., 2008), increased attention to early stimuli in the study list has been implemented by strengthening the associations between items and their contexts. This is accomplished by modulating the step-size or learning rate parameter on encoding these items, itself a standard mechanism to capture competitive attentional effects in associative learning theories more generally (Dayan, Kakade, & Montague, 2000; Pearce & Hall, 1980). eCMR utilises this method to represent the increased attention that emotional items receive at encoding. This decision is based on evidence that enhanced attention to emotional stimuli is linked to tighter associations between stimuli and their context. The priority-binding hypothesis (MacKay et al., 2004) concludes that emotional items are bound more strongly to their presentation context than neutral items. This is evident in that emotional items escape the attentional blink more readily – namely,

they are more likely to be reported when presented in a rapid serial visual stream close to a target stimulus -

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because they are bound better to their encoding context (Anderson, 2005; Mackay, Hadley, & Schwartz,

2005). Attention is thought to be allocated preferentially to features perceived as belonging to the same

emotional object, increasing the degree to which object features are bound together (Mather, 2007),

measured, for example, as increased memory for the source of within-object features, such as the font

colour and screen location of taboo words (MacKay & Ahmetzanov, 2005). Retrieved context models imply

additional consequences of this enhanced binding: In particular, the items with the best chances to be

recalled are those that are most strongly bound to the temporal context, all other factors held constant. One

piece of evidence for this suggestion is the significant covariation between the late positive potential at

study, an ERP sensitive to stimulus-driven attention, and memory success (Chen, Lithgow, Hemmerich, &

Caplan, 2014). In summary, this variant of eCMR encapsulates the baseline variant but also assumes that

items coded as 'high' on an emotional item feature attract more attention, which increases the strength of

their binding to the temporal context.

1.3.3 The final variant of eCMR: Emotional items are represented as belonging to an emotional item

category, they attract extra attention, but alternating item type does not cause context drift

The previous two eCMR variants assumed that whenever item type alternates from emotional to neutral and

vice versa, the temporal context shifts, in keeping with CMR. Motivated by the results of simulation 2, the

final variant no longer makes this assumption. It is identical to the previous variant in all other respects. As

we show in the next section, this variant succeeded in capturing the empirical emotional list composition

effect.

To preview how eCMR works to capture the advantage emotional items have over neutral ones in the recall

of mixed lists, note that emotional stimuli are attended preferentially here, so that they are more strongly

bound to their temporal context at encoding than neutral items. Therefore, they dominate the temporal

context of the memory test. Typically, the emotional items participants encoded also render the emotional context of the test is also more emotional than usual. For both of these reasons, it is more likely that recall would begin with an emotional, rather than a neutral item. Because emotional items always share an emotional context, and often also are more closely related to each other semantically than other items, they promote each other's recall, which adds to their advantage, and additionally impairs memory for neutral stimuli by adding interference that changes the test context away from the encoding context. eCMR thus describes emotional memory enhancement as multiply determined, in keeping with the multiple factors previously posited to contribute to this effect (Talmi, 2013).

1.4 Overview of aims and objectives.

Thus far we have delineated, in broad terms, the limitation of previous models of emotion-enhanced memory and the promise of an extension of CMR – eCMR - to capture the some effects of emotion on episodic memory for items. In section 2 we show that eCMR captures qualitatively the emotional list composition effect, which cannot be explained by existing models of emotional memory: the advantage of emotional over neutral items in the recall of mixed lists, and their diminished advantage in the recall of pure lists. We then probe the retrieval dynamics in eCMR to understand the multiple mechanisms in eCMR that give rise to this effect and render it so robust. We also describe empirical evidence that supports the claim the advantage of emotional stimuli in mixed lists is multiply determined in that it does not rely only on the earlier output of emotional stimuli during recall. In section 3 we show that eCMR also captures a related effect, the emotional oddball effect: the excellent memory for the oddball item, as well as the decrease in memory for items that are encoded close to it in time. In section 4 we examine whether eCMR can capture a classic experiment in the emotional memory literature (LaBar & Phelps, 1998), which presents a pattern of results that is less familiar in the literature of memory modelling, and consider the implications of those results for the predictions eCMR makes for memory after a delay.

2. eCMR captures the emotional list composition effect

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The list composition effect is an umbrella term that refers to an interaction between the typicality of an individual item to be encoded and the global composition of the encoding list (McDaniel & Bugg, 2008). This manipulation could be executed by selecting atypical items that attract special encoding processes because of their own unique attributes, for example those that are unusual, complex, or bizarre; or it could be due to experimental instructions to process a subset of items in a special way, for example by enacting or generating a subset of items while others are silently read. 'Unusual' items are remembered better when they are encoded in the same list as the 'standard' items, but their advantage is minimised or even

eliminated when each item type is encoded separately, in a pure list (McDaniel & Bugg, 2008).

The list composition effect is related to the list strength effect (Ratcliff, Clark, & Shiffrin, 1990), where 'strength' stems from the spaced repetition of some of the items (Malmberg & Shiffrin, 2005). The effects of spaced repetition may not be the same as the effect of unusualness, however, because the latter is thought to be due to the attention and elaboration of unusual stimuli (McDaniel & Bugg, 2008), while longer or deeper processing of standard items does not give rise to the list strength effect (Malmberg & Shiffrin, 2005).

Because emotional stimuli have unique attributes and attract unique processing operations, it is not surprising that emotion also gives rise to an emotional list composition effect. Mixed lists operationalises telling a friend about experiences that include some emotionally arousing aspects (a colleague made an infuriating insinuation, we read a worrying email, and a favourite colleague announced they were leaving during an otherwise unremarkable work day), while pure lists operationalise telling them about more difficult days, with many emotionally arousing aspects (a child broke an arm, we rushed to school, and spent the day in hospital). Across a number of experiments Talmi and colleagues found that while the advantage of emotional stimuli is robust in mixed lists, it is eradicated in pure lists (Barnacle et al., 2016; Talmi, 2013; Talmi & McGarry, 2012). The emotional list composition effect is outside the scope of the modulated consolidation model and the emotional binding account, because it is obtained in immediate memory tests.

It is also difficult to account for the effect using GANE or ABC theory because of evidence that emotional items receive extra attention in both mixed and pure lists. For example, when the task was carried out under divided attention performance on the concurrent auditory choice reaction time task was reduced when participants viewed emotional, compared to neutral pictures in both pure and mixed lists (Talmi & McGary, 2012). In another study EEG was recorded while participants encoded the pictures. Electrophysiological markers of attention and working memory were increased when participants viewed emotional, compared to neutral, pictures (Barnacle et al., in revision). In both of these studies, the list composition did not modulate the increase in attention that emotional stimuli received compared to neutral ones. Furthermore, in a study where we scanned participants with fMRI during encoding in the emotional list-composition paradigm we found no evidence for reduced attention to neutral stimuli or increased attention to emotional stimuli in mixed, compared to pure lists (Barnacle et al., 2016).

These empirical findings motivated us to model increases in attention to emotional compared to neutral items that were equivalent in magnitude across pure and mixed lists in Simulations 2-3. These simulations were expected to decouple the attention and memory effects of emotional arousal, because the attention-driven increase in the strength of the binding of emotional items to the temporal context should only give them a competitive advantage against weakly bound items, such as neutral items in mixed lists. By contrast, attention should not benefit emotional items when they competed against other equally highly attended emotional items (in simulated pure lists). This is because in the simulations presented in this section emotionality was modelled with a binary code, so that all emotional items in pure lists were modelled as equally attended and none should draw attention more than another. In reality, of course, some items will be more emotional to participants than others, attract attention, and would be more likely to win the competition for retrieval during free recall.

Below we describe three ways of operationalising the impact of emotion on CMR, using three straightforward variants of eCMR, based on the considerations discussed in the previous section. The test for each model variant is its ability to mimic qualitatively the empirical pattern of results depicted in Figure 3,

rather than reproduce the numbers themselves. We therefore chose to use very similar parameter values for

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all simulations (Tables 1 and 2) rather than fit the parameters to data. After we describe the simulations of

average recall we describe the dynamics of recall in the third, winning model variant, before describing

additional empirical data that supports the conclusion that the emotional list composition effect depends on

more than one aspect of retrieval dynamics.

2.1 Empirical average recall data

We simulated the average recall data from the emotional and related-neutral conditions in Talmi et al., 2007,

Experiment 2. Details of the methods of that experiment are presented in Appendix 2. The semantic

coherence of the stimuli used in that experiment was matched by selecting neutral items that depicted

domestic scenes, and matching their relatedness in a separate rating study to the relatedness of negative,

arousing emotional stimuli.

The results of this experiment, which are depicted in Figure 3, produced the pattern we refer to in this paper

as the emotional list-composition effect. Emotional stimuli were recalled better than neutral stimuli in the

mixed list condition, but their advantage was diminished, and here non-significant, in the pure list condition.

Qualitatively similar results were replicated in subsequent studies (Barnacle et al., 2016; Barnacle & Talmi,

2016; Talmi, Luk, et al., 2007; Talmi & McGarry, 2012). The emotional list composition resembles non-

emotional list composition effects reported with manipulations such as item generation and enactment

(reviewed in McDaniel & Bugg, 2008).

The results of the pure list condition in this experiment provide a unique insight about the mixed-list results.

This is important, because the majority of emotional memory experiments employ mixed list presentations.

In effect, the pure list condition could be considered a control condition, against which the mixed list

condition should be interpreted. Described in this way, in this experiment, the emotional memory advantage

in mixed lists stemmed entirely from a decrease in memory for neutral items in the mixed-list (compared to

the pure-list) condition rather than from an increase in memory for emotional items in that condition. In fact, in this experiment memory for emotional items was equivalent across pure and mixed lists. Across experiments with emotional and neutral stimuli we always find a decrease in memory for neutral items presented in mixed (compared to pure) lists, while an increase in memory for emotional items in mixed (compared to pure) lists is not always significant. List composition effects are mostly described by reference to the difference between atypical and typical items within list (e.g. predictions 8 and 9 in Table 2 in McDaniel and Bugg, 2008). The conditions that give rise to an advantage of atypical items in mixed,

2.2 Simulations of average recall

compared to pure, lists await further research.

2.2.1 Simulation 1 - the baseline variant of eCMR: Emotional items are represented as belonging to an

emotional item category.

We first examined simulations of the baseline variant of eCMR, which treats emotionality as a category shared among emotional items but not otherwise treated specially. This variant of CMR is closest to CMR, replacing source context in CMR by emotional context in eCMR. Figure 3 shows that, in this case, memory in the mixed lists was decreased compared to memory for pure lists. This decrease was due to the frequent context shifts during the encoding of mixed lists, which decreased the strength of associations between items, and the degree to which items were able to promote each other's recall. In contrast to empirical results, though, the shared emotional context of emotional items did not benefit their recall over that of neutral items. This is to be expected because nothing in the model treated the emotional category differently from the neutral category: in particular, neutral items could also promote each other's recall, because those also shared a neutral context sub-region. The baseline model effectively ignored experimental results that emotion increases attention during encoding. The next model variants attempted to capture these effects.

2.2.2 Simulation 2 - the attention variant of eCMR: Emotional items are represented as belonging to an

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emotional item category and as attracting extra attention

One additional parameter (ϕ_{emot}) was used here compared to CMR to model the effect of emotion. ϕ_{emot} increased the strength of association between item features and the temporal context without concurrently diminishing the strength of association between the current context and previous items. As explained above, this and the next variants of the model simulate an equivalent increase in attention to emotional and neutral stimuli in both mixed and pure lists. Figure 3 shows that this simulation yielded an emotional list-composition effect. Therefore, we can conclude that preferential attention to emotional stimuli, which increases contextual binding, is necessary to the model's ability to simulate this effect. However, because these attentional effects were simulated in both pure and mixed lists differential attention cannot explain the decrease in memory for neutral stimuli seen only in mixed lists. The comparison between simulations 1 and 2 thus shows that attention is necessary, but not sufficient, for eCMR to produce this effect.

The emotional list-composition effect crucially depends on a decrease in memory for neutral items in mixed lists, which was produced here. An intuitive interpretation of this decrease is that enhanced attention protects emotional stimuli somewhat from the impairment to memory that results from the frequent context drifts in mixed lists. In the next simulation we test this interpretation by removing context drifts entirely. This change also serves to address one limitation of Simulation 2, that memory in mixed lists was decreased compared to memory in pure lists, contradicting the empirical results. The results of Simulation 1 suggest that this decrease is due to the context drifts in mixed list, so fixing parameter *d* to zero might help bring memory for mixed lists up, to better match the data. Another interpretation of Simulation 2 is that the attention-dependent advantage of emotional items can only become manifest under conditions of competitive retrieval, as in mixed lists (regardless of any context drifts). Simulation 3 favours this interpretation. In the next section, we describe these competitive retrieval mechanisms in more detail.

2.2.3 Simulation 3 - the final variant of eCMR: Emotional items are represented as belonging to an

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emotional item category, they attract extra attention, but alternating item type does not cause context

drift

The assumption that changing item categories (emotional to neutral and vice versa) shifts the temporal

context was inherited from tasks where the orienting task alternates, but may not be appropriate here,

when item types alternate. To assess whether the success of simulation 2 to capture the emotional list

composition effect depended on that assumption we repeated simulation 2, but now reduced d to 0, a

change that amounts to abolishing the context drift that could occur as a result of the shift between

emotional and neutral stimuli. Figure 3 shows that reducing d to 0 now allowed the model to capture the

empirical results more exactly, implying that context drift is not necessary here. In following simulations we

kept the value of d=0 unless otherwise noted.

In the next section, we examine the retrieval mechanisms that allow eCMR to produce the emotional list-

composition effect in simulation 3. As discussed above, additional attention to emotional items is necessary,

but not sufficient; competition at retrieval is the second, crucial ingredient. Retrieval competition is multiply

determined, and the next section unpacks how it works to favour emotional items only in mixed lists.

2.3 The contribution of retrieval competition to the emotional list-composition effect

In this section, we unpack the retrieval mechanism of the final variant of eCMR, which was described in

Simulation 3. First, we conduct another simulation (Simulation 4) to show that emotional items already have

an advantage when recall commences because of their stronger connection to the temporal context of the

test. Next, we show that the recall advantage when the test commences allows the first emotional item to

promote recall of further emotional items, resulting in an earlier output of emotional compared to neutral

items throughout the recall period. This pattern agrees with available empirical data, and with new data,

reported in Appendix 3. We show that eCMR captures output order for these data. The stronger connection

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of emotional items to the temporal context and to each other implies that they will have a recall advantage

in mixed lists even when they are prevented from being recalled early. We describe new data that support

this hypothesis, and close with an analysis of how transitions during recall multiply determine the emotion

memory advantage compared to less competitive (neutral) items.

2.3.1 Simulation 4: Recall without retrieving the encoding context

Because emotional items are more strongly associated to the temporal context of the test, they should

already have an advantage when recall commences, in the first output position. To show this, in Simulation 4

we use the same model described in Simulation 3, but eliminate the ability of recalled items to retrieve their

study context. The ability of each recalled item to retrieve its encoding context, thereby changing the

retrieval context of subsequent items, is a core aspect of retrieved context models. Therefore eliminating it

was expected to impair memory substantially, but it should not influence the very first recall. This simulation

therefore serves to highlight how binding to the temporal context translates to early recall advantage, free

from the influence of other aspects of the retrieval machinery of eCMR. In Simulation 4 recalled items were

prevented from retrieving their context by setting the parameters that update context during recall, β_{rec}^{temp} ,

 β_{rec}^{emot} = 0. Figure 4 shows that as expected, memory was severely impaired in this simulation, and crucially,

emotional items already had an advantage in the first recall.

Figure 4 plots the probability of recall in Simulation 3 (the final version of eCMR) alongside the probability of

recall in Simulation 4 (where a core retrieval mechanism was eliminated). A comparison of the two plots

serves reveals the effect of retrieval machinery in eCMR in Simulation 3, which contributes to the good recall

of emotional items throughout the recall of mixed lists. We explore this machinery further in the following

sections.

2.3.2 Output order effects in the final variant of eCMR.

In eCMR emotional stimuli are not only more strongly connected to the temporal context, but also share their emotional context. The previous section shows that the former property results in an advantage for emotional items at the first recalled position. When recall is allowed to progress normally the same property should continue to benefit the competitive advantage of emotional items. In addition, when an emotional item is recalled it should promote the recall of items similar to it. Here, emotional items are similar to each other because they share their emotional context, so they should promote each other's recall. For both of these reasons we should expect that emotional items will be recalled earlier than neutral ones throughout the recall period in Simulation 3.

eCMR predicts an earlier output of emotional items in mixed lists (Figure 4). This prediction agrees with empirical data. Talmi et al. (2007) reported a higher probability of free recall for emotional than neutral items in two experiments where a one-minute distractor task was interpolated between study and test, and Siddiqui and Unsworth (2011) found similar results with mixed lists of emotional words. In Appendix 3 we present results from new experiment with mixed lists of emotional and neutral items, which is described more fully Appendix 3. We manipulated retrieval of mixed lists of negatively valenced emotional and neutral pictures by asking participants to recall emotional or neutral items first (the 'emotional first' and 'neutral first' conditions), comparing the results to a 'natural' mixed recall where no such instructions were given. Only the results from the latter condition concern us in this section; emotional items were again recalled earlier than neutral ones. A simulation of that experiment using eCMR (Appendix 3) again predicted the earlier output of emotional items in mixed lists that was obtained in the new experiment (Figure A1). In summary, the analysis of empirical and simulated output order showed that emotional items are recalled earlier than neutral ones, confirming the prediction of eCMR. In the following sections, we explore other aspects of the retrieval that add to the memory advantage of emotional items in mixed lists.

2.3.3 The emotional advantage in mixed lists does not depend solely on interference at retrieval

The earlier recall of emotional items could create output interference, which could produce the emotional memory advantage in mixed lists even without the other mechanisms postulated in eCMR. The logic of eCMR dictates, however, that because emotional items are more strongly associated to the temporal context and to each other, the emotional advantage in mixed lists would remain even when output interference is reduced or eliminated – as long as emotional items compete with recall with non-emotional items. In this section, we describe empirical evidence in support of this hypothesis.

To examine the impact of output order on the emotional memory advantage in mixed lists we conducted a new experiment, described in Appendix 3. In this section, we are only concerned with results from two groups: the 'emotional first' group, who was instructed to recall the emotional pictures first, and then the neutral pictures; and the 'neutral first' group, who was instructed to recall the neutral pictures first, and then the emotional pictures. Let us examine the predictions that stem from the final variant of eCMR. An emotional memory advantage should still obtained even when participants are prevented from recalling emotional items first, because the stronger binding of emotional items to the temporal context should benefit their memory even when recall is a little delayed, as long as participants are able to utilise the temporal context as a retrieval cue and as long as emotional items compete for recall with items that are less strongly bound to the temporal context. Therefore, eCMR predicts that an emotional advantage should be present both when we compare the first recalls of each group (the recall of emotional items in the 'emotional first' group and the recall of neutral items in the 'neutral first' group), and when we compare the second recall of the two groups (the recall of neutral items in the 'emotional first' group and the recall of emotional items in the 'neutral first' group). Crucially, an emotional advantage in the first recall test will contradict the hypothesis that this advantage depends on output interference. As detailed in the appendix, both predictions were confirmed in that both comparisons yielded a significant emotional memory advantage of equivalent magnitude.

One class of models that emphasises output interference are retrieval-induced forgetting (RIF) models. In RIF models items that are recalled do not merely create interference, but suppress items that are concurrently activated but not recalled (Anderson, Bjork, & Bjork, 2000; Norman, Newman, Detre, & Polyn, 2006). The earlier recall of emotional items in 'natural', uninstructed recall of mixed lists could, according to this logic, supress the memory traces of neutral items and yield an emotional memory advantage. This provides a slightly different alternative than the explanation that is solely dependent on output interference, and which also goes against the logic of eCMR. If the RIF interpretation is correct, the emotional advantage should be greatly weakened in the first recall of the 'emotional first' and 'neutral first' groups, where such suppression is prevented, compared to the second recall of those groups, which more closely mimics the 'natural' uninstructed condition. Instead, the size of the emotional memory advantage was equivalent in the first and second recall, in accordance with the prediction of eCMR and going against the RIF-inspired interpretation of

2.3.4 Recall transitions in the final variant of eCMR.

the data.

To further understand the interaction between attention to emotion at encoding and the retrieval machinery of eCMR we analysed the types of transitions the model made between successive recalls (Polyn et al., 2009, 2011). First, we examined the proportion of transitions made based on temporal associations and how those were affected by category membership (emotional/neutral). For each recall transition, we considered the absolute lag of that transition against the distribution of absolute lags from not-yet-recalled items, assigning it a score from 0 to 1, where 1 reflects that the transition was the smallest absolute lag possible. Thus, overall higher temporal clustering scores reflect recall organisation with greater influence from temporal associations, and 0.5 the baseline level expected by chance. Figure 4 shows that temporal clustering within category were very high, reflecting both the shared emotional features, as well as the close temporal proximity, of these items. We also saw a similarly strong between-category temporal clustering, reflecting the strong contribution of temporal associations between items even when they do not share the

same emotional context. Next, we examined the emotional clustering score, defined as the proportion of transitions made to the same emotional category out of all transitions. Figure 4 shows that transitions based on shared emotional context were again more likely than what is expected at chance. Lastly, we considered how transitions between successive recalls were influenced by semantic organisation. A semantic clustering score can be defined in a way analogous to the temporal clustering score, except rather than defining any pair's similarity based on their absolute temporal lag, similarity was defined based on the semantic association. The semantic clustering score was just slightly higher than chance, perhaps because the semantic cohesiveness of the emotional and neutral categories were equated here. Taken together, these results show that the dynamics of recall of mixed lists depends jointly on all of the associations that encoded items share. When an emotional item is recalled, it is most likely to promote the recall of another emotional

2.3.5 Comparison of eCMR and the item-order account

item presented close to it in time.

To some degree, eCMR shares some of the rational of the item-order account, which was developed to explain non-emotional list composition effects (McDaniel & Bugg, 2008). Like retrieved context models, the item-order account also recognizes the central role of the temporal order of items to subsequent memory. But by contrast to retrieved context models, in the item-order account, temporal order only benefits memory to the degree that it is attended, and attention is considered a resource that can be divided between elaboration on the item itself and on the temporal order of items. The item-order account uses the trade-off between attention to items and order to account for the list-composition effect. Specifically, McDaniel and Bugg (2008) suggest that because unusual items attract attention, attention to the temporal order of any list that includes them is decreased. Recall of pure lists of unusual items is often unhurt because the greater attention to the identity of unusual items balances out the lesser attention to their temporal order. But when lists are mixed paying attention to the identity of unusual items comes at the expense not only of attention to their own temporal order, but also to the order of standard items, decreasing recall of

standard items. In support of the item-order account, McDaniel and Bugg examined an implicit measures of memory for temporal order, the "input-output correspondence index" (Asch & Ebenholtz, 1962), which is defined as the proportion of transitions made between successive items at lag=+1 (thus, the input and output order correspond to one another). This index was lower when participants encoded pure unusual lists compared to mixed lists, and higher when participants encoded pure standard list compared to mixed lists (e.g. McDaniel, DeLosh, & Merritt, 2000).

eCMR formally embodies some of the same rationale of the item-order account in that both models assume a trade-off between the reliance of memory on temporal context and aspects of the identity of the item. In CMR and eCMR manipulations that render items "unusual" can be described as source features. Because items can promote the recall of items they share a source context with, recall of mixed lists would rely less on temporal context. For example, Polyn and his colleagues show that when items have differential source features items with the same source context will promote each other's recall, and reducing contiguity effects based on temporal context (Polyn et al., 2011, 2009). Therefore, both eCMR and the item-order account predict a decrease in the effect of temporal context on memory in mixed lists compared to pure lists of neutral stimuli. To make this link between models explicit we computed the input-output correspondence index that McDaniel and Bugg (2008) used, and found a reduced correspondence in mixed lists (0.38) compared to pure neutral lists (0.44) lists.

eCMR differs from the item-order account in that while in the item-order account, attention to identity and temporal order trade off during encoding, in eCMR the importance of the temporal, source, emotional and semantic contexts trade off during retrieval. Therefore, while the item-order account attributes the list-composition effect to differential attention paid to neutral items encoded in pure and mixed lists, eCMR makes the opposite assumption, that standard (neutral) items are encoded in the same way in both pure and mixed lists, and that the differential attention boost to emotional items is also equivalent regardless of list composition. We have discussed empirical evidence that supports these assumptions (Barnacle et al., 2016; Barnacle & Talmi, 2016; Talmi & McGarry, 2012). As we saw above, the retrieval mechanisms in eCMR allows

it to capture the emotional list-composition effect without assuming that the encoding of neutral and emotional items is different. In addition, because it assumes differential attention at encoding, the itemorder account predicts that the input-output correspondence index in pure lists of unusual items would be lower than the input-output correspondence index in mixed lists. This prediction was not supported in the data of Simulation 3. Although the simulation produced a list-composition effect, the input-output correspondence of recalling pure emotional lists were of similar magnitude (0.39) to the index in the recall of mixed lists (0.38). Both the empirical and simulation results therefore support eCMR over the item-order

2.3.6 Summary

account.

The empirical and simulation results in this section deconstruct the emotional memory advantage to its constituting elements. The eCMR variant in simulation 3 captured the pattern of average free recall and the dynamics of the emotional list-composition effect. Emotional arousal was modelled as an emotional feature of items that updates an emotional context sub-region. The emotional item feature was modelled as systematically attended more, thus binding items more strongly to their temporal context and improving their chances of winning the competition for retrieval. The success of eCMR to capture the emotional list composition effect did not depend on context drifts between the encoding of items that are emotional and items that are neutral. Instead, it depended on a number of retrieval mechanisms that interplayed with the additional encoding that emotional items received during encoding. Emotional items that are encoded in mixed lists are more likely to be recalled first because they are more strongly connected to the temporal context. Once one emotional item is retrieved, increased semantic similarity between that emotional item and other emotional items (unless it is controlled experimentally) and the shared emotional context between these items renders additional emotional items more accessible. Because emotional items tend to be recalled early and promote each other's recall they act as a source of interference, making it more difficult for participants to retrieve neutral items. In mixed lists these processes allow emotional items to win

the competition for retrieval over neutral items. In pure lists enhanced attention to emotional stimuli still increased their binding to the temporal context, but because the increased level of binding was equivalent for all of the emotional items in pure lists the competition for retrieval was not affected by emotionality. Therefore, although encoding processes could be very similar in pure and mixed lists, the advantage of emotional items in free recall would be expressed more strongly in mixed lists. Taken together, there are several processes in place that give rise to the emotional advantage in free recall of mixed lists, rendering the emotional list-composition effect a highly robust phenomenon, well-described by eCMR.

3. The emotional oddball effect

List composition effects typically include pure lists, which have 0% or 100% 'strong' items, and mixed lists, which have 50% 'strong' items. It is reasonable to ask what happens when lists have other ratios of emotional to neutral items. An obvious case is the emotional oddball effect, where lists are comprised solely of neutral items, with the exception of one emotional oddball. For example, in a classic paper (Ellis, Detterman, Runcie, McCarver, & Craig, 1971) participants studied lists of line drawings of everyday objects for free recall. The emotional oddball was a picture of a model from a 'sun tanning' magazine, presented in the 9th serial position. The oddball was recalled extremely well, while memory for surrounding items suffered in oddball compared to control lists, a pattern referred to as the emotional oddball effect. This decreased memory for items presented before and after the oddball is often referred to as retrograde and anterograde amnesia, respectively; there is evidence that of the two, the anterograde amnesia effect is the more robust (Schmidt, 2012; Schmidt & Schmidt, 2016). Therefore, the emotional list composition and the emotional oddball effects are similar not only because they represent different ratios of emotional-to-neutral stimuli, but also because in both tasks neutral memory impairments occur when the list includes emotional item(s). Note that the literature on oddball tasks is vast; rather than exploring the many methodological and empirical variations, we focus here on one core, consistent pattern of findings with particular relevance for the current theory.

Although the similarities between the emotional oddball effect and the emotional list composition effect suggest that eCMR should be able to predict both of them, the emotional oddball effect nevertheless presents a challenge for eCMR. Following the same logic discussed above for mixed lists, whenever the emotional oddball is recalled, it should promote the recall of items that are similar to it. Therefore, the variant of eCMR presented in Simulation 3 predicts that an oddball would promote most strongly the recall of those items presented close to them in time – the item presented before, and especially the item presented after, the oddball itself. In fact, the temporal context model was developed to explain the increased likelihood to recall temporally adjacent items contiguously (Howard & Kahana, 2002a). The

problem is that this prediction is exactly the opposite of the retrograde and anterograde amnesia aspects of

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the empirical emotional oddball effect.

A possible resolution to this inconsistency is to revisit the assumption of CMR that the temporal context

drifts whenever the item source (here, the item emotionality) changes. The drift rate is governed by the

parameter d in the model, and in fully mixed lists (which involve continual item category shifts) our

simulations suggested that behaviour was best explained if the drift rate was small or non-existent. In

contrast, reduced memory for items around the oddball, especially after it, implies their weakened temporal

association to the oddball. In this setting, this suggests that the temporal context drifts substantially before

and after the oddball is presented. That temporal drift plays a larger role here is consistent with the intuition

that a single emotional oddball is more surprising to participants, and therefore results in more unique

encoding operations, than a similar emotional item when half the list items are emotional. Related to this, it

is important to note that assuming that the temporal context drifts before and after the oddball is presented

does not influence the emotional context. Thus, the emotional repercussions of viewing a picture of a nude

model or a taboo word were allowed to continue to colour the emotional context when simulated

participants encoded the items that followed the oddball in Simulation 5. As we see below, eCMR captured

the emotional oddball effect.

3.1 Simulation 5: the emotional oddball effect

We simulated a standard oddball paradigm, where the list length (16 items) and the position of the oddball

(9th item) was based on Ellis et al. (1971), and the semantic association between the emotional oddball to

the neutral items was simulated as weaker (on average, 0.15) than their semantic associations to each other

(on average, 0.18, as in Simulation 3). In keeping with Simulation 3, a distractor item was simulated between

the study and the recall test. All other parameters values were kept the same as in Simulation 3, apart from

d, which was initially kept at 0 (in Table 1, this Simulation is denoted as Simulation 5A), as in Simulation 3,

and then increased drastically to 0.95. As expected, while without context drift there was no difference between memory for the oddball and the items presented before and after it, with increased context drift we found excellent memory for the oddball, and decreased memory for the items surrounding it, capturing the emotional oddball effect. With these values, the greater decrease was in memory for oddball-1 positions.

The simulation reflects one other parametric change relative to those used in the previous experiments, which we view as less consequential as it was not strongly constrained by the earlier simulations. The strength of associations between the source context and the temporal item features ($L_{\rm SW}^{CF}$) governs the relative impairment to memory for oddball-1 vs. oddball+1 positions. To better match evidence that the memory decrease is more consistent in the oddball+1 position we increased this parameter (from 0.129 to 0.25). Because there could be other parameter space areas that would capture the emotional oddball effect, and because with this revised parameter value we still observed an emotional list composition effect, we do not believe that this increase represents a meaningful difference between the emotional list composition and the emotional oddball effects. Therefore, Figure 5 depicts the simulated oddball effects from the simulations that used this value. The simulations also predicted that the oddball will be recalled early, in agreement with the predictions the model made for the list composition task, and with empirical data (Elhalal, Davelaar, & Usher, 2014).

The simulation in this section reveals that eCMR can provide a good qualitative fit to generic emotional oddball effects using mostly similar parameter values as those used to model the list composition effect, but with one notable exception: to succeed, the simulation assumed that the emotional oddball shifted the temporal context a lot more than when half the items were emotional, in the list composition task. This stands in contrast to the simulations of the list composition effect, where such a large shift detracted from the model's ability to mimic the empirical data. Together, these considerations suggest future work should endogenize this difference, presumably by deriving the level of context shift from the surprise occasioned by an item.

4. eCMR can account for increased emotion-enhanced memory after a prolonged delay

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A paradigmatic finding in the emotional memory literature is that of a steeper forgetting of neutral compared to emotional stimuli (Yonelinas & Ritchey, 2015). In reports where the memory advantage is greater in a delayed test, the advantage may be smaller immediately and grow with delay (LaBar & Phelps, 1998); sometimes there is no immediate advantage (Sharot & Yonelinas, 2008; Sharot & Phelps, 2004); and in a few classic reports, emotional stimuli were remembered less well than neutral stimuli immediately, and the pattern reversed later (Butter, Training, & Kaplan, 1970; Kleinsmith & Kaplan, 1964). These reports use a variety of methodologies and memory tests which could explain the discrepancy in the immediate memory results, and indeed, eCMR could help buttress their systematic investigation. The point that the emotional memory literature has focused on, and which concerns us in this section, is that such results correspond well to models that emphasise the effect of emotion on the maintenance and storage stage, especially the neuromodulatory effect of catecholoamines on the consolidation of episodic memory traces (Dunsmoor, Murty, Davachi, & Phelps, 2015; Patil, Murty, Dunsmoor, Phelps, & Davachi, 2017).

Readers familiar with work on the neurobiology of memory consolidation may conclude, therefore, that eCMR has no hope of accommodating such findings, because it lacks any mechanism to mimic consolidation effects. Yet retrieved context models had success in accounting for effects attributed to consolidation, typically by assuming increased interference with time, or degraded context reinstatement (Sederberg, Gershman, Polyn, & Norman, 2011; Sederberg et al., 2008). In this section, we use eCMR to simulate a prolonged retention interval, and examine how delay might alter the emotional advantage. Our purpose was to illuminate which cognitive processes influence changes in the magnitude of the emotional memory advantage over time. eCMR is agnostic as to how such changes may be realised at the level of neurobiology.

There are several ways to simulate a prolonged retention interval in retrieved context models. One approach is to insert a temporal context shift at the end of the encoding phase to capture the effect of time delays in

the order of seconds to minutes, by simulating a 'distractor' item (Siegel & Kahana, 2014; Sederberg et al., 2008). We have followed this approach to simulate a short distractor task in previous sections, but this may be a less appropriate way to simulate longer delays, such as those employed in the emotional memory literature, which range from one hour to weeks. In eCMR, although a distractor reduces recall of recency items, once one item is recalled, this leads to retrieval of its encoding contexts and effectively allow the model to 'jump back in time', so that the effects of the retention interval would be limited to the first few recalls. A second approach is to simulate each experimental session as a separate session context. This works well when two stimulus sets are studied in two separate encoding sessions, followed by a memory test; the memory test can be biased towards remembering the context of the earlier or the later session (Sederberg et al., 2011). But this set-up does not quite capture what happens outside the laboratory, when we reminisce about our past. A third approach is to model the retention interval as decreasing the ability of a recalled item to retrieve its temporal context from encoding. This approach has previously been employed successfully to capture the effects of aging on the recency and contiguity effects (Howard, Kahana, & Wingfield, 2006), and we implement it in Simulation 6.

While straightforward, simulating delay as a decreased ability to retrieve the temporal context ignores recent evidence that forgetting is not passive, but involves a transformation of memory traces so that memory for more remote events is more schematic (McKenzie & Eichenbaum, 2011; Moscovitch, Cabeza, Winocur, & Nadel, 2016). For example, animals that learned the location of a platform in a Morris water maze based their trajectory more on the specific location of the platform when memory was recent, but were more sensitive to the probability distribution of platform locations when memory was remote (Richards et al., 2014). A long retention interval is also thought to allow humans to extract generalities (Ellenbogen, Hu, Payne, Titone, & Walker, 2007) and render memory more schematic (Alba & Hasher, 1983). For example, remote memory for film clips relied more on general schemas for films and social scripts, evident in increased number of errors in recalling typical vs. atypical clips after a week (Bonasia et al., n.d.), perhaps because memory for central details of memories is more persistent, while peripheral details are forgotten more quickly (Sekeres et al., 2016). The literature does not, at present, specify exactly what time

frame gives rise to more schematic memory performance. It is also possible that aspects of the experimental

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set-up, such as the stimulus set that is selected or the particular instructions participants receive, influence

the strategies participants apply to the difficult task of delayed recall.

In Simulations 6 and 7 we show how these two ways of conceptualising the effect of time delay - the

increased difficulty to retrieve the encoding context with time (Simulation 6) and an additional

schematisation of memory representations, where retrieval relies less on the temporal associations formed

between items during the experiment (Simulation 7) - impact the predications that eCMR makes for delayed

emotional memory. To show this most clearly, these simulations implement a classic experiment where

emotional items had an increased free-recall advantage in a delayed, compared to an immediate test (LaBar

& Phelps, 1998). Both of the operationalisations of time delay in Simulations 6 and 7 are expected to

decrease the impact of the temporal context on retrieval competition, so eCMR predicts that recall will be

determined more by other associations of items, such as their emotional and semantic context. Because,

drawing on the results of Simulation 3, emotional items should be recalled earlier than neutral ones, they

would promote the recall of items they share an emotional context with, especially when those are more

related to them semantically. Therefore, eCMR predicted that the emotional memory advantage will be

greater in simulated delayed tests, especially when delayed memory is modelled as more schematic.

4.1 Simulation 6: time delay makes it more difficult for a recalled item to retrieve its temporal context of

encoding

LaBar and Phelps (1998) studied healthy controls as well as patients with unilateral temporal lobectomy.

Participants incidentally encoded a single mixed list of 20 low-frequency neutral words and 20 taboo words.

Four buffer words were also included, two in the beginning and two at the end of the list. During encoding

participants rated how arousing the words were. A free recall test was administered immediately and after a

1-hour filled delay. The researchers found an immediate increase in the number of taboo words recalled,

which they attributed to the increased inter-relatedness of these words compared to the neutral words. Strikingly, participants forgot fewer taboo words, so that their memory advantage was greater after one hour than it was immediately, an effect they attributed to the effect of arousal on consolidation. The impact of this particular paper is due to the finding that the participants with temporal lobectomy forgot taboo and neutral words at the same rate, in agreement with the hypothesis that the attenuated forgetting of emotionally arousing material is driven by the amygdala.

We modelled 30 participants who each studied a list of 44 items, half of which were emotional. The first and last two items were considered buffers and not analysed; two of these were emotional, two of these neutral, and they were allocated randomly to the 1^{st} , 2^{nd} , 43^{rd} and 44^{th} list positions for every simulated participant. The immediate test followed the encoding stage immediately without simulating a distractor at the end of the list, which distinguishes this simulation from previous simulations in this paper. The delayed test was modelled by simulating a distractor at the end of the list as well as by decreasing β^{temp}_{rec} (0.55 in the immediate test and 0.4 in the delayed test). In order to reproduce the overall level of recall in Phelps and LaBar's data we altered the decision competition parameter values ($\kappa = 0.25$) and Φ_{emot} (1.25). LaBar and Phelps (1998) discuss semantic cohesiveness as a contributing factor to the immediate enhancement of free recall of taboo words in their data. We assumed (Phelps, personal communication, 2017) that taboo words were more inter-related to each other than they were to neutral words (the average of semantic associations within emotional items was 0.18, as in Simulation 3), and that neutral words, which were all low-frequency words, were not more related to each other than they were to the taboo words (average of 0.15 for all other semantic associations, as in simulations 5).

It is well known that forgetting can be quantified in at least two different ways — the decrease in the number or the proportion of retained (Wixted, 1990). Figure 6 shows that approximately the same number of emotional and neutral items was forgotten in Simulation 6, but these numbers represent a greater proportional forgetting of neutral (46.39%) compared to emotional (22.84%) items. Therefore, the proportional emotional memory advantage score increased with delay: the model recalled 255.43% more

emotional than neutral items immediately, but 367.68% more emotional than neutral items after a delay.

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With these parameters eCMR did not capture the increased memory for emotional items in the delayed test

in LaBar and Phelps' data.

4.2 Simulation 7: time delay makes it more difficult for a recalled item to retrieve its temporal context of

encoding, and renders retrieval more schematic

In addition to the parameter changes for Simulation 6, we also decreased to 0.5 the values of L_{tw}^{CF} and L_{wt}^{FC} ,

which control the temporal context-item associations. Given that recall is competitive in eCMR, if an item is

recalled and temporal item-context associations are weaker, all else being equal this will promote recall of

items that share semantic and emotional, rather than temporal, information with that item. As Figure 7

shows, this change now captures the full pattern of data described by LaBar and Phelps (1998).

4.3 Comparison between Simulations 6 and 7

The difference between the immediate test and the two ways in which time delay was implemented in

Simulations 6 and 7 can be described most clearly by analysing the extent to which recall organisation was

influenced by temporal, semantic and emotional factors (see Simulation 3 for details of this analysis

method). Figure 6 shows that both types of temporal clustering scores were reduced when the temporal

context was less retrievable (Simulation 6), but more so when delayed memory was modelled as more

schematic (Simulation 7). The changes to the model for Simulation 7 led to greater influences of emotional

and semantic organisation.

Both Simulation 6 and Simulation 7 predicted greater emotional memory advantage in the delayed,

compared to the immediate, recall of mixed lists. In Simulation 6 this time-dependent increase was only seen

when we consider the proportion of items the model retained in the delayed test, while in Simulation 7 it

was evident in absolute terms in that emotional items were not forgotten at all. A less extreme decrease in

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the values of L_{tw}^{CF} and L_{wt}^{FC} , the parameters which control the temporal context-item associations, would

have resulted in an intermediate level of forgetting, between these two extremes, corresponding more

exactly to the attenuated forgetting of emotional stimuli that characterise many of the published papers in

the emotional memory literature. Simulation 7 was useful because it suggests that attenuated and even null

forgetting of emotional stimuli with time may be a consequence not only of the duration of the retention

interval but also how much stimuli render themselves to schematisation, and even participants' mindset

when they approach the recall task.

5. Discussion

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The work presented in this paper proposes a shift in the way we understand memory for important experiences. It is well-established that some experiences attract attention and are processed preferentially: those with certain features that a species has evolved to prioritise (e.g. certain spatial frequencies and shapes), those previously associated with reward or punishment, and those that our understanding of our current goals suggests are important. It has previously been thought that the memory traces laid out during the encoding of emotionally arousing experiences are then maintained in a special way so that important events will have the best chance of influencing later fitness-related decisions. eCMR shows that the nature of the memory traces themselves - the increased binding between them and the temporal context, and their inherent associations to other emotionally arousing and semantically related memory traces – is sufficient to give them an advantage during test, particularly delayed tests, when they compete for retrieval with neutral items. The crucial point is that the difference that is already evident at encoding between emotional and neutral items protects and promotes them whenever there is a competition for retrieval later on, and gives rise to emotion-enhanced memory, even without further consolidation advantages. The dynamics of retrieval determine the magnitude of this advantage and could increase or decrease it. eCMR therefore highlights the exquisite sensitivity of memory to the situation in which an agent finds itself - in eCMR, the retrieval context of the memory test – by providing mechanisms which prioritise the retrieval of experiences that best match that test context across multiple dimensions of similarity.

eCMR is the first quantitative model of the emotional enhancement of memory. It explains the improvement in remembering emotionally arousing stimuli as arising from the operation and modulation of retrieved context mechanisms during encoding, maintenance and retrieval. Emotional arousal is operationalised in the model as a feature of items. We assumed, in agreement with the consensus in the literature (reviewed, for example, in Mather & Sutherland, 2011; Pourtois et al., 2013) and our own previous findings (Talmi & McGarry, 2012; Talmi, Schimmack, Paterson, & Moscovitch, 2007), that stimuli that trigger emotional arousal

attract attention obligatorily. Building on previous work, extra attention was described in the model as the strengthening of associations between the attended item and its temporal context (Howard & Kahana, 2002a; Lohnas et al., 2015; Polyn et al., 2009). eCMR therefore is compatible with the suggestion that emotional stimuli are bound more strongly to their context (Hadley & MacKay, 2006; MacKay et al., 2004; MacKay & Ahmetzanov, 2005), although it specifies that the increased binding is with the temporal context. Crucially, eCMR goes beyond previous work, revealing that emotion-enhanced memory is not solely a result of prioritised encoding, but is also the result of retrieval competition, extending to this situation the logic of CMR (Polyn et al., 2009) and its predecessors. The increased association strength between emotional stimuli and their temporal context, and the shared emotional context among emotional items, render emotional items more competitive during retrieval. Therefore, when the model attempts to retrieve emotional and neutral items that were encoded together in mixed lists, the emotional ones are recalled early and promote each other's recall, which interferes with and delays the recall of neutral stimuli. When the memory test takes place after a prolonged interval, the model assumes that the temporal context is less diagnostic, so non-temporal context features such as shared emotional context and the often-stronger semantic associations between emotionally arousing stimuli boost retrieval chances even more. But when emotional items compete against equally highly-attended emotional items, the extra attention they receive at encoding does not help very much at retrieval, so that on average, recall of pure emotional lists resembles recall of pure neutral lists. In summary, eCMR uses the established mechanisms of retrieved context models to describe emotion-enhanced memory as a consequence the interplay between encoding, maintenance, and retrieval effects.

The data presented here support eCMR as a model of the effect of emotional arousal on immediate free recall. eCMR provided a good qualitative fit for the emotional list composition effect and the emotional oddball effect, phenomena related to differences between the average recall of emotional and neutral stimuli. While emotional stimuli are modelled as attracting extra attention and sharing an emotional context regardless of the type of list (pure or mixed) in which they are encoded, these differences between emotional and neutral items only help emotional items win the competition for retrieval in mixed lists,

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where they compete with neutral items. When all candidates for recall are emotional, namely in a recall test that follows the encoding of a pure list of emotional items, the increase in average association with temporal context will no longer matter, rather what would matter would be the fluctuation in attention that individual participants may allocate to individual items. This realisation now provides an explanation to a finding we reported a few years back, using structural equation modelling to relate attention at encoding and free recall performance (Talmi & McGarry, 2012). Participants in that study encoded pure and mixed lists of emotional and neutral pictures under full or divided attention. Performance on the concurrent task worsened in terms of accuracy and reaction time when participants encoded emotional, compared to neutral pictures. We used performance on the concurrent task to compute an attention score for every picture (across participants), a measure which correlated with the arousal ratings each picture received. Intriguingly, we found that in free recall of mixed lists, arousal ratings predicted recall directly, an effect which was not mediated by attention, but in pure lists the effect of arousal on memory was completely mediated by attention. The current modelling explains this findings because a little more attention to particularly arousing pictures can certainly boost retrieval success, but its impact will be drowned out in mixed lists when all emotional items are attended more than all neutral items.

A list with one emotional oddball is also, in a way, a mixed list. eCMR captured the emotional oddball effect too, but only under the assumption that the oddball induces a very large shift in the temporal context. With just one emotional oddball emotional stimuli cannot prime each other during encoding, and more preparation would be needed pre- and post-switch (to and from the oddball), so that it is reasonable to assume a much larger shift in temporal context in the emotional oddball compared task to the emotional list composition task. Without assuming large context shifts, in eCMR the recall of an emotional oddball will promote the recall of items presented close to it in time, in contradiction to the empirical literature where excellent recall of the oddball results in poorer recall of surrounding items.

eCMR also captured well the dynamics of recall. The stronger association between emotional stimuli and their context in eCMR increases the chances that emotional items will win the retrieval competition early in

recall, so the model captured the earlier output of emotional stimuli in the recall of mixed lists and the earlier output of oddball stimuli. Emotional and semantic associations between emotional stimuli help them promote each other recall, increasing the number of transitions between emotional stimuli, which captures the empirical finding of clustering recall around the emotional category. Asking participants to recall only the neutral items prevents them from recalling emotional items first, but emotional items gain the upper hand very quickly as soon as participants are allowed to recall them, too. This occurs because emotional items are not only more strongly bound to the temporal context and therefore likely to win the competition for retrieval when the recall test commences, but also because when they are recalled they retrieve their temporal context, which helps them promote the recall of items close to them in time as well as those that share their emotional and semantic context. This investigation shows a multiply determined effect of emotion on retrieval dynamics, which together with enhanced attention at encoding gives rise to the robust emotional memory enhancement in immediate free recall of mixed lists.

The model we developed here is useful because it can account for many emotional memory phenomena. Some of the effects the model describes, however, which have been discussed in previous work in terms of the contribution of emotional arousal, are here revealed as similar to non-emotional effects. First, the emotional list composition effect is, of course, reminiscent of list composition effects that arise from non-emotional manipulations of unusualness, such as bizarreness, enactment, generation, word frequency and perceptual interference (McDaniel & Bugg, 2008). The increased item-to-context associations, which in eCMR are discussed as a consequence of emotional arousal, may also be true for other neutral categories, such as enacted or generated items. Whether eCMR can account for non-emotional list-composition effects depends on whether additional attention is allocated to each one of these unusual stimuli, whether this occurs in both pure and mixed lists, and on how unusualness impacts on the semantic associations between stimuli. eCMR can perhaps be seen as an extension and quantification of the item-order account, where various item dimensions that receive attention at encoding can balance out memory reductions stemming from reduced attention to others. The emphasis on increased attention at encoding as a driver for the emotional memory enhancement in mixed lists distinguishes the emotional list composition effect — and

other list composition effects for unusual items - from the list strength effect (Ratcliff et al., 1990), which is not obtained when items are rendered 'strong' through manipulations that resemble enhanced attention (either a longer encoding time or deeper elaboration, Malmberg & Shiffrin, 2005). The success of eCMR in modelling the emotional list composition effect can be contrasted with the predictions we can extract from SIMPLE (Brown, Neath, & Chater, 2007). Neath and Brown (Neath & Brown, 2006) proposed that short words are easier to comprehend, which makes them more distinctive compared to long words. Through this insight they showed that SIMPLE captures the findings that memory for a pure list of short words is better than memory for a pure list of long words, and that in mixed lists of short and long words, memory for short and long words is equivalent, at the level of memory for a pure list of short words (Hulme, Stuart, Suprenant, Bireta, & Neath, 2004). We can assume that emotional pictures are also more distinctive than neutral pictures because of all of the unique operations involved in their encoding. Using the same logic, then SIMPLE captures the mirror image of the empirical emotional list composition effect, predicting that memory for memory for pure neutral lists will be *reduced* compared to all other conditions.

Second, the behavioural emotional oddball effect is also reminiscent of semantic and perceptual oddball effects; in a striking demonstration, the same oddball effects are observed either when a picture of a nude model is the oddball item within a list of pictures of clothed models (the standard items), or vice versa. Therefore, it is reasonable to ask whether models developed to explain the generic oddball effect can also explain the emotional oddball effect –including CAN (Elhalal et al., 2014) and SIMPLE (Brown et al., 2007) - as well as whether eCMR can account for non-emotional oddball effects. Since this paper is not focused on the oddball effect, we did not conduct a model comparison and cannot therefore comment on whether eCMR provides a better fit for the data than those other models. In addition to the ability of models to fit the memory data, eCMR uniquely utilises temporal context shifts to account for the oddball effect. Retrospective time estimation is sensitive to the number of different patterns that are encoded into episodic memory (Faber & Gennari, 2015) and are thought to index temporal context shifts (Sahakyan & Smith, 2014). In future research it would be interesting to examine time estimation for oddball and control lists, as well as for pure and mixed lists.

eCMR was confined to the simulation of free recall. The advantage of emotional stimuli would, however, remain evident as long as the recall test is sensitive to some of these processes, in any test that benefits from memory for the temporal context of encoding. Although items do not compete with each other in a recognition test as they do in free recall, the decision to classify a memory trace as a 'Remember' response is inherently defined as the degree to which the encoding context is retrieved at test. This may explain why emotion enhances measures of recollection more than familiarity, as recently reviewed by Yonelinas and Ritchey (2015). The integration of emotion into retrieved context models help us decipher an intriguing, recent dataset, where neutral stimuli that were encoded after a block of emotional stimuli were recollected better than neutral stimuli encoded before a block of emotional stimuli, before a block of neutral stimuli, or after a block of neutral stimuli (Tambini et al., 2017). We comment on this study because as in the emotional list composition effect, here, too, the key comparisons are between conditions that include only neutral items and those that mix emotional and neutral ones, and neutral memory changed based on the presence of emotional items. Following principles of retrieved context models, when emotional stimuli retrieve their temporal context during the recognition test, this might help items that share their encoding context retrieve it during the test. This could increase the recollection of neutral items that are studied after, but not before, the emotional items, because only those share the temporal context of emotional items. In addition, it is likely that participants were still aroused when they encoded neutral items after an emotional block, because the physiological effects of emotional arousal linger for many minutes (Dickerson & Kemeny, 2004), resulting in shared source context as well; and that the arousal state will have increased attention participants allocated towards the post-emotional neutral stimuli (Mather et al., 2015). Therefore, there are a number of reasons compatible with eCMR that could account for the findings, but these speculations could only be examined when eCMR is extended to recognition memory tests.

Retrieved context models do not have a dedicated consolidation module. The core claim is that at the algorithmic level of explanation, time-dependent interference and context changes and reinstatement are sufficient to explain the behavioural phenomena that are typically attributed to consolidation. Retrieved context models are models of the cognitive processes and information processing considerations that give

rise to memory performance, which therefore can be implemented in various ways neurobiologically. Thus, we by no means intend to deny the contribution of mechanisms such as replay or time- or sleep-dependent change in the brain structures that maintain memory traces and even the very structures of synapses that store individual memories (McKenzie & Eichenbaum, 2011). These are simply outside the scope of our model. Future, more neurobiologically minded work might also clarify how these neurobiological mechanisms might implement the computations proposed in eCMR, and conversely the eCMR computations might inform the investigation of the neurobiological mechanism. The step we took in section 4, where we ask how delay might change the nature of memory traces and the operation of retrieval mechanisms, has been inspired by behavioural and neurobiological findings about the way that memories are transformed with time delay, but is similarly blind to the actual mechanism that implement such transformations. Instead, the possibility that an increased reliance on non-temporal dimensions of similarity renders memories more schematic with time can be best tested by its fit to behavioural data, even if it is fundamentally inspired by findings that older memory traces rely less on the hippocampus and more on the neocortex (Moscovitch et al., 2016). Crucially, because eCMR can explain both immediate and delayed effects of emotion, it is the first model of emotional memory that encompasses both parsimoniously, but at the cost of a disconnection from the implementation level of explanation.

The concept of an emotional dimension of similarity, which has been so useful in eCMR, deserves further research. Our previous work (Talmi & Moscovitch, 2004) inspired researchers to control the semantic relatedness of the emotional and neutral stimuli they use. The problem with this approach is that when stimuli are emotional, semantic relatedness ratings may reflect a different construct than they do when stimuli are neutral. Specifically, they may be influenced both by semantic associations and by emotional associations related to how stimuli make participants feel. Participants may therefore rate two negative stimuli, for example, two sad facial expressions belonging to two different people, as more related than a sad and a neutral expression belonging to the same person. How these dimensions of similarity are weighted is a topic that would benefit from further investigation. Notwithstanding that, the qualitative mechanisms of

binding and competition that we investigate here are robust to quantitative variation in the degree of

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similarity across items.

& Sommer, 2017).

The emotional experiences of our lives are rich with personal meaning that defines us as people and connects us to others and to the cultures we live in. They can be positive or negative, happy or calm, fearful or disgusting, and motivate us to approach, avoid, or otherwise behave in multiple bewildering ways. The controversy around defining emotion is well-known (Izard, 2010) and there is no sign yet for an umbrella theory that can bridge the gaps between the different theoretical positions that give rise to the disparate definitions. eCMR concerns only two aspects of emotional experiences – the semantic association between them and their increased intensity, which participants readily rate higher on a calm-to-arousing scale (Bradley & Lang, 1994; Feldman Barrett, 2016; Lindquist, Satpute, Wager, Weber, & Barrett, 2015; Russell, 1980). Arousal was only represented in eCMR inasmuch as it drove enhanced attention. One aspect of emotional experience that deserves additional consideration is valence, because there is evidence that negatively valenced stimuli are remembered better than positive ones even when attention is controlled (Kensinger, 2009a) and that valence may modulate some of the effects we discussed, including the relationship between attention and memory in mixed lists (Talmi, Schimmack, et al., 2007) and the effect of oddballs on surrounding items (Hurlemann et al., 2005). Future research should test whether the empirical results that we drew on here with positive, arousing stimuli. eCMR can be extended to represent a valence

Finally, the current modelling suggests new directions for understanding the adaptive role of emotional memory enhancement in guiding behaviour. These effects have long been understood in terms of prioritizing which individual items to encode and maintain, but situating them within retrieved context models sheds new light on how these effects on retrieved memories might support decision making. We have already noted the striking formal correspondence between item-context associations (as inferred from recall tasks

dimension of context, if such results imply that this is necessary. Another major avenue for future

development of eCMR is to simulate the effect of emotion on associative memory (Madan, Fujiwara, Caplan,

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and embodied in retrieved context models) and predictive world models that have been separately proposed (and verified; Momennejad et al., n.d.) to underlie the evaluation of candidate actions in decision tasks (Gershman et al., 2012). In short, the set of item-context associations amounts to a predictive world model that connects items, situations or events to others they tend to predict. In a decision task, these links can be retrieved at choice time to support a mental simulation of the likely consequences of candidate actions (Shohamy & Daw, 2015). In this framework, the new effect here of emotional modulation of these associations in eCMR would serve to highlight emotionally salient consequences, tending to give them a larger effect on one's deliberations. This, in turn, formally relates these emotional memory enhancements to a set of computational mechanisms and empirical effects (e.g., Huys et al., 2012) that have been proposed to underlie both adaptive control of prospection and maladaptive dysfunction, such as rumination and worry (Eldar et al., 2016; Huys, Daw, & Dayan, 2015) in disorders of mood.

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TABLES

Table 1. Variable parameter values in Simulations 1-6.

Parameter	0	1	2	3	4	5A	5	61	6D	7
eta_{rec}^{temp}	0.510	0.550	0.550	0.550	0	0.550	0.550	0.550	0.400	0.400
eta_{rec}^{emot}	0.588	0.588	0.588	0.588	0	0.588	0.588	0.588	0.588	0.588
L_{sw}^{CF}	0.129	0.129	0.129	0.129	0.129	0.250	0.250	0.129	0.129	0.129
d	0.767	0.300	0.300	0	0	0	0.95	0	0	0
ϕ_{emot}		1.00	1.28	1.28	1.28	1.28	1.28	1.25	1.25	1.25
L_{tw}^{CF}	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.500
L_{wt}^{FC}	0.898	0.898	0.898	0.898	0.898	0.898	0.898	0.898	0.898	0.500
κ	0.111	0.550	0.550	0.550	0.550	0.550	0.550	0.550	0.550	0.550
λ	0.338	0.550	0.550	0.550	0.550	0.550	0.550	0.550	0.550	0.550
β_{dist}		0.976	0.976	0.976	0.976	0.976	0.976	0	0	0

Note: Simulation 0 = Polyn et al. 2009. S5I refers to the simulation of immediate memory; S5D to the simulation of delayed memory. The matrix L scales the magnitude of source associations relative to temporal associations between item and context separately. Subscripts sw: source context-to-item; tw: temporal context to item; wt: item to temporal context.

Table 2. Fixed parameter values in simulations.

Parameter	Value
γ^{FC}	0.898
S	2.780
η	0.159
τ	0.174
ϕ_S	1.070
ϕ_d	0.981

Note: Fixed parameter values for eCMR inherited from Polyn et al. 2009.

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FIGURE CAPTIONS

FIGURE 1: Example neutral and negative, emotionally arousing stimuli.

FIGURE 2: A schematic representation of eCMR

FIGURE 3: The emotional list composition effect

FIGURE 4. Recall dynamics that produce the emotional list composition effect.

FIGURE 5. The emotional oddball effect

FIGURE 6. Forgetting effects

FIGURE 1. Example neutral and negative, emotionally arousing stimuli.





FIGURE 2. A schematic representation of eCMR

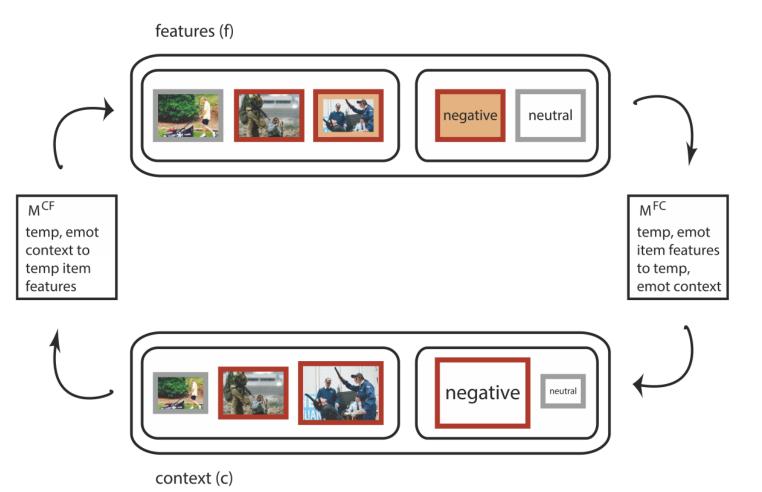


FIGURE 3: The emotional list composition effect

Behavioural data from Talmi et al., 2007, Experiment 2 (left) and the results of Simulations 1, 2 and 3 (right).

eCMR with enhanced attention but without context drifts (Simulation 3) best captured the emotional list composition effect.

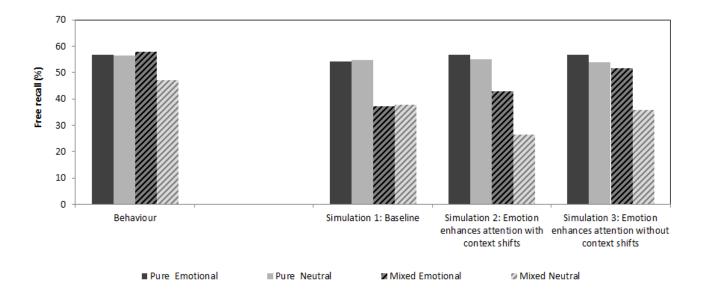
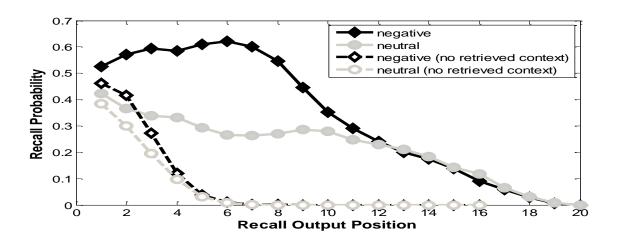


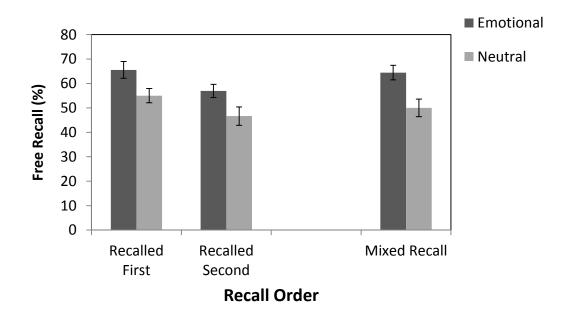
FIGURE 4. Recall dynamics that produce the emotional list composition effect.

Top: Simulated output order for the final eCMR variant with (Simulation 3) and without (Simulation 4) allowing recalled items to retrieve their encoding context. Probability of recall is plotted as a function of recall position, starting with the very first item recalled.

Middle: Empirical data from the instructed recall experiment. Results from the instructed recall (Appendix 3). The two rightmost bars plot recall across both test periods in the group that recalled emotional and neutral items together, namely, the 'natural' mixed recall condition (relevant to section 3). The four leftmost bars plot free recall of the two groups allocated to the 'emotion first' and 'neutral first' conditions (relevant to section 4). The two leftmost bars plot the recall from the first test period in each of these two groups (the emotional list in the 'emotion first' condition and the neutral list in the 'neutral first' condition). The middle two bars plot recall from the second test period in each of these groups (the neutral list in the 'emotion first' condition and the emotional list in the 'neutral first' condition).

Bottom: Parameter estimates describing recall transitions in Simulation 3. Values can range between 0.5 (chance) and 1 (transitions that only depend on one particular set of associations).





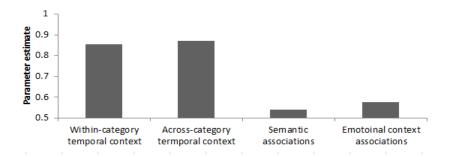


Figure 5: The emotional oddball effect.

Simulated recall probability (Simulation 5) is plotted for serial position 9 (where the oddball was presented to the model), the one before, and the one after. Grey: lists without an oddball item. Black: lists with an oddball item where context drift parameter was set to 0.95. White: lists with an oddball item where context drift parameter was set to 0.

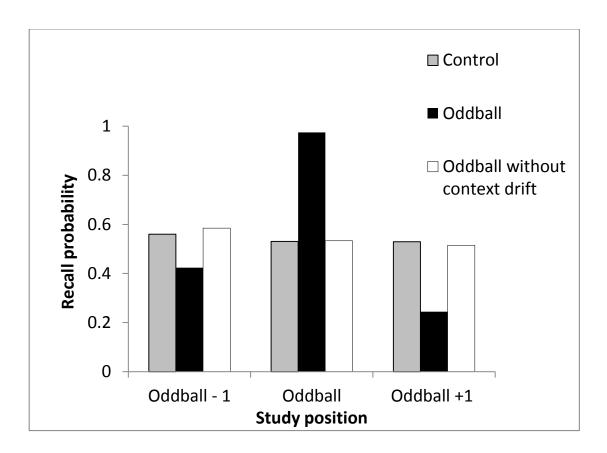
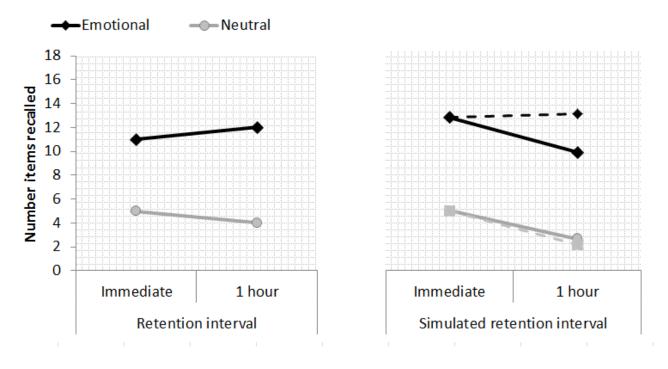
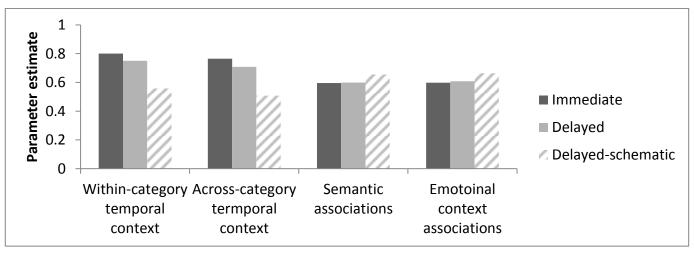


FIGURE 6. Forgetting effects.

Top: Emotional memory advantage as a function of time delay. Left: Original data adapted from Figure 2 in Phelps & Labar (1998). Right. Simulated data (Simulations 6-7). Solid lines: Time delay was modelled as a decrease in β_{enc} temp . Dashed lines: Delayed memory was modelled as more schematic by also decreasing the parameters L_{tw}^{CF} , L_{wt}^{FC} .

Bottom. Parameter estimates for recall transitions in Simulations 6-7.





APPENDIX 1: A FORMAL DESCRIPTION OF ECMR

We begin by describing the assumptions of eCMR that follow directly from those of CMR, before turning to those unique to a model that incorporates the emotional aspect of memory. In eCMR, each studied item i has an associated feature vector, \mathbf{f}_i and context vector \mathbf{c}_i which interact through the association matrices M^{FC} and M^{CF} . When an item is presented to the model, this activates its feature vector \mathbf{f}_i , such that the subscript i denotes that this vectors corresponds to item i. This vector is a concatenation of temporal item features (\mathbf{f}_i^{item}) and emotional item features (\mathbf{f}_i^{emot}), analogous to the definition of item and source features in CMR. For simplicity, each temporal context and emotional context sub-region of \mathbf{f}_i has a localist, orthonormal representation.

This feature vector then creates an input to context. This input to context, \mathbf{c}_i^{IN} , is defined as:

$$\mathbf{c}_{i}^{\mathbf{IN}} = M^{FC} \mathbf{f}_{i} \tag{A1}$$

Like the item vector, the context vector is a concatenation of temporal and emotional representations, and each of temporal and emotional context is updated separately and normalized to have unit length. Next, this input to context, \mathbf{c}_i^{IN} , is used to updated the current context state, \mathbf{c}_i :

$$\mathbf{c}_i = \rho_i \mathbf{c}_{i-1} + \beta \mathbf{c}_i^{\mathsf{IN}} \tag{A2}$$

 β defines how much context is updated for each presented item, and takes on a separate value for the temporal and emotional sub-regions (β_{enc}^{temp} and β_{enc}^{emot} , respectively). This arrangement allows for the emotional context to drift at a different rate than the temporal context. Given that physiological arousal can give rise to slow systemic effects, this was seen as a desirable property. The β parameters are fixed to the same value each presented item. ρ is determined separately for each sub-region to normalize the level of contextual activation to have unit length (see Howard and

Kahana 2002 for a more detailed discussion of the importance of this step):

$$\rho_i = (1 + \beta^2 [(\mathbf{c}_{i-1} \cdot \mathbf{c}_i^{\text{IN}})^2 - 1])^{1/2} - \beta(\mathbf{c}_{i-1} \cdot \mathbf{c}_i^{\text{IN}}). \tag{A3}$$

As each item is presented, the associative matrices (M^{FC} and M^{CF}) are updated according to a standard Hebbian learning rule, such that

$$\Delta M^{FC} = \mathbf{c}_i \mathbf{f}_i^{\mathrm{T}},$$

$$\Delta M^{CF} = \phi_i L^{CF} \mathbf{f}_i \mathbf{c}_i^{\mathrm{T}}. \tag{A4}$$

For early list items, eCMR assumes a primacy gradient of attention such that the change in M^{CF} is scaled by ϕ_i , which is greatest for early list items and decreases exponentially to an asymptotic value over the course of list presentation:

$$\phi_i = \phi_S \, e^{\phi_d \, (i-1)} + 1,\tag{A5}$$

where ϕ_S and ϕ_d are model parameters. L^{CF} in Equation 4 is a matrix that allows CMR to scale the magnitude of source associations relative to temporal associations. L^{CF} has four sub-regions, corresponding to each of the 4 possible association types:

$$L^{CF} = \begin{bmatrix} L_{tw}^{CF} & L_{ts}^{CF} \\ L_{SW}^{CF} & L_{SS}^{CF} \end{bmatrix}. \tag{A6}$$

In the subscript, the first term refers to the context type (temporal (t) or source (s), i.e. emotional), and the second term refers to the feature type (again, temporal (w) or source). For simplicity, only the temporal feature terms are set to non-zero values: the emotional context to temporal feature associations, L_{sw}^{CF} , is a model parameter; the temporal context to temporal feature associations, L_{tw}^{CF} , was fixed at 1 for Polyn et al., 2009, but we consider other values for this parameter, as

described below.

In a similar way, ${\it M}^{FC}$ also has 4 sub-components (i.e. those starting with w), but again only the temporal feature terms are set to non-zero values:

$$L^{FC} = \begin{bmatrix} L_{wt}^{FC} & L_{ws}^{FC} \\ L_{st}^{FC} & L_{ss}^{FC} \end{bmatrix}. \tag{A7}$$

In M^{FC} the relative contribution of the updated experimental associations to the pre-existing associations is controlled by the parameter γ_{FC} :

$$M^{FC} = (1 - \gamma^{FC})M_{pre}^{FC} + \gamma^{FC}M_{exp}^{FC}, \tag{A8}$$

whereas the pre-experimental and experimental components of ${\it M}^{CF}$ do not have this trade-off:

$$M^{CF} = sM_{pre}^{CF} + M_{exp}^{CF}. (A9)$$

Given that the semantic associations are stored in M_{pre}^{CF} as described above, the s parameter thus controls the relative contribution of semantic associations to the experimentally formed (temporal and emotional) associations.

After all list items are presented, if there is an end-of-list distractor, it is simulated in the model by again updating \mathbf{c} according to Equation 2. In this case, the distractor is a single item and updates temporal context with value β_{dist} . Like the shift in temporal context between emotional context types, this disruption item is not incorporated into the association matrices and cannot be recalled.

At the time of recall, cuing with \mathbf{c}_i retrieves a vector $\mathbf{f^{IN}} = M^{CF}\mathbf{c}_i$. To determine which item the model recalls, $\mathbf{f^{IN}}$ serves as the input to a leaky, competitive accumulation process (Usher &

McClelland, 2001) whose value at time step t is determined by

$$\mathbf{x}_t = (1 - \tau \kappa - \tau \lambda \mathbf{N}) \mathbf{x}_{t-1} + \tau \mathbf{f}^{\mathbf{I} \mathbf{N}} + \varepsilon,$$

$$\mathbf{x}_t \to max(\mathbf{x}_t, 0).$$
 (A10)

Each element of \mathbf{x}_t corresponds to an element in $\mathbf{f^{IN}}$. τ is a time constant and κ is a leak parameter decreasing each item by its own strength. λ is a parameter that controls lateral inhibition, by scaling the strength of an inhibitory matrix \mathbf{N} which connects each accumulator to all of the others except itself. ϵ represents randomly distributed noise with mean 0 and standard deviation with model parameter η .

The process in Equation 7 runs iteratively until one of the accumulating elements crosses a threshold or until the recall period is over, determined by a fixed number of time steps in t. This equation is updated until one of the accumulating elements surpasses a threshold (here, set to 1), or until the number of time steps exceeds the amount of recall time that the model is allotted for the recall period. If an element surpasses the threshold, its corresponding item is recalled. The item is re-presented to the model, updating context according to Equation 2. Whereas the drift rate for temporal context varies between encoding and recall (β_{enc}^{temp} and β_{rec}^{temp} , respectively) for simplicity the drift rate of the emotional context region is held constant between encoding and recall (i.e. $(\beta_{enc}^{emot} = \beta_{rec}^{emot})$). Once context is updated, this activates a different set of features on \mathbf{f}^{IN} , and, time permitting, the recall process in Equation 7 begins again.

The modulation of memory representations by emotion

Pre-experimental effects of emotion. Following the assumptions of CMR, we first defined eCMR by

assuming that a change in a non-temporal context sub-region (here, a change between neutral and negative emotional contexts) causes a shift in temporal context. In this way, temporal context is updated and all items studied prior to the novel item become less accessible. Thus, when two successive items are not from the same emotion category, temporal context is updated according to Equation 2. This "disruption item" only updates the temporal context sub-region, is not incorporated into the association matrices, and unlike list items it cannot be recalled. Given that a change in emotional category is qualitatively different than a presented list item, it updates temporal context according to a different model parameter, d, rather than β (Polyn et al., 2009).

Emotion enhances attention. Given that the baseline model failed to account for the list composition effect (see Simulation 1), emotional items were further defined to modulate emotion via the same attentional processes used for primacy items. More explicitly, emotional items increased the strength of association between the item features and the temporal context (M^{CF}) via a new parameter ϕ_{emot} such that experimental context-feature associations are updated as:

$$\Delta M^{CF} = \phi_{emot} \phi_i L^{CF} \mathbf{f}_i \mathbf{c}_i^{\mathrm{T}}$$
(A11)

Note that Equation 11 is identical to Equation 4 if ϕ_{emot} =1, and requires ϕ_{emot} >1 in order for emotional items to benefit from stronger associations and thus improved recall.

Emotional enhances attention without additional temporal context drift. This model was identical to the previous one except d=0.

Emotional enhances attention without additional temporal context drift or retrieval of the encoding context. This model was identical to the previous one except β_{rec}^{temp} , $\beta_{rec}^{emot} = 0$.

APPENDIX 2: DETAILS OF METHODS IN TALMI ET AL.'S (2007) EXPERIMENT 2, SIMULATED IN SECTION 2

In simulations 1-3 we use three variants of eCMR to capture the average recall data from the emotional and

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related-neutral conditions in Talmi et al., 2007, Experiment 2. The semantic coherence of the stimuli used in

that experiment was matched, first, by selecting neutral items that depicted domestic scenes, and second,

by equating the semantic similarity ratings of emotional and neutral stimuli obtained in a separate rating

study.

In the rating study participants were presented with subsets of 5 pictures; all pictures in a subset were

drawn from the same category (emotional negative, related neutral pictures which were all depictions of

domestic scenes, random neutral pictures). The pictures were drawn from the IAPS (Lang & Bradley, 2007)

and supplemented by pictures from the Internet obtained using Google image search. Participants rated all

possible pairs within a subset on a 1-7 scale for their degree of semantic relatedness. A semantic relatedness

score was computed for each picture in the subset based on its relatedness to the other 4 pictures in the

same subset. Each list in the main experiment included three such subsets. The same pictures were used

across the pure and mixed list conditions. The pure lists included 3 subsets of emotional negative pictures; 3

subsets of related neutral pictures; or 3 subsets of randomly selected neutral pictures. The mixed lists

included one subset from each of these categories. There was no significant difference between the average

semantic relatedness of the emotional and the related-neutral pictures, but the relatedness of random-

neutral pictures was lower. The order of pictures in a list was randomised for each participant.

In that experiment two groups of participants studied either 3 pure lists or 3 mixed lists of 15 experimental

pictures. Experimental pictures were preceded by two buffer stimuli of the same type (or one emotional and

one neutral, in mixed lists), and followed by a minute-long arithmetic distractor task, after which participants

recalled the pictures by describing the content of the pictures they have seen in writing. Each recall output

was scored as 'correct' if two independent raters agreed that the description matches that of one, and only

one, of the pictures in the study set. In the rating study participants were presented with subsets of 5

pictures; all pictures in a subset were drawn from the same category (emotional negative, related neutral

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pictures which were all depictions of domestic scenes, random neutral pictures). The pictures were drawn from the IAPS (Lang & Bradley, 2007) and supplemented by pictures from the Internet obtained using Google image search. Participants rated all possible pairs within a subset on a 1-7 scale for their degree of semantic relatedness. A semantic relatedness score was computed for each picture in the subset based on its relatedness to the other 4 pictures in the same subset. Each list in the main experiment included three such subsets. The same pictures were used across the pure and mixed list conditions. The pure lists included 3 subsets of emotional negative pictures; 3 subsets of related neutral pictures; or 3 subsets of randomly selected neutral pictures. The mixed lists included one subset from each of these categories. There was no significant difference between the average semantic relatedness of the emotional and the related-neutral pictures, but the relatedness of random-neutral pictures was lower. The order of pictures in a list was randomised for each participant.

APPENDIX3: THE EFFECT OF RECALL INSTRUCTIONS

We manipulated retrieval of mixed lists of negatively valenced emotional and neutral pictures by asking participants to recall emotional or neutral items first (the 'emotional first' and 'neutral first' conditions), comparing the results to a 'natural' mixed recall where no such instructions were given. Pictures were again drawn from those rated in the rating study reported in Talmi et al. (2007). The semantic relatedness of the pictures was controlled such that the negative and the neutral picture categories were equally cohesive, but between-category associations were weaker.

Three groups of 18 participants took part in this experiment for course credit. They were 18-35 years old and were screened for neurological and psychiatric history. Each group studied 3 mixed lists of 10 negative and 10 neutral pictures, presented in a random order. Participants were informed that they will be viewing negative, arousing pictures and neutral pictures of domestic scenes, and that the order of recall would vary. The first recall in all groups was 'natural'; data from this practice list was discarded. The next two lists were allocated to the same between-participant condition, either natural, emotional first, or neutral first.

When participants encode lists of stimuli that include emotionally arousing ones, the post-encoding emotional context is invariably more emotional than it was before the list was studied. This emotional coloration of the time-of-test context cue before any item is actually retrieved could render emotional stimuli more accessible than a context of a delayed retrieval test, biasing recall to commence with the retrieval of an emotional stimulus first. Therefore, a minute-long arithmetic distractor task separated the study and the picture free recall task to bring the emotional sub-region of the test context back to neutral.

The 'natural' mixed recall group were given 3 minutes to recall all of the pictures at any order. After those 3 minutes have elapsed, participants were invited to continue recall for another 3 minutes, although most participants could no longer recall anything more at that point, and data for that group was aggregated across these two test periods. The 'emotional first' group was given 3 minutes to recall the emotional pictures (first recall test). After 3 minutes, they were asked to recall the neutral pictures for another 3

minutes (second recall test). The 'neutral-first' group was asked to recall the neutral pictures first (first recall test). After 3 minutes, they were asked to recall the emotional pictures for 3 minutes (second recall test).

The results are depicted in Figure 4. Memory in the 'natural' mixed recall condition resembled the results from the mixed list condition reported in section 3, and a paired t-test confirmed that emotion significantly benefitted memory, t(17)=4.34, p<.001, Cohen's d=1.02. We used eCMR to simulate the data from the mixed list condition. This simulation used the semantic association matrix from the rating study and the stimulus order actually administered to participants. All parameters were the same as in Simulation 3, but with a lower ϕ_{emot} (1.05). As in Simulation 3, eCMR captured both the average recall and the recall output data (Figure A1).

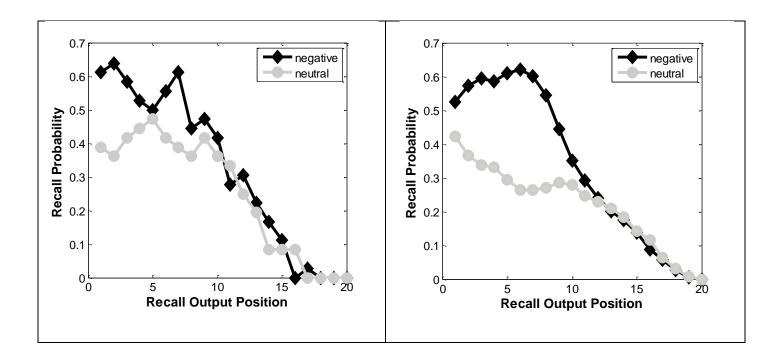


FIGURE A1: EMPIRICAL AND SIMULATED OUTPUT ORDER EFFECTS.

Left: Probability of recall in the experiment reported in Appendix 3 is plotted as a function of recall position, starting with the very first item recalled. **Right:** Simulated recall order from the same experiment using the final variant of eCMR (Simulation 3).

The analysis of the instructed conditions used two independent sample t-tests to compare recall of emotional and neutral items across the 'emotion first' and 'neutral first' groups. The magnitude of the effect of emotion on memory was equivalent and large in the first recall test (comparing recall of emotional items in the 'emotion first' group to neutral items in the 'neutral first' group), t(34)=2.34, p<.05, Cohen's d=0.8, and in the second recall test, (comparing recall of neutral items in the 'emotion first' group to recall of emotional items in the 'neutral first' group), t(34)=2.20, p<.05, Cohen's d=0.76.