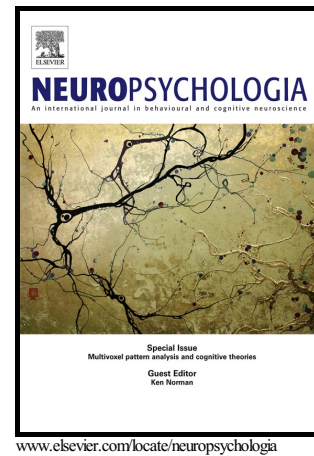# Author's Accepted Manuscript

The list-composition effect in memory for emotional and neutral pictures: Differential contribution of ventral and dorsal attention networks to successful encoding

Gemma E. Barnacle, Daniela Montaldi, Deborah Talmi, Tobias Sommer

Cite this article as: Gemma E. Barnacle, Daniela Montaldi, Deborah Talmi and Tobias Sommer, The list-composition effect in memory for emotional and neutral pictures: Differential contribution of ventral and dorsal attention networks to successful encoding, *Neuropsychologia*, http://dx.doi.org/10.1016/j.neuropsychologia.2016.06.023

The list-composition effect in memory for emotional and neutral pictures: Differential contribution of ventral and dorsal attention networks to successful encoding

Gemma E. Barnacle[ab], Daniela Montaldi[a], Deborah Talmi[a*], Tobias Sommer[b*]

[a] School of Psychological Sciences, University of Manchester, Oxford Road, Manchester. M13 9PL.

[b] Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Martinistr. 52, D-20248, Hamburg, Germany.

[*] Joint senior authors

Gemma Barnacle: gemmaebarnacle@hotmail.com

Daniela Montaldi: daniela.montaldi@manchester.ac.uk

Tobias Sommer: tsommer@uke.uni-hamburg.de

Corresponding author: Deborah Talmi; deborah.talmi@manchester.ac.uk; School of Psychological Sciences, University of Manchester, Oxford Road, Manchester, UK. (0161) 275 1968.

Abstract

The Emotional enhancement of memory (EEM) is observed in immediate free-recall memory tests when emotional and neutral stimuli are encoded and tested together ("mixed lists"), but surprisingly, not when they are encoded and tested separately ("pure lists"). Here our aim was to investigate whether the effect of list-composition (mixed versus pure lists) on the EEM is due to differential allocation of attention. We scanned participants with fMRI during encoding of semantically-related emotional (negative valence only) and neutral pictures. Analysis of memory performance data replicated previous work, demonstrating an interaction between list-composition and emotional valence. In mixed lists, neural subsequent memory effects in the dorsal attention network were greater for neutral stimulus encoding, while neural subsequent memory effects for emotional stimuli were found in a region associated with the ventral attention network. These results imply that when life experiences include both emotional and neutral elements, memory for the latter is more highly correlated with neural activity representing goal-directed attention processing at encoding.

1.   Introduction

The Emotional Enhancement of Memory (EEM) effect refers to the better memory of emotional compared to neutral information or events. Cahill & McGaugh's modulation model of the EEM has amassed a wealth of supporting evidence (McGaugh, 2013, 2004). In brief, the modulation model is principally concerned with the functional connection of the amygdala (AMY), hippocampus (HPC) and caudate nucleus which are said to perform different functions. The amygdala is said to be the modulatory hub which influences brain regions, e.g. particularly the hippocampus and the caudate nucleus. Activation of the amygdala may be achieved by several routes, but most commonly cited are the actions of stress hormones such as epinephrine and cortisol. The levels of these hormones may rise due to a stress reaction (for example witnessing a traumatic event), or may rise due to experimental drug administration. Epinephrine activates the amygdala indirectly as it cannot permeate the blood brain barrier. It is proposed that peripheral elevation of these hormones (for example during a stress response) leads to the activation of beta-adrenoceptors on the vagus nerve, which connects via the nucleus of the solitary tract (Miyashita & Williams, 2006) and the locus coeruleus (McIntyre, McGaugh, & Williams, 2012) to the amygdala which in turn releases norepinephrine (NE).

In support of this model, evidence from neuroimaging research demonstrates enhanced activation in the amygdala (AMY) and medial temporal lobe (MTL) during the successful encoding of emotionally arousing stimuli compared to neutral stimuli (Cahill et al., 1996; Schwarze, Bingel & Sommer, 2012; for reviews see Hermans et al., 2014; McIntyre, McGaugh, & Williams, 2012). Furthermore, there is some evidence that these activations are more strongly associated with subsequent delayed- compared to immediate-memory (Ritchey et al., 2008), in agreement with the modulation model and with human lesion findings (LaBar & Phelps, 1998; Sharot et al., 2007). Yet the EEM is often pronounced immediately after study (e.g. Harris & Pashler, 2005; Kensinger & Corkin, 2004), before synaptic consolidation has been completed (Alberini and Kandel, 2015); a finding for which the modulation model cannot account. The correlation between activations in the MTL that correspond to the EEM effect could support either immediate or delayed EEM, and have indeed been shown to correlate with EEM in immediate memory tests (Kensinger and Corkin, 2004; Sommer et al., 2008). An emerging body of research (Mather, Clewett, Sakaki, & Harley, 2015; Talmi, 2013) seeks to specifically explain the correlates of the *immediate* EEM effect. This research has expanded the current literature by

examining the role of cognitive factors at encoding as mediators of this effect (Mather & Sutherland, 2011; Talmi, 2013), and the contribution of brain regions outside the MTL (Mickley Steinmetz et al., 2010; Murty et al., 2010).

This growing area of research has already demonstrated convincing results regarding the contribution of several cognitive factors to the immediate EEM, such as attention and semantic relatedness. These are factors which typically provide a processing advantage for emotional stimuli (Talmi & Moscovitch, 2004; Talmi, Schimmack, Paterson & Moscovitch, 2007; Talmi et al., 2013), because such stimuli are typically preferentially attended to and are more related to each other compared to neutral stimuli. To test whether cognitive factors play a role in EEM we have, in recent years, manipulated the encoding conditions in various ways and examined which manipulation(s) abolish the EEM in immediate free recall. We found that this outcome only occurs when three conditions are in place (Talmi & McGarry, 2012): (1) when attention resources are not constrained, for example by presenting items with relatively long inter-stimulus intervals under full-attention, intentional encoding conditions; and when emotional stimuli are prevented from competing for resources with neutral stimuli; (2) when emotional and neutral items are equally inter-related to each other; and (3) when emotional and neutral items are studied separately. These conditions control organization, attention, and distinctiveness processing, in turn. Once any of these controls is relaxed, the EEM effect reappears. Here we focus on the list composition effect on EEM (Buchanan, Etzel, Adolphs, & Tranel, 2006; Dewhurst & Parry, 2000; Hadley & MacKay, 2006; MacKay et al., 2004; Schmidt & Saari, 2007; Sommer et al., 2008; Talmi, Schimmack, et al., 2007; Talmi, Luk et al., 2007; Talmi & McGarry, 2012), namely, on what happens when instead of encoding emotional and neutral items separately ("pure lists") the two item types are encoded and tested together with neutral items ("mixed lists"). We have previously shown that the EEM effect is only observed in the latter condition (Talmi, Luk et al., 2007; Talmi & McGarry, 2012).

The studies cited above demonstrate the list-composition effect on EEM. They used a variety of stimuli and experimental tasks: e.g. positive and negative words and a remember/know recognition test (Dewhurst & Parry, 2000); taboo and neutral words and free recall (Hadley & MacKay, 2006; Schmidt & Saari, 2007); positive, negative and neutral words in recognition (Sommer et al., 2008; note – only pure lists were included); and negative/arousing (non-taboo) and neutral pictures and free recall (Talmi, Schimmack, et al., 2007; Talmi, Luk et al., 2007; Talmi & McGarry, 2012). Here we used picture stimuli, and all our emotional pictures were negative and arousing. This is because research demonstrates a key role for arousal in EEM (e.g. Kensinger and Corkin, 2004; Mather & Sutherland, 2011). Indeed, once semantic relatedness is controlled, EEM in mixed lists is consistently found only for highly arousing stimuli, such as

taboo words and emotional scenes, but not for negatively-valenced emotional words (Buchanan et al., 2006; Madan, Caplan, Lau, & Fujiwara, 2012; Talmi & Moscovitch, 2004). In our laboratories, negatively-valenced pictures generate more consistent ratings of high arousal (Talmi, 2013).

When participants process a mixed study list, emotional items stand out because while all list items share some attributes by virtue of experimental selection – e.g. all may be pictures depicting social scenes – the emotional items possess additional attributes that are not shared by the neutral items in the list, nor by the majority of items thought to be stored in long-term memory. This greater salience of emotional over neutral items within the 'active framework' that participants hold in mind while they encode a study list is referred to as 'primary distinctiveness' (Schmidt, 1991). Mediation theory (Talmi, 2013) suggests that distinctiveness contributes to the EEM. Primary distinctiveness may be essential for the role emotion plays in our memory for important life events, because life outside the laboratory is not 'pure' - our experiences always include a mixture of emotional and neutral elements. The aim of the present study was to use functional MRI (fMRI) neuroimaging to illuminate the neural mechanism that underlies the effect of primary distinctiveness processing on EEM, by comparing mixed- and pure-list encoding. Specifically, we asked whether the list-composition effect on the EEM is due to differential attention to emotional and neutral items during encoding.

A number of findings suggest that the effect of list-composition on the EEM is a result of the processing that happens at the encoding stage. Processing resources are allocated to emotional pictorial stimuli at the expense of neutral stimuli when these compete with each other (MacKay et al., 2004; Mather, Clewett, Sakaki, & Harley, 2015; Schimmack, 2005; Schmidt & Saari, 2007; Talmi, Schimmack, Paterson, & Moscovitch, 2007; Vuilleumier, 2005). Therefore, it is likely that participants allocate more resources to emotional than neutral materials in mixed lists, while the resources allocated to these two material types in pure lists may be equivalent. We found evidence for this in an EEG study, where Event-Related Potentials (ERPs) known to be associated with enhanced processing had higher amplitude for emotional than neutral pictures in mixed, but not pure lists (Barnacle & Talmi, in press), although others disagree (Codispoti, Ferrari, & Bradley, 2007; Schupp, Schmälzle, Flaisch, Weike, & Hamm, 2012). In support of this attentional explanation of the EEM in mixed lists, Nguyen and McDaniel (2014) found that list composition influenced the memory advantage of complex over simple neutral pictures: additional processing time was allocated to complex than simple pictures when they were encoded in mixed lists, but that processing time for the two types of pictures was equivalent when they were encoded in pure lists. The attentional explanation for the picture complexity effect is relevant to the current study because participants judge emotional pictures as more

vivid and complex than neutral pictures (Madan, Bayer, Gamer, Lonsdorf, & Sommer, in preparation; Todd, Talmi, Schmitz, Susskind, & Anderson, 2012) even when they are equated on objective measures. Linking differential attention and its memory consequences, Talmi et al. (Talmi, Anderson, Riggs, Caplan, & Moscovitch, 2008) showed that the fusiform gyrus was sensitive to the effect of emotion during the encoding of mixed lists, and that this activation overlapped with subsequent neural EEM.

To put the current investigation into context, it is known that list-composition influences a number of human memory phenomena (for review see Malmberg & Shiffrin 2005; Nguyen & McDaniel, 2014). In memory tests of free recall, many well-known effects are present in mixed lists but disappear or reverse in pure lists (Nguyen & McDaniel, 2014). One of these is the list-strength effect; namely, the greater advantage of 'strong' over 'weak' stimuli in mixed compared to pure lists in free recall (Ratcliff et al., 1990). The list-strength effect is relevant here because emotional items are conceivably "stronger" than neutral ones, a point we discuss in more detail in the discussion section. Thus, the same mechanisms that have been put in place to account for this list-strength effect may explain the list composition effect on the EEM. According to current memory models, the list-strength effect is a result of the better differentiation of 'strong' memory traces at encoding, a process that free recall tests are particularly sensitive to (Criss and Koop, 2015; Dennis and Humphreys, 2001; Shiffrin and Steyvers, 1997). Therefore, if the list-composition effect on the EEM is an exemplar of the list-strength effect, we should be able to observe its neural correlates during encoding. In free recall participants rely a lot more on a search process and are affected more by the context than in recognition. This allows the stronger items to better compete for retrieval resources in the free recall of mixed lists, while the more uniform context in the free recall of pure lists attenuates their advantage.

Yet other findings challenge the encoding interpretation of the effect of list-composition on EEM. Emotional pictures attract more attention than neutral ones even in pure lists, evident in equivalent reductions in concurrent task performance in pure or mixed lists (Talmi & McGarry, 2012); and in enhanced attention-related ERPs to emotional pictures that follow a sequence of pictures with the same emotional valence (Codispoti, Ferrari, & Bradley, 2007; Schupp, Schmälzle, Flaisch, Weike, & Hamm, 2012). That attention allocation may be important even within pure lists is also evident in Talmi & McGarry's finding that attention mediated the effect of emotion on memory in pure lists, and that although EEM is abolished in pure lists, it can be observed even in pure lists when encoding takes place under divided attention conditions. The fact that the list-strength effect is abolished in recognition memory tests clarify that differential encoding resources may not be sufficient for the effect to become manifest (Ratcliff et al., 1990). Unpublished results from our laboratory suggest that the effect of list composition on EEM

reverses when memory is tested with cued recall or recognition, results that highlight the importance of retrieval processes for the effect of list-composition on EEM. Clearly, the relative distinctiveness of emotional items may play a role not only at encoding, but also at retrieval, bestowing memory advantages through similar mechanisms to those that benefit stimuli that are temporally distinct (e.g. recency effects, Brown et al., 2007).

Here, we collected neuroimaging data during encoding to investigate whether the list-composition effect on the EEM was due, in part, to encoding processes. Participants encoded negatively-valenced arousing pictures (referred to henceforth as "emotional") and neutral pictures in mixed and pure lists. The behavioural interaction between list composition and emotional valence in three previous studies (Barnacle, Tsivilis, Schaefer & Talmi, in prep; Talmi & McGarry, 2012; Talmi, Luk, et al., 2007) was driven by a memory advantage for emotional, compared to neutral stimuli in mixed but not pure lists, and a reduction in memory for neutral stimuli presented in mixed compared to pure lists. We predicted that the same behavioural results would be obtained here, despite the altered encoding conditions in the scanner environment. We used the subsequent memory paradigm which involves the measurement of brain activity at encoding and the categorisation of experimental events according to their later memory status as remembered or forgotten. To ensure that our results related specifically to successful encoding in long-term memory, and not to encoding items only in working memory, we employed a distractor task after encoding (see Methods sections for more details). Specifically, we wanted to find out whether differential activation in attention networks during successful encoding would explain the behavioural pattern of EEM results, where EEM is present in mixed-, but absent pure-lists.

A meta-analysis of subsequent memory effects (Uncapher and Wagner, 2009) has shown that encoding activation in dorsal regions of lateral posterior parietal cortex (PPC) is associated with successful encoding. This effect was insensitive to stimulus type and the nature of the testing, and was therefore interpreted as a general-purpose mechanism associated with goal-directed attention to the encoded material. Building on that work, our key prediction of the neural data was that attention would be differentially involved in the successful encoding of emotional compared to neutral stimuli in mixed- but not pure-lists. We predicted that under intentional encoding, subsequent memory effects in the dorsal attention network (DAN), associated with top-down attention allocation (Corbetta and Shulman, 2002; Corbetta et al., 2008), would track the pattern of the behavioural results; that is, we predicted that DAN activation would be greater for neutral items in pure lists than neutral items in mixed lists.

In their meta-analysis, Uncapher and Wagner (2009) also reported ventral-parietal subsequent memory effects when the retention interval was short (<15 minutes). They suggested that such activations express reflexive attention to salient, incongruent or infrequent stimuli; in other words, stimuli that are relatively distinct, triggering memory-enhancing processes that have more impact on immediate memory. Because we used an immediate memory test here, we expected to confirm their hypothesis, and predicted that in mixed lists we would observe greater subsequent memory effects in regions belonging to the ventral attention network (VAN) for emotional compared to neutral stimuli (Corbetta, Patel, & Shulman, 2008; Viviani, 2013; Vossel, Geng, & Fink, 2014).

2.   Materials

Stimuli consisted of semantically related neutral, and semantically related emotional colour pictures which were arousing and negatively-valenced (no positively valenced emotional pictures were used); taken from Barnacle, Madan and Talmi (in prep.). Stimuli were previously rated for arousal and valence using the SAM scales (Bradley & Lang, 1994); and for semantic relatedness as measured by how similar a trial stimulus was to a set of category exemplars (emotional / neutral). Controlling the stimulus sets (1 x emotional, 1 x neutral) for semantic relatedness eliminated a confound present in much emotional memory research – i.e. differential semantic relatedness is known to contribute to the EEM, but the EEM can be eliminated (given other controls) when semantic relatedness is equated between stimulus sets (Talmi, Luk, McGarry, & Moscovitch, 2007; Talmi & McGarry, 2012; Talmi, Schimmack, et al., 2007).

Participants saw a total of 224 experimental pictures (50% emotional, 50% neutral), and all participants saw the same pictures, presented in different orders. Each stimulus set (both emotional and neutral) contained 96 experimental pictures and 16 buffer pictures. Pictures were randomly assigned to form part of the pure or mixed encoding lists, resulting in three experimental conditions: pure neutral, pure emotional, and mixed (containing neutral and emotional stimuli). Pictures were presented in 16 encoding lists (8 mixed, 4 pure neutral, 4 pure emotional) containing 14 stimuli each. The order of lists and of pictures within lists was pre-randomised. This was achieved by scripting a random permutation of list order (1-16), stimulus order within lists (1-14), and the allocation of stimuli to conditions (mixed/pure as per detailed above).

The first two pictures in each list were buffers which were removed from analysis. Mixed lists contained two buffers - one emotional and one neutral, followed by six pictures from both the emotional and neutral sets, randomised in order. Pure lists contained two same-emotion buffers

followed by twelve same-emotion pictures, either all neutral or all emotional. Stimulus check-lists were created for real-time coding of free recall responses. The total number of pictures analysed in each condition reflected the removal of three pictures (two unintentional emotional stimulus duplicates, and one poor quality neutral stimulus).

Stimulus presentation for this experiment was realised using Cogent 2000 (Wellcome Department of Imaging Neuroscience, UCL, UK; http://www.vislab.ucl.ac.uk/cogent_2000.php). A digital audio recording device (SONY IC Recorder) was placed next to the fMRI experimenter-participant intercom to record all free recall responses for later playback and coding verification.

Table 1. Mean scores of arousal, valence, and semantic relatedness for each stimulus type

Measure	Stimulus type	
	Neutral	Emotional
Arousal*	2.34 (1.36)	5.65 (1.47)
Valence*	5.34 (0.49)	2.81 (0.66)
Semantic Relatedness	5.22 (1.31)	4.81 (1.24)

Mean rating on three stimulus measures, standard deviation in parentheses. *Indicates significant difference between stimulus types at $p<.001$. Arousal and valence measures were rated on a scale 1-9 (as per SAM scale, Bradley & Lang, 1994); semantic relatedness was scored on a scale of 1-7, 1 = low, 7 = high.

3. Methodology

3.1. Participants

Twenty three female participants were recruited via online advertising on a job exchange website of the University of Hamburg. One was removed from analysis due to non-compliance with instructions, leaving a total of 22 participants (mean age 26 years). Female-only subjects were chosen due to the gender-dependent lateralisation of amygdala activity suggested to occur in such emotional memory paradigms (Cahill et al., 2004, 2001). Participants provided informed consent, and consulted with a medical physician before scanning commenced to ensure suitability for the experiment. Ethical approval was obtained from the local ethics committee.

3.2   Procedure

After providing informed consent, participants underwent a practice session containing all tasks that they would complete during scanning with full, detailed instructions and opportunities to ask any questions. The stimuli used in this practice session were 14 additional pictures (50% emotional, 50% neutral) that were not shown in experimental sessions. After the practice session, participants underwent 16 experimental blocks which each contained four tasks: baseline task, list encoding, distractor task, and free recall.

3.2.1.   Baseline Task

Participants were instructed to respond by button press to an arrow presented on the screen. Single arrows were presented for a fixed duration of 1500ms and pointed either to the left or right of the participants' field of view. Each block contained 14 trials. This task was chosen in order to provide a hippocampus-independent task on which to contrast encoding data instead of using imaging data from the distractor task or fixation (Mayes and Montaldi, 2010; Stark and Squire, 2001), but this method was not used in the final analysis.

3.2.2.   List Encoding

In each block participants passively viewed 14 pictures under intentional encoding instructions. Participants were instructed to passively view each picture for a later memory test. Participants were explicitly asked not to use a specific memory strategy – e.g. the loci memory strategy. During list encoding a fixation cross was presented 500ms before each image. Each image was presented for 2000ms (conforming to Talmi & McGarry, 2012) with a jittered inter-stimulus interval (ISI) of 4000ms +/- 500ms.

3.2.3.   Distractor Task

After viewing the pictures participants engaged in an arithmetic task, which aimed to reduce recency effects. Two simple sums were presented concurrently on the right and left of the display. Participants were asked to compute the sums mentally and identify the highest value sum by pressing one of two buttons. The distractor task lasted for 60 seconds, after which scanning stopped and the words 'free recall' were presented on screen.

3.2.4.   Free Recall

The inclusion of buffer pictures at the beginning of each encoding list, which were excluded from analysis, were intended to reduce the effect of primacy on memory performance. This approach was complemented by the inclusion of a distractor task before the free recall test,

ensuring that differential working memory activation and recency effects could not influence memory performance. Immediately after the distractor task, when the words 'Free Recall' appeared on the screen, participants were instructed to begin freely recalling the stimuli of the current list in any order. In mixed lists participants were free to recall emotional or neutral pictures in any order they came to mind (the subsequently coded trials are referred to as mixed emotional recalled/forgotten, and mixed neutral recalled/forgotten throughout). All participants were allowed 3 minutes for this task regardless of whether they had finished recalling. This served to encourage further recall, especially in those participants with low motivation to continue recalling. It is notable that this time period was deemed sufficient for the task – no participants were still actively recalling at the end of the task, and on more than one occasion participants had recalled all items successfully within this time.

3.3.   Analysis

3.3.1.   Behavioural Analysis

Each trial was coded as one of eight trial types: mixed emotional recalled / forgotten, pure emotional recalled / forgotten, mixed neutral recalled / forgotten, pure neutral recalled / forgotten. Free recall responses were coded during the recall period by two raters who referred to prepared image checklists. Because pictures were selected to be highly distinct, ambiguities were minimal and were resolved through discussion after each list. In order to examine the behavioural data for EEM effects, we computed proportion recalled scores for each condition. These were calculated as the number of recalled items of a given condition (e.g. mixed emotional) divided by the total number of stimuli of that kind presented. We also calculated the behavioural EEM as the difference between the proportion of recalled emotional and the proportion of recalled neutral stimuli.

To further investigate the strategy participants used during retrieval we also computed a clustering score for each participant using the LBCsem – list-based semantic clustering index (Stricker et al., 2002). Using this method, any two consecutive same-category items (emotional or neutral) produced as output during the free recall of mixed lists were counted as one cluster. For each participant an average score across the eight mixed lists was calculated. Given the number of stimuli used and their category, the LBCsem scores of this experiment could have ranged from LBCsem = -6 (all items of the list recalled but no clusters present) to the maximum score of LBCsem = 6 (all items of the list remembered, with all same-category items recalled consecutively). However, it is notable that such extremes were not expected (and indeed were not found) in the data.

3.3.2. Functional MRI Analysis

3.3.2.1. Image acquisition and pre-processing

Functional MRI data was obtained using a Siemens Trio 3-tesla scanner, with an echo planar imaging (EPI) T2*-sensitive sequence, acquiring 38 contiguous axial slices in descending order (3mm thickness; TR, 2210ms; TE 30ms; flip angle, 80°; FOV, 216 x 216mm2; matrix 64 x 64).

Functional MRI data were pre-processed using Statistical Parametric Mapping (SPM8; Wellcome Department of Imaging Neuroscience, London, UK), and analysed using SPM12, running under MATLAB R2012a (Mathworks, Inc., Natick, MA, USA). The first six images of a volume were discarded because of spin saturation and because participants were adjusting to the scanner noise. Functional data were corrected for differences in acquisition time ('slice timing'), rigid body motion, and susceptibility artefacts ('realign and unwarp'). Then, the individual structural T1 image was co-registered to the mean functional image generated during realignment. Co-registered T1 images were then segmented using the 'New Segment' routine in SPM8. During this pre-processing step, tissue-class images for grey and white matter were generated and subsequently used within the DARTEL toolbox to create structural templates as well as individual flow fields which in turn were used for normalization to MNI (Montreal Neurological Institute) space. Functional images were resliced with an isotropic voxel size of 2 mm. Finally, images were smoothed with a full-width half maximum Gaussian isotropic kernel of 8 mm.

3.3.2.2. Functional MRI Statistical Analysis

First-level single subject models. Encoding trials were coded as recalled or forgotten post-hoc based on the participant's free recall descriptions, and categorised by encoding list (pure or mixed) and valence (emotional or neutral) – resulting in 8 experimental regressors to model. We also modelled a number of regressors of no interest: 4 buffer regressors (mixed emotional/neutral; pure emotional/neutral); the arrow-, and distractor-tasks. Individual regressors were created for all experimental conditions by convolving delta functions marking the onsets of the particular condition with the canonical hemodynamic response function. The arrow and distractor tasks were modelled as blocks of 30, and 60 seconds respectively. We included regressors modelling the buffer items as well as the arrow and distractor tasks in the first level model as regressors of no interest in order to include all experimentally induced variance in the GLM. Data from the buffer items and these tasks were not analysed further. The regressors and functional images of the 16 runs were concatenated and 16 session constants were modelled accordingly. The time series of each run was corrected for baseline drifts by applying a high-pass filter (128 seconds). Within each run serial dependency was corrected by

application of an AR(1) autocorrelation model. Parameter estimates pertaining to the amplitude of the hemodynamic response function were computed at each voxel for each condition and each subject. Finally, difference due to memory (Dm) contrast images were computed by subtracting in each voxel the parameter estimate corresponding to subsequently forgotten from subsequently recalled pictures for each of the conditions.

Second-level (group) model. These Dm contrast images (recalled minus forgotten) for each condition were entered into a flexible factorial design as implemented in SPM12. This design modelled the effects of subject, list-type, and valence. In order to control for multiple comparisons we used a combined voxel-wise significance threshold of p<.005 together with an extent threshold of kE = 20 (based on recommendation from Lieberman and Cunningham, 2009). Applying this combination thresholding procedure acted to balance type I and type II errors.

4.   Results

4.1.   Behavioural Data

4.1.1.   Proportions Recalled

The proportions of recalled items per condition were entered into a 2 x 2 repeated measures ANOVA with list-type and emotion as factors (Figure 1). We found a significant main effect of emotion, $F(1,21) = 13.340$, $p = .001$, $\eta p^2 = 0.38$; but no significant main effect of list-type $F(1,21) = 2.51$, $p = .13$. A significant list-type x emotion interaction was found $F(1,21) = 11.016$, $p = .003$, $\eta p^2 = 0.33$. Further post-hoc Tukey tests were used to understand this interaction, and found no significant difference between memory for emotional and neutral pictures in pure lists ($p>.05$). There was however, a significant difference between memory of neutral and emotional items in mixed lists, $t(21) = 4.243$, $p<.001$, $d_z = 0.90$. There was also a significant difference between memory for neutral items in mixed compared to pure lists, $t(21) = -3.651$, $p=.001$, $d_z = -.78$. Finally, we also found a non-significant trend for better memory of emotional items in mixed compared to pure lists, $t(21) = 1.803$, $p = .09$, $d_z = 0.38$.

Figure 1. Proportions of recalled items per condition
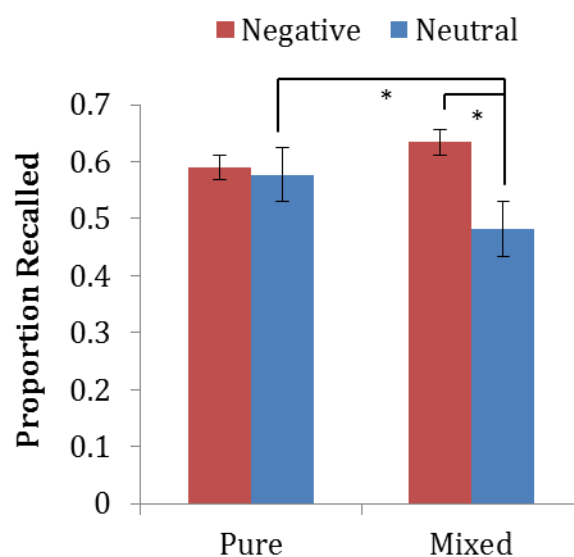
EEM was observed in the mixed condition but not the pure condition. Error bars represent standard error. *p<.001

4.1.2. Clustering Scores

For each participant an average clustering score was calculated across the eight mixed lists using the LBCsem – list-based semantic clustering index (Stricker et al., 2002). There was a moderate clustering effect evident in the data which ranged between LBCsem = -0.71 and LBCsem = 2.69 (mean LBCsem = 0.73, S.D LBCsem = 0.83). Clustering correlated significantly with overall mixed-list memory performance r(22) = .61, p < .01. However, clustering did not correlate significantly with the behavioural EEM.

4.1.3. Functional MRI Results

We first checked the results of the main effect of subsequent memory, i.e. the general Dm effect contrast (recalled > forgotten; [1 1 1 1] at the second level), to ensure that these were consistent with previously published results. In accordance with Kim (2011), we found activations in left inferior frontal cortex (IFC; peak xyz = -50, 26, 20; Z = 6.04; K_E = 3085; peak p < .001); bilateral fusiform gyrus (e.g. [right] peak xyz = 28, -62, -16; Z = 5.84; K_E = 22133; peak p < .001) extending into bilateral hippocampus (e.g. [right] peak xyz = 22, -8, -24) and bilateral posterior parietal cortex (PPC; e.g. [left] peak xyz = -18, -72, 50; Z = 5.71); and bilateral pre-motor cortex

(PMC; e.g. [right] peak xyz = 50, 8, 36; Z = 3.72; K_E = 526; peak p < .001); consistent with Dickerson et al. (2007) and Kim (2011).

Next we investigated the two-way interaction, i.e. list-type (pure vs. mixed) x valence (neutral vs. emotional) interaction, using the contrast [1 -1 -1 1] (see figure 2), to explore the neural data for any corresponding activations that would explain the observed behavioural results. We used t-contrasts in SPM to test the interaction between list-type and valence, to examine in which areas the Dm-effect for emotional pictures in mixed lists was greater than the Dm effect for neutral pictures in mixed lists compared to the same difference in pure lists. Our analysis revealed 3 significant clusters in the following regions: left anterior superior temporal gyrus (aSTG; peak xyz = -40, 6, -22; Z = 3.35; K_E = 71; peak p < .001); right insula (peak xyz = 38, 6, 16; Z = 2.99; K_E = 30; peak p = .001) and part of the ventral attention network in the right supramarginal gyrus (rSMG; peak xyz = 54, -24, 34; Z = 3.17; K_E = 62; peak p = .001) (Uncapher & Wagner, 2009). In all of these regions we found a significant subsequent memory effect ('Dm' effect) only for the mixed emotion condition. To shed light on the drivers of the behavioural interaction we unpacked the neural interactions by conducting simple effects analyses, masked by the interaction SPM, to check where the neural Dm activity for mixed neutral trials was less than that of mixed emotional and pure emotional and neutral trials. In the ATL and the rSMG the Dm effect was greater in the mixed emotional trials compared to the mixed neutral trials. No significant clusters survived the contrast of pure neutral Dm > mixed neutral Dm. For completion, we also investigated where the emotional Dm was greater in mixed- compared to pure-lists for emotional encoding, (using the same masking procedure as above), an effect that was only present as a trend in the behavioural results. Using the same masking procedure as above, the same clusters were again present in aSTG, rSMG, and right insula.

Figure 2. Ventral activation identified in two way interaction analysis
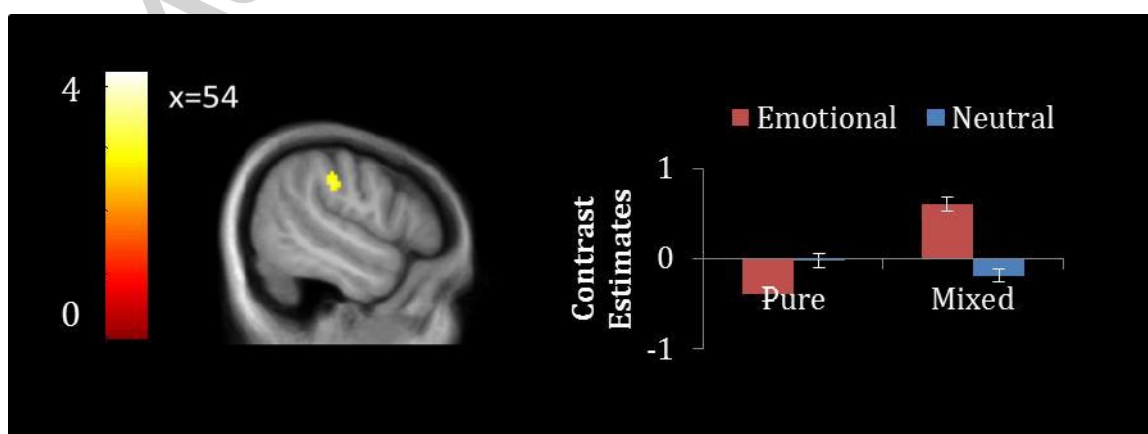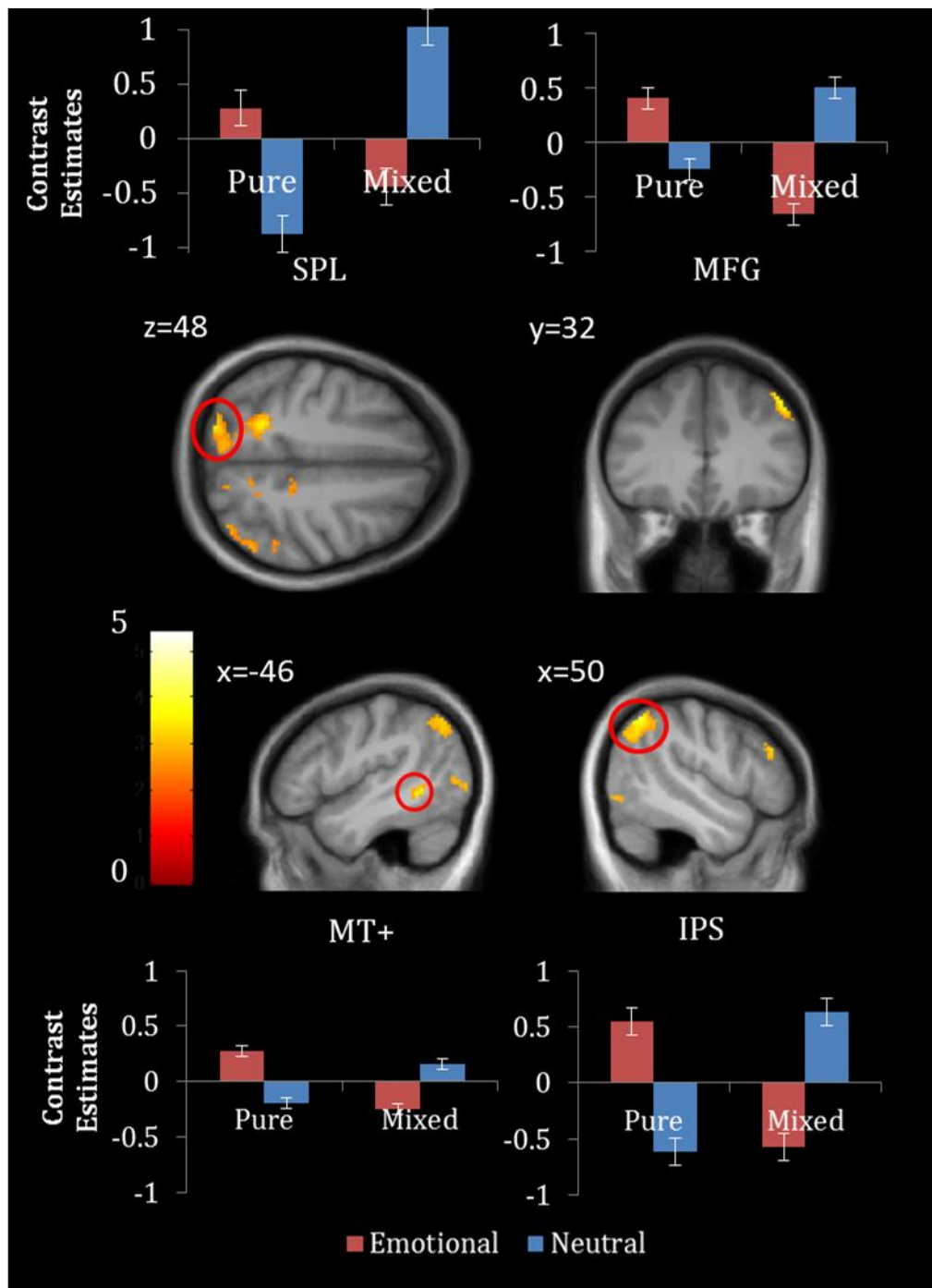
Significant activations at p<.005, K_E = 20 in right SMG. Significant activations are overlaid on the mean high resolution T1 image. Accompanying graph (right) shows contrast estimates and standard error of each Dm regressor.

We also investigated whether there were regions with a larger neural Dm effect despite subsequent poorer memory, an analysis we refer to as the inverse two-way interaction. The rationale of this analysis was to identify areas that are stronger or additionally recruited for successful memory encoding in conditions that render memory formation more difficult as it is the case for the neutral pictures in mixed lists. In particular, this analysis queries where the neural Dm activity for neutral pictures in mixed lists was greater than that of emotional pictures in mixed lists, compared to that difference in pure lists. As such the contrast implemented was a literal inversion of the interaction reported above i.e. the contrast [-1 1 1 -1. In the dorsal attention network (Corbetta et al., 2008; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Uncapher & Wagner, 2009) we found significant clusters in the right posterior inferior parietal sulcus (IPS, peak xyz = 38, -68, 48; Z = 4.21; K_E = 550; peak p < .001) extending into right anterior IPS (peak xyz = 50, -56, 48); left middle temporal complex (MT+; peak xyz = -46, -48, -4; Z = 3.56; K_E = 87; peak p < .001); and left superior parietal lobule (SPL; peak xyz = -26, -76, 48; Z = 3.12; K_E = 157; peak p = .001). We also found significant activation in the right middle frontal gyrus (MFG; peak xyz =40, 32, 42; Z = 3.77; K_E = 174; peak p < .001); considered to govern top-down and bottom up control (Corbetta et al., 2008), and sometimes considered a mediator between attentional networks (Vossel et al., 2014). In addition we identified significant activations in memory / visual areas in right lingual gyrus (peak xyz = 24, -68, -2; Z = 4.87; KE = 1710; peak p < .001) extending into fusiform gyrus (peak xyz = 24, -74, -8) and parahippocampal gyrus (peak xyz = 24, -50, -8).

As before, we unpacked the inverse interaction by testing for three simple effects guided by the behavioural data, masked by the inverse interaction SPM (Figure 3). For the contrast examining where mixed neutral Dm was greater than mixed emotional Dm, the dorsal attention network (IPS, MT+), was identified. We also found significant activation in the MFG region for this contrast. For the contrast examining where neutral encoding activity was greater for mixed compared to pure conditions, again regions in the dorsal attention network (IPS, SPL) was identified. Finally, dorsal regions were identified also in the contrast examining where encoding activity was greater for pure emotional compared to mixed emotional: in IPS, MT+. Again, we found significant activation in the MFG region for this contrast.

Figure 3. Regions of Dorsal attention network activations that explain the inverse two way interaction results

Significant activations at p<.005, K_E = 20 in left MT+ and SPL, and right IPS and MFG. Significant activations are overlaid on the mean high resolution T1 image. Accompanying graphs show contrast estimates and standard error of each Dm regressor.

5.   Discussion

As expected, the behavioural results in this study replicated the effect of list composition on EEM. We found that for stimuli that were controlled for semantic relatedness, the behavioural data demonstrated an interaction of list-composition (list-type) and emotional valence: no pure-list EEM but a significant mixed-list EEM (Barnacle, Tsivilis, Schaefer & Talmi, in prep.; Talmi & McGarry, 2012; Talmi, Schimmack, et al., 2007). As in previous work, the interaction was driven by a reduction in memory for neutral stimuli compared to emotional stimuli in mixed lists, and compared to neutral stimuli in pure lists. Clustering was correlated with neutral and emotional memory performance for mixed lists, suggesting that clustering during free recall of mixed lists was a helpful strategy. However, clustering was not positively correlated with the EEM effect, suggesting that clustering is not important for the EEM effect when participants encode and retrieve stimuli in a mixed list context (Talmi et al., 2007). This result weakens the support for the hypothesis that the list-composition effect on EEM stems from retrieval processes.

Our research question focused on subsequent memory effects in regions related to attention allocation. We hypothesised first, that if the effect of list composition on EEM was a result of attention allocation at encoding, we would observe subsequent memory effects in those regions, and second that the pattern of activations would track the interaction between list composition and emotion observed in memory performance. As expected, the interaction between list-composition and emotional valence was expressed in several of the peak nodes of the ventral and dorsal attention networks, according to the coordinates reported by Corbetta and colleagues (Corbetta et al., 2008; Fox et al., 2006). Activity in the areas of the dorsal, top-down attention network have been identified before to correlate with successful encoding (Uncapher & Wagner 2009). The neural interaction pattern in those regions tracked some of the behavioural results, in the sense that it differentiated the condition where memory was worst – mixed neutral – from those where it was significantly better – mixed emotional and pure neutral. Of these three conditions, subsequent memory effects in the dorsal attention network were stronger and were only positive in the mixed neutral condition. We had expected the opposite direction to hold, because the literature on subsequent memory effects suggests that typically, weaker Dm effects are found in conditions where memory is poor. For example, while both deep and shallow encoding has been associated with subsequent memory effects, the former condition is associated with more widespread activations in the brain (Fletcher et al., 2003; Otten et al., 2001). Our results show, however, that the typical positive association between the neural subsequent memory effects and behavioural memory levels is not obligatory, and that the same logic applies regardless of the direction of this association. Here the Dm-related activations found during successful encoding of neutral pictures in mixed lists

suggests that goal-directed attention was more important in the mixed neutral condition – a condition where stimuli suffered most from competition for resources; compared to the mixed emotional and pure neutral conditions. The increased recruitment of DAN in the mixed compared to the pure neutral conditions corresponds to Talmi & McGarry's finding that divided attention impaired memory for neutral stimuli in mixed, more than pure, lists. Thus, while the dorsal parietal network at encoding may have protected memory for some neutral stimuli in mixed lists, it may have been unable to bring memory performance for these stimuli any higher. Notably, because on average participants recalled about 50% of the pictures they saw, we had similarly strong power to detect subsequent memory effects in all conditions.

As predicted, we also observed an interaction between emotional valence and list composition in in the ventral lateral parietal cortex, associated with the ventral attention network. The neural subsequent memory effect in the rSMG was only positive in the mixed emotional condition. Previously activity in this area has been associated with subsequent forgetting, rather than remembering, a finding which was interpreted as a consequence of bottom-up attention to task, namely, encoding of irrelevant stimuli (Uncapher & Wagner 2009). The current results suggest that participants' attention was captured reflexively by the relative distinctiveness of emotional stimuli in mixed lists, and that those additional resources which emotional stimuli received translated to better subsequent memory for them (Pourtois, Schettino, & Vuilleumier, 2013). These results support the speculation of Uncapher and Wagner (2009) that positive subsequent memory effects in ventral attention networks can be observed for stimuli that are relatively distinct, when those are tested after a short retention interval. They add to the finding that positive subsequent memory effects in this region have also been reported during the successful encoding of the first-, and therefore, the contextually-distinct item presented in a study list; but not the proceeding items (distinctiveness theory of the primacy effect; Sommer, Rose, & Büchel, 2006).

When items do not differ with respect to their distinctiveness, activity in this ventral attentional area is greater for subsequently forgotten compared to subsequently recalled trials, i.e. a subsequent forgetting effect is observed (Uncapher and Wagner, 2009). This effect has been attributed to the attraction of bottom-up attention by non-task-relevant stimuli, which leads to less efficient parallel encoding of task relevant stimuli (Kim, 2011; Uncapher & Wagner, 2009). Whereas the attraction of bottom-up attention detracts from encoding of the relevant stimuli in many contexts, here we speculate that emotional stimuli in mixed lists triggered bottom-up attention and that this aided encoding of the distinctive emotional pictures; evident in greater activation for subsequently recalled compared to forgotten trials. The activation of the bottom-up attention network is likely to be related to the involuntary attention participants allocate to

emotional pictures under conditions of divided attention, evident in worse performance on a concurrent task. Reflexive attention appears to protect emotional items, so that they suffer less from divided attention.

Taken together, in the mixed list condition, emotional items enjoyed more reflexive attention and required less goal-directed attention than neutral items; resulting in an increased subsequent memory effect in ventral attention regions, and reduced subsequent memory effects in dorsal attention regions. Neutral items, by comparison, did not have the benefit of reflexive attention, so their successful encoding relied more on goal-directed attention, resulting in increased subsequent memory effects in dorsal attention regions, possibly reflecting goal-directed attention to some neutral stimuli.

Although our investigation was particularly focussed on neural attentional effects, it should be acknowledged that our study may also provide supporting evidence for a task-switching function executed by the insula (Goulden et al., 2014; Sridharan, Levitin, & Menon, 2008). Recent analyses of resting state data suggests that the salience network (Seeley et al., 2007) may govern the mental 'switch' between active cognition (i.e. requiring attention, assessed in relation to the central executive network; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006) and rest (i.e. not requiring attention, assessed in relation to the default mode network). In our data, activation in the insula was greatest for subsequent memory effects in the mixed emotion condition suggesting that this proposed task-switching mechanism governed by the insula may confer a particular mnemonic benefit in that condition; possibly by triggering reflexive attention networks when emotional stimuli are observed in a mixed list context. However, this was not something we tested directly, and therefore we exercise caution in asserting this interpretation.

While both behavioural and fMRI datasets revealed an emotion by list-composition interaction, the fMRI pattern nevertheless differed from the behavioural pattern. In behaviour the neutral mixed condition differed from all other conditions, in which memory performance was similar. By contrast, an examination of the interaction pattern in the neural data showed that in the same regions where Dm effects were positive for mixed neutral (compared to mixed emotional, mixed emotional, and pure neutral), they were also positive for the pure emotional compared to mixed emotional encoding. While the behavioural difference between the two emotional conditions did not reach significance here and in our previous work (Barnacle, Tsivilis, Schaefer & Talmi, in prep.; Talmi & McGarry, 2012; Talmi, Luk, et al., 2007), this is the second study where we find a trend towards better memory for emotional material in the mixed compared to pure lists (currently unpublished data). The neural result suggests that goal-directed attention benefits the encoding of emotional pictures in pure lists more than in mixed lists. The direction

of the effect corresponds to the rest of the interaction pattern, where Dm effects are greater in the condition where behaviourally, memory was poorer. This pattern is in keeping with the finding that attention – indexed via performance on a concurrent task – mediated the relationship between arousal and memory for emotional pictures in pure but not mixed lists (Talmi & McGarry, 2012). This finding is particularly interesting when considering that emotional stimuli likely trigger a "general-purpose defence mechanism" (Algom, Chajut & Lev, 2004), or an early, stimulus-driven pre-attentive system (Ohman et al., 2001), resembling the VAN, regardless of list composition. Our findings suggest that when emotional stimuli do not enjoy a relative distinctiveness advantage, they utilise goal-directed attention resources to achieve successful memory. However, the finding that divided attention did not have a more severe impact on emotional memory in pure than mixed lists (Talmi & McGarry, 2012) suggests that emotional stimuli may utilise the VAN when encoding resources are severely constrained.

Finally, although the subsequent memory paradigm we used meant that we focused on processes that occur at the encoding stage, it is possible that the effect of list composition on EEM is also due to retrieval processes. For example, the relative distinctiveness of emotional items may play a role not only at encoding, but also at retrieval, bestowing memory advantages through similar mechanisms to those that benefit stimuli that are temporally distinct (e.g. recency effects, Brown et al., 2007). Differential attention to emotional and neutral stimuli may also interact with relative distinctiveness at retrieval. For example, participants may be relying more on stimulus category – emotional/neutral – in the mixed list condition, but more on how much attention was allocated to each and every one of the stimuli when they recall pure lists. This suggestion is supported by Talmi & McGarry's (2012) analysis across items, where attention to individual pictures, indexed through performance on a concurrent task while participants viewed that picture, mediated the effect of arousal ratings on free recall in pure, but not mixed lists.

5.1. The list-composition effect in EEM: is it all simply a list-strength effect?

The list-composition effect on the EEM resembles the list-strength effect, which has been studied extensively; so it is important to discuss whether the present investigation can learn from, or indeed inform, that disparate literature. The ''strength' in the list-strength effect is a result of experimental manipulations at encoding, typically the spaced repetition of those stimuli compared to others that were only presented once, which gives 'strong' items a memory advantage. According to current memory models, the list-strength effect is due to the differentiation of 'strong' memory traces at encoding. This only influences memory tests, such as free recall, that are sensitive to that particular differentiation mechanism, which is why the

list-strength effect disappears in recognition memory tests (Criss and Koop, 2015; Dennis and Humphreys, 2001; Shiffrin and Steyvers, 1997).

The intuition that emotional stimuli are 'stronger' than neutral ones probably stems from the fact that they trigger deeper processing, including an appraisal of the meaning of stimuli for the self (Lazarus, 1991), are attended to for longer (e.g. Algom, Chajut, & Lev, 2004; Fox, Russo, Bowles, & Dutton, 2001), and are prioritized over other stimuli (Mather & Sutherland, 2011). Importantly, the manner with which neutral items are 'strengthened' in the literature on the list-strength effect is quite different. The list-strength effect appears when strength is induced through spaced repetition, but – crucially – not through deeper semantic analysis or massed repetition, which may mimic priority or longer study time (Malmberg & Shiffrin, 2005). The conceptual differences in what makes emotional and neutral items 'strong' in memory already suggests that the list-strength effect may not be relevant to EEM.

Additionally, although the empirical similarity between the two phenomena is intriguing, there are also a number of differences between the specific pattern of free recall of 'strong' and 'weak' neutral words (the stimuli of choice in the list-strength literature), complex and simple neutral pictures (Nguyen & McDaniel, 2014), and emotional and neutral pictures. First, while strong words are recalled better than weak words in mixed lists, emotional words are not recalled better than neutral ones, unless they are taboo words (Buchanan et al., 2006; Madan, Caplan, Lau, & Fujiwara, 2012; Talmi & Moscovitch, 2004); while emotional pictures, such as those used here, are always recalled better than neutral ones in mixed list. The effect of stimulus type may hold important clues as to the way the list-strength effect is modelled (Osth et al., 2014). Second, while in the literature on the list-strength effect strong items are recalled better than weak items in pure lists, there is no advantage to emotional over neutral pictures in pure lists. Third, the only study of the list-strength effect for pictures reported a pattern that differed from the one we observed with emotional pictures (Nguyen and McDaniel, 2014). In that study, participants took longer to encode complex than simple neutral pictures in a self-paced encoding task when the pictures were presented in mixed lists, but the study time was equivalent in pure lists. By contrast, emotional stimuli are processed more slowly in a variety of tasks (Algom, Chajut & Lev, 2004), and attract more attention than neutral ones even when presented in pure lists (Talmi & McGarry, 2012). Additionally, the memory advantage for complex pictures in mixed lists reversed under divided attention (Nguyen and McDaniel, 2014, Experiment 2), but the EEM is robust and even larger under divided attention (Talmi, Schimmack et al, 2007).

In summary, further research is needed to understand how the effect of list-composition on EEM is related to the list-strength effect. It would be particularly interesting to use differentiation models (Shiffrin and Steyvers, 1997) to account for the current findings, that subsequent memory effects in goal-directed attention regions supported memory for neutral mixed and emotional pure lists.

5.2 Conclusions

In conclusion, our results suggest that the list-composition effect for emotional and neutral pictures depends at least partly on the encoding stage, reflected in a differential engagement of ventral and dorsal parietal areas. The distinctiveness of emotional pictures in mixed lists resulted in enhanced activity in an area involved in bottom-up attention, whereas the successful encoding of neutral pictures in mixed lists relied on the additional engagement of areas associated with goal-directed attention. This latter finding is of particular interest as it shows that enhanced activity during encoding does not always correlate with superior memory performance.

Acknowledgements

References

Alberini, C.M., Kandel, E.R., 2015. The regulation of transcription in memory consolidation. Cold Spring Harb. Perspect. Biol. 7, 1–18.

Algom, D., Chajut, E., Lev, S., 2004. A rational look at the emotional stroop phenomenon: a generic slowdown, not a stroop effect. J. Exp. Psychol. Gen. 133, 323–38. doi:10.1037/0096-3445.133.3.323

Bradley, M.M., Lang, P.J., 1994. Measuring emotion: The self-assessment manikin and the semantic differential. J. Behav. Ther. Exp. Psy. 25(1), 49-59.

Brown, G.D.A., Neath, I., Chater, N., 2007. A temporal ratio model of memory. Psychol. Rev. 114, 539–76. doi:10.1037/0033-295X.114.3.539

Buchanan, T.W., Etzel, J.A., Adolphs, R., Tranel, D., 2006. The influence of autonomic arousal and semantic relatedness on memory for emotional words. Int. J. Psychophysiol. 61, 26–33. doi:10.1016/j.ijpsycho.2005.10.022

Cahill, L., Haier, R.J., Fallon, J., Alkire, M.T., Tang, C., Keator, D., Wu, J., McGaugh, J.L., 1996. Amygdala activity at encoding correlated with long-term, free recall of emotional information. Proc. Natl. Acad. Sci. U. S. A. 93, 8016–21.

Cahill, L., Haier, R.J., White, N.S., Fallon, J., Kilpatrick, L., Lawrence, C., Potkin, S.G., Alkire, M.T., 2001. Sex-related difference in amygdala activity during emotionally influenced memory storage. Neurobiol. Learn. Mem. 75, 1–9. doi:10.1006/nlme.2000.3999

Cahill, L., Uncapher, M., Kilpatrick, L., Alkire, M.T., Turner, J., 2004. Sex-related hemispheric lateralization of amygdala function in emotionally influenced memory: an FMRI investigation. Learn Mem 11, 261–6.

Codispoti, M., Ferrari, V., Bradley, M.M., 2007. Repetition and event-related potentials: distinguishing early and late processes in affective picture perception. J. Cogn. Neurosci. 19, 577–86. doi:10.1162/jocn.2007.19.4.577

Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: from environment to theory of mind. Neuron 58, 306–24. doi:10.1016/j.neuron.2008.04.017

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev. Neurosci. 3, 201–215. doi:10.1038/nrn755

Criss, A.H., Koop, G.J., 2015. No Title. Cogn. Model. Percept. Mem. A Festschrift Richard M. Shiffrin.

Dennis, S., Humphreys, M.S., 2001. A Context Noise Model of Episodic Word Recognition. Psychol. Rev. 108, 452–478.

Dewhurst, S.A., Parry, L.A., 2000. Emotionality, distinctiveness, and recollective experience. Eur. J. Cogn. Psychol. 12, 541–551. doi:10.1080/095414400750050222

Dickerson, B.C., Miller, S.L., Greve, D.N., Dale, A.M., Albert, M.S., Schacter, D.L., Sperling, R.A., 2007. Prefrontal-Hippocampal-Fusiform Activity During Encoding Predicts Intraindividual Differences in Free Recall Ability : An Event-Related Functional-Anatomic MRI Study. Hippocampus 1070, 1060–1070. doi:10.1002/hipo

Dolcos, F., Labar, K.S., Cabeza, R., 2004. Interaction between the Amygdala and the Medial Temporal Lobe Memory System Predicts Better Memory for Emotional Events. Neuron 42, 855–863.

Fletcher, P., Stephenson, C., Carpenter, T., Donovan, T., Bullmore, E., 2003. Regional Brain Activations Predicting Subsequent Memory Success: An Event-Related Fmri Study of the Influence of Encoding Tasks. Cortex 39, 1009–1026. doi:10.1016/S0010-9452(08)70875-X

Fox, E., Russo, R., Bowles, R., Dutton, K., 2001. Do threatening stimuli draw or hold visual attention in subclinical anxiety? J. Exp. Psychol. Gen. 130, 681–700.

Fox, M.D., Corbetta, M., Snyder, A.Z., Vincent, J.L., Raichle, M.E., 2006. Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. PNAS 103, 10046–10051.

Goulden, N., Khusnulina, A., Davis, N.J., et al. 2014. The salience network is responsible for switching between the default mode network and the central executive network: replication from DCM. Neuroimage 99, 180-190.

Hadley, C.B., MacKay, D.G., 2006. Does emotion help or hinder immediate memory. Arousal versus priority-binding mechanisms. J. Exp. Psychol. Learn. Mem. Cogn. 32(1), 79-88.

Harris, C.R., Pashler, H., 2005. Enhanced memory for negatively emotionally charged pictures without selective rumination. Emotion 5(2), 191–199.

Hermans, E.J., Battaglia, F.P., Atsak, P., de Voogd, L.D., Fernández, G., Roozendaal, B., 2014. How the amygdala affects emotional memory by altering brain network properties. Neurobiol. Learn. Mem. doi:10.1016/j.nlm.2014.02.005

Kensinger, E.A., Corkin, S., 2004. Two routes to emotional memory: distinct neural processes for valence and arousal. Proc. Natl. Acad. Sci. U. S. A. 101, 3310–5. doi:10.1073/pnas.0306408101

Kim, H., 2011. NeuroImage Neural activity that predicts subsequent memory and forgetting : A meta-analysis of 74 fMRI studies. Neuroimage 54, 2446–2461. doi:10.1016/j.neuroimage.2010.09.045

LaBar, K.S., Phelps, E.A., 1998. Arousal-Mediated Memory Consolidation: Role of the Medial Temporal Lobe in Humans. Psychol. Sci. 9, 490–493.

Lazarus, R., 1991. Cognition and Motivation in Emotion. Am. Psychol. 46, 352–367.

Lieberman, M.D., Cunningham, W.A., 2009. Type I and Type II error concerns in fMRI research: re-balancing the scale. Soc. Cogn. Affect. Neurosci. 4, 423–8. doi:10.1093/scan/nsp052

MacKay, D.G., Shafto, M., Taylor, J.K., Marian, D.E., Abrams, L., Dyer, J.R., 2004. Relations between emotion , memory , and attention : Evidence from taboo Stroop , lexical decision , and immediate memory tasks. Mem. Cognit. 32, 474–488.

Madan, C.R., Caplan, J.B., Lau, C.S.M., Fujiwara, E., 2012. Emotional arousal does not enhance association-memory. J. Mem. Lang. 66, 695–716. doi:10.1016/j.jml.2012.04.001

Malmberg, K.J., Shiffrin, R.M., 2005. The " One-Shot " Hypothesis for Context Storage. Cognition 31, 322–336. doi:10.1037/0278-7393.31.2.322

Mather, M., Clewett, D., Sakaki, M., Harley, C.W., 2015. Norepinephrine ignites local hot spots of neuronal excitation: How arousal amplifies selectivity in perception and memory. Behav. Brain Sci. 1–100. doi:10.1017/S0140525X15000667

Mather, M., Sutherland, M.R., 2011. Arousal-Biased Competition in Perception and Memory. Perspect. Psychol. Sci. 6, 114–133. doi:10.1177/1745691611400234

Mayes, A.R., Montaldi, D., 2010. The Neuroimaging of Long-term Memory Encoding Processes. Memory 7, 613–659.

McGaugh, J.L., 2013. Making lasting memories: Remembering the significant. Proc. Natl. Acad. Sci. 110 Suppl , 10402–7. doi:10.1073/pnas.1301209110

McGaugh, J.L., 2004. The amygdala modulates the consolidation of memories of emotionally arousing experiences. Annu. Rev. Neurosci. 27, 1–28. doi:10.1146/annurev.neuro.27.070203.144157

McIntyre, C.K., McGaugh, J.L., Williams, C.L., 2012. Interacting brain systems modulate memory consolidation. Neurosci. Biobehav. Rev. 36, 1750–62. doi:10.1016/j.neubiorev.2011.11.001

McReynolds, J.R., Mcintyre, C.K., 2012. Emotional modulation of the synapse. Rev. Neurosci. 23, 449–461. doi:10.1515/revneuro-2012-0047

Mickley Steinmetz, K.R., Addis, D.R., Kensinger, E. A, 2010. The effect of arousal on the emotional memory network depends on valence. Neuroimage 53, 318–24. doi:10.1016/j.neuroimage.2010.06.015

Miyashita, T. & Williams, C. L. (2006). Epinephrine administration increases neural impulses propagated along the vagus nerve: Role of peripheral beta-adrenergic receptors. Neurobiology of Learning and Memory, 85, 116-124.

Murty, V.P., Ritchey, M., Adcock, R.A., Labar, K.S., 2010. fMRI studies of successful emotional memory encoding : A quantitative meta-analysis. Neuropsychologia 48, 3459–3469. doi:10.1016/j.neuropsychologia.2010.07.030

Nguyen, K., McDaniel, M.A., 2014. The Picture Complexity Effect: Another List Composition Paradox. J. Exp. Psychol. Learn. Mem. Cogn. doi:10.1037/xlm0000071

Osth, A.F., Dennis, S., Kinnell, A., 2014. Stimulus type and the list strength paradigm. Q. J. Exp. Psychol. (Hove). 37–41. doi:10.1080/17470218.2013.872824

Otten, L.J., Henson, R.N., Rugg, M.D., 2001. Depth of processing effects on neural correlates of memory encoding: relationship between findings from across- and within-task comparisons. Brain 124, 399–412.

Poutois, G., Schettino, P., Vuilleumier, P., 2013. Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. Biol. Psychol. 92(3), 495-512.

Ratcliff, R., Clark, S.E., Shiffrin, R.M., 1990. List-strength effect: I. Data and discussion. J. Exp. Psychol. Learn. Mem. Cogn. 16, 163–78.

Ritchey, M., Dolcos, F., Cabeza, R., 2008. Role of amygdala connectivity in the persistence of emotional memories over time: an event-related FMRI investigation. Cereb. cortex 18, 2494–504. doi:10.1093/cercor/bhm262

Schimmack, U., 2005. Attentional interference effects of emotional pictures: threat, negativity, or arousal? Emotion 5, 55–66. doi:10.1037/1528-3542.5.1.55

Schmidt, S.R., 1991. Can we have a distinctive theory of memory? Mem. Cognit. 19, 523– 42.

Schmidt, S.R., Saari, B., 2007. The emotional memory effect: Differential processing or item distinctiveness? Mem. Cognit. 35, 1905–1916. doi:10.3758/BF03192924

Schupp, H.T., Schmälzle, R., Flaisch, T., Weike, A.I., Hamm, A.O., 2012. Affective picture processing as a function of preceding picture valence: an ERP analysis. Biol. Psychol. 91, 81–7. doi:10.1016/j.biopsycho.2012.04.006

Schwarze, U., Bingel, U., Sommer, T., 2012. Event-related nociceptive arousal enhances memory consolidation for neutral scenes. J. Neurosci. 32, 1481–7. doi:10.1523/JNEUROSCI.4497-11.2012

Seeley, W.W., Menon, V., Schatzberg, A.F., 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. J. Neuro. 27(9), 2349-2356.

Sharot, T., Verfaellie, M., Yonelinas, A.P., 2007. How emotion strengthens the recollective experience: a time-dependent hippocampal process. PLoS One 2, e1068. doi:10.1371/journal.pone.0001068

Shiffrin, R.M., Steyvers, M., 1997. A model for recognition memory: REM-retrieving effectively from memory. Psychon. Bull. Rev. 145–166.

Sommer, T., Gläscher, J., Moritz, S., Büchel, C., 2008. Emotional enhancement effect of memory : Removing the influence of cognitive factors. Learn. Mem. 15, 569–573. doi:10.1101/lm.995108

Sommer, T., Rose, M., Büchel, C., 2006. Dissociable parietal systems for primacy and subsequent memory effects. Neurobiol. Learn. Mem. 85, 243–51. doi:10.1016/j.nlm.2005.11.002

Sridharan, D., Levitin, D.J., Menon, V., 2008. A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. PNAS 105(34), 12569-12574.

Stark, C.E., Squire, L.R., 2001. When zero is not zero: the problem of ambiguous baseline conditions in fMRI. Proc. Natl. Acad. Sci. U S A 98, 12760–6.

Stricker, J.L., Brown, G.G., Wixted, J., Baldo, J. V, Delis, D.C., 2002. New semantic and serial clustering indices for the California Verbal Learning Test – Second Edition: Background , rationale , and formulae. J. Int. Neuropsychol. Soc. 8, 425–435.

Talmi, D., 2013. Enhanced Emotional Memory: Cognitive and Neural Mechanisms. Curr. Dir. Psychol. Sci. 22, 430–436. doi:10.1177/0963721413498893

Talmi, D., Anderson, A.K., Riggs, L., Caplan, J.B., Moscovitch, M., 2008. Immediate memory consequences of the effect of emotion on attention to pictures. Learn. Mem. 15, 172–82. doi:10.1101/lm.722908

Talmi, D., Luk, B.C., McGarry, L.M., Moscovitch, M., 2007. Memory and Language The contribution of relatedness and distinctiveness to emotionally-enhanced memory. J. Mem. Lang. 56, 555–574. doi:10.1016/j.jml.2007.01.002

Talmi, D., McGarry, L.M., 2012. Accounting for immediate emotional memory enhancement. J. Mem. Lang. 66, 93–108. doi:10.1016/j.jml.2011.07.009

Talmi, D., Moscovitch, M., 2004. Can semantic relatedness explain the enhancement of memory for emotional words? Mem. Cognit. 32, 742–51.

Talmi, D., Schimmack, U., Paterson, T., Moscovitch, M., 2007. The role of attention and relatedness in emotionally enhanced memory. Emotion 7, 89–102. doi:10.1037/1528-3542.7.1.89

Talmi, D., Ziegler, M., Hawksworth, J., Lalani, S., Herman, C.P., Moscovitch, M., 2013. Emotional stimuli exert parallel effects on attention and memory. Cogn. Emot. 27, 530–8. doi:10.1080/02699931.2012.722527

Todd, R.M., Talmi, D., Schmitz, T.W., Susskind, J., Anderson, A.K., 2012. Psychophysical and neural evidence for emotion-enhanced perceptual vividness. J. Neurosci. 32, 11201–12. doi:10.1523/JNEUROSCI.0155-12.2012

Uncapher, M.R., Wagner, A.D., 2009. Posterior parietal cortex and episodic encoding: insights from fMRI subsequent memory effects and dual-attention theory. Neurobiol. Learn. Mem. 91, 139–54. doi:10.1016/j.nlm.2008.10.011

Viviani, R., 2013. Emotion regulation, attention to emotion, and the ventral attentional network. Front. Hum. Neurosci. 7, 746. doi:10.3389/fnhum.2013.00746

Vossel, S., Geng, J.J., Fink, G.R., 2014. Dorsal and ventral attention systems: distinct neural circuits but collaborative roles. Neuroscientist 20, 150–9. doi:10.1177/1073858413494269

Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. Trends Cogn. Sci. 9, 585–94. doi:10.1016/j.tics.2005.10.011

Highlights:

- Neural subsequent memory effects in the dorsal attention network were greater for neutral encoding
- This effect was greater in the ventral attention network for emotional stimulus encoding
- When life experience is emotional and neutral, neutral memory requires goal-directed attention
- Neural subsequent memory effects do not always correspond to memory performance