TEMPORO-SPATIAL DYNAMICS OF THE IMPACT OF EMOTIONAL CONTEXTS ON VISUAL PROCESSING AND MEMORY

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1.SUMMARY

It has frequently been observed that single emotional events are not only more efficiently processed, but also better remembered, and form longer-lasting memory traces than neutral material. However, when emotional information is perceived as a part of a complex event, such as in the context of or in relation to other events and/or source details, the modulatory effects of emotion are less clear. The present work aims to investigate how emotional, contextual source information modulates the initial encoding and subsequent long-term retrieval of associated neutral material (item memory) and contextual source details (contextual source memory). To do so, a two-task experiment was used, consisting of an incidental encoding task in which neutral objects were displayed over different contextual background scenes which varied in emotional content (unpleasant, pleasant, and neutral), and a delayed retrieval task (1 week), in which previously-encoded objects and new ones were presented. In a series of studies, behavioral indices (Studies 2, 3, and 5), event-related potentials (ERPs; Studies 1-4), and functional magnetic resonance imaging (Study 5) were used to investigate whether emotional contexts can rapidly tune the visual processing of associated neutral information (Study 1) and modulate long-term item memory (Study 2), how different recognition memory processes (familiarity vs. recollection) contribute to these emotion effects on item and contextual source memory (Study 3), whether the emotional effects of item memory can also be observed during spontaneous retrieval (Sstudy 4), and which brain regions underpin the modulatory effects of emotional contexts on item and contextual source memory (Study 5). In Study 1, it was observed that emotional contexts by means of emotional associative learning, can rapidly alter the processing of associated neutral information. Neutral items associated with emotional contexts (i.e. emotional associates) compared to neutral ones, showed

enhanced perceptual and more elaborate processing after one single pairing, as indexed by larger amplitudes in the P100 and LPP components, respectively. Study 2 showed that emotional contexts produce longer-lasting memory effects, as evidenced by better item memory performance and larger ERP Old/New differences for emotional associates. In Study 3, a mnemonic differentiation was observed between item and contextual source memory which was modulated by emotion. Item memory was driven by familiarity, independently of emotional contexts during encoding, whereas contextual source memory was driven by recollection, and better for emotional material. As in Study 2, enhancing effects of emotional contexts for item memory were observed in ERPs associated with recollection processes. Likewise, for contextual source memory, a pronounced recollection-related ERP enhancement was observed for exclusively emotional contexts. Study 4 showed that the long-term recollection enhancement of emotional contexts on item memory can be observed even when retrieval is not explicitly attempted, as measured with ERPs, suggesting that the emotion enhancing effects on memory are not related to the task embedded during recognition, but to the motivational relevance of the triggering event. In Study 5, it was observed that enhancing effects of emotional contexts on item and contextual source memory involve stronger engagement of the brain's regions which are associated with memory recollection, including areas of the medial temporal lobe, posterior parietal cortex, and prefrontal cortex.

Taken together, these findings suggest that emotional contexts rapidly modulate the initial processing of associated neutral information and the subsequent, long-term item and contextual source memories. The enhanced memory effects of emotional contexts are strongly supported by recollection rather than familiarity processes, and are shown to be triggered when retrieval is both explicitly and spontaneously attempted. These results provide new insights into the modulatory role of emotional information

on the visual processing and the long-term recognition memory of complex events. The present findings are integrated into the current theoretical models and future ventures are discussed.

2. ZUSAMMENFASSUNG

Es wurde häufig beobachtet, dass einzelne emotionale Ereignisse effizienter verarbeitet und besser erinnert werden und länger anhaltende Gedächtnisspuren bilden als neutrales Material. Wenn jedoch emotionale Informationen als Teil eines komplexen Ereignisses wahrgenommen werden, wie beispielsweise im Kontext oder in Bezug auf andere Ereignisse und/oder Quellendetails, sind die modulierenden Einflüsse von Emotionen weniger klar. Die vorliegende Arbeit zielt darauf ab zu untersuchen, wie emotionale, kontextuelle Quelleninformationen die anfängliche Kodierung und den anschließenden langfristigen Abruf von zugehörigem neutralen Material (Itemgedächtnis) und kontextuellen Quellendetails (Quellengedächtnis) modulieren. Dazu wurde ein Zwei-Aufgaben-Experiment verwendet, bestehend aus einer nicht instruierten Enkodierungsaufgabe, bei der neutrale Objekte eingebettet in verschiedene kontextuelle Hintergrundszenen dargeboten wurden, die in ihrem emotionalen Inhalt variierten (unangenehm, angenehm und neutral), und einer verzögerten Abrufaufgabe (1 Woche), bei der zuvor enkodierte und neue Objekte präsentiert wurden. In einer Reihe von Studien wurden Verhaltensindizes (Studien 2-5), ereigniskorrelierte Potenziale (EKPs; Studien 1-4) und funktionelle Magnetresonanztomographie (Studie 5) verwendet, um zu untersuchen, ob emotionale Kontexte die visuelle Verarbeitung der zugehörigen neutralen Informationen kurzfristig verändern können (Studie 1) und das Langzeitgedächtnis modulieren (Studie 2), wie verschiedene Prozesse des Wiedererkennens (Vertrautheit vs. Rekollektion) zu diesen Emotionseffekten auf das Item- und das kontextuelle

Quellengedächtnis beitragen (Studie 3), ob die emotionalen Effekte auf das Itemgedächtnis auch bei der spontanen Abfrage beobachtet werden können (Studie 4) und über welche Hirnregionen die modulierenden Effekte emotionaler Kontexte auf das Item- und kontextuelle Quellengedächtnis vermittelt werden (Studie 5).

In Studie 1 wurde beobachtet, dass emotionale Kontexte durch emotionales assoziatives Lernen die Verarbeitung der zugehörigen neutralen Informationen kurzfristig verändern können. Neutrale Elemente, die mit emotionalen Kontexten verbunden sind (im Folgenden „emotional Assoziierte“ genannt), zeigten nach einer einzigen Paarung im Vergleich zu neutralen Elementen eine verbesserte perzeptuelle und elaboriertere Verarbeitung, wie durch höhere Amplituden in den P100- bzw. LPP-Komponenten nachgewiesen wurde. Studie 2 zeigte, dass emotionale Kontexte länger anhaltende Gedächtniseffekte erzeugen, was sich in einer besseren Itemgedächtnisleistung und größeren EKP-alt/neu Unterschieden für emotional Assoziierte zeigte. In Studie 3 wurde eine mnemonische Differenzierung zwischen Item- und kontextuellem Quellengedächtnis beobachtet, die durch Emotionen moduliert wurde. Das Itemgedächtnis wurde durch den Prozess der Vertrautheit getrieben unabhängig von den emotionalen Kontexten während der Enkodierung. Das kontextuelle Quellengedächtnis wurde dagegen durch Rekollektion getrieben und war besser für emotionales Material. Wie in Studie 2 wurden in EKPs, die mit Rekollektionsprozessen in Verbindung stehen, verstärkende Effekte von emotionalen Kontexten für das Itemgedächtnis beobachtet. Ebenso wurde für das kontextuelle Quellengedächtnis eine ausgeprägte Rekollektionsbezogene Potenzierung der EKPs ausschließlich für emotionale Kontexte beobachtet. Studie 4 zeigte, dass die langfristige Verstärkung der Rekollektion, die emotionale Kontexten im Itemgedächtnis verursachen, auch dann beobachtet werden kann, wenn der Abruf nicht explizit instruiert wird. Dieser Befund zum spontanen Erinnern deutet darauf hin, dass die gedächtnissteigernden Effekte von Emotionen nicht mit der Aufgabe zusammenhängen, die während des Abrufs gestellt wurde, sondern mit der motivationalen Relevanz des auslösenden Ereignisses. In Studie 5 wurde beobachtet, dass an der verstärkenden Wirkung von emotionalen Kontexten auf das Item- und kontextuelle Quellengedächtnis solche Hirnregionen beteiligt sind, die mit der Rekollektionsprozessen assoziiert werden, einschließlich der Bereiche des medialen Temporallappens, des posterioren parietalen Kortex und des präfrontalen Kortex.

Zusammengenommen deuten diese Ergebnisse darauf hin, dass emotionale Kontexte die anfängliche Verarbeitung der zugehörigen neutralen Informationen und der nachfolgenden, langfristigen Erinnerungen an Items und kontextuelle Quellen schnell modulieren. Die durch emotionaler Kontexte ausgelösten Gedächtniseffekte werden eher durch Rekollektions- und weniger durch Vertrautheitsprozesse vermittelt und zeigen sich sowohl bei expliziten als auch bei spontanen Abruf. Diese Ergebnisse liefern neue Erkenntnisse über die modulierende Rolle emotionaler Informationen bei der visuellen Verarbeitung und der Langzeiterinnerung an komplexe Ereignisse. Die vorliegenden Erkenntnisse werden in aktuelle theoretische Modelle integriert und zukünftige Forschungsperspektiven werden diskutiert.

3. EMOTIONAL ASSOCIATIVE LEARNING

One important survival strategy of living organisms is detecting fluctuating changes that occur in contiguous environments in order to readjust the momentary motivational relevance of incoming information and generate adaptive responses to their surroundings (Miskovic & Keil, 2012). The continuous update of the motivational value of encountered information takes place by means of emotional associative learning processes (Hamm, Greenwald, Bradley, & Lang, 1993; Hebb, 1949). Emotional associative learning in humans is most often studied using the differential fear conditioning paradigm. Here, a presented stimulus (aversive conditioned stimulus; CS+) is consistently associated with an aversive event (unconditioned stimulus; UCS), while a comparable stimulus (CS-) is unpaired with a UCS or associated with a non-emotional UCS (neutral CS+). While emotional CS+ and neutral CS+ or CS- are considered equally relevant before pairing, after CS/aversive-UCS association, the aversive CS+ stimulus, (but not CS- or neutral CS+ ones) acquires motivational relevance in relation to the aversive UCS.

Most of the paradigms traditionally employed in investigating associative learning in animals and humans are characterized by the use of a few or a single CS event(s) and a highly aversive UCS (i.e. electrical shocks), presented together for a large number of occurrences in order to generate “strong” CS/UCS associations (Lissek, Pine, & Grillon, 2006). As a consequence, physiological markers of motivational activation, (i.e., increased skin conductance, decreased heart rate, or potentiation of the startle response) are enhanced for aversive CS+ when compared to CS- or neutral CS+ stimuli (Hamm et al., 1993; Lonsdorf et al., 2017). Changes in the motivational significance of events repeatedly paired with a UCS can also be captured with more time-sensitive neuroimaging techniques like electro- (EEG) and magnetoencephalography (MEG). In one of the first EEG studies of this kind, Pizzagalli and colleagues (Pizzagalli, Greischar, & Davidson, 2003) presented four different fearful faces, either associated with an electric shock (two CS+ faces) or not (2 CS- faces). The authors observed that CS+ faces, when compared to CS- ones, showed a larger positive peak in occipital regions at an early time point of ~ 120 ms after stimulus onset, coinciding with the latency of the P100 component. The P100 is an event-related potential (ERP) associated with the amplification of sensory visual information, reflecting perceptual processing in visual cortical areas (Clark, Fan, & Hillyard, 1995; Di Russo, Martínez, Sereno, Pitzalis, & Hillyard, 2002). In the same vein, larger P100 amplitudes have been observed for emotional visual stimuli (e.g. scenes, faces, words) when compared to neutral ones (e.g. Carretié, Martín-Loeches, Hinojosa, & Mercado, 2001; Pourtois, Dan, Grandjean, Sander, & Vuilleumier, 2005; Rellecke, Palazova, Sommer, & Schacht, 2011). This result may therefore indicate that CS+ faces receive a prioritized amplification of sensory visual processing. Similarly, Pizaggali et al. (2003) observed that CS+ faces generated a more positive-going waveform over parietal areas in a later time epoch when compared to CS- faces (ca 400 to 700 ms), corresponding to the late positive potential (LPP) component. Research on emotional visual processing has consistently found larger LPP amplitudes for emotional information (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Foti, Hajcak, & Dien, 2009; Schupp et al., 2000). Given that the LPP has been interpreted as an index of attentional orientation and elaborate processing, especially heightened for emotional information (Bradley, 2009), larger LPP amplitudes for CS+ faces suggest that, due to the acquisition of emotional relevance, conditioned stimuli undergo deeper processing (see for similar results, Dolan, Heinze, Hurlemann, & Hinrichs, 2006; Fritsch & Kuchinke, 2013). Altogether, this evidence suggests that changes in the motivational value of incoming information by means of emotional associative learning processes occur at different stages of processing, which are perceptual earlier and later more elaborated.

However, the use of single, unambiguous, and/or isolated, multiple CS/UCS pairings models simplistic scenarios from which associative learning processes are difficult to extrapolate for diverse and complex environments such as those encountered in real life (Lissek et al., 2006). The employment of paradigms that generate “weak” CS/UCS associations, using less salient UCS, multiple complex pairings, and/or few CS/UCS contingencies may, thus, provide a better understanding of the underpinnings of associative learning (Beckers et al., 2012; Hur et al., 2016; Lissek et al., 2006; Steinberg, et al., 2013).

This idea was addressed by Junghöfer and colleagues in a series of studies (Brockelmann et al., 2011; Pastor et al., 2015; Rehbein et al., 2014; Steinberg et al., 2012; Steinberg, Bröckelmann, Dobel, & Elling, 2013) in which they investigated the magneto- and electrophysiological correlates of emotional associative learning using a MultiCS paradigm. In this paradigm, numerous neutral stimuli are used as CS (e.g., pictures of neutral faces) and either associated with emotionally relevant UCS (aversive and appetitive sounds, electric shocks) or remain unpaired or associated with neutral information. The results showed that after multiple pairings, aversive and/or appetitive CS+ stimuli generated enhanced neural activity at prefrontal and sensory cortical regions during earlier (< 300 ms; Brockelmann et al., 2011; Rehbein et al., 2014; Steinberg, Bröckelmann, Dobel, et al., 2013; Steinberg et al., 2012) and later stages of processing (>300 ms; Pastor et al., 2015) when compared to CS- or neutral CS+, irrespective of contingency awareness. Extending prior results using strong CS/UCS associations, these findings indicate that in life-like challenging circumstances, associative learning mechanisms occur in a rapid fashion: emotional CS+ stimuli are learned to predict the UCS and, consequently, their perceptual and more elaborate processing is facilitated.

3.1 STUDY 1: BRAIN DYNAMICS OF RAPIDLY FORMED ASSOCIATIONS BETWEEN NEUTRAL STIMULI AND EMOTIONAL CONTEXTS

It must be noted that the above-mentioned studies have mostly used highly salient UCS. Although most studies employ aversive cues as UCS (Miskovic & Keil, 2012), highly salient appetitive events such as monetary gain or a sweet taste can also stimulate associative learning processes (Blechert, Testa, Georgii, Klimesch, & Wilhelm, 2016; Hammerschmidt, Kagan, Kulke, & Schacht, 2018; Hammerschmidt, Sennhenn-Reulen, & Schacht, 2017; Martin-Soelch, Linthicum, & Ernst, 2007; Schacht, Adler, Chen, Guo, & Sommer, 2012). Thus, it remains unclear whether less prominent aversive and appetitive UCS may promote equally rapid associative processes. Study 1 of this thesis aimed to investigate the electrophysiological signature of emotional associative learning processes under these circumstances (Ventura-Bort, Löw, Wendt, Dolcos, Hamm & Weymar, 2016a). To do so, 144 neutral objects were presented in the context of various emotionally arousing, pleasant and unpleasant background scenes, which served as appetitive and aversive UCS, and neutral background scenes, which serve as non-emotional UCS. Object and scene presentation always occurred in the same sequential order: objects, also referred to as associates[1], were first presented on a black screen and afterward a picture scene was added as background context. Emotional associative processes were boosted by instructing the participants to imagine the object as part of the scene. Pairings were presented in two blocks, allowing for a comparison of the processing of emotional (paired with emotional scenes) and neutral associates (paired with neutral scenes), before (first

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[1] Previous literature on emotional associative learning uses the term *conditioned stimulus* (CS) to refer to events associated to aversive or appetitive unconditioned stimuli (UCS). However, this terminology is rarely used in memory literature. Because in the present thesis the effects of emotional contexts on both the initial encoding (where emotional associative learning processes are carried out) and the subsequent long-term memory retrieval were investigated, the term *associate* was used to consistently refer to objects embedded in emotional and neutral contexts across various studies.

block) and after (second block) a single pairing. Because prior evidence has shown enhanced perceptual and sustained elaborative processing for emotional conditioned stimuli, it was expected that emotional associates would evoke larger amplitudes at earlier (P100) and later stages of processing (LPP).

As predicted, after a single pairing with either a pleasant or an unpleasant context, emotional associates evoked an enhanced P100 at occipital regions in the 140–184 ms time window. Similar to prior work using highly relevant appetitive (Schacht et al., 2012) and aversive UCS (Fritsch & Kuchinke, 2013; Pizzagalli et al., 2003), visual perceptual processing was amplified for emotional associates, as indicated by larger P100 amplitudes. Enhanced perceptual activation for emotionally conditioned events has been attributed to the learning history of the individual, modulating the sensitivity of sensory neural populations to specific emotional features by means of re-shaping the processing of incoming sensory information (Miskovic & Keil, 2012; Steinberg, Bröckelmann, Rehbein, et al., 2013). This finding demonstrates that after a single pairing with an emotional context, an update of the motivational value of the emotional associate is carried out, evoking a rapid readjustment of perceptual processing to match the current relevance state.

Likewise, emotional associates elicited a larger LPP at parieto-occipital electrodes between 450 and 750 ms after stimulus onset than neutral ones. This finding is consistent with previous studies using emotionally relevant material (Cuthbert et al., 2000; Foti et al., 2009; Schupp et al., 2000), and conditioned events paired with highly aversive (Pizzagalli et al., 2003) and appetitive UCS (Blechert et al., 2016; Schacht et al., 2012), as well as multiple CS/UCS pairings (Pastor et al., 2015). Because the LPP has been related to attentional orienting and sustained processing (Bradley, 2009; Lang & Bradley, 2010), these data suggest that objects associated with both appetitive and aversive scenes receive more attention and are deeper encoded due to the acquired motivational value.

Taken together, the findings from Study 1 (Ventura-Bot et al., 2016a) provide evidence for the existence of rapid emotional associative processes (i.e. after a single pair). Neutral objects paired with emotional relative to neutral contexts acquired emotional relevance in relation to emotional contexts, engaging heightened perceptual and attentional, more elaborate processes, as indexed by enhanced P100 and LPP amplitudes respectively. From a functional perspective, rapid readjustments to the relevance of incoming information should be retained in memory, in order to enable rapid adaptive responses in the future. Thus, in the next studies (Studies 2-5), whether the deepened processing of emotional associations observed is also reflected in enhanced long-term memory for these items was investigated, along with how this presumably enhanced memory is characterized. Before detailing the results of these studies, however, an overview of the temporo-spatial characteristics and neurobiology of emotional episodic memory will be presented, in order to provide a theoretical and empirical background for the interpretation of the findings on the impact of emotional contexts on recognition memory.

4. EMOTIONAL EPISODIC MEMORY

From an evolutionary perspective, events associated with survival (e.g., finding food, spotting a predator) should be stored preferentially in one's memory to guarantee an adaptive response in future encounters (Dolan, 2002; Dolcos, LaBar, & Cabeza, 2005). In line with this view, a great deal of empirical evidence has confirmed that episodic memory for single events, also termed item memory, is enhanced if such events are emotionally relevant (Ochsner, 2000; Bradley, Greenwald, Petry, & Lang, 1992; Dolcos et al., 2017; Dolcos, LaBar, & Cabeza, 2004, 2005; Weymar, Löw, Melzig, & Hamm, 2009). When emotional and neutral information (e.g. images or sounds) is presented and memory is subsequently tested, emotionally arousing items are retrieved in more detail and their memories last longer than for their neutral counterparts, an effect that extends across paradigms (recognition and recall paradigms; Bradley et al., 1992; Dolcos et al., 2005; Weymar et al., 2009) and stimulus material (images, faces and sounds; Ringhi et al., 2012; Bradley 2000; Weymar et al., 2011; see Dolcos et al., 2017 and Weymar & Hamm, 2013 for reviews).

Experimental evidence suggests that episodic memory recognition is not a single process (single process-account; Dunn, 2004), but is supported by two types of mnemonic information (dual-process account; see for review Yonelinas, 2002). According to dual-process accounts, episodic memory can be based upon two qualitatively different processes: the recognition of information of undifferentiated strengths, also referred to as familiarity; or the recognition of specific information about the study episode, also termed recollection (Mandler, 1980; Rugg & Curran, 2007; Yonelinas, 2002). Familiarity-based recognition is assumed to be fast-acting and does not provide specific details of the encoded event, whereas recollection-driven recognition is considered a slower process that gives rise to the conscious retrieval of an event and specific contextual information about the learning episode. It should be noted that, although the retrieval of additional information linked to an event is typically supported by recollection processes, in some instances, memory for associated information can be mediated by familiarity. This is particularly true when the specific event and related information are encoded as a single configuration, forming unitized representations (Yonelinas, Kroll, Dobbins, & Soltani, 1999)

Within the dual-process frame, research has consistently shown that the mnemonic advantage for emotional information is accompanied by specific details, indicating that such an effect is driven by recollection rather than by familiarity processes (Ochsner, 2000; Sharot et al., 2004; Dolcos et al., 2005; Ritchey et al., 2008; Weymar et al., 2009, 2010).

4.1. TEMPORO-SPATIAL CHARACTERIZATION OF EMOTIONAL EPISODIC MEMORY

In recent decades, the implementation of neuroscientific techniques has provided better insights into the neural mechanisms underlying episodic memory. The use of temporally and spatially accurate brain imaging technology, like EEG or functional magnetic resonance imaging (fMRI), has allowed for a detailed characterization of the time course and brain regions involved in mnemonic recognition.

4.1.1 Temporal dynamics

ERP studies investigating the temporal dynamics of episodic memory have found that correctly classified old items consistently evoke a more positive-going ERP waveform than correctly classified new items (Rugg & Curran, 2007). This difference in ERP responses has been termed the ERP Old/New effect (Rugg & Curran, 2007). Two temporally and topographically different ERP Old/New effects have been detected which, in line with dual-process accounts, may distinctly reflect familiarity- and recollection-based retrieval. An early Old/New effect (also labeled FN400; Curran, 1999), maximal over fronto-central (Rugg & Curran, 2007) or left-frontal sites (Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010) that peaks around 300-500 ms, has been associated with the subjective experience of familiarity (see also other literature linking the early Old/New effect to implicit memory processes: Leynes, Bruett, Krizan, & Veloso, 2017; Paller, Voss, & Boehm, 2007; Voss, Lucas, & Paller, 2012; Voss & Paller, 2006, 2007); and a late ERP Old/New effect, typically evident over centro-parietal (Weymar & Hamm, 2013) or left-parietal regions (Rugg & Curran, 2007), starting around 400 ms after stimulus presentation, which has been related to the subjective experience of recollection (Curran, 2000; Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Rugg & Curran, 2007). Similarly, and in line with the greater involvement of recollection with the retrieval of contextual details, it has been observed that the late Old/New effect is more pronounced with the increase of accuracy of source cues (Wilding & Rugg, 1996; MacLeod & Donaldson, 2017), or the report of associative information (Donald and Rugg, 1998), and enhanced by ‘Remember’ rather than ‘Know’ judgements (Düzel et al., 1997; MacLeod & Donaldson, 2017).

Further ERP evidence for a dissociation between familiarity and recollection comes from the employment of different stimuli and encoding strategies. In one study, Jäger and colleagues (2006) investigated how the similitude of two associated events modulates memory retrieval. To do so, either two very similar (the same face with a different facial expression) or two different, associated events (two different faces) were presented and their memory tested in an immediate recognition task. The authors observed that when the associated events were very similar, correct recognition evoked a pronounced early Old/New effect (Jäger, Mecklinger, & Kipp, 2006). However, when the associated events were distinct, larger, late Old/New differences were observed during recognition. In much the same vein, Bader and colleagues (2010) observed that the retrieval of two associated words was differentially influenced by recollection and familiarity, depending on the associative strategy used (integrative vs. non-integrative) during encoding. When words were integrated as one single concept, memory retrieval was driven by familiarity, as indicated by an early Old/New effect, whereas memory for non-integrative words was related to recollection processes as indexed by larger, late Old/New effects (Bader, Mecklinger, Hoppstädter, & Meyer, 2010; see Diana, Van den Boom, Yonelinas, & Ranganath, 2011 for similar results). These findings thus indicate that familiarity and recollection processes make a differential contribution to memory retrieval, depending on the characteristics of the stimuli and the approach used during encoding.

A large number of studies have focused on the impact of emotion on the electrophysiological correlates of memory retrieval for single events, using different stimulus material such as words (Dietrich et al., 2001; Inaba, Nomura, & Ohira, 2005; Maratos, Allan, & Rugg, 2000; Weymar, Bradley, Hamm, & Lang, 2014), faces (Graham & Cabeza, 2001; Kissler & Strehlow, 2017; Righi et al., 2012), or scenes (Pérez-Mata, López-Martn, Albert, Carretié, & Tapia, 2012; Schaefer, Pottage, & Rickart, 2011; Weymar, Löw, & Hamm, 2011; Weymar, Löw, Schwabe, & Hamm, 2010). Results, however, have been mixed for the ERP Old/New effect for emotional and neutral content, with some studies finding enhanced late ERP Old/New differences, while others reporting no ERP differences as a function of emotionality. This discrepancy could be related to factors such as arousal or stimulus type (words vs. faces vs. scenes), but also to differences in the retention interval used across studies (Weymar & Hamm, 2013).

In this sense, the length of the retention interval for sufficient consolidation (Bradley, Greenwald, Petry, & Lang, 1992; McGaugh, 2004; Schümann, Bayer, Talmi, & Sommer, 2017; Sharot & Phelps, 2004; Yonelinas & Ritchey, 2015) has been shown to mediate the enhancing effect of emotion on episodic memories (Sharot & Phelps, 2004; Sharot & Yonelinas, 2008; but see Wirkner et al., 2018). Whereas short consolidation periods (e.g. 3-5 min after encoding) result in comparable recognition rates for emotional and neutral items (Sharot & Phelps, 2004; Sharot & Yonelinas, 2008), longer delays (>24 hours) lead to a prominent memory advantage for emotional materials - that is, with longer delays recognition rates prevail for emotional items, but decline for neutral items (Sharot & Phelps, 2004; Sharot & Yonelinas, 2008). Similarly, during immediate retrieval tests, divergent ERP results have been often reported. While in some studies larger ERP Old/New effects for emotionally arousing (both pleasant and unpleasant) items have been observed (Dietrich et al., 2001; Langeslag & Van

Strien, 2008; Pérez-Mata et al., 2012; Schefter, Knorr, Kathmann, & Werheid, 2012; Wirkner et al., 2018), in others these effects were absent (Koenig & Mecklinger, 2008; Weymar, Bradley, El-hinnawi, & Lang, 2013). However, when memory is tested after long consolidation periods (> 24 h), enhanced late parietal Old/New differences have reliably been found for emotional items (Weymar & Hamm, 2013).

Evidence for this comes from a series of studies by Weymar and colleagues, in which the brain dynamics of emotional, long-term mnemonic advantages were investigated. To do so, emotional and neutral image scenes were presented, and memories of the scenes were tested in a subsequent recognition task (with a one day, one week or one year delay). At a behavioral level, the authors found a typical enhanced long-term memory performance for emotional images (Weymar et al., 2011, 2009; Weymar, Löw, Schwabe, & Hamm, 2010), reflected by higher memory discrimination, and ‘Remember’ judgments (Weymar et al., 2009, 2011). This emotional mnemonic advantage was accompanied by larger, late Old/New effects at a neural level, further indicating that emotionally arousing contents facilitate recollection-based memory (Figure1; Weymar & Hamm, 2013).

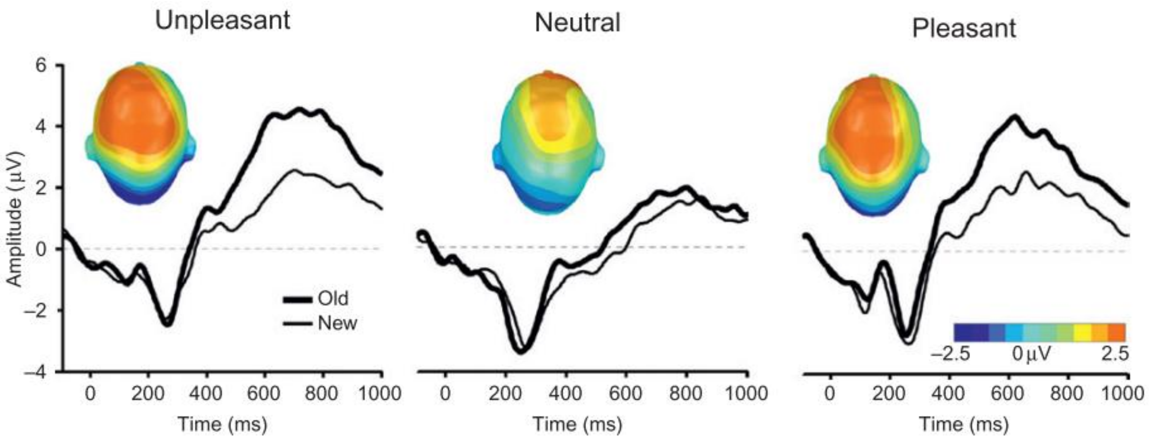

Figure 1. Late ERP Old/New effect and difference topographies (old vs. new) for unpleasant, neutral and pleasant scenes (adapted from Weymar & Hamm, 2013).

4.1.2 Spatial dynamics

Functional MRI studies investigating the underlying brain structures of episodic retrieval show that the successful recognition of information is associated with greater activation in various brain regions such as the medial temporal lobe (MTL, which encompasses the hippocampus, perirhinal cortex, and parahippocampal cortex), the prefrontal cortex (PFC, which includes the medial and orbital areas), and the posterior parietal cortex (PPC, which includes the angular gyrus, retrosplenial/posterior cingulate cortex and cuneus/precuneus; see Davachi, 2006; Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Ranganath, 2010; Ranganath & Ritchey, 2012 and Rugg & Vilberg, 2013 for reviews). These anatomical regions seem to have both distinct and shared (or complementary) functions within the retrieval network, including their involvement in recollection and familiarity-based processes. For instance, Rugg et al. (2012) found, in a detailed review of eight studies from their own group, that hippocampus activation consistently increased with the amount of information retrieved both during item and source recognition tasks, suggesting that the hippocampus is modulated by the quantity of retrieved information. Successful retrieval of associated source information of an event has not only been related to the hippocampus but also to the parahippocampal cortex (Düzel et al., 2003; see for review Diana et al., 2007), medial PFC (e.g., Schlichting & Preston, 2015), as well as PPC activity (Vilberg & Rugg, 2007, 2009a, 2009b; see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Rugg & King, 2018; Sestieri et al., 2017; Vilberg & Rugg, 2008 and Wagner, Shannon, Kahn, & Buckner, 2005 for reviews), particularly when memory retrieval was based on recollection rather than familiarity judgments (Wheeler & Buckner, 2004). The activation of PPC regions seems to be closely related to the recollection-sensitive, late ERP Old/New effect, as suggested by studies using combined fMRI-ERP methodologies (Vilberg et al., 2006) and ERP source localization analysis (Hoppstädter, Baeuchl, Diener, Flor, & Meyer, 2015; Weymar et al., 2011a; Weymar, Löw, Modess, et al., 2010).

Prior brain imaging studies also suggest that, as for the ERP Old/New effect (e.g., Weymar et al., 2009; 2011), the retrieval of single emotional events (e.g. scenes) is associated with enhanced PPC activity (Keightley, Chiew, Anderson, & Grady, 2011; Sterpenich et al., 2009). Furthermore, emotion-specific retrieval effects have also been observed in the MTL and PFC (Dolcos, LaBar, & Cabeza, 2005; Keightley et al., 2011; Sterpenich et al., 2009; see LaBar & Cabeza, 2006 for reviews), as part of a putative recollection network (Gilmore, Nelson, & McDermott, 2015; King, de Chastelaine, Elward, Wang, & Rugg, 2015; Rugg & Vilberg, 2013). In addition, the amygdala, as a crucial node that helps establish long-lasting emotional memories (McGaugh, 2004; Mcintyre, Mcgaugh, & Williams, 2012), also shows larger activation during episodic retrieval (Dolcos et al., 2005). Indeed, the amygdala interacts with the PFC and MTL regions to generate a synergic mechanism in which emotion and recollection enhance one another (Dolcos et al., 2005; Smith, Stephan, Rugg, & Dolan, 2006) via top-down and bottom-up processes (Figure 2; Dolcos, Denkova, & Dolcos, 2012; Dolcos et al., 2017).

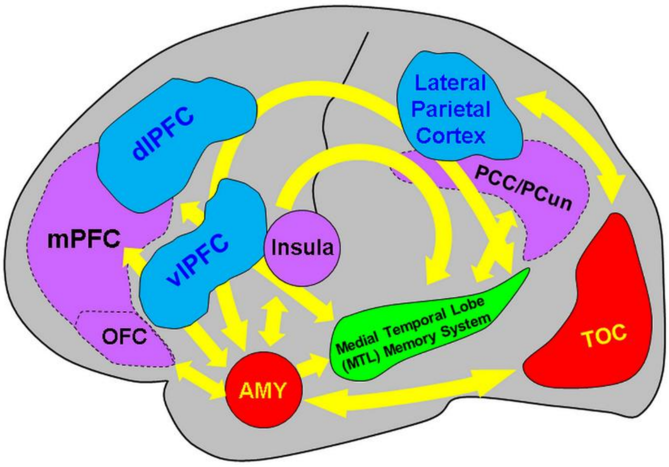

Figure 2. Diagram summarising the neural substrates involved in the memory-enhancing effects of emotion. The MTL-AMY interactions contribute to the memory-enhancing effects of emotion via bottom-up mechanisms. PFC-AMY interactions, through The enhancement of strategic, working memory, and attentional processes, have an indirect influence on the memory-enhancing effects of emotions driven by top-down mechanisms. In addition, larger involvement of temporo-occipital and parietal cortices also facilitate encoding and retrieval of emotionally relevant stimuli. AMY: amygdala; MTL: medial temporal lobe; PFC: prefrontal cortex; mPFC: medial PFC, OFC: orbital PFC; dlPFC: dorsolateral PFC; vlPFC: ventral-lateral PFC; PCC/PCun: posterior cingulate cortex/precuneus; TOC: temporo-occipital cortices (adapted from Dolcos et al., 2017).

On the level of synaptic transmission, the interplay between these brain areas that results in enhanced memory for emotional events is mainly mediated by cathecolamines and glucocorticoids, as detailed in the next section.

4.2. NEUROBIOLOGY OF EMOTIONAL EPISODIC MEMORY

When encountering an emotionally relevant event, multiple physiological responses are initiated, exerting influence on the mnemonic processes of encoding, consolidation, and retrieval, depending on their temporal actions (Schwabe, 2017). These effects are mainly influenced by the release of two major classes of chemical transmitters: catecholamines and glucocorticoids (Hermans, Henckens, Joels, & Fernandez, 2014; Joëls, Fernandez, & Roozendaal, 2011; Schwabe, 2017). Immediately after the encounter, the release of monoamines, including noradrenaline, dopamine, and serotonin, occurs in specific brain areas and rapidly spreads to subcortical and cortical regions (Joëls & Baram, 2009). Simultaneously, a fast chain of physiological reactions in the autonomic nervous system (ANS) originates in brainstem regions and acts in different organs, including the adrenal glands, which initiate the release of catecholamines (i.e., epinephrine and norepinephrine) in the first few seconds following the encounter. Via afferents of the vagal nerve to the nucleus of the solitary tract (NTS), the peripheral release of catecholamines feeds back to the brain (Roozendaal, McEwen, & Chattarji, 2009), allowing for the release of central norepinephrine in the locus coeruleus (LC), the main brain source of norepinephrine (NE). Critically, the released neuromodulator NE acts upon the beta-adrenergic receptors on the basolateral amygdala and in the hippocampus, modulating the crosstalk of these two regions (Cahill, Prins, Weber, & McGaugh, 1994).

In parallel to the activation of the ANS, the hypothalamus initiates an endocrine response via the hypothalamic-pituitary-adrenal (HPA) axis, stimulating the release of glucocorticoid hormones with a delay of about 15 minutes after the encounter (Ulrich-Lai & Herman, 2009). Glucocorticoids access the brain by crossing the blood-brain barrier and modulate the stress-induced brain reactions, acting on the high-affinity mineralocorticoid receptors (MRs) and low-affinity glucocorticoid receptors (GRs) that are widely distributed in limbic and prefrontal areas (Reul & De Kloet, 1985). After reaching the brain, NE and cortisol interact with each other to exert modulatory effects on regions involved in the consolidation of episodic emotional memories (Figure 3; McGaugh, 2000; McGaugh, 2004; McIntyre, McGaugh, & Williams, 2012).

Consistent with these assumptions, an increase in the concentration of epinephrine and cortisol via direct administration or cold press stressors during encoding improves memory retrieval (Cahill & Alkire, 2003). Moreover, the administration of antagonist drugs that prevent the epinephrine action (e.g. propranolol) blocks the effects of this treatment on memory (Cahill et al., 1994) and exerts a special influence on the recollection-based enhancement of emotional episodic memory (Cahill et al., 1994; Cahill & Van Stegeren, 2003; Schwabe, Nader, & Pruessner, 2013; van Stegeren, 2008; Weymar, Löw, Schwabe, et al., 2010; Weymar, Schwabe, Löw, & Hamm, 2012). Neuroimaging studies have further confirmed that the amygdala, when interacting with the hippocampus (Roozendaal, Okuda, De Quervain, & McGaugh, 2006; Roozendaal & McGaugh, 1997; Roozendaal et al., 2009), appears to be primarily responsible for the modulatory effects of glucocorticoids and catecholamines in emotional episodic memory. Indeed, pharmacological variations of glucocorticoid and norepinephrine levels modulate the amygdala activation during the processing of emotional material (Henckens, Hermans, Pu, Joels, & Fernandez, 2009; Schwabe, Höffken, Tegenthoff, & Wolf, 2013; Strange & Dolan, 2004), and the subsequent hippocampal reactivity during episodic emotional memory retrieval (Strange & Dolan, 2004).

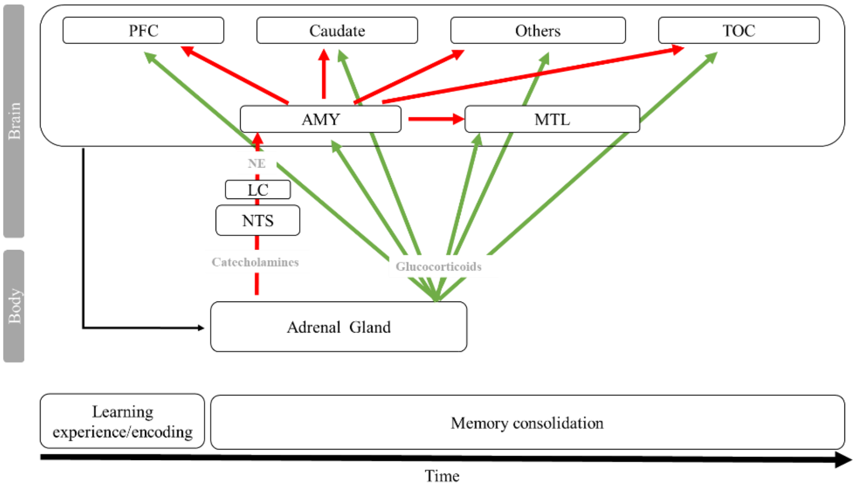

Figure 3. Schematic representation of the interaction of catecholamines (red arrows) and glucocorticoids (green arrows) with memory-related brain regions to enhance memory consolidation. AMY: amygdala, MTL: medial temporal lobe; PFC: prefrontal cortex: LC: locus coeruleus; NTS: nucleus of the solitary tract.

Despite the great amount of empirical evidence demonstrating the memory advantage of emotional events (i.e. item memory), the effects of emotion for associated information or contextual details, also termed source or relational memory, are less clear (see Chiu, Dolcos, Gonsalves, & Cohen, 2013; Dolcos et al., 2017; Mather & Sutherland, 2011; Mather, Clewett, Sakaki, & Harley, 2016 and Murray & Kensinger, 2013 for reviews). In the next sections, existing knowledge on this topic will be summarized, open research questions derived and the contributions of this thesis to gaining more knowledge in the field of emotional context effects on episodic memory detailed.

5. SOURCE MEMORY AND EMOTION

Over the last chapters, a modulatory effect of emotion on item memory has been firmly established. Extending upon this research, recent approaches have been centered on the effects of emotion on memory for real-world scenarios in which items are not isolated, but in the context of or in relation to other items and/or source details (e.g. spatial, physical, temporal features), a phenomenon referred to as relational or source memory (Chiu et al., 2013). In this sense, some studies have observed that the retrieval of source details is facilitated when encoded as part of an emotional item (e.g. a scene or word). These effects have been shown for the recognition of colors, spatial location and temporal order of the items (D'Argembeau & Van der Linden, 2004, 2005; Doerksen & Shimamura, 2001; MacKay & Ahmetzanov, 2005; Mather, Gorlick, & Nesmith, 2009; Mather & Nesmith, 2008; Nashiro & Mather, 2011; Rimmele, Davachi, & Phelps, 2012; Schmidt, Patnaik, & Kensinger, 2011; but see Koenig & Mecklinger, 2008; MacKenzie, Powell, & Donaldson, 2015; Maddock & Frein, 2009; Mather & Knight, 2008). Several studies have also shown that memories of neutral objects or words integrated within emotional contexts (e.g. arousing words or emotional scenes) are better retrieved than when encoded in neutral or less arousing contexts (Martinez-Galindo, & Cansino, 2016; Guillet & Arndt, 2009; Luck, Leclerc, & Lepage, 2014; Maratos & Rugg, 2001; Pierce & Kensinger, 2011; Smith, Dolan, & Rugg, 2004; Smith, Henson, Rugg, & Dolan, 2005). However, others have reported negative effects of emotional information on memory for associated material (e.g. objects or words) and/or source details (e.g. frames, spatial location or language; Bisby & Burgess, 2014; Bisby, Horner, Horlyck, & Burgess, 2016; Cook, Hicks, & Marsh, 2007; Ferré, Comesaña, & Guasch, 2019; Guo, Li, Bi, & Chen, 2018; Kensinger, Garoff-Eaton, & Schacter, 2007; MacKenzie et al., 2015; Madan, Fujiware, Caplan, & Sommer, 2017;

Madan, Caplan, Lau, & Fujiwara, 2012; Mao, You, Li, & Guo, 2015; Mather et al., 2006, 2009; Mather & Knight, 2008; Murray & Kensinger, 2012; Nashiro & Mather, 2011; Pierce & Kensinger, 2011; Rimmele, Davachi, Petrov, Dougal, & Phelps, 2011; Touryan, Marian, & Shimamura, 2007). Altogether, these findings point to divergent effects of emotion on source memory, i.e., in some cases enhancing and in others decrementing memory retrieval.

Mather and colleagues integrated the divergent findings about emotion on source memory in their Arousal-Biased Competition Theory (ABC Theory; Mather et al., 2016; Mather & Sutherland, 2011). According to this model, the modulatory effects of emotion depend upon the attentional priority that the critical material receives during learning. This prioritization or bias can be determined via bottom-up processes which are automatic and driven by the perceptual characteristics of a stimulus, via top-down processes derived from specific goals, or through a past experience with particular stimuli. Emotional arousal can thus have opposing effects on associated source information, enhancing memory if highly prioritized or integrated with emotional information (likely through the promotion of associative learning processes), or weakening memory if lowly prioritized or perceived as a resource competitor for emotional material (Mather et al., 2016; Mather & Sutherland, 2011). The mixed results of emotional source memory could, therefore, be explained in terms of prioritization. On the one hand, when high prioritization is facilitated for physical, temporal or spatial characteristics, as well as for related neutral information via past experiences, bottom-up, or top-down processes, memory for such information is enhanced if associated with an emotionally arousing event. On the other hand, if no prioritization is given, the attentional resources needed to encode source details may be limited in favor of the arousing characteristics of the event, resulting in a detrimental effect on source memory. In a recent study by Sakaki and colleagues, the role of prioritization on the contrasting effects of memory arousal was systematically tested (Sakaki, Fryer, & Mather, 2014). In their study, a series of neutral objects mixed in with a neutral or arousing oddball object were presented, at the end of each series, participants were instructed to retrieve, either the oddball object or the object presented prior to the oddball (oddball-minus-one object). After the presentation, memory for the oddball-minus-one object was tested for both conditions. When participants were instructed to focus on the oddball object, memory for oddball-minus-one objects was reduced when followed by highly arousing compared to neutral oddballs. However, when participants were instructed to focus on the oddball-minus-one objects, highly arousing oddballs in comparison to neutral ones amplified memory for oddball-minus-one objects. These results indicate that arousal can both impair and amplify memory for related neutral information, depending on priority.

Neurobiological support for this assumption stems from research on synaptic transmission mostly conducted in animals, showing that NE and glutamate may interact with each other to both potentiate and diminish neuronal activation. When glutamate is released, some of it escapes the synaptic cleft and spreads over the surroundings, an effect termed glutamate spillover (Okubo et al., 2010). The spilled glutamate binds to the adjacent presynaptic glutamatergic NMDA receptors of the LC varicosities and promotes the release of NE, which will bind to its presynaptic high-affinity alpha-adrenoreceptors or low-affinity beta-adrenoreceptors, further inhibiting or amplifying NE release. Thus, if NMDA receptors in the LC varicosities receive only lower levels of glutamate, NE will be released in lower concentrations, binding mainly to alpha-adrenoreceptors which will inhibit further NE release. As a consequence, the impact of NE on the presynaptic beta-adrenoreceptors of the glutamatergic neurons will be reduced. In turn, the neuronal activation of the mental representation will be weakened. However, if the impact of glutamate on presynaptic NMDA receptors in LC varicosities is high, larger amounts of NE will be released and will bind to the presynaptic beta-adrenoreceptors. Consequently, more NE will be spread, will bind to the presynaptic beta-adrenoreceptors of the glutamatergic neuron, and promote the release of more glutamate. This positive feedback loop between NE and glutamate release will strengthen the neuronal activation of mental representation (Figure 4).

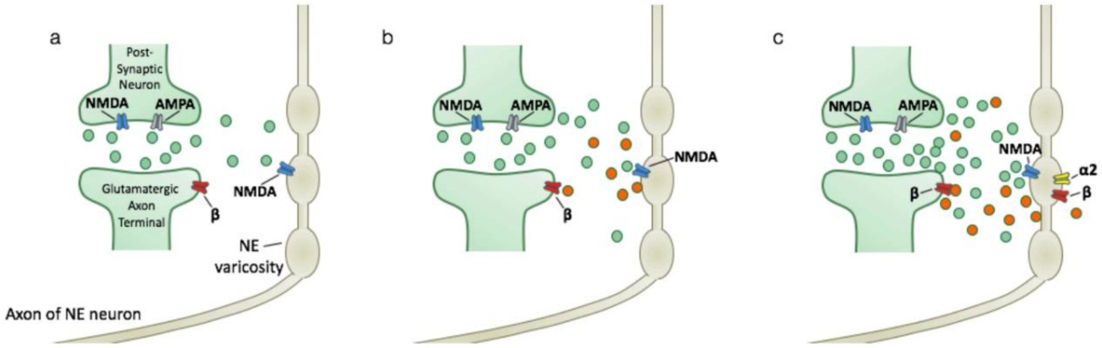

Figure 4. Graphic depiction of the proposed glutamate-NE interaction. When an event is perceived, a) glutamate (green circles) spill-over reaches LC varicosities. b) The glutamate spill-over will attach itself to the NMDA receptors of the LC and trigger NE (orange circles) release. c) Elevated local levels of NE will activate beta-adrenergic receptors that will further stimulate NE release, the released NE will reach to presynaptic beta-adrenergic receptors of glutamatergic neurons, promoting further release of glutamate, leading to high neuronal excitation, and ultimately a stronger mental representation of the event. If the release of NE occurs in lower amounts, NE will attach to alpha-adrenoreceptors of LC varicosities, inhibit further NE release, and subsequently the increase of glutamate release, which will, in turn, produce a weaker mental representation of the triggering event (adapted from Lee et al., 2018).

Importantly, the LC has widespread projections to different cortical and subcortical regions that are vitally important for memory encoding and consolidation, including the hippocampus (e.g., Harley, 2007; Mello-Carpes & Izquierdo, 2013), amygdala (e.g., Chen & Sara, 2007; Williams, Men, & Clayton, 2000; Williams, Men, Clayton, & Gold, 1998; for a review, see McIntyre et al., 2012), and prefrontal cortex (Arnsten, Wang, & Paspalas, 2012; Clayton, 2004). Through these afferent projections, the NE varicosities of the LC, when interacting with glutamatergic neurons, modulate the activation of these regions. The amplification or reduction of the mental representations as a function of priority will determine the longevity of the memory trace (Mather et al., 2016).

5.1. STUDY 2: LONG-TERM MEMORY FOR OBJECTS ENCODED IN EMOTIONAL AND NEUTRAL CONTEXTUAL BACKGROUNDS.

As reviewed above, along with the priority-dependent effects, retention interval is another important feature that may exert crucial influence on the effects of emotion on source memory (Mather et al., 2016; Mather & Sutherland, 2011). Indeed, longer retention intervals favor memory retrieval for items paired with emotional (particularly unpleasant) information in comparison to neutral material, likely by facilitating consolidation processes (Pierce & Kensinger, 2011). Thus, memory for neutral information and/or source details may be enhanced if integrated with emotional material, particularly if the retention interval is long enough to allow for consolidation processes. In our second study (Ventura-Bort, Löw, Wendt, Moltó, Poy, Dolcos, Hamm & Weymar 2016b), we tested these assumptions -by examining the behavioral and electrophysiological correlates of long-term memory for neutral items encoded in emotional and neutral contexts. In the first session of a two-session experiment[2], participants incidentally encoded 144 common objects, presented in one of the four quadrants of the screen, and overlaid on 144 different background scenes (i.e. contexts) that were either pleasant, neutral or unpleasant. To facilitate object/context integration, participants were instructed to imagine the object as a part of the scene. Moreover, object/context pairs were presented twice in two different runs. One week after encoding, participants were presented with the 144 encoded objects intermixed with 144 new objects and were to decide whether each object had previously been seen during encoding or not, using an “old/new” paradigm (e.g., Weymar et al., 2009).

Results showed that emotional contexts enhanced item memory for associated objects (i.e. emotional associates) as indicated by larger memory performance. At an

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[2] Results from the encoding session are presented in Study 1 of this thesis.

electrophysiological level, the mnemonic advantage for emotional associates was observed at different stages of processing. In an early time window (180-220 ms) over frontal electrodes, emotional associates elicited larger P2 amplitudes than their neutral counterparts. The frontal P2 has been related to the activation of visual representations in long-term memory (Curran & Dien, 2003). Concretely, frontal P2 amplitudes increase when the visual input matches with efficiently stored relevant information (Schaefer et al., 2011; Voss & Paller, 2009), suggesting that the P2 might be related to the phenomenological salience of activated representations (Voss & Paller, 2009). Consistent with this idea, Schaefer et al. (2011) observed that the P2 amplitudes of correctly retrieved unpleasant images increased with their arousal level. Thus, larger P2 amplitudes for emotional compared to neutral associates suggest that they may have acquired long-lasting emotional relevance due to the integration with emotional contexts.

In addition, the memory-sensitive ERP components also showed emotional modulation. The early Old/New effect (300-500 ms) was prominent for unpleasant associates, however, neither neutral nor pleasant associates showed such effect. These findings suggest that unpleasant contextual source information facilitated familiarity-based retrieval processes. Although it was initially proposed that source memory depends upon recollection-based processes (Rugg & Curran, 2007; Wilding & Rugg, 1996), later evidence has showed that familiarity-related processes could also contribute to source recognition by means of unitization, that is, the representation of separate components (e.g., an object and its color or location) as a single unit (Addante, Ranganath, & Yonelinas, 2012; Diana, Van den Boom, Yonelinas, & Ranganath, 2011). Shedding light on this differentiation, Diana et al. (2011) examined the effects of unitization on the electrophysiological correlates of memory. The authors observed that when item/context associations are highly unitized (i.e. encoded as single units), memory for items is driven by familiarity-related process, as indicated by more pronounced frontal Old/New differences, whereas when item/context associations are lowly unitized, memory retrieval is based on recollection, as shown by larger parietal Old/New differences (see also, Bader et al., 2010). Although in Study 2 no unitization instructions were emphasized, the experimental setting was intended to promote object/context associations at encoding. It might, therefore, be that through these mechanisms, object/context unitization for unpleasant associations was accentuated, facilitating to some extent familiarity-based recognition. It was also found that emotional (but not neutral) associations generated pronounced late Old/New differences. The enhanced late ERP Old/New effect observed for emotional (but not neutral) associates is in line with previous long-term memory ERP studies for emotional single items (e.g., Weymar et al., 2009) and extends prior findings, demonstrating that emotional relevance can facilitate memory for associated neutral information. Given the recollective nature of the late ERP Old/New effect (Rugg & Curran, 2007), the emotional mnemonic advantage is, at least in part, driven by recollection processes.

In summary, in Study 2 it was found that emotional contextual information can have long-lasting effects on the mnemonic trace of associated neutral material when object/context integration is encouraged and the retention interval allows for consolidation. These effects seem to occur at different stages of processing, facilitating visual identification and explicit mnemonic processing. In this study, however, memory performance was evaluated using an old/new procedure, therefore no distinction could be made in terms of the differential effects of recollection and familiarity for item and source information at the behavioral level. Furthermore, brain dynamics associated with the long-term retrieval of contextual source information were not explored. Study 3 aims to gain more insights into the mnemonic processes underlying long-term item and source memory, along with the associated electrophysiological correlates.

5.2. STUDY 3: DISENTANGLING RECOLLECTION AND FAMILIARITY IN ITEM AND SOURCE MEMORY FOR EMOTIONAL ASSOCIATES.

In an attempt to disentangle the differential contribution of emotional contexts on recollection and familiarity-based processes during the retrieval of neutral associated information and source details, the well-established ‘Remember/Know’ procedure (Tulving, 1985) was used in Study 3 (Ventura-Bort, Dolcos, Wendt, Wirkner, Hamm and Weymar, 2017). In this procedure, participants are asked to indicate whether their memory for emotional stimuli comprises rich contextual details of the contiguous attributes conforming the encoding episode (‘Remember’ judgments) or lacks contextual specifics (‘Know’ judgments). This distinction allows for a differentiation between recollection (measured by ‘Remember’ judgments) and familiarity-based retrieval (measured by ‘Know’ judgments). Here, unlike in Study 2 (Ventura-Bort et al., 2016), the modulatory effects of emotion on the brain dynamics underlying contextual source memory was examined. Similar to Study 2, a two-session task was used, however, in order to generate more realistic scenarios this time no object/context integration was encouraged. Instead, participants were instructed to watch the object and the scene attentively when displayed together on the monitor. Moreover, object/context pairs were presented only once. One week later, item and source memory were tested, using the ‘Remember/Know’ paradigm while EEG activity was recorded.

Behavioral results revealed that item memory performance was mainly driven by familiarity-related judgments, as indicated by larger hit rates for ‘Know’ than ‘Remember’, irrespective of the emotional category of the contexts. Contextual source memory, however, was more related to recollection processes, especially for emotionally arousing backgrounds. In line with item memory performance, for the ERPs, early Old/New differences (300-500 ms) were observed for both neutral and emotional associates. Late Old/New differences (600-800 ms) were, however, found particularly for emotional associations. For contextual source memory, ERPs paralleled the enhanced recollection-based memory performance for emotional contextual information, as indicated by pronounced late ERP Old/New differences for objects with correctly recognized emotional, but not neutral, contexts.

Convergent behavioral and electrophysiological results for item memory suggest that long-term memory for associations is guided by familiarity judgments when tested one week after encoding. These findings concur with a recent study, showing that long-term memory (4 week delay) for neutral objects relies more on familiarity than on recollection processes (Tsivilis et al., 2015). In contrast to Study 2 (Ventura-Bort et al., 2016b), the memory advantage for emotional associates was only partially replicated. While no emotion effects were observed on memory performance, the late Old/New effect was observed exclusively for emotional associates. The dissimilarities in memory performance between both studies could have been due to methodological reasons. In Study 2, object/context integration was facilitated by instructing participants to actively imagine the objects in context. Moreover, object/context pairings were presented twice. Here, no integration-related instruction was given and only a single object/context pairing was presented. According to the ABC theory, it is likely that these variations (no integration-related instruction and single presentation) weakened object/context association and lessened attentional priority for the objects during encoding (Mather and Sutherland, 2011), impacting on mnemonic recognition, particularly at a behavioral level. Given that ERPs are considered a fine-grained tool for detecting changes in cognitive processing, even in the absence of behavioral indicators (Jaeger et al., 2009), these methodological changes may have led to a lack of emotional effects on memory performance in the presence of enhanced late ERP Old/New effects.

For contextual source memory, emotion enhancing effects were observed both at the behavioral and electrophysiological levels. These findings are consistent with previous studies assessing memory for single emotional and neutral events (Dolcos et al., 2005; Ochsner, 2000; Sharot et al., 2004; Weymar et al., 2009, 2010) in which participants were more likely to experience vivid memories for emotionally arousing events than neutral ones, as indicated by higher 'Remember' judgments and recognition confidence rates. Furthermore, these results extend previous studies using immediate recognition testing (Rimmele et al., 2011, 2012; Smith et al., 2004), showing that long-term memory for emotional contextual information is based on recollection processes.

Taken together, Study 3 revealed that familiarity-based processes guide item memory, irrespective of context category, whereas recollection-based processes are more involved in contextual source memory. Importantly, emotion was found to enhance recollection memory for item and contextual source information, as indicated by pronounced late parietal ERP Old/New effects. These findings highlight the importance of distinguishing between mnemonic processes, such as familiarity and recollection, to provide a better understanding of the mechanisms underlying item and contextual source memory when interacting with emotion. The previous studies of the thesis, as well as the revised literature, suggest that retrieval of emotional items and associates is particularly driven by recollection-based processes, especially during explicit recognition tasks. The question arises, however, whether emotion may alter less controlled, but also frequent, forms of memories, namely involuntary or spontaneous memories. Study 4 aims to investigate the effects of emotional contexts on the spontaneous retrieval of associated neutral information.

5.3. STUDY 4: ELECTROPHYSIOLOGICAL EVIDENCE OF SPONTANEOUS RETRIEVAL FOR EMOTIONAL ASSOCIATES

Spontaneous memories are understood to be memories that are retrieved without deliberate intention (Berntsen, 2010). Typically, these memories are evoked by highly salient past events and/or by the presence of a specific feature which matches previously stored information (Berntsen, 2010; Hintzman, 2011). Spontaneous memories are as recurrent in daily life as voluntary memories (Rubin & Berntsen, 2009), and such recurrences may be an advantageous mechanism, by means of which the effortless retrieval of relevant information can facilitate adaptive responses (Berntsen, 2009). However, spontaneous memories can also become maladaptive, as occurs in different mental disorders (American Psychiatric Association, 2013). For instance, in individuals suffering from post-traumatic stress disorder (PTSD), the retrieval of spontaneous, highly emotional autobiographical memories is frequently experienced and accompanied by strong vividness, exerting a notable influence on their behavior. Due to their involuntary nature, these memories are less linked to the mechanism of emotion regulation, being more likely to produce many PTSD symptoms (Rubin, Boals, & Berntsen, 2008).

Despite its relevance, emotional spontaneous memory has rarely been studied, mainly due to methodological limitations, such as the absence of behavioral reports. As outlined above, however, ERP methodology may provide reliable information about the mnemonic processes carried out, and therefore may be a well-suited approach for identifying the processes underlying spontaneous emotional memory in the absence of behavioral indices (Ferrari, Bradley, Codispoti, Karlsson, & Lang, 2013; Jaworek, Weymar, Löw, & Hamm, 2014; Rosburg, Mecklinger, & Frings, 2011; Weymar, Bradley, El-Hinnawi, & Lang, 2013). The few existing ERP studies on spontaneous emotional memory found enhanced parietal Old/New effects exclusively for single emotional events (e.g. images) during immediate recognition (Ferrari et al., 2013; Weymar et al., 2013), suggesting that the mere exposure to previously-seen, emotionally-relevant information triggered spontaneous recollection, independently of task demands during retrieval. However, when spontaneous memory was prompted one week after encoding, single emotional events generated larger ERP Old/New differences over frontal regions, suggesting that for long-term delays, implicitly remembered emotional scenes may be mediated by familiarity-based processes (Jaworek et al., 2014).

In order to extend the existing evidence, in Study 4 (Ventura-Bort, Wirkner, Dolcos, Wendt, Hamm & Weymar, submitted), ERPs were used to investigate whether the memory enhancing effect of emotion during spontaneous retrieval is also evident for neutral information previously encoded in emotional contexts. Similar to previous studies (Studies 2 and 3; Ventura-Bort et al., 2016b, 2017), participants encoded neutral objects in emotionally arousing, pleasant, unpleasant, or neutral contexts (background scenes). One week later, all the previously encoded neutral items were again presented and mixed with new ones, while participants were instructed to attentively watch the material presented (free viewing procedure).

In line with previous explicit item memory testing (e.g. Study 3; Ventura-Bort et al., 2017), the results of Study 4 showed early and late ERP Old/New differences during the viewing of old and new objects (Study 4: Ventura-Bort et al., submitted). Most interestingly, only emotional associates showed a pronounced late (504-1144 ms) Old/New effect, whereas the early Old/New effect was observed for both neutral (392-548 ms) and emotional associates (360-484 ms).

The observed modulatory effects of emotional contexts on spontaneous item memory compliment previous explicit recognition memory research with an identical encoding procedure (Ventura-Bort et al., 2017), in which emotional and neutral associates evoked a comparable early Old/New effect, whereas only correctly recognized emotional associates generated prominent late Old/New differences. The convergent findings between explicitly and spontaneously triggered retrievals are in line with recent theoretical proposals stating that the retrieval of voluntary and involuntary memories, although may differ in terms of the executive control exerted (Berntsen, 2010), is carried out by the same memory processes (Rubin et al., 2008). The results thus give further evidence that the long-term, memory enhancing effects of emotional contexts are not related to the task embedded during recognition, but to the motivational relevance of the triggering event.

So far, the studies of this thesis have provided electrophysiological evidence for a long-term, recollection-guided advantage of emotional contexts for item and contextual source information (Ventura-Bort et al., 2016, 2017, submitted). From these studies, however, no conclusions can be drawn in terms of the brain regions involved in these processes. The next study aims at exploring this question using fMRI to investigate the neural substrates engaged in memory retrieval of emotional associates and contextual source information.

5.4. STUDY 5: NEURAL SUBSTRATES OF LONG-TERM ITEM AND SOURCE MEMORY FOR EMOTIONAL ASSOCIATES

To examine the brain structures underlying the modulatory effects of emotional contexts on item and source memory, in Study 5 (Ventura-Bort, Wendt, Wirkner, König, Lotze, Hamm, Dolcos & Weymar, submitted), an fMRI-adapted design similar to previous ERP studies (e.g. Study 1: Ventura-Bort et al., 2016b) was used. During the first session, neutral objects were integrated into emotional or neutral contexts (background scenes), while participants imagined the object as part of the scene. One week later, the same encoded objects were mixed in with new ones and participants were asked to indicate whether objects were seen or not during encoding (item memory), and which background category the object was paired with (contextual source memory). To directly assess the contribution of recollection and familiarity-based memory, 'Remember' and 'Know' judgments were obtained (Tulving, 1985).

In line with Study 3 (Ventura-Bort et al., 2017), behavioral results showed a mnemonic dissociation between item and contextual source information. Specifically, item memory was driven by familiarity-based judgments, whereas contextual source memory was guided by recollection-based judgments. Most interestingly, emotional contexts enhanced recollection-based memory for both item and contextual source memory, as indicated by larger 'Remember' hit rates.

During the episodic retrieval of item and contextual source information, functional MRI results revealed that regions embedded in a network related to recollection-based memory, including regions in the medial temporal lobe (MTL), posterior parietal cortex (PPC), and prefrontal cortex (PFC), were more strongly engaged (Rugg & Vilberg, 2013; Gilmore et al., 2015). Critically, the retrieval of both emotional associates and contextual source material activated more intensely these regions.

In the MTL, the hippocampus (HC) and parahippocampal cortex (PHC) showed differential activation for item and contextual source memory: whereas the HC was more strongly activated during the retrieval of both emotional associates and contextual source material, the PHC was exclusively involved in the retrieval of emotional contextual information. Although both brain regions participate in the retrieval of episodic memories, the HC and PHC have been attributed to different functions (Diana et al., 2007). The PHC is thought to process spatial contextual information (the where) of an event (Burgess, Maguire, Spiers, & O'Keefe, 2001; Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011), whereas the HC binds together all aspects of the event (the what, when, where, how, and why), generating a compound representation and creating a rich episodic memory trace (Ekstrom et al., 2011; Staresina & Davachi, 2009; see Davachi, 2006; Eichenbaum et al., 2007 and Ranganath, 2010 for reviews). Thus, a larger PHC engagement elicited by recognized, emotionally arousing contextual information may indicate that emotion facilitates the retrieval of contextual details. Additionally, the observed larger HC activity for recognized emotional associates further suggests that emotion enhances the retrieval of multiple aspects integrated into the encoding episode.

The involvement of the HC during retrieval of emotional associates is in line with findings by Dolcos and colleagues, who observed enhanced HC activity for emotional scenes during both memory encoding (Dolcos, LaBar, & Cabeza, 2004b), interacting with the amygdala (Dolcos et al., 2004b; Keightley et al., 2011; McGaugh, 2004; Ritchey et al., 2008; Smith, Stephan, Rugg, & Dolan, 2006) and retrieval (Dolcos et al., 2005). In the present study, stronger hippocampal activation was observed when retrieving emotional associates from long-term memory, which expands upon prior work by Smith et al. (2004), using an immediate recognition task.

Regions of the PPC, including the precuneus (PCUN)/cuneus, and posterior cingulate cortex (PCC), also showed greater activation during the retrieval of emotional associates and contextual source details.

The precuneus/cuneus as a part of the memory network has also been reliably related to episodic retrieval (Cavanna & Trimble, 2006; Rugg, Otten, & Henson, 2002; Wagner et al., 2005). The PCUN, is integrated in the dorsal parietal cortex and is said to participate in top-down, goal-directed attentional processes during memory retrieval (Cabeza et al. 2008). However, recent evidence has also found similar activations during involuntary retrieval, in which old stimuli were merely presented, without explicit recognition instructions (Bradley et al., 2015; Weymar et al., 2018), suggesting that the precuneus/cuneus region may be involved in both top-down and bottom-up attentional mechanisms (Gilmore et al., 2015). In Study 5, a stronger precuneus/cuneus activation during item memory was observed, particularly for emotional associates (cuneus). This result extends prior findings using emotional images and faces (Keightley et al., 2011), indicating a larger deployment of attentional resources during the retrieval of motivationally relevant memory representations.

Results also showed stronger activation of the PCC during the recognition of emotional associations and emotional contextual source information, in line with prior memory retrieval studies (Natu et al., 2018; Rugg & Vilberg, 2013). Importantly, PCC activation has been related to the retrieval of self-relevant information such as autobiographical or emotionally salient events (Maddock, Garrett, & Buonocore, 2003; Maratos, Dolan, Morris, Henson, & Rugg, 2001). Thus, stronger PCC engagement for emotionally-laden material may indicate that due to its motivational value, such information becomes more self-relevant than neutral information.

Finally, different prefrontal areas involved in the recollection network, namely the medial and orbital PFC, also showed stronger activation during item memory and were modulated by emotion for contextual source memory retrieval. It has been suggested that the PFC modulates mnemonic processes in an indirect fashion, by means of strategic, semantic, working memory and attentional processes (Roy, Shohamy, & Wager, 2012). The medial PFC, as one of the most important prefrontal regions involved in retrieval, is thought to guide behavior through the integration of current information with prior experiences. The medial PFC works together with MTL regions (e.g. HC), continuously updating the attributes that define an event by means of integrating past and current experiences (Schlichting & Preston, 2015). Furthermore, emotional relevance seems to enhance the integrative role of the medial PFC (Barron, Dolan, & Behrens, 2013; Maratos et al., 2001; Smith et al., 2004). Greater involvement of the medial PFC during successful retrieval may indicate an update of the information from the reinstated event. Most interestingly, medial PFC activity was specifically related to emotional contextual source memory. These findings suggest that the ongoing integration between previous and current encounters with an event may be particularly enhanced by the emotional relevance of the event (Schlichting & Preston, 2015). Turning to the orbital PFC, this region has been shown to play an important role in decision making (Krawczyk, 2002), and has been associated with affective, reward-related valuation (Heinzel & Northoff, 2009). Emotional relevance has been shown to increase orbital PFC activation during retrieval processes (Smith et al., 2004). In this vein, a larger orbital PFC activation during the retrieval of emotional contextual source information was found, suggesting that the orbital PFC may signal the significance of the to-be-retrieved stimulus.

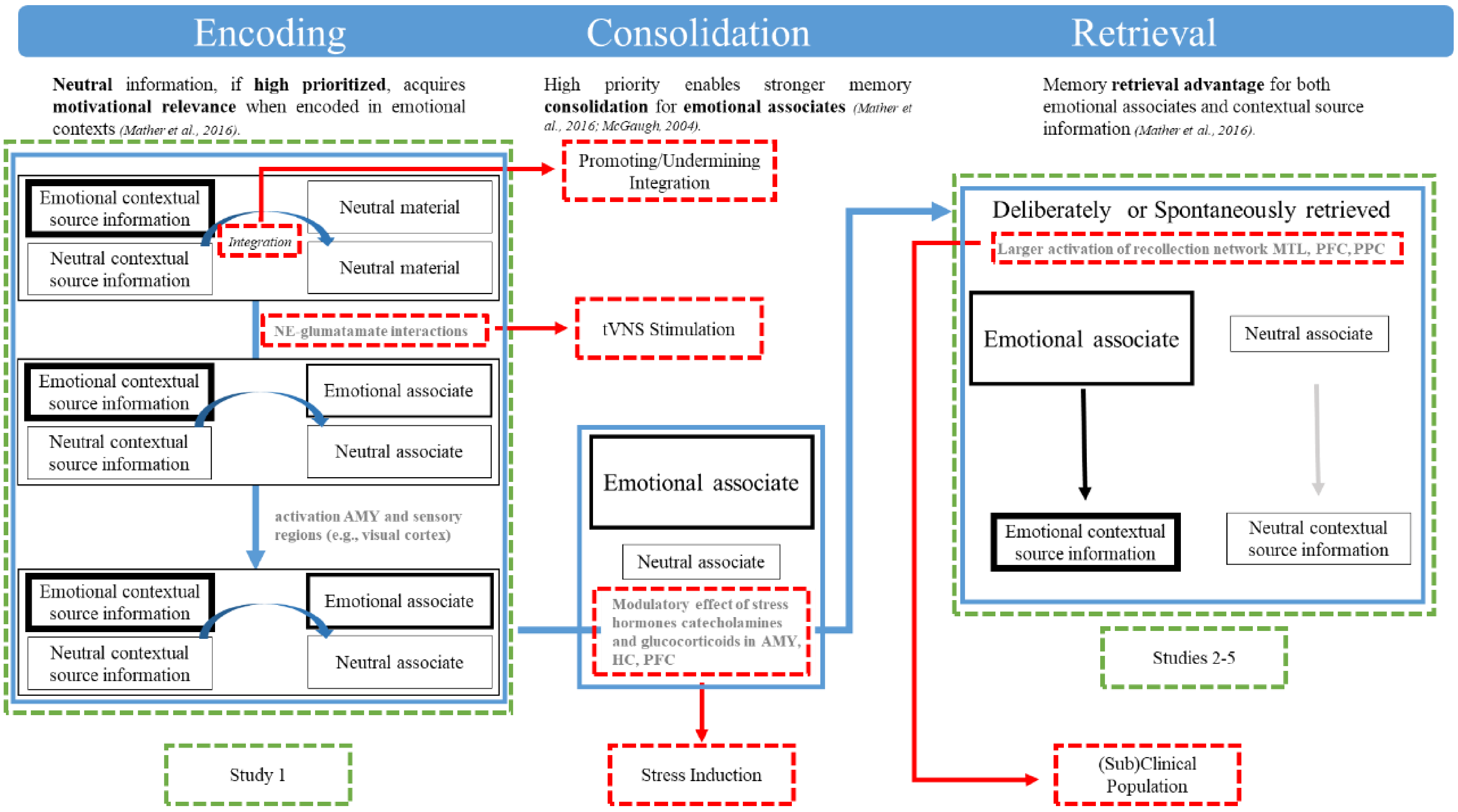
In summary, Study 5 provides behavioral and neural evidence for enhanced long-term recollection memory of emotional associates and contextual source details. Extending upon prior ERP studies (studies 2-4), Study 5 showed that the retrieval of emotional associates and contexts is related to stronger activation in regions previously associated with episodic recollection, such as the PFC, MTL and PPC. these findings suggest that, in line with episodic memory for single events, the memory enhancing effects of emotion for associated information and source details involve the engagement of bottom-up and top-down processes (Dolcos et al., 2017).

6. INTEGRATIVE SUMMARY, LIMITATIONS AND FUTURE DIRECTIONS

The present work has examined the role of emotional contexts in the initial processing and subsequent long-term retrieval of associated neutral information and source details. First, it was demonstrated that neutral information can become emotionally relevant by means of associative processes, if briefly encoded in emotional contexts (one single pair), as indicated by a rapid tuning of earlier perceptual and later, more elaborate, stages of processing (Study 1: Ventura-Bort et al., 2016a). Second, memory retrieval of neutral material deliberately integrated into a context (item memory), and of contextual source details (source memory) are enhanced if encoded in emotionally relevant contexts (Studies 2, 3 and 5: Ventura-Bort et al., 2016b; 2017, submitted), an effect evidently driven by recollection processes, indicated by greater ‘Remember' hit rates (Studies 3 and 5: Ventura-Bort et al., 2017, submitted). By using different neuroscientific techniques, it was possible to characterize the temporo-spatial features of these mnemonic effects. In line with behavioral performance, exclusively emotional associates and contextual source information showed a pronounced recollection-related, late ERP Old/New effect during explicit (Studies 2 and 3: Ventura-Bort et al., 2016; 2017) and spontaneous long-term retrieval conditions (Study 4: Ventura-Bort et al., submitted). In addition, brain areas associated with the so-called recollection network, including the MTL, PPC and PFC regions showed stronger engagement during the retrieval of emotional associates and contextual source details when compared to their neutral counterparts (Study 5: Ventura-Bort et al., submitted). Altogether, these findings show that emotional contexts produce a recollection-based memory advantage for associated neutral material and source details. This enhancement occurs independently of the demands of the task during retrieval, suggesting that it is driven by the emotional relevance of the triggering material.

In Figure 5, results from this thesis are integrated (green, dotted boxes) within the current theoretical proposals (blue, solid boxes) and future research ventures are addressed (red, dotted boxes). According to the theoretical models, emotion enhances initial processing and subsequent memory for neutral information and source details, if highly-prioritized or integrated with emotional material during encoding (Mather et al., 2016; Mather & Sutherland, 2011). The mnemonic enhancing effects are particularly pronounced after long retention intervals that facilitate consolidation processes (McGaugh, 2004). A key neuromodulator for the memory enhancing effects of emotion is NE. During encoding, emotionally relevant information facilitates the release of NE in the brain, and consequently allows for the activation of noradrenergic and glutamatergic neurons in AMY, as well as in the MTL, and PFC, increasing the neural representations of the encoded material. Additionally, catecholamine release (e.g. epinephrine and norepinephrine) takes place in the adrenal gland and feeds back to the brain via afferent paths of the vagus nerve. This vagal-mediated feedback reaches the brain shortly after the initial encoding and produces an NE release in the AMY, MTL and PFC which, in interaction with glucocorticoids, facilitates consolidation processes. Finally, the NE-mediated encoding and consolidation enhancements of emotionally relevant material result in stronger recollection-mediated, long-term memories. The results presented here give support to the existing theoretical proposals, demonstrating that, during encoding, neutral information integrated with emotional material receives prioritized processing. Moreover, after a long retention period which facilitates memory consolidation, memory retrieval is enhanced for emotional associates and source details. Despite the relevance of these results for the understanding of the mechanism underlying the enhancing effects of emotion on encoding and memory retrieval, the current findings open up new questions to be addressed in future research, namely the role of explicit object background integration, the neurobiology underlying encoding and consolidation processes, and their significance with regard to the development and maintenance of mental disorders.

It could be demonstrated that by promoting object-background integration to facilitate the generation of item/context compounds, emotion enhanced long-term memory for associated information and source details. Indeed, when such integration was not explicitly instructed, no differences were observed on the behavioural level between neutral and emotional associations (Ventura-Bort et al., 2017). However, no systematic comparisons of the effects of integration (vs. non-integration) on the modulatory effects of emotion on memory were carried out. Thus, future research should focus on directly investigating the effects of both promoting and undermining item-context binding processes between emotional and neutral information on item and source memory, in order to better delineate the predicted opposing effects.



Encoding

Neutral information, if **high prioritized**, acquires **motivational relevance** when encoded in emotional contexts *(Mather et al., 2016)*.

Consolidation

High priority enables stronger memory **consolidation** for **emotional associates** *(Mather et al., 2016; McGaugh, 2004)*.

Retrieval

Memory **retrieval advantage** for both emotional associates and contextual source information *(Mather et al., 2016)*.

Figure 5: Summary of the findings of this thesis integrated into the current theoretical models of emotional episodic memory and potential future research avenues. The blue, solid boxes represent the current theoretical models of emotional episodic memory which suggest that neutral information, if highly prioritized, acquires emotional relevance when encoded in emotional contexts. The item/context association is mediated by NE-glutamate interaction that takes place in memory-related regions, including the AMY, HC and PFC. Acquired high priority enables stronger consolidation for emotional associates due to the interaction of the stress-neuromodulators in memory-related brain regions. Consequently, during retrieval, recollection-related brain regions show stronger engagement, facilitating a more accurate and longer-lasting recognition of emotional associates and contexts. The green boxes depict the findings of the current thesis, which provide evidence for enhancing processing of emotional associates and better memory retrieval. By using ERP and fMRI evidence for the neural underpinnings and processes underlying this memory enhancing effects were further provided. The red boxes represent proposed new directions for future investigations, including the examination of the promotion/undermining of integration, the effects of transcutaneous vagus nerve stimulation (tVNS), the effects of stress, and the study of these processes in clinical and/or subclinical populations.

From a neurobiological perspective, the mechanisms underlying the enhancing effects of emotional contexts on visual processing for emotional associates have not yet been demonstrated. Although prior research suggests that NE reacting with glutamate plays an important role in these effects (Mather et al., 2016), studies systematically manipulating the effects of NE release during encoding, for instance via transcutaneous vagus nerve stimulation (tVNS; Ventura-Bort et al., 2018), may further shed light on these underlying mechanisms. Similarly, it has been shown that the interaction of NE and glucocorticoids in memory-related regions (AMY, MTL and PFC) modulate the consolidation processes of emotional episodic memories (McGaugh, 2004). Thus, studies examining the role of these neuromodulators may also bring more insights into the neurobiological architecture of these processes for emotional associates and contextual information. One possible approach to investigate this may require the usage of well-established stress-induction paradigms that have been proven to reliably increase the release of NE and glucocorticoids (Schwabe & Schächinger, 2018) and modulate the consolidation of emotional memories (Wirkner, Weymar, Löw, & Hamm, 2013).

The retrieval of past events and the surrounding contextual information, although it could be adaptive for survival (Dolcos et al., 2005), might bring back emotional and motivational states that could facilitate the development and/or maintenance of clinical conditions in some instances, such as stress and trauma-related disorders and addiction (Dolcos, 2013; Ehlers & Clark, 2000; Robinson & Berridge, 1993), when source details are bound to traumatic events or to impulsive behaviour. Thus, from a clinical perspective, future investigations translating the current research to clinical scopes by, for instance, examining the retrieval processes of individuals showing high symptomatology severity, may help elucidate upon the (mal)functioning of neural mechanisms associated with certain disorders.

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8. APPENDIX A: MANUSCRIPTS

Manuscript 1: Ventura-Bort, C., Löw, A., Wendt, J., Dolcos, F., Hamm, A. O., & Weymar, M. (2016). When neutral turns significant: Brain dynamics of rapidly formed associations between neutral stimuli and emotional contexts. *European Journal of Neuroscience, 44*, 2176–2183. https://doi.org/10.1111/ejn.13319

Manuscript 2: Ventura-Bort, C., Löw, A., Wendt, J., Moltó, J., Poy, R., Dolcos, F., Hamm, A. O., & Weymar, M. (2016b). Binding neutral information to emotional contexts: Brain dynamics of long-term recognition memory. *Cognitive, Affective and Behavioral Neuroscience* (Vol. 16). https://doi.org/10.3758/s13415-015-0385-0

Manuscript 3: Ventura-Bort, C., Dolcos, F., Wendt, J., Wirkner, J., Hamm, A. O., & Weymar, M. (2017). Item and source memory for emotional associates is mediated by different retrieval processes. *Neuropsychologia*, (December), 0–1. https://doi.org/10.1016/j.neuropsychologia.2017.12.015

Manuscript 4: Ventura-Bort, C., Wirkner, J., Dolcos, F., Wendt, J., Hamm, A. O., & Weymar, M. (submitted). Enhanced spontaneous retrieval of cues from emotional events: An ERP study.

Manuscript 5: Ventura-Bort, C., Wendt, J., Wirkner, J., König, J., Lotze, M., Hamm, A. O., Dolcos, F., & Weymar, M. (submitted) Neural substrates of long-term item and source memory for emotional associates: an fMRI study

8.1. MANUSCRIPT 1

When neutral turns significant: brain dynamics of rapidly formed associations between neutral stimuli and emotional contexts

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CVB, FD, MW and AOH design the experiment. CVB and MW supervised the data acquisition. CVB analyzed the data and provided the first draft of the manuscript. All authors contributed to the interpretation of the data and wrote the manuscript.

When Neutral Turns Significant: Brain dynamics of rapidly formed associations between neutral stimuli and emotional contexts

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Abstract

The ability to associate neutral stimuli with motivationally relevant outcomes is an important survival strategy. In the present study, we used event-related potentials (ERPs) to investigate brain dynamics of associative emotional learning when participants were confronted with multiple heterogeneous information. Participants viewed 144 different objects in the context of 144 different emotional and neutral background scenes. During each trial, neutral objects were shown in isolation and then paired with the background scene. All pairings were presented twice to compare event-related potentials (ERPs) in response to neutral objects before and after single association. After single pairing, neutral objects previously encoded in the context of emotional scenes evoked a larger P100 over occipital electrodes compared to objects that were previously paired with neutral scenes. Likewise, larger late positive potentials (LPP) were observed over parieto-occipital electrodes (450-750 ms) for objects previously associated with emotional relative to neutral contexts. The LPP — but not P100 — enhancement was also related to subjective object/context binding. Taken together, our ERP data provide evidence for fast emotional associative learning, as reflected by heightened perceptual and sustained elaborative processing for neutral information previously encountered in emotional contexts. These findings could assist in understanding binding mechanisms in stress and anxiety, as well as in addiction and eating-related disorders.

Introduction

One important survival strategy is to perceive fluctuating changes that occur in contiguous environments in order to readjust the momentary motivational relevance of incoming information. This ability allows developing flexible and adaptive responses based on the history of contingencies encountered by the individual (Miskovic & Keil, 2012). In this sense, it has been observed that a previously neutral stimulus (conditioned stimulus; CS+) continuously associated with an aversive event (unconditioned stimulus; UCS) acquires motivational relevance, compared to a neutral stimulus (CS-) unpaired with a UCS or associated with a non-emotional UCS, a process called associative learning. Traditionally, a large number of pairings between few and/or simple CS+ and a strongly aversive UCS have been used in learning paradigms to generate strong associations (Lissek et al., 2006). However, rather than single, unambiguous, and/or isolated CS/UCS pairings, we are constantly confronted with multiple different events that imply associations between neutral and moderately relevant stimuli. Thus, the use of paradigms involving “weak” ambiguous situations (e.g., less salient UCS, multiple complex pairings and/or few contingencies CS/UCS) would provide a better understanding of the underpinnings of associative learning (Beckers et al., 2012; Hur et al., 2016; Lissek et al., 2006; Steinberg, et al., 2013b). In the present study, we investigated the role of UCS heterogeneity on the formation of associations using electrophysiological correlates of associative learning for multiple neutral events paired with multiple emotional contingencies (emotional scenes).

Recent studies from Junghöfer and colleagues (e.g., Pastor et al., 2015; see for review, Steinberg et al., 2013b) used the so-called MultiCS conditioning, in which multiple CSs+ (e.g., pictures of different faces) were associated with emotionally relevant UCSs (e.g., aversive and appetitive sounds, electric shocks), while other CSs- remained unpaired or were associated with neutral events. Brain activation was measured using electro- and magnetoencephalography

(EEG, MEG) during these conditioning procedures. After multiple pairings, CSs+ compared to CSs- evoked enhanced neural activity at prefrontal and sensory cortical regions during earlier (<300ms; Bröckelmann et al., 2011; Rehbein et al., 2014, 2015; Steinberg et al., 2012, 2013a) and later stages of processing (>300ms; Pastor et al., 2015), irrespective of contingency awareness. These results suggest the existence of a rather automatic learning mechanism that rapidly transfers the emotional properties of the UCS to CSs, leading to a facilitated perceptual and a more elaborated processing of the CS+.

Nevertheless, these studies have only used highly salient UCS. Therefore, it is unclear whether such associative learning processes also occur in the presence of less intense emotional events — e.g., reproducing daily interactions — or whether the formation of associations is exclusively facilitated in survival-specific contexts (Ohman & Mineka, 2001). It is also unclear whether the acquired motivational significance leading to neural response enhancement for emotion-associated stimuli occurs rapidly after one single pairing (e.g., Morel et al., 2012; Rehbein et al., 2014), or whether more than one repetition is needed to form such associations (e.g., Steinberg et al., 2012). While most of the electrophysiological conditioning studies have used aversive cues as UCS (see for review Miskovic & Keil, 2012), it has recently been observed that pleasant information can also serve as effective, intrinsically motivating UCSs (Blechert et al., 2016; Schacht et al., 2012; Steinberg et al., 2013a; see for neuroimaging findings: Martin-Soelch et al., 2007). Both, aversive and appetitive conditioning processes likely contribute to various disorders, such as trauma-and stress-related disorders, but also to substance abuse and eating-related disorders (e.g., Martin-Soelch et al., 2007; Pape & Pare, 2010). Thus, more evidence regarding the effect of valence on associative conditioning is needed.

In the present study, we therefore investigated brain dynamics of associative emotional learning when participants viewed neutral objects in the context of different emotionally arousing (both pleasant and unpleasant) and neutral background scenes. Object and scene presentation occurred always in the same order: first objects were presented in isolation (CS), and then a picture scene was added as background (see Figure 1). Pairings were presented in two consecutive blocks, allowing to compare the processing of CS+ objects — paired with emotional scenes — and CS- objects — paired with neutral scenes, *before* (first block) and *after* single pairing (second block). Based on previous EEG and MEG conditioning studies (see for review, Miskovic & Keil, 2012), we predicted enhanced processing of neutral cues previously paired with emotional contexts, irrespective of valence, relative to cues previously paired with neutral contexts at different stages of processing. Because both perceptual and sustained elaborative processing have been found to be enhanced for stimuli associated with CS+, we predicted enhanced positivity for the CS+ compared with the CS- at (a) earlier (P100), and (b) later stages of processing (late positive potential [LPP]).

Materials and Methods

Participants

Thirty-one students (27 women, 4 men; mean age = 22.7 years; 3 left-handed) from the University of Greifswald participated in the study for course credits or financial compensation. All participants had normal or corrected-to-normal vision, and provided written informed consent for a protocol approved by the Review Board of the German Psychological Society (DGPs). Data from 6 participants were excluded due to software problems (1 participant) or excessive artifacts in the EEG data (5 participants).

Stimulus Materials

Overall, 288 neutral objects (CSs) together with 96 emotionally arousing (UCSs) and 48 neutral background scenes were used as stimulus material. Neutral objects were selected from two different standardized sets: *The Bank of Standardized Stimuli* (BOSS; Brodeur et al., 2010), and the *ecological adaptation of Snodgrass and Vanderwart* (Moreno-Martínez, & Montoro, 2012). In order to assure variability between multiple CSs, objects were selected to belong to different semantic categories (e.g., office supplies, electronics, household objects). Objects were grouped in six different sets of 48 items each, carefully matched in terms of semantic category, familiarity, object agreement, and manipulability according to the normative ratings of the standard samples (see BOSS and ecological adaptation of Snodgrass and Vanderwart norms). Each participant viewed three (out of six) different sets, consisting of a total of 144 neutral objects. Half of the neutral objects (144) were used in a recognition memory task that occurred one week later (published elsewhere, see Ventura-Bort et al., 2016). One hundred and forty-four background scenes — 48 pleasant, 48 neutral, and 48 unpleasant — were selected from the *International Affective Picture System* (IAPS; Lang et al., 2008) as UCS. To ensure the heterogeneity between the UCSs, the pictures were carefully selected to include different contents. Specifically, the pleasant category comprised pictures of erotica, adventure, and nurturance contents; the neutral category contained pictures of buildings, landscapes, and neutral human faces; and the unpleasant category included pictures showing mutilation, attack, and disgust/accident. Mean (SD) valence and arousal ratings were 6.94 (0.63) and 5.84 (0.77) for pleasant; 5.27 (0.82) and 3.51 (0.57), for neutral; and 2.73 (0.85) and 5.93 (0.57) for unpleasant pictures. Pleasant and unpleasant pictures did not differ in emotional arousal ($F< 1$). All pictures were matched for complexity, brightness, and contrast (all *p*s >.23). Object sets were counterbalanced across participants, so that each set was paired with each emotional picture category equally often.

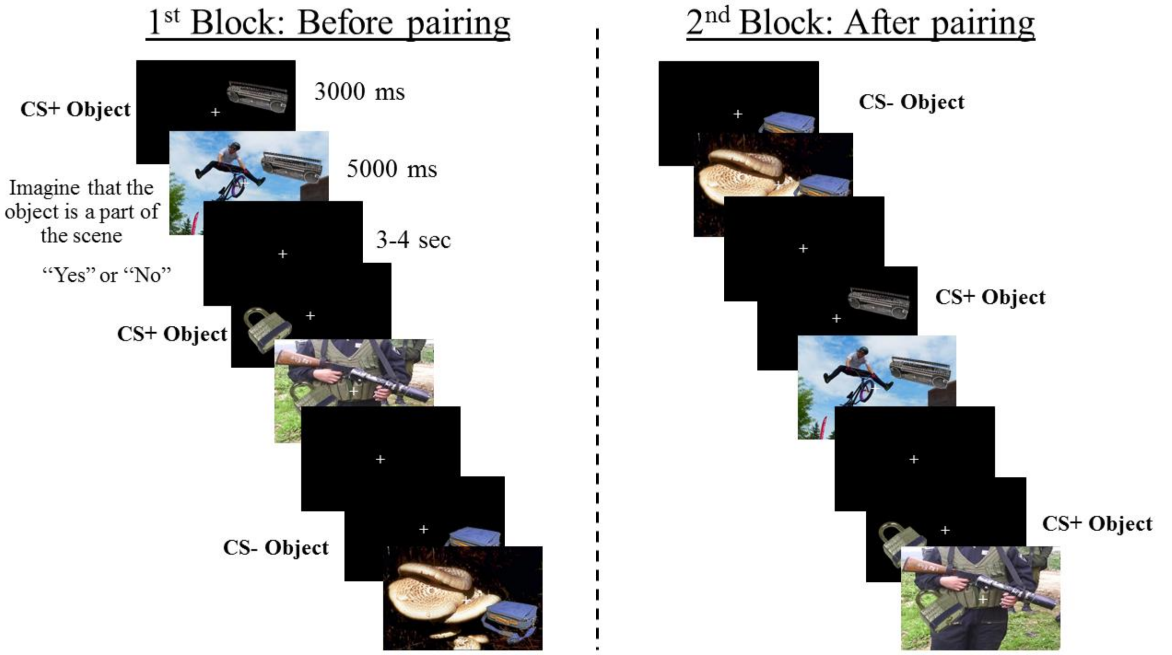

Figure 1. Schematic view of the stimulus presentation during first and the second associative learning blocks. When an object was seen during the first block, the object/background association has not yet taken place, and when the object was seen in the second block, object and background scene have been associated once.

Procedure

The experiment took place in a sound-attenuated, dimly lit room. After electrodes were attached, participants were seated in a reclining chair and were instructed to avoid eye blinks and body movements during ERP measurement. The session consisted of two blocks in which 144 different neutral CS objects were presented superimposed on 144 different background scenes. Each CS was first presented alone for 3000 ms in one of the four quadrants of a blank screen. The four positions of the CS were selected randomly and with the same probability for each background scene category. Then, while the CS remained on the screen, the UCS was added as background. Each CS/UCS pairing was presented for 5000 ms. Inter-trial intervals (ITIs) were 3000, 3500 or 4000 ms. One of the 48-objects set (CS+) was paired with an unpleasant UCS, one set (CS+) with a pleasant UCS, and one set (CS-) with a neutral scene (i.e., no motivationally relevant UCS was presented). Sets were counterbalanced across participants. To facilitate CS/UCS associative binding, participants were instructed to imagine that the object was a part of the scene and to indicate after CS/UCS offset whether the imagination was successful or not by pressing a “yes” or a “no” button on a response pad (see Figure 1). Finally, all 96 CS/UCS pairings and all 48 CS/neutral pairs were presented in a first block and, after one minute break, the same 144 CS and UCS/neutral scenes were repeated in a second block, but in a different randomized order.

Apparatus and Data Analysis

EEG signals were recorded continuously from 257 electrodes using an Electrical Geodesics (EGI) HydroCel high-density EEG system with NetStation software (4.3.1) and a NA 300 amplifier on a Macintosh computer. The EEG recording was digitized at a rate of 250 Hz, using vertex sensor (Cz) as recording reference. Scalp impedance for each sensor was kept below 30 kΩ, as recommended by manufacturer guidelines. All channels were band-pass filtered online from 0.1 to 100 Hz. Offline reduction was performed using Electro-Magnetic-

EncephaloGraphy Software (EMEGS; Peyk et al., 2011) and included lowpass filtering at 40 Hz, artifact detection, sensor interpolation, baseline correction, and conversion to the average reference (Junghöfer et al., 2000). Stimulus-synchronized epochs were extracted from 100 ms prior to 1200 ms after onset of the object and baseline corrected (100 ms prior to stimulus onset). Each extracted epoch was corrected for eye movement and blink artifacts using the MATLAB-based toolbox BioSig (Vidaurre et al., 2011).

For each participant, separated ERP averages were computed for each sensor and condition. Based on previous research (Liu et al., 2012b; Pastor et al., 2015; Pizzagalli et al., 2003; Schacht et al., 2012), two ERP components were analyzed: the P100 component, as an index of early perceptual processing (Liu et al., 2012b; Pizzagalli et al., 2003; Schacht et al., 2012) and the LPP considered as an index of motivationally-driven, sustained attentional processing (Bradley, 2009; Ferrari et al., 2008; Heim & Keil, 2006; Pastor et al., 2015; Pizzagalli et al., 2003; Schupp et al., 2000). For the P100, ERP mean amplitudes were averaged over lateral occipital brain regions that encompassed the EGI sensors 95, 96, 104, 105, 106, 107,113, 114, 115, 122 (left), and 159, 160, 167, 168, 169, 170, 176, 177, 178, 189 (right; see inset Figure 2A). To determine the time window, we identified the maximum P1-peak latency (162 ms) based on the overall grand average across conditions and defined a symmetrical time epoch from 140 to 184 ms for subsequent analysis. For the LPP, mean ERP amplitudes were analyzed over a cluster of parieto-occipital sensors (EGI sensors: 85, 86, 87, 88, 89, 96, 97, 98, 99, 100, 101, 106, 107, 108, 109, 110, 118, 119, 127, 128, 129, 130, 140, 141, 142, 151, 152, 153, 160, 161, 162, 169, 170, and 171; see inset Figure 3A). Due to the difficulty to extract a maximum peak for the LPP (Schupp et al., 2000), a 450-750 ms time window was selected for the LPP based on previous literature and visual inspection of the waveforms.

To investigate the emotion’s role in subjective object/context binding, we also compared responses rates of successful object/context imaginations. Response rates were analyzed using a repeated-measures ANOVA including the within-subjects factors *Block* (First block vs. Second block) and *Category* (Pleasant vs. Neutral vs. Unpleasant).

To determine associative learning, we compared ERPs in response to CS objects in the first block, relative to ERP responses to CS objects in the second block. Therefore, mean ERP data were analyzed using a repeated-measures ANOVA including the within-subjects factors *Block* (First block vs. Second block) and *Category* (Pleasant vs. Neutral vs. Unpleasant). When no significant *Block* x *Category* interaction was observed, additional exploratory analyses were performed collapsing both emotional picture categories together into one *Emotional* category. Then, a repeated-measures ANOVA was conducted including the within-subjects factors *Block* and *Emotion* (Neutral vs. Emotional). The factor *Laterality* (Left vs. Right) was added as a further within-subjects factor for the P100 component.

Finally, a correlation analysis was performed to determine possible relations between ERP and behavioral data. Therefore, subjective object/context imagination (CS/UCS; CS/neutral scene) was correlated with the mean amplitudes of the P100 and LPP.

Results

Behavioral Data

Analyses revealed a main effect of *Block* ($F[1, 24] = 4.29$, $p = .049$, $\eta_p^2=.15$) and *Category* ($F[2, 48] = 16.46$, $p < .0001$, $\eta_p^2=.4$), but there was no interaction *Block* x *Category* ($F[2, 48] = 1.12$, $p = 33$, $\eta_p^2=.04$). Post-hoc comparisons revealed that subjective object/context imagination was less successful in aversive CS+ (mean = .74) compared to appetitive CS+ (mean = .86): $t(24) = 5.79$, $p < .0001$, $d =1.15$; and CS- (mean = .88): $t(24) = 5.12$, $p < .0001$, $d =1.02$. No differences were observed between appetitive CS+ and CS- ($t[24] = 1.37$, $p < .18$, $d = 0.27$).

ERP Data

P100 (140-184 ms). Figure 2A illustrates grand-averaged ERPs collapsed across the occipital cluster for objects paired with emotional backgrounds (CS+ objects) and objects paired with neutral backgrounds (CS- objects) during the first and the second block.

A main effect of *Block* ($F[1, 24] = 5.71$, $p = .03$, $\eta_p^2=0.19$) and *Category* were observed: $F(2, 48) = 5.35$, $p = .008$, $\eta_p^2=.19$. Although, the interaction *Block* x *Category* did not reach significance ($F[2, 48] = 1.99$, $p = .15$, $\eta_p^2=0.08$), a significant quadratic trend was observed ($F[1, 24] = 4.59$, $p = .043$, $\eta_p^2=0.16$), suggesting that the activity for appetitive and aversive CS+ increased in the second block compared to CS- objects. Neither a main effect of *Laterality* ($F< 1$, $p> .36$) nor other interaction effects were found (Fs<1, ps> .42). Post-hoc comparisons revealed that both CS+ objects, relative to CS- objects prompted a larger P100 in the second block (objects paired with pleasant scenes vs. objects paired with neutral scenes: $t[24] = 3.04$, $p = .006$, $d = 0.61$; objects paired with unpleasant scenes vs. objects paired with neutral scenes: $t[24] = 3.31$, $p = .003$, $d = 0.66$; see Figure 2B), but not in the first block (ts< 1, ps> .45). No differences were observed between the appetitive and aversive CS+ objects during the second block (*t*< 1, *p*> .61).

When pleasant and unpleasant objects were collapsed into an *Emotional* category, statistical analyses showed a main effect of *Emotion*, indicating a larger P100 for those objects associated with emotional background scenes (CS+) compared to objects paired with neutral scenes (CS-; *Emotion: F*[1, 24] = 8.16, *p* = .009, η_p^2= 0.25). Critically for demonstrating an associative learning process, this effect was driven by CS+/CS- differences during the second block, supported by an interaction between *Block* and *Emotion* (*F*[1, 24] = 4.58, *p* = .043, η_p^2 = 0.16). Neither the main effect of *Block* (*F*[1, 24] = 2.47, *p* = .13, η_p^2 = 0.1) nor *Laterality* (*F*<1, *p*> .5) reached significance. No other interaction effects were found (*F*s<1, *p*s>.44). Follow-up comparisons confirmed that CS+ items prompted a larger positivity in the second compared to the first block (*t*[24] = 3.04, *p* = .006, *d* = 0.61). Moreover, CS+ objects presented in the second block also elicited an enhanced P100 in comparison to CS- objects presented in the first (*t*[24] = 2.95, *p* = .007, *d* = 0.6), and in the second block (*t*[24] = 3.77, *p* = .001, *d* = 0.75; See Figure 2C). No ERP differences were found between blocks for CS- objects, or between CS- and CS+ objects during the first block (*t*s< 1, *p*s> .34).

In sum, we found that single pairing of neutral information with emotional experience modulates subsequent early visual processing when encountering this stimulus again.

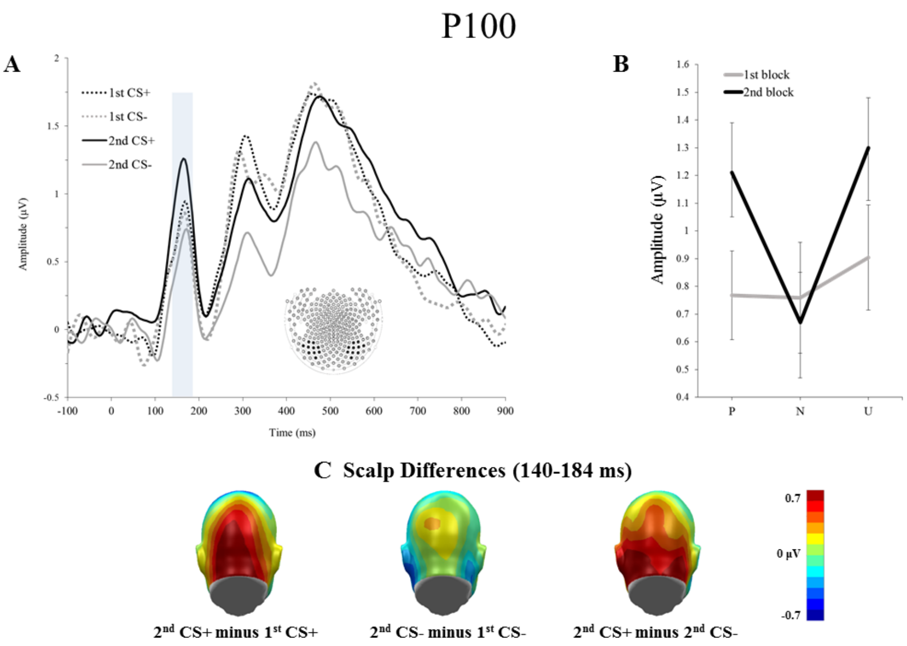

Figure 2: Objects encoded in emotional contexts modulate early visual processing (P100). A: Grand average ERPs prompted by CS+ objects (black lines) and CS- Objects (grey lines) presented during the first (dotted lines) and the second block (thick lines). ERPs were averaged across channels within a specific occipital cluster (see inset). B: Mean (standard error) ERPs collapsed across lateralized clusters during the 140-184 ms for CS+ objects previously paired with pleasant images (P), CS- objects paired with neutral images (N), and CS+ objects associated with unpleasant images (U). C: Display of the scalp topographies for the ERP differences during the 140-184 ms time window between first and second block for CS+ (left) and CS- (middle) objects, and between CS+ and CS- objects during the second block (right).

LPP (450-750 ms). Figure 3A illustrates grand average ERPs extracted from parieto-occipital regions for CS+ and CS- objects during the first and the second block.

Analyses showed a main effect of *Block* ($F[1,24] = 7.92$, $p = .01$, $\eta_p^2 = .25$), and *Category* ($F[2,48] = 4.88$, $p = .02$, $\eta_p^2 = .18$). Moreover, The interaction *Block x Category* approached significance: $F(2, 48) = 2.51$, $p = .09$, $\eta_p^2 = .1$, showing a significant quadratic trend ($F[1, 24] = 4.74$, $p = .039$, $\eta_p^2 = .17$) that suggests that the activity for appetitive and aversive CS+ objects increased in the second block compared to CS- objects. Post-hoc comparisons showed that both objects bound with pleasant and unpleasant relative to neutral background scenes elicited an enhanced LPP after the first pairing (objects paired with pleasant scenes vs. objects paired with neutral scenes: $t[24] = 2.51$, $p = .02$, $d = 0.5$; objects paired with unpleasant scenes vs. objects paired with neutral scenes: $t[24] = 3.31$, $p = .003$, $d = 0.66$; see Figure 3B), but not before the pairing (ts< 1, ps> .45). No differences were observed between objects associated with unpleasant and pleasant scenes during the second block ($t[24] = 1.27$, $p= .23$, $d= 0.25$).

After collapsing pleasant and unpleasant CS+ into an *Emotional* category, a trend main effect for the factor *Block* ($F[1,24] = 3.73$, $p = .07$, $\eta_p^2 = .13$), and a main effect of the factor *Emotion* ($F[1,24] = 7.96$, $p = .009$, $\eta_p^2 =.25$) were observed. As for the P100, larger ERP positivity was present for CS+, compared to CS- after single pairing with UCS as indicated by the *Block* x *Emotion* interaction ($F[1,24] = 4.74$, $p = .04$, $\eta_p^2 = .17$). Single comparisons revealed that, CS+ items evoked a significantly larger ERP activity in the second compared to the first block ($t[24] = 3.75$, $p = .001$, $d = .75$). Larger ERP positivity was also observed for CS+ relative to CS- objects during both the first ($t[24] = 3.35$, $p = .003$, $d = .66$), and the second block ($t[24] = 3.36$, $p = .007$, $d = .67$; see Figure 3C). No differences were found between CS+ and CS- objects during the first block, or between the first and the second block for CS- objects (ts< 1, ps> .69).

To summarize, neutral information from emotional, but not neutral, contexts prompt elaborative processing as indicated by enhanced late positive potentials.

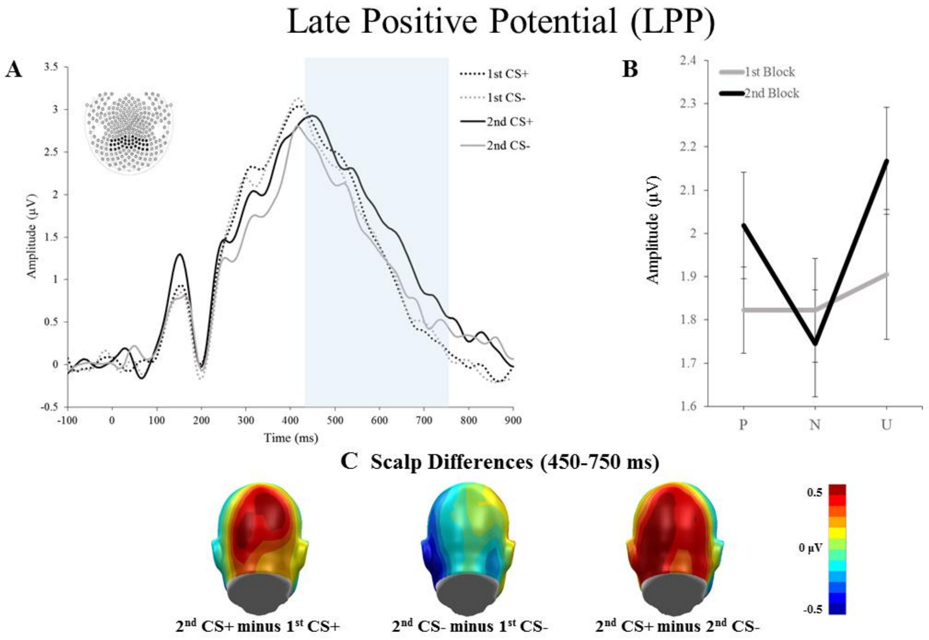

Figure 3: Objects from emotional contexts prompt larger late positive potentials (LPPs) indicating motivational relevance. A: Grand average ERPs prompted by CS+ objects (black lines) and CS- Objects (grey lines) presented during the first (dotted lines) and the second block (thick lines). ERPs were averaged across channels within a specific parieto-occipital cluster (see inset). B: Mean (standard error) ERPs collapsed across electrodes during the 450-750 ms for CS+ objects from pleasant contexts (P), CS- objects from neutral contexts (N), and CS+ objects from unpleasant contexts (U). C: Display of the scalp topographies for the ERP differences during the 450-750 ms time window between first and second block for CS+ (left) and CS- (middle) objects, and between CS+ and CS- objects during the second block (right).

Correlation between subjective object/context association (CS/UCS) and ERPs.

Correlational analyses showed a positive relation between successful object/context imagination rates during the first block and LPP activity during the second block for both objects bound with neutral ($r_s = .42$, $p = .04$) and emotional ($r_s = .64$, $p = .0005$) contexts. Furthermore, a significant correlation between LPP amplitudes for objects bound with emotional contexts and successful object/context imagination rates in the second block was found ($r_s = .42$, $p = .03$). This relation was not found for objects paired with neutral backgrounds ($r_s = .07$, $p = .71$). No significant correlations were found between behavioral performance and P100 amplitudes (r_ss $< .24$, $p < 24$).

In sum, successful subjective object/context binding was related to larger LPP — but not P100 — amplitudes. LPP amplitudes were associated with better subjective object/context association when the context was emotional.

Discussion

In the present study, brain potentials were used to investigate neural processing when multiple neutral objects were associated with either emotional or neutral background scenes. Our results showed that, (a) after a single pairing with an emotional event, neutral CS+ objects compared to objects paired with neutral events (CS-) evoked an enhanced positivity (P100) at occipital regions in the 140-184 ms time window. These differences in ERP positivity can be interpreted as a result of an associative learning process because they were not present prior to the initial pairing (first block). Likewise, (b) objects paired with emotionally arousing scenes, compared to objects paired with neutral scenes, elicited a larger LPP at parieto-occipital electrodes between 450 and 750 ms after stimulus onset. The LPP enhancement was also related to better subjective context/item binding. Our data provide evidence for rapid item/context learning (i.e., after one pairing), as reflected by enhanced perceptual and sustained elaborated processing for items from emotional contexts.

The P100 component is assumed to indicate amplification of sensory visual information, reflecting perceptual processing in the extrastriate visual cortex (Clark et al., 1995; Di Russo et al., 2002). Some studies have observed enhanced P100 amplitudes for emotional compared to neutral visual stimuli (e.g., Carretié et al., 2004; Pourtois et al., 2005; Rellecke et al., 2011), suggesting that perceptual attentional resources may be allocated towards emotionally, arousing events, via amygdala projections (Rotshtein et al., 2010). Learning studies also showed that conditioned visual stimuli associated with positive (Schacht et al., 2012) or negative UCS evoke more pronounced P100 ERP (Fritsch & Kuschinke, 2013; Pizzagalli et al., 2003) and electromagnetic field activation (Dolan et al., 2006; Steinberg et al., 2012, 2013a), reflecting activity in visual-related areas (Dolan et al., 2006; Pizzagalli et al., 2003). Enhanced perceptual activation for emotionally conditioned events has been attributed to the learning history of the individual that tunes the sensitivity of sensory neural populations to specific emotional features by means of re-shaping the processing of incoming sensory information (Miskovic and Keil, 2012; Steinberg et al., 2013b). Some studies suggest that the short-term neural reorganization in sensory-related regions occurs after several associations (Hintze et al., 2014; Keil et al., 2007; Stolarova et al., 2006). Recent research using MultiCS paradigms, however, found that CS+ could also produce changes in visual- and auditory-related areas in a very fast fashion — i.e., after few or single associations (Bröckelmann et al., 2011; Steinberg et al., 2012; Rehbein et al., 2014). The present study extends these findings showing that one single association between neutral objects and relatively weak UCSs (images) is enough to readjust the visual processing of relevant information based on a rapid update of its motivational value, evoking enhanced P100 amplitudes in response to neutral cues bound to or associated with emotional contexts.

In addition, CS+ objects also evoked a larger positive-going waveform over parieto-occipital electrodes between 450 and 750 ms, relative to the CS- objects. This later component corresponds to the LPP and extends previous findings using aversive (Pizzagalli et al., 2003) and appetitive UCSs (Blechert et al., 2016; Schacht et al., 2012), and multiple CS/UCS pairings (Pastor et al., 2015). Enhanced LPP during encoding of motivationally significant — appetitive and aversive — stimuli is a hallmark finding in affective neuroscience (Cuthbert et al., 2000; Foti et al., 2009; Schupp et al., 2000). In the current study, we found similar ERP positivity for neutral objects paired with emotional scenes as consistently found for emotional images[2]. While enhanced LPPs to emotional scenes have been reliably found over central-parietal areas (Cuthbert et al., 2000), which may represent aggregated activity from ventral, dorsal and occipital visual cortex (e.g., Sabatinelli et al., 2013), the current study showed a more posterior distribution of the enhanced LPP, which is likely due to the involvement of occipito-temporal regions in contextual object-processing (Bar, 2004). Because LPPs are related to initial orienting, sustained perceptual processing, and motivated actions (Bradley, 2009; Lang & Bradley, 2010), our data suggest that objects associated with both appetitive and aversive scenes received sustained elaborated processing due to the acquired motivational relevance.

In a recent study, Mueller & Pizzagalli (2016) demonstrated that rapid perceptual enhancement for fear-conditioned events could occur when conditioning acquisition took place in a remote past. These authors observed that CS+ faces produced enhanced early ERP activity one year after the CS/UCS association, suggesting that associative learning processes can produce long-lasting changes, even when participants were fully-unaware of the CS/UCS contingency. In another study, Dolcos and Cabeza (2002) observed that enhanced elaborated processing during encoding, as indexed by LPP amplitude, predicted better long-term memory performance for emotional information. In line with this, we have recently observed that objects paired with emotional, relative to neutral contexts, elicited enhanced electrophysiological correlates implicated in mnemonic retrieval processing (Ventura-Bort et al., 2016). The present study, thus, indicate that faster enhanced perceptual and elaborative processes of neutral information bound to emotional compared to neutral contexts might also promote memory storage (Dolcos & Cabeza, 2002; Weymar et al., 2012; Ventura-Bort et al., 2016).

Human brain imaging studies (Vuilleumier et al., 2004; Vuilleumier & Driver, 2007; Wendt et al. 2011) have observed that the amygdala plays an important role in the processing of stimulus salience (e.g., Adolphs, 2010; Weymar & Schwabe, 2016). Moreover, there are strong associations between high cortical areas, and the amygdala (e.g., Sabatinelli et al., 2005, 2014; Liu et al., 2012a), suggesting that the affective evaluation of visual stimulation results from re-entrant projections between subcortical and cortical brain regions (Pessoa & Adolphs, 2010; Vuilleumier, 2005). It has been proposed that the amygdala is responsible of identifying the conditioned stimuli as emotionally relevant and providing ongoing feedback to higher cortical brain regions such as inferotemporal, occipital, and prefrontal cortex (Keil et al., 2009; Liu et al., 2012a; Sabatinelli et al., 2009, 2014) that give rise to a cascade of perceptual, attentional and action preparation processes (Lang & Bradley, 2010). Substantiating this view, using simultaneous EEG-fMRI recording, Liu and colleagues (2012a) demonstrated that the amygdala activity modulates the LPP amplitude for emotional stimuli. In the present study, we observed that the encoding of conditioned stimuli was modulated after one pairing with an emotional background scene, which can be mediated by such re-entrant influences from the amygdala.

Taken together, the present findings provide evidence for fast emotional learning when emotional contexts and neutral cues are present. Neutral objects paired with emotional relative to neutral scenes rapidly acquired motivational relevance, engaging heightened perceptual and attentional processes, as indexed by enhanced P100 and LPP amplitudes. On the one hand, the ability to rapidly processing changes for stimuli that signal motivationally significant events may facilitate the detection of relevant information, and the execution of fast motivational responses (Lang et al., 1997), when encountered in the future. On the other hand, however, such cues might also become maladaptive when bound to traumatic memories, by their ability not only to grab attention but also to activate the traumatic memory including exaggerated fear responses. In the same vein, appetitive cues linked to addiction- and food-related contexts are able to prompt impulsive consuming behaviors.

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Conflict of Interest

The authors declare no competing financial interests.

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Footnote

[1] P100 latency was relatively high (140-184 ms), compared to previous studies (e.g., Pizzagalli et al., 2003: 84-152 ms; Schacht et al., 2012: 136-164 ms; Rotshtein et al., 2010: 100-150 ms). To elucidate the timing of the P100 evoked by the objects, we also extracted the P100 latency for the background scenes. For scenes, the P100 peaked earlier than for objects (136 ms and 162 ms, respectively). One likely explanation for this P100 latency difference could be the stimulus location on the screen. That is, there is evidence showing that the P100 latency is affected by the eccentricity of the stimuli (Busch et al., 2004). Busch et al. (2004) observed that the P100 latency for objects located peripherally was higher compared to stimuli presented in the center of the screen. In the present study, the background scenes were presented full-screen and, therefore, centered on the monitor, whereas the objects were peripherally located in one of the four quadrants of the screen. Another factor that might contribute to the latency difference is the continuous change of the stimulus location. Specifically, it has been observed that variation of the location affects the latency of the brain activation from very early stages of processing (Isik et al., 2013). Here, in contrast to the scenes, which were always presented underneath the objects, object presentation was randomized and, therefore, the location of the upcoming object was always unpredictable. Thus, it could be that these two differences delayed the latency of the P100 for the objects.

[2] To confirm that the LPP component elicited by CS+ objects was comparable to the LPP generated by intrinsically visual relevant stimuli, we assessed the LPP emotional effects generated by the background scenes (neutral vs. emotional), using the same cluster and time window as for CS objects. For this analysis, the mean ERPs elicited by the neutral and emotional images were entered into a repeated-measure ANOVA with *Emotion* and *Block* as within subject factors. Results showed a trend effect of *Block* ($F[1,24] = 3.4$, $p = .08$, $\eta_p^2 = .12$), and a clear effect of *Emotion* ($F[1,24] = 10.32$, $p = .004$ $\eta_p^2 = .30$), emotional scenes eliciting

larger LPP amplitudes than neutral background scenes ($M\underline{\Delta}$ =.33). No *Emotion* X *Block* interaction was observed ($F < 1$, $p > .7$).

We also analyzed the Early Posterior Negativity (EPN) elicited by the background scenes. The EPN is a well-known ERP observed between 150 and 300 ms after stimulus onset on posterior sites that is modulated by emotionality (e.g., Schupp et al., 2003). Results showed a clear main effect of *Emotion* ($F[1,24] = 7,12$, $p = .015$, $\eta_p^2 = .23$), indicating that emotional background scenes evoked more negative EPN amplitudes than neutral images ($M\underline{\Delta} = -.38$), in line with previous studies. No effect of *Block*, or interaction were observed (Fs<1, ps> .43).

8.2. MANUSCRIPT 2

Binding neutral information to emotional contexts: Brain dynamics of long-term recognition memory.

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CVB, FD, MW and AOH design the experiment. CVB and MW supervised the data acquisition. CVB analyzed the data and provided the first draft of the manuscript. All authors contributed to the interpretation of the data and wrote the manuscript.

Binding Neutral Information to Emotional Contexts: Brain Dynamics of Long-Term Recognition Memory

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Running head: Long-term emotional relational memory

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Keywords: Event-related potentials, ERPs, Emotion, Context, Relational memory, Associative memory, Old/New effect, Recognition

Abstract

There is abundant evidence in memory research that emotional stimuli are better remembered than neutral stimuli. However, effects of an emotionally charged context on memory for associated neutral elements is also important particularly in trauma and stress-related disorders, where strong memories are often activated by neutral cues due to their emotional associations. In the present study, we used event-related potentials (ERPs) to investigate long-term recognition memory (one week delay) for neutral objects that had been paired with emotionally arousing or neutral scenes during encoding. Context effects were clearly evident in the ERPs: An early frontal ERP old/new difference (300-500 ms) was enhanced for objects encoded in unpleasant compared to pleasant and neutral contexts; and a late central-parietal old/new difference (400-700 ms) was observed for objects paired with both pleasant and unpleasant contexts, but not for items paired with neutral backgrounds. Interestingly, objects encoded in emotional contexts (and novel objects) also prompted an enhanced frontal early (180-220 ms) positivity compared to objects paired with neutral scenes indicating early perceptual significance. The present data suggest that emotional —particularly unpleasant— backgrounds strengthen memory for items encountered within these contexts and engage automatic and explicit recognition processes. These results could help in understanding binding mechanisms involved in the activation of trauma-related memories by neutral cues.

Introduction

There is considerable evidence that emotions play a critical modulatory role in episodic memory (Dolcos, Denkova, & Dolcos, 2012; Weymar & Hamm, 2013). For instance, when presenting emotional and neutral materials and memory is subsequently tested, emotionally arousing items are better remembered and are more robust against forgetting than emotionally neutral items (e.g., Bradley, Greenwald, Petry, & Lang, 1992; Dolcos, LaBar, & Cabeza, 2005; Jaworek, Weymar, Löw, & Hamm, 2014; Ochsner, 2000; Weymar et al., 2009, 2010a, 2010b, 2011; Wirkner, Weymar, Löw, & Hamm, 2013; Wirkner, Löw, Hamm, & Weymar, 2015). Despite convincing evidence for a memory enhancing effect of emotion, neutral cues can also activate strong emotional memories (e.g., in patients suffering from trauma or stress-related disorders), if these events were associated with an emotional context in which these items were encountered during encoding (e.g., Davachi, 2006; Ranganath, 2010). To understand how emotion interacts with these "real-world" situations, recent research has therefore focused on the emotion's effects on memory for items as a part of, or in relation to other items, the so-called contextual relational binding (Chiu, Dolcos, Gonsalves, & Cohen, 2013). Here, we investigated the brain dynamics of contextual/relational memory using event-related potentials (ERPs) recorded during retrieval.

It is a robust finding in memory research that ERPs generated by correctly recognized old stimuli evoke more positive-going waveforms than those elicited by correctly detected new stimuli (for reviews, Rugg & Curran, 2007; Weymar & Hamm, 2013). This difference in ERP positivity has been labeled the ERP old/new effect. Two ERP old/new differences have been identified reflecting different processes involved in recognition memory: An early old/new effect (300-500 ms) located over frontal brain regions has been related to a-contextual familiarity-based remembering, while centro-parietal old/new differences (> 500 ms) have been associated with recollection-based remembering (i.e. retrieval of specific contextual information about the learning episode; Rugg & Curran, 2007; Weymar & Hamm, 2013). ERP studies exploring the electrophysiological correlates of long-lasting enhancing memory effects of emotion showed that emotional events, compared to neutral ones, are associated with larger old/new effects over parietal areas (e.g., Jaworek et al., 2014; Schaefer, Pottage, & Rickart, 2011; Weymar et al., 2009, 2010a, 2010b, 2011; Wirkner et al., 2013, 2015), suggesting that remembering of emotional events is most likely guided by recollection, rather than familiarity (Dolcos et al., 2005).

The few available behavioral and ERP studies investigating the effect of emotion on memory for associated contextual information, however, have produced mixed results. Some researchers found better memory for contextual features of emotional items (e.g., Doerksen & Shimamura, 2001; Mather & Nesmith, 2008; Nashiro & Mather, 2011) and neutral items embedded in arousing contexts (e.g., Guillet & Arndt, 2009; Pierce & Kensinger, 2011), whereas others found impairments in memory performance (e.g., Bisby, & Burgess, 2014; Nashiro & Mather, 2011; Rimmele, Davachi, Petrov, Dougal, & Phelps, 2011; Touryan, Marian, & Shimamura, 2007) or no effects (e.g., Koenig & Mecklinger, 2008; Sharot & Phelps, 2004) when retrieving emotional, relative to neutral, contextual source information (e.g., paired words, background scenes or features). Smith et al. (2004a) explored ERPs related to immediate recognition of emotionally neutral objects associated with emotional and non-emotional background scenes. These authors found no ERP old/new differences between context categories in early frontal or late parietal regions (replicated by Jaeger, Johnson, Corona, & Rugg, 2009). Similarly, Maratos and Rugg (2001) also did not observe ERP old/new differences when source information (contextual pairings) was tested for neutral words encoded in emotionally arousing sentences, compared to emotionally neutral sentences. Hence, compared to ERP results from episodic memory studies using single items, ERP findings related to relational memory seem to indicate no emotional modulation in contextual memory processes.

One potential contributing factor for the lack of emotional effects might be the length of the retention interval (for discussion concerning item memory, see Weymar & Hamm, 2013). Most available studies have used immediate testing but emotional advantages in single item memory have often been augmented over time, in part, by facilitating consolidation processes (e.g., Quevedo et al., 2003; McGaugh, 2004; LaBar & Cabeza, 2006; Ritchey, Dolcos, & Cabeza, 2008). For delayed intervals, greater memory accuracy (Weymar & Hamm, 2013), stronger recollective experience, and larger ERP old/new differences have been reported for emotionally arousing stimuli (Schaefer et al., 2011; Sharot, Delgado, & Phelps, 2004; Weymar et al., 2010a), especially for unpleasant events (Weymar et al., 2011). Thus, emotion might also facilitate contextual or relational binding after a longer delay (as suggested by Pierce & Kensinger, 2011). In accordance with this suggestion, in behavioral research it has been observed that recognition of emotional contextual cues compared to neutral ones is enhanced after long (such as 1 or 7 days), but not after short delays (Pierce & Kensinger, 2011; Sharot & Phelps, 2004). Recently, two ERP studies have investigated emotional contextual binding (Jaeger et al., 2009; Jaeger & Rugg, 2012) on a delayed test (24 hours). However, Jaeger and colleagues (2009, 2012) found no better memory for neutral objects encoded in emotionally unpleasant background scenes, compared to those neutral objects associated with neutral scenes, indicating that beneficial effects of contexts may occur after longer consolidation periods (c.f., Pierce & Kensinger, 2011).

One other important factor to be considered in emotional relational memory is the manner in which stimuli are bound (MacKay, Shafto, Taylor, Marian, Abrams, & Dier, 2004; Mather, 2007). According to the arousal-biased competition (ABC) theory (Mather & Sutherland, 2011), emotional arousal can lead to enhancement and impairment among neutral stimuli competing for attention depending on high or low priority (due to bottom-up perceptual salience or top-down attentional focus). The theory further suggests that emotional arousal may enhance associative memory for features of high priority items (e.g., color or location of an item) and impair memory for neutral items, when presented at the same time with emotional items. However, if the association between emotional cues and neutral items is well integrated, memory for neutral items may improve due to the acquisition of high priority. In order to prevent competition between emotional and neutral stimuli, in the current study participants were instructed to imagine the object as a part of the scene to promote the binding between object and background (cf. Awipi & Davachi, 2008). Moreover, unlike prior studies (e.g., Smith et al., 2004a; Jaeger & Rugg, 2012) in which objects were presented visually separated from the background scenes (e.g., surrounded with white background and yellow frame), objects were unframed and presented with transparent background to further facilitate object/context integration. Finally, objects were presented first followed by the background scene, to avoid direct competition between emotional backgrounds and neutral objects, as it might occur when the emotional stimulus is introduced first (cf. Jaeger & Rugg, 2012).

Thus, to further investigate the role of emotion on context binding, we explored electrophysiological correlates of recognition memory for neutral events embedded in emotional contexts taking into account various critical factors facilitating emotional context memory (i.e., delayed retention interval and event-context integration). Furthermore, some memory studies (e.g., Bradley, et al., 1992; Dolcos et al., 2005; Weymar et al., 2009) found that emotionally arousing stimuli are better remembered than low arousing neutral stimuli, observing no differences in the retrieval of unpleasant and pleasant material, whereas others observed a preference in remembering negative information over positive and neutral information (e.g., for associative memory, see Pierce & Kensinger, 2011; for item memory, see Weymar et al., 2011). In order to explore the effects of arousal and emotional valence on memory binding in healthy individuals, both high arousing pleasant and unpleasant pictures were included as contexts in the present study.

The experimental procedure consisted of two phases (see Smith et al., 2004a for a similar design): An incidental encoding task where emotionally neutral objects were presented in the context of emotionally neutral or emotionally arousing background scenes; and a recognition memory task in which item (old vs. new) and context (pleasant vs. unpleasant vs. neutral background picture) was tested. Based on previous studies reporting memory enhancing-effects in the context of emotion (e.g., Guillet & Arndt, 2009; Pierce & Kensinger, 2011), we made a first prediction concerning behavioral performance: *(i)* we expected that objects encoded in emotional contexts would be better remembered than objects encoded in neutral contexts after a 1-week retention interval. Concerning associated brain dynamics we made a second prediction: *(ii)* we expected to find larger parietal ERP old/new differences (500-700 ms) for neutral objects previously paired with emotional, relative to neutral background pictures, possibly reflecting explicit recollection.

Materials and methods

Participants

Participants were 30 healthy students (26 women, 4 men; mean age = 22.7 years; 3 left-handed, 27 right-handed) from the University of Greifswald, with normal or corrected-to-normal vision, who participated for course credits or financial compensation. All participants were native German speakers. Each individual provided written informed consent for a protocol approved by the Review Board of the German Psychological Society (DGPs). Data from 3 participants were excluded due to excessive artifacts in the electroencephalogram (EEG) data.

Stimulus materials

A total of 288 neutral objects and 144 background scenes were used in the present experiment. Neutral objects were selected from two different standardized sets: The Bank of Standardized Stimuli (BOSS; Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010), and the ecological adaptation of Snodgrass and Vanderwart (Moreno-Martínez & Montoro, 2012)[1].

Objects belonged to a variety of different semantic categories (e.g., office supplies, electronics, household objects) and were grouped in six different sets carefully matched in terms of semantic category, familiarity, object agreement, and manipulability, according to the normative ratings of the standard samples (see BOSS and ecological adaptation of Snodgrass and Vanderwart norms). Background scenes were selected from the *International Affective Picture System* (IAPS; Lang, Bradley & Cuthbert, 2008), consisting of 48 pleasant (e.g., erotic, adventure, babies and small animals), 48 neutral (e.g., buildings, landscapes, and neutral human faces), and 48 unpleasant (e.g., mutilation, attack, disgust and accident) pictures[2]. Mean (SD) valence and arousal ratings (respectively) for the three picture valence categories were as follows: Pleasant: 6.94 (0.63), 5.84 (0.77); neutral: 5.27 (0.82), 3.51 (0.57); and unpleasant: 2.73 (0.85), 5.93 (0.57). Pleasant, neutral and unpleasant pictures did not differ in complexity, brightness, and contrast (all *p*s > .23).

During encoding, neutral objects were presented superimposed on an emotional or neutral background scene. Participants were presented with one of six encoding lists (for list construction, see Jaeger et al., 2009; Smith et al., 2004a), each consisting of 144 object/background pairs, with no more than two pictures from the same valence presented consecutively. Each neutral object set was paired with a neutral background scene in one list, an unpleasant background in another, a pleasant background scene in a third, and was available as a novel object set for the remaining three lists.

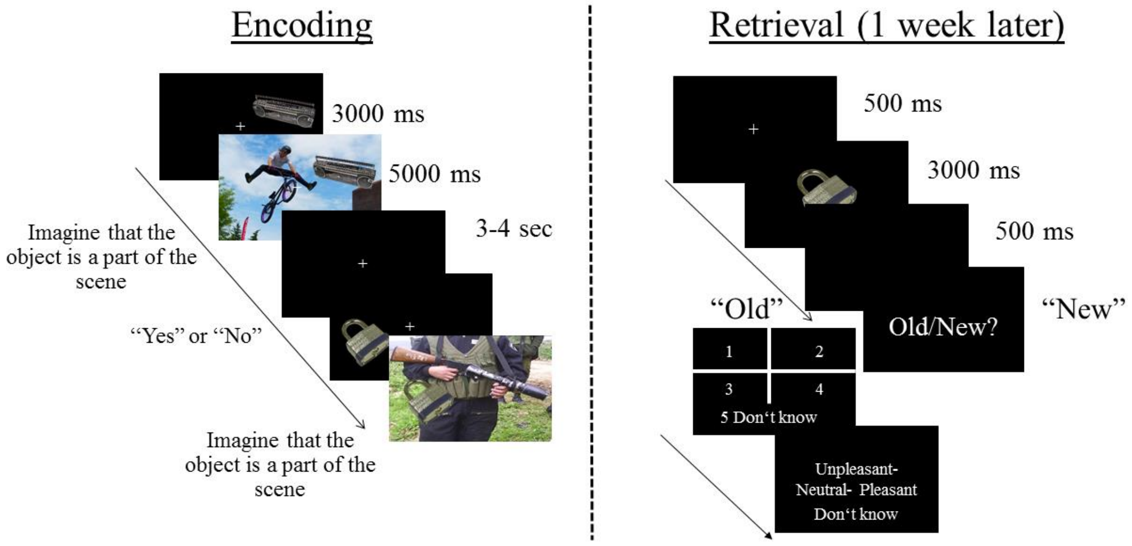
Procedure

During encoding, 144 objects were superimposed on 144 background scenes. Objects (mean vertical and horizontal visual angle of 4.96º) and background scenes (vertical visual angle of 7.73º, horizontal visual angle of 10.93º) were presented on a 20” computer monitor located 150 cm in front of the participant. In contrast to previous studies (e.g., Jaeger et al., 2009; Jaeger & Rugg, 2012; Smith et al., 2004a, 2004b, 2005), in which objects were visually separated (white background and/or yellow frame), here objects were presented with transparent background and without frame to facilitate object-scene binding. Objects were presented in one of four quadrants of the screen. The four positions of the objects were selected randomly and with the same probability for each background category. After 3000 ms, an emotional or neutral scene was added as background. Each object and scene pairing was presented for 5000 ms with an inter-trial interval (ITI) of 3000, 3500 or 4000 ms. The encoding phase was separated into two blocks in which all 144 object-scene pairings were presented and after a break of one minute, the exact 144 same object/scene pairings were repeated (but in randomized order). Participants were instructed to imagine that the object is a part of the scene and to indicate after object/scene offset whether the imagination was successful or not by pressing a “yes” or a “no” button on a response pad (see Figure 1). No mention of a memory test was made (incidental encoding).

One week after encoding, participants returned to the lab for a memory task, in which old and new objects were presented. The task took place in a sound-attenuated dimly lit room. Each participant viewed 288 objects (i.e., 144 old and 144 novel objects). Of the 144 old objects, 48 objects had been encoded in the context of an unpleasant scene, 48 objects in the context of a pleasant scene, and 48 objects in the context of a neutral scene. Each object was presented in the center of the screen (mean vertical and horizontal visual angle of 5.92º) without context for 3000 ms with a preceding fixation cross of 500 ms.

Participants were instructed to decide whether each object had previously been seen during encoding or not. Following object offset[3], the question "Old/New?" appeared on the screen, and participants pressed an "old" button on a keyboard if they remembered the object, or else a "new" button. When the object was recognized as old, subjects were asked to remember source information cues: the location the object was presented at during encoding (i.e., which quadrant of the screen), and the background paired with (i.e., pleasant, neutral or unpleasant; see Figure 1). Participants were instructed to avoid eye blinks and body movements.

Figure 1. Schematic view of the stimulus presentation during encoding and retrieval.



Apparatus and data analysis

EEG signals were recorded continuously from 257 electrodes using an Electrical Geodesics (EGI) HydroCel high-density EEG system with NetStation software on a Macintosh computer. The EEG recording was digitized at a rate of 250 Hz, using vertex sensor (Cz) as recording reference. Scalp impedance for each sensor was kept below 30 kΩ, as recommended by manufacturer guidelines. All channels were band-pass filtered online from 0.1 to 100 Hz. Offline reduction was performed using ElectroMagnetic EncephaloGraphy Software (EMEGS; Peyk, De Cesarei, & Junghöfer, 2011) and included lowpass filtering at 40 Hz, artifact detection, sensor interpolation, baseline correction, and conversion to the average reference (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). Stimulus-synchronized epochs were extracted from 100 ms before to 1200 ms after picture onset and baseline corrected (100 ms prior to stimulus onset). Extracted epochs were corrected for eye movement and blink artifacts using the MATLAB-based toolbox BioSig (Vidaurre, Sander, & Schlögl, 2011).

For each participant, separated ERP averages were computed for each sensor and condition. Only trials with correct responses for old and new objects were included in ERP averages. Due to the low number of hits in the source memory task (location and background) only ERPs during the item recognition task (old vs. new) were analyzed. The identification of sensor clusters representative for maximal old/new effects were based on visual inspection of the waveforms and based on previous studies (Jaeger et al., 2009; Jaeger & Rugg, 2012; Maratos & Rugg, 2001; Smith et al., 2004a; Weymar et al., 2009, 2010a, 2010b; Wirkner et al., 2013, 2015). Because recent studies observed context effects at earlier (< 300 ms) stages of processing (Curran & Dien, 2003; Tsivilis, Otten, & Rugg, 2001; Voss & Paller, 2009), especially for emotionally arousing events (Jaeger et al., 2009, 2012; Schaefer et al., 2011; Smith et al., 2004a), we also examined ERP differences in an early time window. Mean ERP amplitudes were analyzed in a 180-220 ms and 300-500 ms time window over frontal brain regions (EGI HydroCel sensors 5, 6, 7, 8, 14, 15, 16, 22, 23, and 29), and in a 400-700 ms time window over centro-parietal brain regions (EGI HydroCel sensors 9, 45, 80, 81, 89, 90, 130, 131, 132, 186, and 257). Recognition-related ERP data for each time window were analyzed in two separate ANOVAs including the factors *Memory* (old objects vs. new objects) and *Context* (neutral objects encoded in pleasant contexts vs. neutral contexts vs. unpleasant contexts). If there was no difference between objects encoded in pleasant and unpleasant contexts, an ANOVA with the factor *Emotion* (neutral objects encoded in pleasant and unpleasant contexts vs. neutral context) was performed.

For behavioral performance data, hit rate was analyzed using an ANOVA involving the factor *Context* (objects encoded in pleasant context vs. neutral context vs. unpleasant context). For the source task, hit rates for stimulus location (hit location/hit old object) and background recognition (hit context/hit old object) were analyzed in separate ANOVAs involving the factor *Context*. Again, if pleasant and unpleasant contexts did not differ, an ANOVA with the factor *Emotion* (objects encoded in emotional context vs. neutral context) was performed. For effects involving repeated measures, the Greenhouse-Geisser correction for non-sphericity was used when necessary.

Results

Behavioral data

Memory performance for old (item and source memory data) and new objects is listed in Table 1.

Item memory. Hit rates for objects previously paired with emotional pictures tended to be higher than for objects encoded in a neutral context, Emotion: *t*(29) = 1.96, *p* = .059, *d* = .19. No differences were found between hit rates for objects that had been paired with pleasant and unpleasant backgrounds (*t*[29] = 1.08, *p* = .28, *d* = .13), suggesting that memory for neutral objects benefits from binding with emotionally arousing contexts irrespective of their valence during encoding.

Source accuracy rates. Hit rates for remembered objects location were low and similar for emotional and neutral contexts ($F < 1$), indicating that emotional context did not influence memory for source location. Overall, correct source memory for background pictures was low, and did not differ from the probability of guessing, that is, from the proportion of randomly choosing a correct contextual source (.33; ps > .286). However, there were differences as a function of picture content (Context: $F[2,58] = 10.37$, $p < .001$, $\eta_p^2 = .26$): Unpleasant ($F[1,29] = 5.13$, $p < .05$, $\eta_p^2 = .15$) and neutral ($F[1,29] = 19.9$, $p < .001$, $\eta_p^2 = .41$) contexts were better classified than pleasant contexts. Recognition for correct background also differed for unpleasant and neutral scenes ($F[1,29] = 5.5$, $p < .05$, $\eta_p^2 =.16$). The probability of committing a false alarm by mistakenly identifying a context as neutral (.53) significantly differed from the chance level ($t\,[29]= 5.8$, $p < .001$), and from the probability of erroneously identifying a context as pleasant (.4; $t[29] = 3.6$, $p < .001$, $d = .63$), and unpleasant (.4; $t[29] = 3.59$, $p < .001$, $d = .63$), indicating a response bias toward neutral contexts. Based on the assumption that the response bias is a good estimate of the bias operating for object recognition, Maratos & Rugg (2001), suggest that the probability of recollection of context information can be obtained from the following formula: pCorrect source = pRecollection + pGuess x (1 - pRecollection). After applying the formula, the probabilities of correct background recognition are higher for pleasant (.77) and unpleasant (.76) compared to neutral contexts (.74), in accordance with the item memory performance.

Table 1. Hit rate means (standard deviation) for new and old objects encoded in pleasant, neutral and unpleasant contexts.

	Hit rates		
	Item recognition	*Source location*	*Source background*
New objects	.93 (.04)		
Old objects			
Pleasant context	.65 (.14)	.13 (.09)	.25 (.13)
Neutral context	.62 (.15)	.12 (.08)	.36 (.20)
Unpleasant context	.64 (.14)	.14 (.10)	.30 (.16)
Emotional context [a]	.65 (.13)	.13 (.08)	.27 (.14)

[a] Combining pleasant and unpleasant contexts.

ERP encoding data

To exclude a-priori object differences, we compared ERPs in response to neutral objects subsequently encoded in emotional or neutral context in the first block of the encoding session. No ERP differences were found at any time window or sensor location ($F < 1$).

ERP recognition data

Frontal ERP effect. Figure 2A illustrates the grand average ERPs extracted from the frontal cluster for old objects previously encoded in the context of a pleasant, neutral and unpleasant scene, and new objects.

Early ERP Emotional effect (180-220 ms). For the early time window, no ERP old/new difference was found (Memory: $F < 1$). However, frontal positivity in the time window between 180 and 220 ms was modulated by context ($F[2,52] = 3.83$, $p < .05$, $\eta_p^2 = .13$). Follow-up testing showed that objects previously paired with emotional pictures prompted a larger positivity than objects paired with neutral pictures (Emotion: $F[1,26] = 4.17$, $p = .05$, $\eta_p^2 = .14$; see Figure 2C). No significant ERP differences were found between objects paired with unpleasant scenes compared to objects paired with pleasant scenes, $F[1,26] = 3.2$, $p = .09$, $\eta_p^2 = .09$. When comparing new objects with old objects from different encoding contexts, we observed that novel objects also produced a larger ERP positivity than objects previously encoded in neutral contexts ($F[1,26] = 4.96$, $p < .05$, $\eta_p^2 = .16$; see Figure 2C).

Early ERP Old/New effect (300-500 ms). ERPs for old objects were modulated by Context ($F[1,52] = 3.81$, $p < .05$, $\eta_p^2 = .13$). Enhanced positivity was found for objects previously paired with unpleasant contexts, compared to pleasant ($F[1,26] = 8.54$, $p < .01$, $\eta_p^2 = .25$) and neutral contexts ($F[1,26] = 4.09$ $p = .05$, $\eta_p^2 = .14$). Although the main effect of memory was not significant (Memory: $F[1,26] = 1.55$, $p = .22$, $\eta_p^2 = .05$), only objects from unpleasant backgrounds showed a significant old/new effect: unpleasant contexts vs. new objects, $F(1,26) = 8.58$, $p < .01$, $\eta_p^2 = .25$. Objects paired with pleasant and neutral backgrounds did not show such an old/new difference ($F < 1$; see Figure 2C).

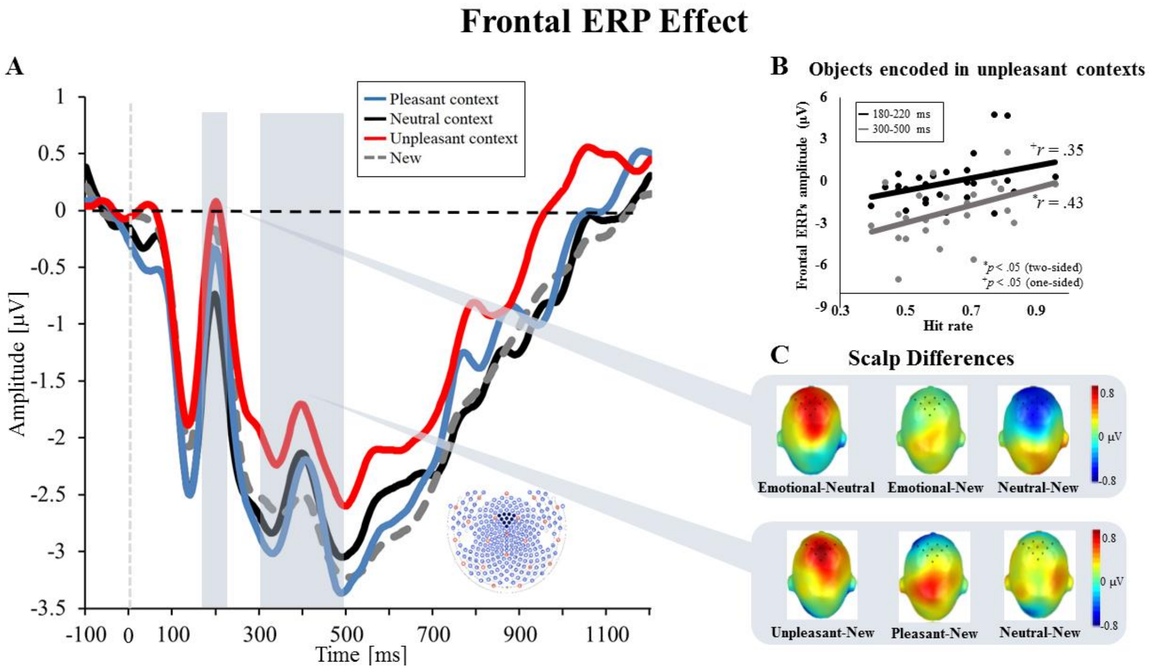


Figure 2. Frontal ERP Effect. A: Grand average ERPs in response to correctly recognized new (grey dotted line) and old objects encoded in pleasant (blue line), neutral (black line), and unpleasant (red line) contexts. ERPs are averaged across electrodes within a frontal sensor cluster. B: Correlations between the mean amplitude of the frontal ERPs positivity at 180-220 ms (black line) and 300-500 ms (grey line) time window, and hit rate for objects encoded in unpleasant contexts. C: Display of the scalp topographies of the ERP differences. The upper scalp differences plot the early (180-200 ms) emotional ERP effects; the lower topographies represent the ERP old/new effect at 300-500 ms.

Parietal ERP Effect. Figure 3A illustrates the grand average ERPs for correctly recognized neutral objects encoded in the context of a pleasant, neutral or unpleasant scene, and for new objects from a representative centro-parietal cluster.

Late ERP Old/New effect (400-700 ms). As expected, correctly recognized old objects elicited a larger positive-going waveform than correctly detected new objects (Memory: $F[1,26] = 12.12$, $p < .005$, $\eta_p^2 = .32$). This old/new difference was modulated by context during encoding (pleasant objects vs. neutral objects vs. unpleasant objects: $F[2,52] = 3.14$, $p = .05$, $\eta_p^2 = .11$).

Specifically, objects paired with emotional backgrounds elicited a larger ERP positivity than novel objects (unpleasant contexts vs. new objects: $F[1,26] = 4.52$, $p < .05$, $\eta_p^2 = .15$; pleasant contexts vs. new objects: $F[1,26] = 24,74$, $p < .001$, $\eta_p^2 = .49$). However, objects paired with neutral background scenes did not show the parietal old/new effect (neutral contexts vs. new objects: $F[1,26] = 1.53$, $p = .23$, $\eta_p^2 = .06$); see Figure 3C).

Correlations between recognition performance and ERP effects. Significant correlations between hit rate performance and ERPs were only observed for unpleasant contexts in the 180-220 ms, 300-500 ms (Figure 2B), and 400-700 ms (Figure 3B) time window. Hit rates for objects encoded in unpleasant contexts showed a positive relation with the ERP amplitude (180-220 ms, $r = .37$, $p = .03$, one-tailed; 300-500 ms, $r = .43$, $p < .05$; 400-700 ms, $r = .35$, $p = .035$, one-tailed), suggesting that higher memory accuracy was related to larger positivity for objects encoded in the unpleasant context (see Figure 2B, and Figure 3B). This relation was not found for objects encoded with pleasant or neutral contexts in either time windows (*r*s < .27, *p*s > .17).

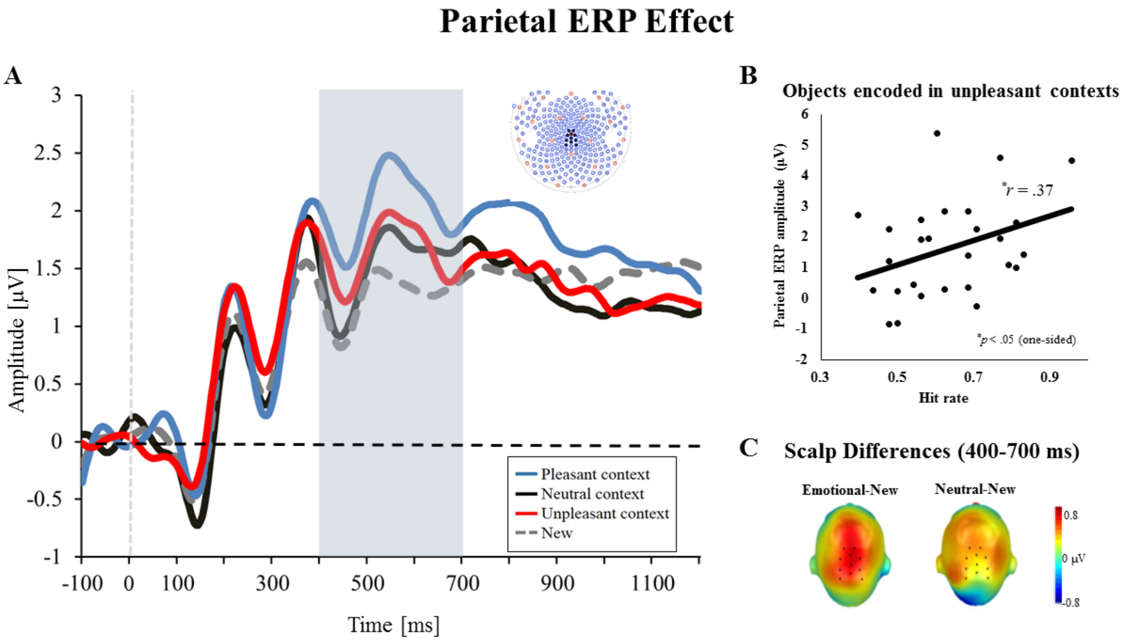


Figure 3. Parietal ERP effect. A: Grand average ERPs evoked by correctly recognized new (grey dotted line) and old objects encoded in pleasant (blue), neutral (black), and unpleasant (red) contexts. The waveforms represent the ERPs averaged across electrodes within a centro-parietal sensor cluster. B: Correlation between the mean amplitude of the parietal ERP positivity (400-700 ms) and hit rate for objects encoded in unpleasant contexts. C: Display of the scalp topographies of the ERP old/new differences (objects in emotional contexts and neutral contexts vs. new objects).

Discussion

In the current study, ERPs were used to investigate long-term recognition memory for neutral objects that had been encoded in an emotionally arousing or neutral context. We found that ERPs during retrieval were sensitive to context differences at encoding at three different time windows. We observed that old objects previously paired with emotional contexts prompted an enhanced early (180-220 ms) positivity (P2) over frontal sites. Furthermore, correct recognition was associated with larger centro-parietal ERP old/new differences (400-700 ms) for objects encoded in both pleasant and unpleasant, but not in neutral contexts, and associated with early frontal ERP old/new differences (300-500 ms), particularly for unpleasant contexts. Our results indicate that emotion improves associative binding and engages both automatic perceptual mechanisms and explicit recognition processes at retrieval, such as familiarity and recollection processes.

Although the effect was only marginal in the current experiment, we found enhanced memory performance for neutral objects associated with emotional contexts, in comparison to neutral contexts. This finding is in line with many previous studies reporting emotional memory-enhancing effects for single items and contexts (Bradley et al., 1992; Doerksen & Shimamura, 2001; Dolcos et al., 2005; Guillet & Arndt, 2009; Jaworek et al., 2014; Maratos et al., 2001; Mather & Nesmith, 2008; Nashiro & Mather, 2011; Pierce & Kensinger, 2011; Smith et al., 2004a; Weymar et al., 2009; 2010a; 2010b; 2011; Wirkner et al., 2013, 2015; but see Jaeger et al., 2009, 2012), suggesting that emotional arousal improves long-term associative memory.

In ERPs, correctly recognized old items compared to correctly classified new items elicited enhanced ERP positivity, replicating a large body of previous work on memory research with short and long retention intervals (e.g., Rugg, Mark, Walla, Schloerscheidt, Birch, & Allan, 1998; see for reviews Rugg & Curran, 2007; Weymar & Hamm, 2013). As expected, larger

ERP old/new differences were observed for neutral objects encoded in emotionally arousing, but not in emotionally neutral contexts over parietal regions. Because a parietal ERP old/new effect has been related to the process of contextual remembering (Wilding, 2000; Wilding & Rugg, 1996; see Rugg & Curran, 2007 for review), our finding indicates that retrieval of emotional (unpleasant and pleasant) contexts engages recollection processes. This clearly replicates previous ERP picture memory studies that found enhanced parietal ERP old/new effects for emotional pictures (e.g., Jaworek et al., 2014; Weymar et al., 2009, 2010, 2011; Wirkner et al., 2013, 2015; Ferrari, Bradley, Codispoti, Karlsson, & Lang, 2013). Interestingly, our result contrasts with prior work where comparable ERP old/new effects were found when measuring emotional and neutral pictures as contexts (Jaeger et al., 2009; Jaeger & Rugg, 2012; Smith et al., 2004a). One reason for this discrepancy could be related to item-context binding processes (Mackay et al., 2004; Mather, 2007), which were facilitated methodologically in the present study. It has been observed that contextual memory increases when neutral items are well integrated with other items or contexts (Murray & Kensinger, 2012, 2013), especially when the latter are arousing (Guillet & Arndt, 2009; Pierce & Kensinger, 2011). Compared to previous studies (e.g., Jaeger & Rugg, 2012), we facilitated item-context pairing by integrating the object into the scene.

Another reason that might be critical is stimulus order presentation (Sakaki, Fryer, & Mather, 2014; Sutherland & Mather, 2012). Based on the ABC theory (Mather & Sutherland, 2011), recent studies have observed that emotionally arousing stimuli distinctly modulate memory for preceding and following neutral target stimuli (Sakaki, Fryer, & Mather, 2014; Sutherland & Mather, 2012). Thus, if emotional events are preceded by a neutral target stimulus (i.e., high priority), emotional arousal further enhances memory for highly prioritized neutral items; however, if the emotional event is followed by a neutral target stimulus, emotional arousal captures attentional resources and impairs perceptual processing of the neutral target item, hindering the memory-enhancing effects (Sakaki et al., 2014; Sutherland & Mather, 2012). Contrary to prior studies (e.g., Jaeger et al., 2009; Jaeger & Rugg, 2012), we intended to avoid competition for attention resources by presenting the object before the context image appeared.

However, most critically contributing to the emotional enhancing effects observed in the present data is probably the one-week interval between the encoding and the retrieval session. A number of studies have demonstrated that longer retention periods facilitate consolidation processes, resulting in memory enhancing-effects (e.g., LaBar & Cabeza, 2006), especially for emotionally, compared to neutral, arousing events (e.g., Dolcos et al., 2005; Pierce & Kensinger, 2011; Weymar et al., 2009; see Weymar & Hamm, 2013 for review). In contrast to a number of previous emotional associative memory studies (e.g., Smith et al., 2004a; Maratos et al., 2001; Jaeger et al., 2009), we promoted consolidation processes by means of long retention periods.

To summarize, the ERP parietal old/new effect findings seem to indicate that emotional contexts enhance electrophysiological correlates of long-term recollection memory for integrated neutral material. In addition to the parietal ERP old/new effects, emotional context modulated frontal ERP correlates of familiarity-based recognition. Compared to pleasant and neutral contexts, objects embedded in unpleasant background scenes generated enhanced frontal ERP old/new differences between 300 and 500 ms. A number of studies propose that relational memory depends upon recollection-based mechanisms (Rugg & Curran, 2007; Wilding & Rugg, 1996). However, recent behavioral (Diana, Yonelinas, & Ranganath, 2008, 2010) and electrophysiological studies (Addante, Raganath, & Yonelinas, 2012; Diana, Van den Boom, Yonelinas, & Ranganath, 2011; Ecker et al., 2007a, 2007b; Mollison & Curran, 2012; Peters & Daum, 2009; Speers & Curran, 2007; Tibon et al., 2014a, 2014b, 2014c; Tsivilis et al., 2001; Zheng, Li, Xiao, Broster, & Jiang, 2015) have evidenced that familiarity-related processes could also contribute to source recognition (Johnson, Hashtroudi, & Lindsay, 1993;

Yonelinas, 2002). In an attempt to shed light on the familiar-related processes embedded in source memory, Diana et al. (2008, 2010, 2011) investigated the impact of encoding processes on familiarity-based recognition. These authors observed that exclusively high-unitized associations —i.e., item-context pairings encoded as a single unit— elicited frontal ERP old/new effects, whereas low-unitized associations only elicited recollection-related ERPs (Diana et al., 2011). In the same direction, a number of studies have observed that when item-source associations can be processed together at encoding, familiarity processes are also enhanced during recognition. Thus, when item and source information are encoded in the same modality (visual) vs. different modality (visual and auditory; Tibon et al., 2014a, 2014b, 2014c), when the nature of the association item-source is intrinsic vs. extrinsic (Ecker et al., 2007a, 2007b; Zheng et al., 2015), or when source refers to salient contextual information (Mollison & Curran, 2012), source recognition prompts larger familiarity-related ERPs, suggesting that memory for source information is strengthened (Addante et al., 2012; Chiu et al., 2013; Curran, 2004). In the present study, no explicit instructions for unitization were given, however, as commented above, we promoted item-context binding processes at encoding. It might be that this instruction accentuated item-context unitization for unpleasant associations and, thus, promoted stronger familiarity-based recognition of negative source information. However, clear conclusions cannot be derived because judgments regarding the strength of the associations were not directly recorded in the present study. Future research should assess the emotional effect on strength/unitization of item-context associations in order to clarify the present finding.

Intriguingly, we found differences of context association at early stages of processing. Neutral stimuli encoded in emotional, compared to neutral contexts, elicited a larger early (180-220 ms) positive-going waveform over frontal sites. This early emotional effect resembles those reported by previous source memory studies (Jaeger et al., 2009; Jaeger & Rugg, 2012; Smith et al., 2004a), suggesting that neutral stimuli acquired emotionally arousing properties. This emotion effect may relate to the transmission of emotional attributes from contexts to objects by means of associative binding mechanisms (Smith et al., 2004a), enhancing their processing (e.g., Öhman & Mineka, 2001; Vuilleumier, 2005). A substantial body of research has suggested the existence of highly elaborated networks, involving the amygdala (Ohman & Mineka, 2001), and cortical regions (Pessoa & Adolphs, 2010; Van Gaal & Lamme, 2012), that rapidly identify motivationally relevant events (Brosch, Sander, Pourtois, & Scherer, 2008; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Steinberg, Bröckelmann, Rehbein, Dobel, & Junghöfer, 2013; Wieser, Gerdes, Büngel, Schwarz, Mühlberger, & Pauli, 2014) and further provide rapid learning capacity and an excellent resolving power (cf. Steinberg et al., 2013). Thus, our data seem to indicate that neutral objects embedded in emotional contexts have rapidly —after two pairings!— acquired long-lasting emotional relevance.

An alternative but not excluding interpretation could link the early frontal ERP also with memory-related mechanisms. The frontal P2 has been related to the activation of representations retrieved in long-term memory due to the detection of visual information (Curran & Dien, 2003; Tsivilis et al., 2001; Voss & Paller, 2009) under explicit memory testing (Curran, 1999; Voss & Paller, 2009; but see Jaeger & Rugg, 2012). Specifically, it has been observed that the frontal P2 increases when the visual input matches with efficiently stored information, suggesting that the extent of activation of representations in memory indexed by P2 might relate to the phenomenological salience of the stimuli (cf. Voss & Paller, 2009). Consistent with this idea, Schaefer et al. (2011) found that frontal P2 was modulated by the memory strength of emotional events, that is, remembered unpleasant scenes —but not neutral ones— evoked frontal P2 old/new effects; moreover, P2 amplitudes in response to unpleasant images increased with their arousal. In the current study, larger P2 was evoked by neutral objects embedded in emotional compared to neutral background scenes, suggesting that emotional contexts increase the saliency of the events bound with, facilitating their later recognition.

From a dual-process model perspective (Yonelinas, 2002) however, it remains unclear which mnemonic mechanisms underlie the P2 old/new effects. On the one hand, the spatio-temporal attributes of the P2 matches with the frontal familiarity-related old/new effects, suggesting the existence of similar processes between both components. On the other hand, the P2 old/new effect has only been found when the events where labeled as remembered, but not when they were considered familiar (Voss & Paller, 2009), indicating that P2 might be related to recollection. Schaefer et al. (2011) found distinct patterns of modulation across arousal levels between P2, frontal and parietal old/new effects, suggesting that different memory sub-processes might be involved for each component (cf. Schaefer et al., 2011). We, however, did not find clear evidence that would allow us to disentangle this question. Future research should focus on elucidating the memory sub-processes underlying this frontal memory index, assessing, for instance, which recognition processes (remember vs. know) have been employed.

Surprisingly, we found that correctly identified new objects also elicited a larger P2 than old objects paired with neutral background scene. A plausible explanation of this effect could be that early frontal activity is related to the processing of novelty/relevant stimuli (Ecker et al., 2007c; Tsivilis et al., 2001; Voss & Paller, 2009). In this line, Ecker et al. (2007c) observed that novel neutral events generated larger early frontal activity than correctly recognized old neutral stimuli. These authors suggest that the brain response difference between new and old information at early stages of processing might be associated with an enhanced attentional capture (Ecker et al., 2007c). Thus, based on previous research, we interpret this finding as a result of enhanced processing of new objects, along with decreased processing of relatively non-relevant (associated with neutral source information) old events.

Although pleasant and unpleasant background scenes were matched in terms of emotional arousal, we found that frontal old/new effects were exclusive for unpleasant-related associations. We further observed that memory performance for objects paired with unpleasant background scenes predicted larger electrophysiological activity at the three ERP memory-related components (P2, frontal and parietal old/new effects). These results are in line with recent memory studies that report enhanced long-term explicit memory for unpleasant-related stimuli, compared to pleasant ones (Pierce & Kensinger, 2011; Ochsner, 2000; Weymar et al., 2011). For instance, Pierce and Kensinger (2011) investigated emotional valence and arousal on associative binding after a short (15 min) and longer (1 week) delay and observed that memory performance for unpleasant word pairs was better in comparison to pleasant and neutral word pairs after long, but not after short retention intervals, suggesting that unpleasant-related stimuli acquire a higher long-term relevance. From an evolutionary perspective, memory for stimuli related to potentially dangerous events should be consistent, salient, and stable over time in order to facilitate their detection and avoid them in the future (Dolan, 2002). Furthermore, it has been suggested that pleasant contexts (animals or nurture scenes) do not contain the same type of survival-relevant information as unpleasant contexts (accidents or attacks), making them less relevant for future purposes than negative situations (Ashby, Isen, & Turcken, 1999; Fredrickson, 1998, 2001; Ochsner, 2000). Thus, the current findings may indicate that especially unpleasant contexts facilitate associative long-term memory processes.

One further interpretation of the present results might be related to post-encoding arousal effects (Anderson, Wais & Gabrieli, 2006; Knight & Mather, 2009) that might have facilitated memory for neutral objects. Some studies have observed that presenting neutral stimuli shortly prior to emotionally arousing materials can result in enhanced memory (1-week later) for the preceding event (Anderson et al., 2006). A potential mechanism might be that stress hormones (rapid nongenomic effects of catecholamines and glucocorticoids) released in response to arousing emotional contexts might increase vigilance via interactions between the amygdala and hippocampus formation (e.g., McGaugh, 2013), and facilitate memory storage for the context itself but also for recently experienced-related events.

Although the ability to remember cues associated with potentially threatening events could protect us from dramatic consequences, when these events are extremely distressing, memories can become maladaptive and clinically relevant (Ehlers & Clark, 2000). For instance, in patients suffering from posttraumatic stress disorder (PTSD), events associated with traumatizing contexts can involuntarily trigger vivid distressing memories in form of intrusive thoughts, flashbacks or nightmares (Parson & Ressler, 2012) and, on the other hand, can result in impaired episodic memory for the traumatic event itself (e.g., Brewin, 2013; Flor & Nees, 2014; Hayes, VanElzakker, & Shin, 2012; McNally, 2008; Wilker, Elbert, & Kolassa, 2014). A prominent hypothesis of PTSD etiology suggests that trauma memories are poorly integrated into their context (e.g., time and place) during encoding, thus resulting in retrieval distortions of trauma-related information (Dolcos, 2013; Pannu Hayes et al., 2011), overgeneralization and easy triggering of physically similar cues (Ehlers & Clark, 2000), which might relate to deficits in long-term contextual binding processes. Despite its relevance, little is known about the neural processing of emotional binding mechanisms in PTSD. ERPs might be a useful tool to elucidate the long-term binding deficits in PTSD, providing new insights into the neurobiological alterations of the memory systems in trauma and stress-related disorders.

Conclusion

In summary, we found that neutral information can activate long-term memories due to their emotional associations. Neutral objects encoded in emotional contexts showed prioritized automatic perceptual, and explicit mnemonic processing during recognition that was also related to long-term memory performance. Our findings highlight the importance of emotional binding mechanisms in long-term memory processes, which could have also direct clinical relevance for trauma- and stressor-related disorders.

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Footnotes

[1] BOSS: bib, clamp, headphones02b, mallet01b, powercable, bottlecap, calculator01, cookiecutter, flask, makeupbrush04, nailpolish03b, pictureframe04, razor01, scotchtape, tennisball01b, circuitboard, pacifier02d, wheel01, bracket01, beermug01a, nail, strainer02, chalkboard, log, petcarrier, dustpan, giftbag01a, plunger02, studiolight, balloon01b, cane, globe, jar02, chessboard, hanger02a, pitcher02b, ring01, swimgoggles, iron01b, mitten04, tripod, electricrazor, lego03b, tshirt, CD, hinge, highheelshoe01, rearviewmirror, wallet02a, boxcutter03a, cottonpad, envelope03a, glass02a, horsefigurine, leaf02a, match, screwdriver04b, sunglasses04, walkman, medal02b, watch02a, rope03, bag, coffeepot03a, plate01b, flyswatter, microscope, pillow01a, vase02, cooler, kettle01, notebook03a, pylon, oilbottle01, laptop01a, clothespin03b, eraser, divider02, violin, number3, scale01a, videocamera01a, speaker04, lunchbox, cigarette, corkscrew03a, carkeys, key01, mixer01d, starfish, toothbrush03b, remotecontrol04, camera01a, holepunch04, reflector, waterbottle01b, bandaid01, bracelet01, cell phone, diaper01c, hosenozzle, paperclip01b, pingpongracket, thimble, tweezers02a, hourglass, scissors01, tile, manshoe, folder03a, milkcontainer, wateringcan, bikehelmet, fan, sewingmachine01a, tambourine, plasticgallon, papertowel, kitchenscale01a, broom, candle08b, playingcard04, toycow, exercisebench, comb02a, kleenexbox01b, sock01a, alarmclock, fork03c, icecubetray01a, peeler01, sponge01, baseball01a, chain, dice05a, filmroll, gluestick, lighter01, pen04b, stapler03a, taperecorder, thread02, wrench01b, pencilsharpener02a, lock03a, tongs01b, glassmop, keyboard02, printer02, bleachbottle, hairdryer02a, wood, axe, drill01b, fireextinguisher, lamp04a, teapot, winerack, plant01, fishinghook03, teabag, foodprocessor, plasticbasket01a, lifejacket, suitcase, propanetank, pinecone01, monitor, painttray, visegrippliers, brush05b, mousetrap, thermometer02b, cassettetape01a, handfan01b, peppermill02b, spoon01, whisk, bubbleblower, chisel02b, compactpowder, diskette02a, hairclip03, lipstick02a, pliers02b, safetypin, stapleremover, thumbtack02a, usbkey, belt02a, staples, vikingmask01b, antenna,

spraybottle01, bowl01, ridinghelmet, babyseat, boot02b, drum, pants, sportbag, toaster, cardboardbox, squeegee01b, earrings01, glasses01a, cameracase01a, babybottle, pot02a, chair, binder03b, dropper, umbrella04, icepack, battery02b, chalkboarderaser, hat03b, magnifyingglass01b, plugs, spraycan, 50dollarsbill, birdie, bungeecord02, christmasball, computermouse06, flashlight02b, highlighter02b, keychain, nailclipper03b, perfume01a, puzzlepiece, telephone01b, toiletpaper01a, bucket01a, saw02b, handbag02a, radio01, scarf, paintroller01, strawbasket01, backpack01a, clipboard, fryingpan02a, iceskate, rollingpin01a; the ecological adaptation of Snodgrass and Vanderwart: chest of drawers, skirt, saxophone, harp, diabolo, bedside table, skate, rocking chair, clarinet, saucepan, skittle, wardrobe, ludo, undershirt, racket, balalaika, trumpet, bathrobe, trowel, bed, couch, showel, coat, bugle, stool, chair, biretta, piano, soccer ball, sofa, filling cabinet, dartboard, table, ski, drum, fondue, guitar, tuba, jacket, accordion, armchair, bookcase, table football.

[2] Pleasant pictures: 1440, 1590, 1640, 1650, 1659, 1811, 2035, 2045, 2075, 2158, 2160, 2165, 2208, 2340, 2345, 4598, 4599, 4604, 4643, 4645, 4647, 4658, 4659, 4660, 4680, 4687, 4690, 4694, 4800, 5470, 5621, 5626, 8001, 8030, 8041, 8080, 8158, 8170, 8186, 8191, 8192, 8206, 8211, 8260, 8300, 8470, 8490, and 8620; neutral pictures: 2026, 2038, 2039, 2102, 2104, 2190, 2206, 2211, 2273, 2359, 2377, 2383, 2390, 2410, 2511, 2513, 2595, 2840, 2850, 5201, 5390, 5510, 5535, 5593, 5711, 5836, 5875, 5982, 7033, 7037, 7041, 7130, 7161, 7179, 7205, 7234, 7491, 7495, 7504, 7510, 7546, 7550, 7590, 7595, 7620, 7920, 9210, and 9469; unpleasant pictures: 1019, 1026, 1205, 1220, 1302, 1931, 1932, 3015, 3019, 3051, 3064, 3100, 3102, 3110, 3150, 3180, 3181, 3190, 3191, 3195, 3280, 3530, 6212, 6370, 6410, 6560, 6562, 6563, 6571, 6832, 8480, 9008, 9042, 9230, 9253, 9301, 9420, 9490, 9520, 9561, 9570, 9599, 9622, 9635.1, 9908, 9910, 9921, and 9930.

[3] Behavioral recognition responses were delayed until offset of the 3 sec picture presentation in order to avoid contamination by motor potentials. Reaction times are therefore not informative and were not analyzed.

8.3. MANUSCRIPT 3

Item and source memory for emotional associates is mediated by different retrieval processes

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CVB, MW and AOH design the experiment. CVB supervised the data acquisition. CVB analyzed the data and provided the first draft of the manuscript. All authors contributed to the interpretation of the data and wrote the manuscript

Item and source memory for emotional associates is mediated by different retrieval processes

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Running head: Dissociative effects in item and source emotional memory.

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Keywords: Event-related potentials, Emotion, Source memory, Remember/Know, Old/New effect.

Highlights

- Memory performance for neutral items encoded in emotional and neutral contexts is mainly driven by the subjective experience of familiarity, irrespective of context.
- Memory performance for correct background sources is based on recollection processes, particularly for emotional ones.
- Correctly recognized old items evoke an overall early frontal (300-500 ms) ERP Old/New effect.
- Late parietal (600-800 ms) ERP Old/New effects are exclusively evoked by old items associated with emotional backgrounds.
- In light of a differential contribution of familiarity- and recollection-based retrieval to item and contextual source memory, emotion effects on item and (background) source memory are driven by recollection processes.

Abstract

Recent event-related potential (ERP) data showed that neutral objects associated with emotional background pictures during encoding were better remembered than objects encoded in neutral contexts, when recognition memory was tested one week later. In the present study, we investigated whether this item long-term memory advantage is also associated with correct memory for contextual source details. Furthermore, we were interested in the contribution of recollection and familiarity processes (using a Remember/Know procedure). The results revealed that item memory performance was mainly driven by the subjective experience of familiarity, irrespective of whether the objects were previously encoded in emotional or neutral contexts. Correct source memory for the associated background picture, however, was driven by recollection and enhanced when the content was emotional. In ERPs, correctly recognized old objects evoked frontal ERP Old/New effects (300-500 ms), irrespective of context category. As in our previous study (Ventura-Bort et al., 2016b), retrieval for objects from emotional contexts was associated with larger parietal Old/New differences (600-800 ms), indicating stronger involvement of recollection. Thus, the results suggest a stronger contribution of recollection-based retrieval to item and contextual source memory for neutral information associated with an emotional event.

Introduction

It has long been known that emotional arousal modulates episodic memories (see for review, Dolcos et al., 2012, 2017, in press; Weymar & Hamm, 2013). For instance, when emotional and neutral items (e.g. words, faces or scenes) are presented in isolation and item memory is tested at a later time, emotionally arousing items are better recalled (Bradley et al., 1992; Dolcos et al., 2004) and recognized (Dolcos et al., 2005; Weymar et al., 2009) than emotionally neutral items. Better memory accuracy is also associated with a stronger sense of remembering (e.g. Dolcos et al., 2005; Weymar et al., 2010) as tested by means of a Remember/Know procedure (Tulving, 1985): When participants are asked to indicate whether their memory for emotional stimuli comprises rich contextual details of the contiguous attributes conforming the encoding episode (recollection-based retrieval, measured by Remember judgments), or rather lacks contextual specifics (familiarity-based retrieval, measured by Know judgments), the memory advantage of emotional stimuli is often driven by the subjective experience of recollection (Ochsner, 2000; Sharot et al., 2004; Dolcos et al., 2005; Weymar et al., 2010). If memories are related to emotional episodes (e.g. a traffic accident), the associated adjacent, contextual neutral details (e.g. the color of surrounding cars, or the weather that day) can be integrated into the memory representation, which, by means of associative processes (Davachi, 2006; Ventura-Bort et al., 2016a) can also be better recollected (Ventura-Bort et al., 2016b). Conversely, later exposure to such associated contextual cues alone can also trigger reactivation of past emotional experiences. Hence, binding individual features associated with an episodic event, such as items and context (e.g. time, place, and other associative cues) is an important aspect of human memory, and clarifying the neural mechanisms underlying these associative processes is relevant for understanding alterations associated with clinical conditions, such as stress-related disorders and addiction.

Despite abundant data showing enhancement of emotional information in item memory (see for review, Dolcos et al., 2017, in press; Weymar & Hamm, 2013), the evidence regarding emotional influences on the accuracy of remembering contextual details (source memory) is mixed (for reviews, see Chiu et al., 2013; Kensinger, 2009; Mather & Sutherland, 2011). Emotion can facilitate memory for intrinsically associated features of emotional stimuli, but can also impair memory for associated extrinsic cues of the emotional information (Chiu et al., 2013; Mather, 2007). For instance, memory for within-item associated details, such as color (Doerksen & Shimamura, 2001; D’Argembeau & Van der Linden, 2004), spatial location (D’Argembeau & Van der Linden, 2004; MacKay & Ahmetzanov, 2005; Mather & Nesmith, 2008; Schmidt et al., 2011), or temporal order (D’Argembeau & Van der Linden, 2005; Schmidt et al., 2011; but see Koenig & Mecklinger, 2008) is enhanced for emotional stimuli (e.g. scenes or words), in comparison to their neutral counterparts. Conversely, emotion can have a negative impact on memory for between-item contextual features, when emotional objects are accompanied by neutral scenes (Kensinger et al., 2007), when neutral stimuli (e.g. objects or words) are embedded in emotional contexts (Murray & Kensinger, 2012; Nashiro & Mather, 2011; Touryan et al., 2007; Rimmele et al., 2011; Zhang et al., 2015), or when emotional scenes are presented with color frames (Rimmele et al., 2011).

Mather and Sutherland have recently proposed a solution to reconcile these controversies in the so-called *Arousal-Based Competition Theory* (ABC; Mather & Sutherland, 2011). The authors argue that modulatory effects of emotion on memory binding depend upon the attentional priority that the critical cue receives during learning (via bottom-up perceptual salience or top-down attentional focus). This suggests that emotional arousal enhances memory for neutral features of high priority information, as it occurs in within-item binding processes, while arousal weakens memory for neutral information (low priority) presented at the same time with emotional cues, as it is the case for between-item binding processes. Substantiating this view, some studies showed that memory for neutral objects or words simultaneously presented with emotional cues (e.g. high arousing words or emotional scenes) can benefit from the emotional arousal, if participants are instructed to learn word-word associations (Guillet & Arndt, 2009; Pierce & Kensinger, 2011) or to mentally connect objects and images at encoding (Luck et al., 2014; Maratos & Rugg, 2001; Smith et al., 2004a, 2005; Ventura-Bort et al., 2016b, but see Nashiro & Mather, 2011; Bisby et al., 2014). Hence, when surrounding neutral stimuli are highly prioritized by becoming an intrinsic feature of the emotional event, emotion is also able to enhance memory for such neutral information (Mather & Sutherland, 2011; see also Murray & Kensinger, 2013). The question arises, however, whether enhanced memory for neutral information intrinsically related to emotional events also includes correct source information (i.e. details about the associated emotional event). Furthermore, it is unclear whether memory for emotional item and source information is related to such distinct processes as recollection or familiarity.

Event-related potential (ERP) recording is considered a suitable brain imaging technique to explore such distinct memory processes (Tsivilis et al., 2001; Wilding & Ranganath, 2012). Due to its high temporal resolution, this tool is fundamental for disentangling the contribution of different mechanisms involved in the accomplishment of a specific behavior. Thus, applied to memory research, ERPs together with fine-grained behavioral measures (e.g. Remember/Know paradigm; Diana et al., 2006; Tulving, 1985) can shed light on the distinct mnemonic processes involved in retrieval (Duarte et al., 2004; Tsivilis et al., 2001; Wilding & Ranganath, 2012). ERP memory research has shown that previously encoded items that are correctly recognized, generate larger positive-going ERPs than correctly identified new information (for reviews, see Rugg & Curran, 2007; Weymar & Hamm, 2013; Wilding & Ranganath, 2012), an effect known as the ERP Old/New effect. Two dissociable ERP Old/New effects have been identified: (i) an early ERP Old/New effect maximal at fronto-central (Rugg & Curran, 2007) or left-frontal (Woodruff et al., 2006; Yu & Rugg, 2010) sites (300-500 ms after stimulus onset), which has been associated with the subjective experience of *familiarity*, a process that seems to be mediated by the perirhinal cortex (PrC; e.g. Eichenbaum et al., 2007), and (ii) a late ERP Old/New effect typically evident over centro-parietal (Weymar & Hamm, 2013) or left-parietal (Rugg & Curran, 2007) regions (>400 ms after stimulus presentation), which has been linked to *recollection*, (e.g. Bridson et al., 2006; Curran, 2000; Duarte et al., 2004; Düzel et al., 2001; Rugg et al., 1998; Woodruff et al., 2006; Yu & Rugg, 2010; see for review Rugg & Curran, 2007), a process associated with hippocampus (HC) and parahippocampal cortex (PhC) activation (Düzel et al., 2001; Eichenbaum et al,. 2007; Ranganath & Ritchey, 2012).

Prior ERP studies testing item memory found that the retrieval of emotional pictures is associated with an enhanced centro-parietal ERP Old/New effect in the recollection-sensitive time window (Schaefer, et al., 2011; Weymar et al., 2009, 2010, 2011, 2013; Wirkner et al., 2013, 2015; reviewed in Weymar & Hamm, 2013), an effect that is also related to Remember rather than Know judgments (Weymar et al., 2010). In a recent study (Ventura-Bort et al., 2016b), enhanced ERP positivity during retrieval was also observed for objects previously associated with emotional background scenes. When participants were instructed to actively integrate neutral objects in emotional and neutral scenes (instruction supporting within item/context binding; c.f., Kensinger, 2009, Mather & Sutherland, 2011), emotion enhanced memory was found for the arousing contexts and the associated objects, in comparison to their neutral counterparts (for similar results, see also Maratos & Rugg, 2001; Martinez-Galindo & Cansino, 2017; Smith et al., 2004). In ERPs, neutral objects paired with emotional contexts produced larger early fronto-central and late centro-parietal Old/New differences than objects from neutral contexts, indicating better memory for this material (Ventura-Bort et al., 2016b). In this study, however, based on the ERPs, no clear conclusion could be drawn on whether memory for emotional associates was based on rich contextual details or not (acontextual remembering). Therefore, the main goal of the present study was to follow up on this matter and clarify (1) the differential contribution of recollection and familiarity processes, by assessing remember/know judgments (Ochsner, 2000; Sharot et al., 2004; Tulving, 1985), and (2) the associated electrophysiological correlates, by assessing the ERP Old/New effects. Considering the possible hemispheric asymmetries in the early and late ERP Old/New effects (Rugg & Curran, 2007; Woodruff et al., 2006; Yu & Rugg, 2010), the Old/New differences were analyzed in two symmetrically lateralized sensor clusters in frontal and parietal regions.

It has been observed that the retrieval of contextual information is associated with recollection, as indexed by larger parietal Old/New differences, when contextual details of a previous event are correctly recognized (Wilding & Rugg, 1996; Wilding, 2000). However, recent evidence suggests that when context and item are processed as a single unit (i.e. unitized), source memory can also be supported by familiarity-related processes (Diana et al., 2008; Bader et al., 2010), eliciting larger frontal Old/New effects (Diana et al., 2011). Additionally, it has been shown that enhanced memory for emotional compared to neutral backgrounds is specifically supported by recollection (Murray & Kensinger, 2012), as indexed by more accurate remember judgments (Rimmele et al., 2011), and larger parietal Old/New effects (Smith et al., 2004a; but see Maratos & Rugg, 2001), in comparison to neutral contextual information. Therefore, based on these prior studies (Diana et al., 2008; Smith et al., 2004a; Weymar et al., 2009, 2010; Wilding, 2000), we expected that both familiarity and recollection processes would facilitate memory performance for item and source memory, but that increased memory for objects encoded in emotional contexts and the associated source information would be primarily driven by recollection processes .

Method

Participants

Thirty-three healthy students (30 women, 3 men; mean age = 21.8) from the University of Greifswald participated for course credits or financial compensation. All participants had normal or corrected-to normal vision and were perfect German speakers. Each individual provided written informed consent for a protocol approved by the Review Board of the German Psychological Society. Data from five participants (5 females) could not be analyzed due to various reasons (i.e. technical problems, poor EEG quality).

Stimulus material

Stimuli consisted of 360 neutral objects and 180 background scenes. Neutral objects were selected from *The Bank of Standardized Stimuli* (BOSS; Brodeur et al., 2010, 2014) and *the Ecological Adaptation of Snodgrass and Vanderwart* set (Moreno-Martínez & Montoro, 2012). Objects belonged to a heterogeneous variety of semantic categories (e.g. office supplies, electronics, household objects) and were distributed in 6 different sets of sixty items each (see Ventura-Bort et al., 2016b, for more details about the sets construction).

Background scenes were selected from the *International Affective Picture System* (IAPS; Lang et al., 2008) and consisted of 60 pleasant (e.g. erotic, adventure, babies, animals), 60 neutral (e.g. buildings, neutral views, neutral human faces) and 60 unpleasant (e.g. mutilation, attack, disgust, accident) pictures. The three categories were matched for complexity, brightness and contrast (*p*s > .14). Normative valence and arousal ratings were 7.02 (0.52) and 5.88 (.077) for pleasant scenes; 5.08 (0.45) and 3.37 (0.45) for neutral scenes; and 2.58 (0.73) and 6.00 (.54) for unpleasant scenes. The three picture categories did not overlap in the valence x arousal space (see for similar approach Iordan et al., 2017). Pleasant, neutral and unpleasant scenes differed in normative valence ratings (*p*s< .001). The arousal ratings did not differ for pleasant and unpleasant pictures (*t*s < 1), and were reliably higher for emotional (both pleasant and unpleasant) compared to neutral scenes (*p*s < .001).

During the encoding session, neutral objects were presented in an emotional or neutral background scene. In order to counterbalance object/scene pairings across participants, the six object sets were arranged in six different lists (for list construction see Jaeger et al., 2009; Smith et al., 2004a; Ventura-Bort et al., 2016b).

Procedure

The experimental design is displayed in Figure 1. During encoding, 180 objects were superimposed on 180 background scenes. Objects (mean vertical and horizontal visual angle of 4.96º) and background scenes (vertical visual angle of 7.73º, horizontal visual angle of 10.93º) were presented on a 20” computer monitor located 150 cm in front of the participant. Unlike previous studies (e.g. Jaeger et al., 2009; Jaeger & Rugg, 2012; Smith et al., 2004a), in which objects were visually separated from the scenes (white background and/or yellow frame), we facilitated object-scene integration by presenting the objects unframed and with transparent background (Ventura-Bort et al., 2016b). For each trial, objects were presented on a black background in one of the four quadrants of the screen. The four positions of the objects were randomly selected and balanced across context categories. After 3000 ms, an emotional or neutral scene was added as background. Each object and scene pairing was presented together for 5000 ms, with an inter-trial interval (ITI) of 3000, 3500, or 4000 ms. In an attempt to simulate automatic, everyday-life item/ context binding, participants were not encouraged to actively bind object and scene (unlike our previous study: Ventura-Bort et al., 2016b), but to attentively watch the object and the image when displayed together on the monitor. Moreover, item/ context pairings were presented only once (and not twice, as in Ventura-Bort et al., 2016b). No mention of a memory test was made (i.e. incidental encoding).

One week after the encoding session, participants returned to the lab for a memory task, in which old and new objects were presented. The task took place in the same sound-attenuated dimly lit room. Each participant viewed 360 objects (i.e. the three old-objects sets and three novel-objects sets). To reduce fatigue, the recognition task was split in two experimental blocks. Object presentation was pseudo-randomized, so that an equal number of objects per condition was presented in each block with the restriction that no more than six objects of the same condition (old or new) were presented in consecutive fashion.

For each retrieval trial, an object was presented in the center of the screen (mean vertical and horizontal visual angle of 5.92º) without context for 3000 ms. After the object's offset, the question "Remember/Know/New?" appeared on the screen for 3000 ms, and participants made Remember, Know, or New judgments (Figure 1). Participants were instructed to press the Remember button on the keyboard when they were certain that they had seen the object during encoding and they could bring back specific associated information that occurred at study (e.g. thoughts evoked by the object when seen for the first time). The Know button was to be pressed if the object was recognized as presented during encoding but no specific information could be recollected. Participants were instructed to press the 'New' button when the object was not seen during encoding. When objects were judged as remembered or known, participants had to retrieve specific source information associated with the object (location and picture content). Therefore, two consecutive images appeared on the screen, each presented for 3000 ms. Firstly, four possible positions (i.e. upper right, upper left, lower right, and lower left) were shown and participants had to indicate in which quadrant of the screen the object was displayed during encoding. Secondly, the words "Unpleasant, Pleasant, and Neutral" were displayed, and participants had to indicate the correct content of the picture the object was associated with. During all parts of the study, participants were instructed to avoid eye blinks and body movements, to reduce recording artifacts.

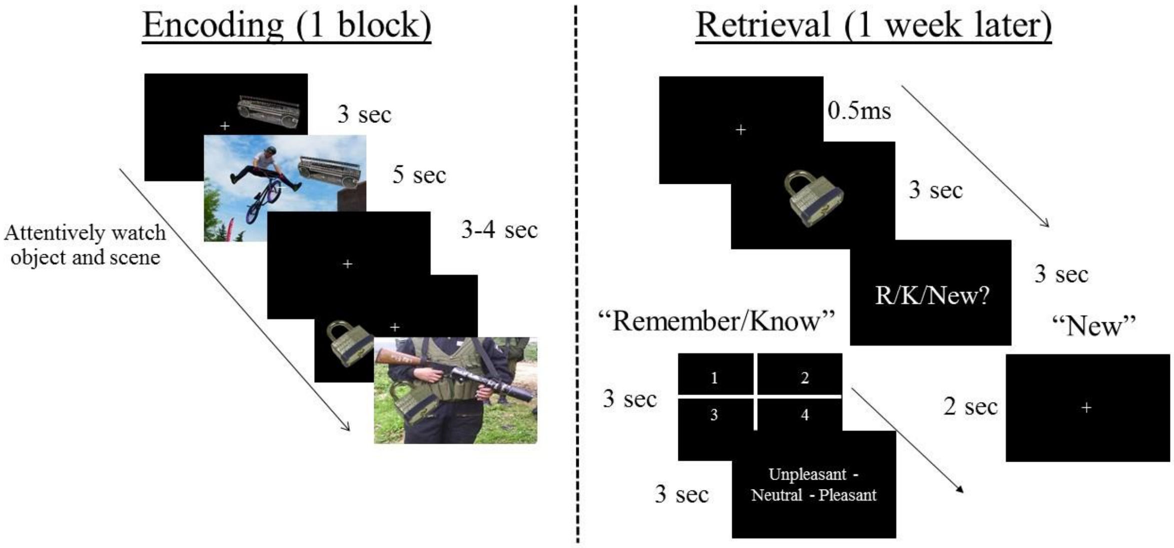

Figure 1. Schematic view of the stimulus presentation during encoding and retrieval.

Apparatus and data analysis

EEG signals were recorded continuously from 257 electrodes using an Electrical Geodesics (EGI) high-density EEG system with NetStation software on a Macintosh computer. The EEG recording was digitized at a rate of 250 Hz, using vertex sensor (Cz) as recording reference. Scalp impedance for each sensor was kept below 30 kΩ, as recommended by manufacturer guidelines. All channels were band-pass filtered online from 0.1 to 100 Hz. Stimulus-synchronized epochs were extracted from 100 ms before to 1200 ms after stimulus onset and then submitted to the procedure proposed by Junghöfer and colleagues (2000) as implemented in the EMEGS software provided by Peyk *et al.* (2011) that included lowpass filtering at 40 Hz, artifact detection, sensor interpolation, baseline correction, and conversion to the average reference (Junghöfer *et al.*, 2000). The MATLAB-based toolbox BioSig (Vidaurre et al., 2011) was used for eye movement and blink artifacts corrections of the extracted epochs. This method is based on linear regression to reliably remove electrooculogram activity from the EEG (Schlögl et al., 2007). For each participant, separated ERP averages were computed for each sensor and each condition. Due to the low number of hits for the Remember and Know conditions, both response types were merged into one 'old' condition. For item memory, only the trials correctly identifying old and new objects were included for ERP averaging (number of trials per condition: *M* = 21.1 [min= 8, max= 75], *SD* = 6.9). Furthermore, the low number of valid trials for correct contextual information did not allow reliable ERP analyses of contextual source memory (number of trials per condition: *M* = 7.6 [min= 3, max= 39], *SD* = 2.7). However, given the evidence regarding larger late ERP Old/New effects when contextual information is retrieved (Wilding & Rugg, 1996), especially when these are emotionally charged (Maratos & Rugg, 2001), exploratory analyses were performed to investigate the ERP correlates of correctly retrieved contextual information.

Based on previous studies (Duarte et al., 2004; Woodruff et al., 2006; Yu & Rugg, 2010; Ventura-Bort et al., 2016b; Tsivilis, et al., 2015; Weymar et al., 2009), and based on visual inspection of the waveforms, sensor clusters and time windows were identified where the difference between old and new conditions was maximal. The early ERP Old/New effect was analyzed in a 300-500 ms time window over frontal regions (EGI HydroCel sensors left: 16, 17, 22, 23, 24, 27, 28, 29, 30, 34, 35, 36, 42, 43, and 44; right: 4, 5, 6, 7, 12, 13, 14, 20, 185, 197, 198, 206, 207, 215, and 225), and the late ERP Old/New effect was analyzed in a window 600 and 800 ms over a central-parietal cluster (EGI HydroCel sensors left: 9, 17, 44, 45, and 53; right: 132, 144, 185, 186, and 198). Emotion effects (late positive potential, LPP) were also recorded irrespective of context judgments. For this analysis, mean ERP amplitudes were calculated for the time windows 600-800 ms and 800-1200 ms over central-parietal brain regions, as in previous ERP studies (see for review Hajcak et al., 2012).

To investigate item memory performance, hit rates were analyzed using a repeated-measures ANOVA involving the within factors *Memory Type* (Remember vs. Know) and *Emotion* (neutral objects encoded in pleasant contexts vs. neutral contexts vs. unpleasant contexts). If the interaction reached significance, follow-up analyses were performed to elucidate the cause of the interaction effect. Because Know responses are mathematically constrained by Remember responses, hit rates for Remember and Know judgments (irrespective of context category) were further scored with respect to the independence-of-redundancy assumption (Yonelinas & Jacoby, 1995). That is, remember responses (indexed by Remember hit rate - Remember false alarm) were compared to independent Know responses (as indexed by [Know hit rate/1- (Remember hit rate)] - [Know false alarm /1- (Remember false alarm)]), which represent the probability that an old object is recognized as known given that it was not categorized as remembered. For source memory performance, hit rates were calculated for correct location of each object (hit location/ hit object). For correct background picture, the unbiased hit rate

(*Hu*) was calculated (Wagner, 1993). The Hu index takes into account not only the stimulus performance, but also the judge performance, and is defined as the conjoint probability of the correct identification of a stimulus and the correct use of a response (Wagner, 1993). For instance, for pleasant contexts of objects restricted to Know judgments, the Hu is calculated as follows:

$$\frac{Hit\ Pleasant\ Context}{(Hit\ Pleasant\ Context + Error\ Pleasant\ Context)} * \frac{Hit\ Pleasant\ Context}{N°\ of\ times\ Pleasant\ Context\ is\ chosen}$$

Memory performance for both location and background recognition was analyzed using a repeated-measures ANOVA involving the factors *Memory Type* and *Emotion.* If the interaction reached significance, follow-up analyses were performed to elucidate the cause of the interaction effect.

Preliminary ERP analyses demonstrated that ERP amplitudes for objects from pleasant and unpleasant categories contexts did not differ in the chosen time windows and clusters (*p*s > .29; see for similar results Smith et al., 2004, 2005). Therefore, these two conditions were collapsed into one "emotion category" for the subsequent statistical analyses. To examine the electrophysiological correlates of item and context source memory, analyses were performed using repeated-measures ANOVAs with the within-subject factors *Memory* (old objects vs. new objects) and *Laterality* (left vs. right) over the fronto- and centro-parietal clusters. If a main effect of *Memory* or interaction was significant, follow-up analyses were performed testing the Old/New effects for each background picture category, separately. To investigate emotional differences in object processing, a 2 (*Emotion:* neutral objects encoded in emotional contexts vs. neutral contexts) x 2 (*Laterality*: Left vs. Right) repeated-measures ANOVA was performed over the centro-parietal cluster.

Results

Behavioral data

Table 1 summarizes the mean (standard deviation) hit rates for item and source memory by context category.

Item Memory.

Item memory was driven by Know judgments irrespective of emotional context. The analysis of item memory performance showed a main effect of *Memory Type* ($F[1,28] = 29.79$, $p < .001$ $\eta_p^2 = 0.52$), indicating that objects were more often categorized as known ($M = .34$, $SD = .14$) than as remembered ($M = .14$, $SD = .1$; see Figure 2A). No effect of *Emotion* ($F[1,28] = 1.02$, $p = .37$ $\eta_p^2 = 0.04$) or *Memory Type* x *Emotion* interaction ($F < 1$) were observed. After correcting for the dependency of *Know* and *Remember* responses, the analysis still revealed that memory for objects was predominantly based on knowing ($M = .15$, $SD = .08$), than remembering ($M = .09$, $SD = .06$), $t(28) = 3.87$, $p < .001$, $d = 0.7$. *Know* and *Remember* judgments also significantly differed from 0 (ps <.001), after correcting for the response dependency, indicating that participants deliberately distinguished between old and new items (no judgment based on chance).

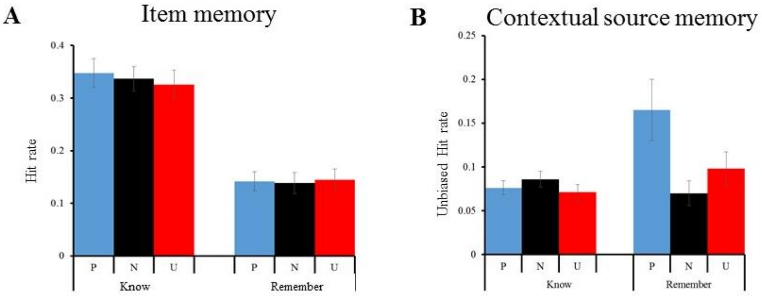

Figure 2. Memory performance in the *Remember/ Know* paradigm. **A:** Know (left) and Remember (right) hit rates for objects encoded in pleasant (blue), neutral (black), and unpleasant (red) contexts. **B:** Unbiased hit rates for contextual source memory based on Remember and Know judgments for objects encoded in pleasant (blue), neutral (black), and unpleasant (red) contexts.

Source Memory.

For location source memory, no main effect of *Memory Type* ($F < 1$) and *Emotion* ($F < 1$) was found, replicating the results of our previous study (Ventura-Bort et al., 2016b). No *Memory Type* x *Emotion* interaction was observed ($F < 1$). The hit rates did not significantly differ from chance level (.25; *t*s <1.43, *p*s > .16), indicating that participants were guessing the location of the object during encoding.

Contextual source memory was driven by Remember judgments and enhanced for emotional background contents. For correct background pictures, the analysis revealed a significant effect of *Memory Type* ($F[1,28] = 4.49$, $p = .043$, $\eta_p^2 = 0.14$), indicating that, overall, memory for contextual backgrounds was driven by Remember judgments. A trend effect for *Emotion* $F(2,56) = 2.79$, $p = .07$, $\eta_p^2 = 0.09$) was also observed. Interestingly, we found an interaction between *Emotion* and *Memory Type* ($F[2,56] = 4$, $p = .024$, $\eta_p^2 = 0.13$). Subsequent one-way ANOVAs with the factor *Emotion* were computed for each *Memory Type*, separately: For Know judgments, the *Emotion* effect did not reach significance ($F < 1$). For Remember judgments, however, the main effect of *Emotion* was significant ($F[2,56] = 3.78$, $p = .028$, $\eta_p^2 = 0.12$). Post-hoc t-comparisons showed that memory was better for the emotional contextual information compared to neutral contextual information (pleasant contexts vs. neutral contexts: $t[28] = 2.36$, $p = .025$, $d = 0.44$; unpleasant contexts vs. neutral contexts: $t[28] = 1.61$, p [one-tailed]= .059, $d = 0.31$; see Figure 2B). No differences were observed between pleasant and unpleasant contexts ($t[28] = 1.55$, $p = .13$, $d = 0.29$; see Figure 2B). Furthermore, unbiased hit rates were significantly higher than the estimated expectancy of chance level for each judgment (*t*s>2.85, *ps*< .009), suggesting that the observed memory effects were not related to chance.

In summary, item memory performance was mainly driven by the subjective experience of familiarity, irrespective of whether the objects were previously encoded in emotional or neutral contexts. Although location source memory was at chance level, contextual source memory for backgrounds was enhanced when item memory was driven by recollection. Interestingly, recognition for contextual cues (correct background picture assignment) varied as a function of the emotional properties of the contexts. Although no emotional facilitation was observed when item memory was driven by familiarity, emotional contextual cues, especially pleasant ones, were retrieved more often when item memory was based on recollection. Thus, behavioral findings, confirm our hypotheses about the involvement of both familiarity and recollection in item and context memory. However, our predictions about the emotional modulatory effects on memory performance for both item and context were only partially confirmed.

Table 1. Correct rejection and Hit rate means (standard deviation) for correctly identified new objects and Hit rates for correctly recognized old objects encoded in pleasant, neutral, and unpleasant contexts.

	Item recognition				***Source location***		***Source background (Hu)***	
	Correct Rejection	*Total hits*	*Remember*	*Know*	*Remember*	*Know*	*Remember*	*Know*
New objects	.72 (.12)	.28 (.12)	.05(.06)	.23 (.1)				
Old objects								
Pleasant context		.49 (.15)	.14 (.10)	.35 (.15)	.20 (.20)	.23 (.08)	.17 (.2)	.08 (.05)
Neutral context		.48 (.15)	.14 (.11)	.34 (.12)	.28 (.23)	.24 (.09)	.07 (.08)	.08 (.05)
Unpleasant context		.47 (.15)	.14 (.11)	.33 (.15)	.24 (.16)	.24 (.13)	.1 (.1)	.07 (.08)
Overall		.48 (.14)	.14 (.1)	.33 (.14)				
Correcting for Dependency			.08 (.06)	.15 (.07)				

ERP data

Item Memory

Early ERP Old/New effect (300-500 ms) irrespective of emotional context. Figure 3 illustrates grand average ERPs for representative frontal sensor clusters for correctly recognized old objects encoded in emotional and neutral contexts, and correctly identified new objects. At frontal regions, correctly recognized old objects elicited a larger positivity than correctly identified new objects, as shown by a main effect of *Memory*: $F(1,27) = 5.45$, $p = .027$, $\eta_p^2 = 0.17$. A main effect of *Laterality* was also found ($F[1,27] = 10.1$, $p = .004$, $\eta_p^2 = 0.27$), indicating larger overall activity over left electrode locations. However, a *Memory* x *Laterality* interaction was not observed ($F[1,27] = 2.71$, $p = .11$, $\eta_p^2 = 0.09$; see Figure 3A).

To follow-up on this interaction, the Old/New effect was assessed separately for objects encoded in emotional contexts and for those encoded in neutral contexts. Objects paired with emotional contexts elicited a larger ERP activity than new objects (neutral objects encoded in emotional contexts vs. new objects: $F[1,27]= 5.19$, $p = .031$, $\eta_p^2 = 0.16$; see Figures 3). No interactions with *Laterality* were observed ($F < 1$). For objects associated with neutral contexts, overall, ERPs did not show a larger positivity activity than new objects (neutral objects encoded in neutral contexts vs. new objects: $F < 1$), however a significant interaction with *Laterality* was found ($F[1,27]= 4.29$, $p = .048$, $\eta_p^2 = 0.14$). Follow-up comparisons revealed that objects associated with neutral contexts elicited an Old/New effect over left ($t[27]= 2.14$, $p = .041$, $d = 0.40$), but not over right brain regions ($t < 1$; see Figures 3B).

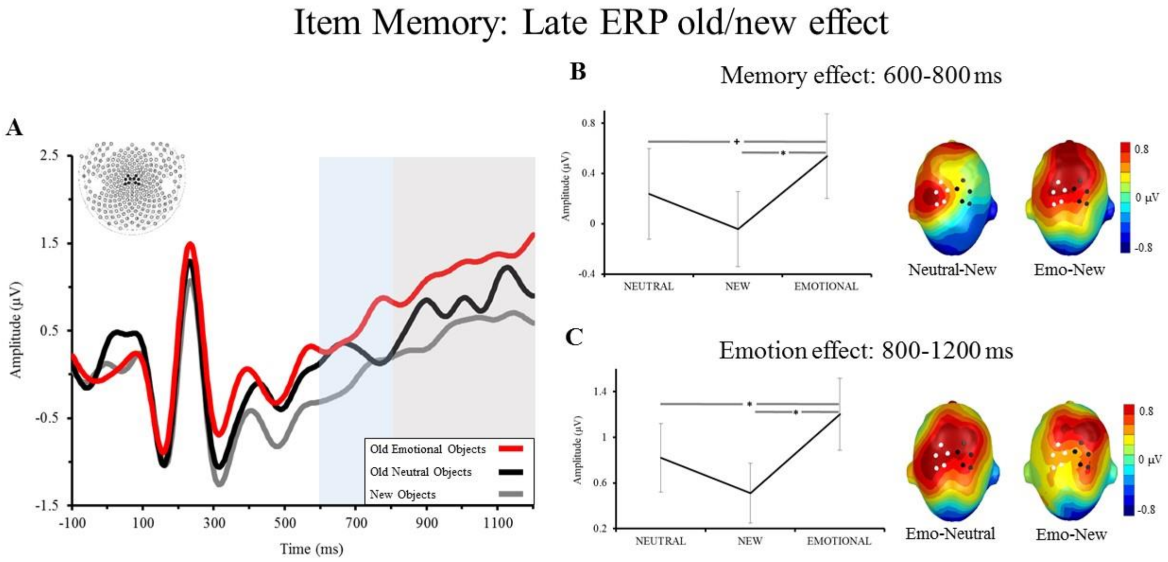

Figure 3. Early ERP Old/New effect for item memory. **A:** Grand average ERPs in response to correctly recognized new objects (gray), old objects previously encoded with neutral backgrounds (black), and old objects previously encoded with emotional backgrounds (red). ERPs were averaged across electrodes within left and right frontal clusters (see upper right inset). Lower right inset, scalp topographies for the ERP Old/New differences for each context category during the 300-500 ms time window between correctly identified old objects encoded in neutral contexts (N) and new objects (left), and correctly identified old objects encoded in emotional contexts (E) and new objects (right).**B:** Upper: Mean (standard error) ERPs of the left frontal cluster during 300-500 ms. Lower: Mean (standard error) ERPs on the right frontal cluster during 300-500 ms. * *p* < .05; + *p* < .05 one-sided.

Late ERP Old/New effect (600-800 ms) for objects encoded in emotional contexts. Figure 4 illustrates grand average ERPs for correctly recognized old objects encoded in emotional and neutral backgrounds, and correctly identified new objects for representative centro-parietal sensor clusters. At parietal sites, ERP differences were found between correctly recognized old objects and correctly identified new objects, as indicated by a main effect of *Memory* ($F[1,27] = 5.14$, $p = .031$, $\eta_p^2 = 0.16$). Neither a main effect of *Laterality* ($F < 1$) nor a *Memory* x *Laterality* interaction ($F[1,27] = 1.71$, $p = .20$, $\eta_p^2 = 0.06$) were observed. Because no *Laterality* effects were found, follow-up analyses were performed collapsing sensors across sites. T-test comparisons revealed that objects associated with emotional contexts showed Old/New differences (*t*[27] = 3.06, *p* = .005, *d* = 0.57), whereas ERPs did not differ between objects associated with neutral contexts and new objects (*t*[27] = 1.27, *p* = .21, *d* = 0.24; see Figure 4B), replicating our previous work (Ventura-Bort et al., 2016b).

<u>Enhanced Emotion effect (LPP) for objects encoded in emotional contexts.</u> During the 600-800 ms time window over parietal regions, objects associated with emotional backgrounds scenes showed a more positive-going waveform than objects paired with neutral contexts, but this difference was only significant at trend level (*Emotion: F*[1,27] = 3.61, *p* = .07, η_p^2 = 0.12). Laterality effects were not significant (*Laterality*: *F* < 1; interaction*: F*[1,27] = 2.5, *p* = .12, η_p^2 = 0.09) . During 800-1200 ms, however, analyses revealed that objects associated with emotional compared to neutral contexts evoked significantly larger LPP amplitudes (*Emotion: F*[1,27] = 5.61, *p* = .025, η_p^2 = 0.17 see Figure 4C). Again, no *Laterality* effects were observed (*Laterality*: *F* < 1; interaction*: F* < 1).

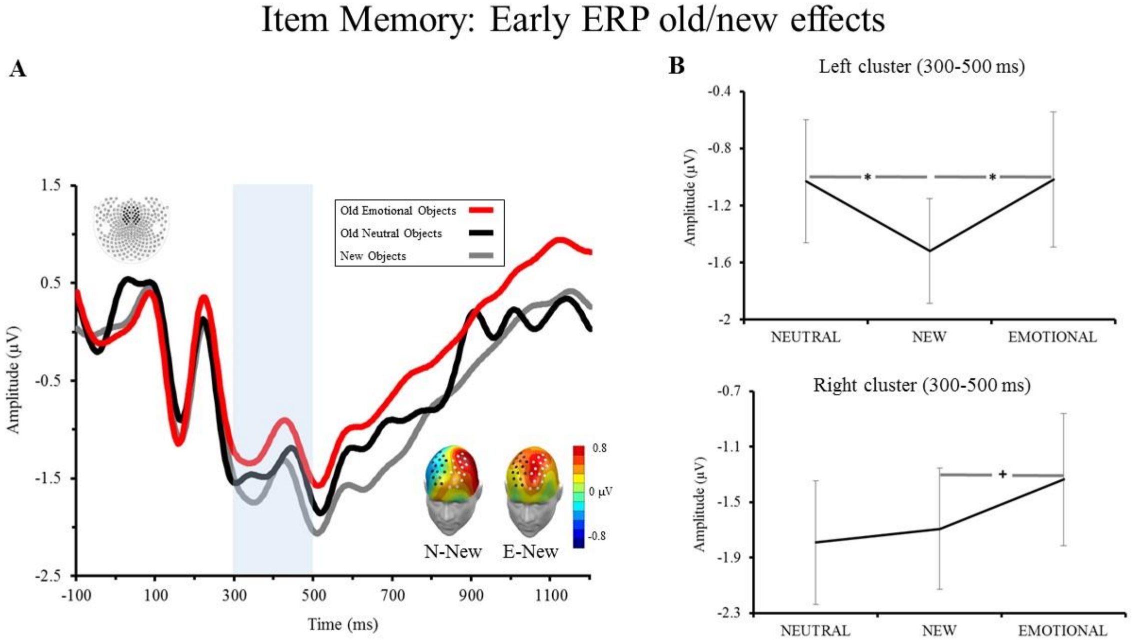

Figure 4. Late ERP Old/New effect for item memory. **A:** Grand average ERPs prompted by correctly recognized new objects (gray), old objects previously encoded with neutral backgrounds (black), and old objects previously encoded with emotional backgrounds (red) of representative lateralized centro-parietal clusters (see inset). **B:** Memory effect. Left: Mean (standard error) ERPs across electrodes within left and right centro-parietal clusters during 600-800 ms. Right: Scalp topographies for ERP Old/New differences during 600-800 ms for each context category. **C:** Emotion

effect. Left: Mean (standard error) ERPs of the whole centro-parietal cluster (800-1200 ms.) Right: Scalp topographies for tERP Old/New differences (800-1200) ms for each context category. * $p < .05$; + $p < .05$ one-sided.

Contextual Source Memory for backgrounds

Figure 5 illustrates grand average ERPs for old neutral objects presented in correctly recognized contextual emotional and neutral backgrounds and correctly identified new objects for representative frontal (Figure 5A) and centro-parietal electrode clusters (Figure 5B).

Early ERP Old/New effect (300-500ms) was not modulated by correct contextual background source memory. When contextual cues (background pictures) were correctly recognized, ERP amplitudes for the associated objects did not differ from new objects, *Memory*, $F<1$. Neither *Laterality* ($F<1$) nor interaction ($F < 1$) effects were observed (see Figure 5A).

In contrast, late ERP Old/New effect (600-800ms) was modulated by correctly recognized contextual background source. Over centro-parietal regions, ERPs to old objects with correctly recognized background pictures showed larger positivity when compared to new objects, as indicated by a significant main effect of *Memory* ($F[1,22] = 4.37$, $p = .048$, $\eta_p^2 = 0.17$). *Laterality* effects did not reach significance level (main effect: $F[1,22]$ 3.35, $p = .08$, $\eta_p^2 = 0.14$; interaction: $F<1$). Again, because no *Laterality* effects were found, follow-up analyses were performed collapsing both sensor sites. T-comparisons revealed that, when emotional contextual cues were correctly recognized, the associated neutral objects elicited a parietal ERP Old/New difference ($t[22] = 2.83$, $p = .01$, $d = 0.59$), whereas the recognition of neutral contextual cues did not evoke such an effect ($t[22] = 1$, $p = .32$, $d = 0.21$; see Figure 5B).

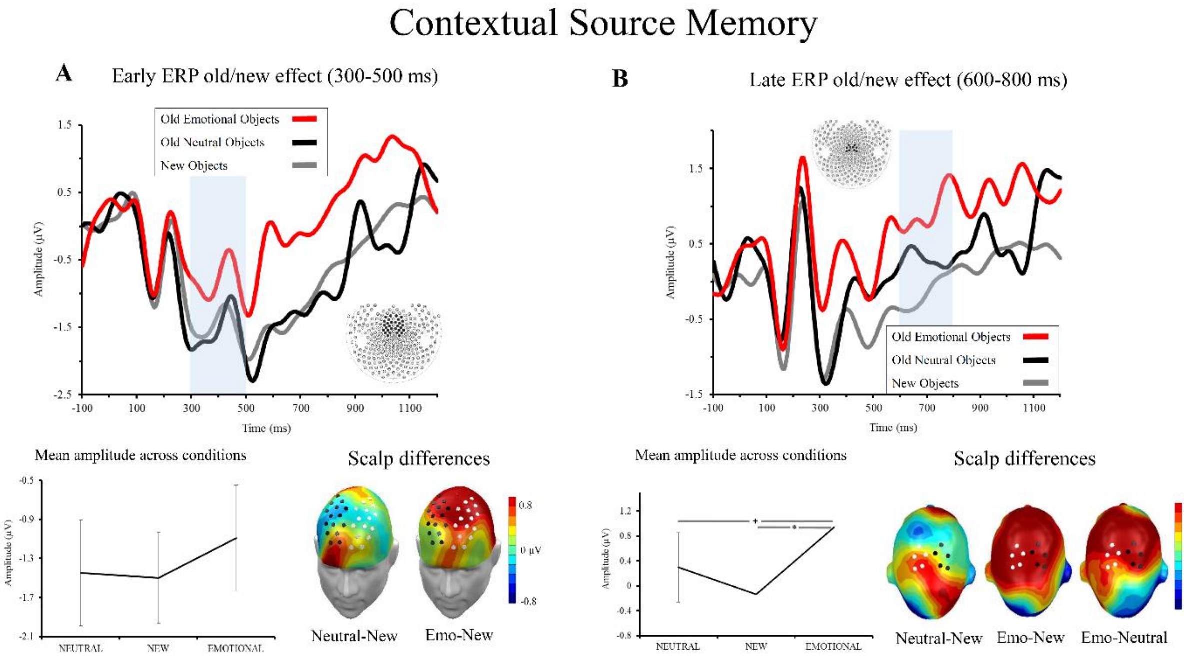

Figure 5. Early and late ERP Old/New effects related to contextual background source memory. **A:** Early ERP Old/New effect. Upper: Grand average ERPs in response to correctly recognized new objects (gray), old objects with correctly recognized neutral backgrounds (black), and old objects with correctly recognized emotional backgrounds (red). ERPs were averaged across electrodes within two frontal clusters (see inset). Lower left: Mean (standard error) ERPs across frontal clusters during 300-500 ms. Lower right: Display of the scalp topographies of the ERP Old/New differences. **B:** Late ERP Old/New effect. Upper: Mean ERPs evoked by correctly recognized new objects (gray), old objects with correctly recognized neutral backgrounds (black), and old objects with correctly recognized emotional backgrounds (red). Waveforms represent ERPs averaged across electrodes over centro-parietal sensors (see inset). Lower left: Mean (standard error) ERPs across centro-parietal clusters during 600-800 ms. Lower right: Acalp topographies of the ERP Old/New differences and ERP emotional differences. * *p* < .05; + *p* < .05 one-sided.

In summary, correctly recognized old objects evoked frontal ERP Old/New effects (300-500 ms) irrespective of context category. In a later time-window (600-800 ms), parietal Old/New differences were exclusively observed for objects encoded in emotional, but not in neutral contexts. In addition, larger LPPs were observed over parietal electrodes (800-1200 ms) for objects associated with emotional contexts, compared to neutral ones. In contrast to item memory, contextual background source memory did not show ERP Old/New effects at frontal regions. However, parietal ERP Old/New effects (600-800 ms) were observed particularly for correctly recognized emotional contexts, indicating recollection-based remembering. These ERP findings support our second hypothesis concerning the modulatory effect of emotion on the Old/New effect: for both item and background source memory, emotional enhancing effects were observed in the late ERP Old/New effect, reflecting a greater involvement of recollection-based memory.

Discussion

In the present study, we investigated item and source recognition for episodic events that involved neutral objects in emotional and neutral contexts. Using a Remember/Know paradigm, a dissociation of the mnemonic mechanism underlying item and contextual background source memory was observed. Whereas memory performance for neutral objects was mainly driven by familiarity-related judgments, independently of the emotional contexts, memory for contextual background sources was more related to recollection processes, especially for emotionally arousing backgrounds. In line with the behavioral performance, we found early frontal Old/New differences (300-500 ms) in the ERPs during object retrieval irrespective of encoding context. Parietal Old/New differences (600-800 ms), however, were found particularly for objects associated with emotional contexts. Emotional differences between objects emerged in parietal areas during 800-1200 ms, as indexed by larger LPP amplitudes for emotional compared to neutral associates. These findings will be discussed in detail below.

We observed that memory for neutral objects encoded in both emotional and neutral contexts was strongly guided by familiarity (rather than recollection) judgments, when given one week after encoding. This behavioral finding was also visible in the ERPs, in which Old/New differences were observed over frontal regions irrespective of contextual information, supporting previous studies that associate this component to familiarity (e.g. Curran, 2000; Duarte et al., 2004; Woodruff et al., 2006; Yu & Rugg, 2010; see for review Rugg & Curran, 2007). A recent ERP study (Tsivilis et al., 2015) also observed that long-term memory (4-weeks delay) for neutral objects relies more on familiarity than recollection, supporting our item memory finding.

Contrary to our predictions, we did not observe memory-enhancing effects on performance for neutral objects paired with emotional contexts. The current finding contrasts with our previous results in which memory recognition was enhanced for objects associated with emotional compared to neutral contexts (Ventura-Bort et al., 2016b). In ERPs, similar to our prior research (Ventura-Bort et al., 2016b), enhanced parietal Old/New differences were found for neutral objects encoded in emotionally arousing context, suggesting a stronger recollective experience for these items. The dissimilarities in memory performance between the present and our former study could have methodological reasons. In our previous study, we facilitated item/context binding by instructing participants to actively imagine the objects in the background contexts. We also presented the object/ context pairings twice to ensure deeper encoding (Kensinger, 2009; Mather & Sutherland, 2011). In the current study, however, we attempted to generate a more realistic scenario, avoiding the “artificial” item/ context binding instruction and presenting each pairing only once. According to the ABC theory, it is possible that these variations weakened object/ context binding and lessened the attentional priority for the objects during encoding (Mather & Sutherland, 2011), which might have impacted the behavioral but not the neural mnemonic enhancement. Given that ERPs are considered a fine-grained tool to detect changes in cognitive processing, even in the absence of behavioral indicators (e.g. Jaeger et al., 2009), these methodological changes may have led to the lack of emotional effects on memory performance in the presence of enhanced parietal ERP Old/New effects.

Interestingly, we observed ERP differences over parietal regions in a later time window (800-1200 ms) between objects from emotional and neutral backgrounds. This slow positive-going waveform resembles the LPP in time and location (e.g. Cuthbert et al., 2000; Foti et al., 2009; Hajcak & Olvet, 2008; see for review, Hajcak et al., 2012; Lang & Bradley, 2010). The LPP is a sustained positive-going waveform maximal at central posterior sites from 500 ms to several seconds after stimulus presentation (e.g. Hajcak & Olvet, 2008), and is larger following the presentation of both pleasant and unpleasant compared to neutral stimuli (Cuthbert et al., 2000; Dolcos & Cabeza, 2002; Foti et al., 2009; Schupp et al., 2000 see for review, Hajcak et al., 2012). The LPP is considered a neural index that reflects facilitated allocation of attention to motivational stimuli by means of which relevant information received increased processing resources (Ferrari et al., 2008). Associative learning studies have also observed that neutral stimuli (e.g. faces or objects) associated with emotionally relevant information (e.g. shocks or emotional pictures) evoke larger LPP amplitudes than prior to association and compared to neutral stimuli associated with non-relevant information (Pastor et al., 2015; Pizzagalli et al., 2003; Ventura-Bort et al., 2016a), indicating an increase of motivational relevance toward the emotional associates. In line with these results, the present finding seems to indicate that objects from emotional contexts, acquired motivational value, leading to a more sustained processing.

We further observed that emotion enhanced the recollection of contextual background sources. This result is consistent with prior studies assessing memory for neutral and emotional scenes (Dolcos et al., 2005; Ochsner, 2000; Sharot et al., 2004; Weymar et al., 2009, 2010), in which participants were more likely to experience vivid memories for emotionally arousing images compared to neutral ones, as indicated by higher Remember judgements and recognition confidence rates. The present finding also replicates previous results showing that memory for emotional contextual cues is related to recollection processes (Rimmele et al., 2011; Rimmele & Phelps, 2012). Moreover, the exploratory ERP analyses showed larger late parietal ERP Old/New effects exclusively when emotional information was correctly retrieved, giving further support to the greater involvement of recollection processes in emotional contextual memory.

It should be noted, however, that memory for location source information was at chance level. The inability to remember the position of the objects at encoding could be related to the relevance given to the specific information about the locus of the items (Mather & Sutherland, 2011). Indeed, attention towards irrelevant information diminishes in favor of more relevant emotional information (Schupp et al., 2007). In the present study, emotional context effects were observed during retrieval, suggesting that participants considered the background information, compared to object location as more potentially relevant, leading to better memory storage.

In terms of the underlying neural mechanisms of item and contextual background source memory, there is a large number of studies reporting that memory-related subregions of the medial temporal lobe (MTL), involving the PRc, PHc and the HC, may have different influence on the retrieval of item and source information (see for reviews, Davachi, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Ranganath, 2010; Ranganath & Ritchey, 2012). The PRc receives projections from multiple perceptual regions that collect information about unidimensional characteristics of items (the ‘what’ stream), whereas the PHc receives projections from posterior cortical areas, gathering information about contextual details (the ‘where’ stream). The ‘what’ and ‘where’ routes converge in the HC where contextual- and item-related information are elaborated and integrated to form the representation of the episodic event (e.g. Diana et al., 2007). Consistent with this, neuroimaging and lesion studies have observed that the PRc activity is related to item, but not to source memory, while the PHc and the HC (and to some extent also the retrosplenial cortex) activation is associated with source memory (e.g. Davachi et al., 2003; see for review Davachi 2006; Ranganath & Ritchey, 2012). In turn, the PRc activity can support item representations in long-term memory, when no specific contextual information is retrieved, as it is the case in familiarity-based recognition. Alternatively, PHc activity is involved in the representation of the contextual information associated with such items in long-term memory, as it occurs in recollection. Evidence for this distinction comes from studies showing that activity in the PRc is increased for items that are later recognized as familiar, whereas activity in the PHc (and HC) selectively predicts later recollection processes (e.g. Dolcos et al., 2005; Ranganath et al., 2003; see for reviews, Eichenbaum et al., 2007; Diana et al., 2007).

The fact that in the present study item recognition was mainly based on familiarity, independently of the contextual details, concurs with evidence for the involvement of the PRc in item memory (e.g. Diana et al., 2010; Staresina et al., 2008, 2011). Greater influence of recollection processes in the retrieval of contextual cues is also consistent with a greater contribution of the PHc to source memory (e.g. Davachi et al., 2003; Ranganath et al., 2003). Finally, the modulatory effects of emotion on recollection-based memory also seems coherent with the greater involvement of the PHc (Smith et al., 2004b), mediated by the amygdala (Ritchey et al., 2008) in emotional memory. The present findings therefore expand prior evidence in favor of the existence of two processes influencing recognition (Yonelinas, 2002), demonstrating that familiarity and recollection are distinct memory processes that differently contribute to item and contextual memory. Our data also support the view that memory for emotionally relevant information is based on recollection processes (Dolcos et al., 2005; Weymar et al., 2010). However, we can only draw tentative conclusions regarding the brain structures underlying the different mnemonic mechanisms. Thus, future neuroimaging studies are needed to shed light on the specific brain regions involved in item and source (background) emotional memory.

Prior source memory studies have observed that the enhanced memory for source information may be the result of a greater unitization (Diana et al., 2011). Unitization is understood as a process by means of which source and item information are codified as a single event (e.g. Bader et al., 2010), which is associated with familiarity-based memory and larger frontal ERP Old/New effects (Diana et al., 2011). When this integration involves emotionally relevant information, memory for the integrated neutral events seems to be enhanced (e.g. Guillet & Arndt, 2009). This is in line with our previous study, in which we instructed participants to actively bind item and emotional source information, and found larger frontal ERP Old/New effects for items previously associated with unpleasant backgrounds, which may, in part, be due to stronger unitization processes (Ventura-Bort et al., 2016b). In the present study, in the absence of any integration-related instructions during encoding, the observed frontal ERP Old/New effect was emotion-unspecific and only present for item memory, suggesting that the involvement of unitization was rather scarce. In contrast, the emotional enhancing effects on item and contextual background source memory were only observed for the parietal Old/New effect, indicating a greater involvement of recollection-based (likely PHc and HC-mediated) processes.

Although this study provides new insights on distinct processes involved in item and contextual background source memory, some limitations need to be mentioned. Of note, the encoding instruction (attend to item and context) meant to simulate automatic, everyday-life binding seemed to come with memory detrimental costs, as observed in an overall low hit rate which is not optimal to study the electrophysiological correlates of contextual memory. Indeed, compared to our previous study (Ventura-Bort et al., 2016b), in which participants were encouraged to actively bind object and background scene, memory performance was notably reduced (.48 vs .63, $t[57] = -4.43$, $p < .001$, $d = 1.15$). Consequently, for ERP analyses, the number of valid trials per condition was also diminished. In order to overcome this limitation, future studies should try to ensure a larger number of trials for ERP analyses, for instance, by instructing the participants to bind object and scene, duplicating the number of item/ background presentation and/ or reducing the time interval between encoding and recognition.

Conclusion

Taken together, we found that familiarity guided object recognition, irrespective of context category. On the other hand, contextual background information seems to facilitate recollection-based memory. Interestingly, emotion enhanced recollection memory for item and correct contextual background source as indicated by larger late parietal ERP Old/New effects. Our findings highlight the importance of considering mnemonic processes, such as familiarity and recollection, to provide a better understanding of the mechanisms underlying item and contextual background source memory in interaction with emotion. The ability to trigger past contextual information is crucial for the survival of the individual (McGaugh, 2000). However, in some circumstances, when the contextual cues are bound to traumatic events or to impulsive behaviors, the retrieval of these cues might bring back emotional and motivational states that, in extreme cases, could lead to the development and/ or maintenance of clinical conditions, such as stress- and trauma-related disorders and addiction (Dolcos, 2013; Ehler & Clark, 2000; Robinson & Berridge, 1993).

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Footnote

[1] ERPs were reanalyzed using a linked-mastoids reference in order to assess the reference dissimilarities with other ERP memory studies. Compared to the average reference used in the current study, the results yielded essentially the same results.

8.4. MANUSCRIPT 4

Enhanced spontaneous retrieval of cues from emotional events: An ERP study.

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Mathias Weymar

Submitted

Authors contributions:

CVB, and MW design the experiment. CVB supervised the data acquisition. CVB analyzed the data and provided the first draft of the manuscript. All authors contributed to the interpretation of the data and wrote the manuscript

Enhanced Spontaneous Retrieval of Cues from Emotional Events: An ERP Study

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Abstract

Recent evidence points to enhanced episodic memory retrieval not only for emotional items but also for neutral information encoded in emotional contexts. However, prior research only tested instructed explicit recognition, and hence here we investigated whether memory retrieval is also heightened for cues from emotional contexts when retrieval is not explicitly probed. During the first session of a two-session experiment, neutral objects were presented on different background scenes varying in emotional and neutral contents. One week later, objects were presented again (with no background) intermixed with novel objects. In both sessions, participants were instructed to attentively watch the stimuli (free viewing procedure), and during the second session, ERPs were also collected to measure the ERP Old/New effect, an electrophysiological correlate of episodic memory retrieval. Analyses were performed using cluster-based permutation tests in order to identify reliable spatio-temporal ERP differences. Based on this approach, old relative to new objects, were associated with larger ERP positivity in an early (364-744 ms) and late time window (760-1148 ms) over distinct central electrode clusters. Interestingly, significant late ERP Old/New differences were only observed for objects previously encoded with emotional, but not neutral scenes (504 to 1144 ms). Because these ERP differences were observed in a non-instructed retrieval context, our results indicate that long-term, spontaneous retrieval for neutral objects, is particularly heightened if encoded within emotionally salient contextual information. These findings may assist in understanding mechanisms underlying spontaneous retrieval of emotional associates and the utility of ERPs to study maladaptive involuntary memories in trauma- and stress-related disorders.

Keywords: Event-related potentials, ERP, Emotion, retrieval, spontaneous memory, Old/New effect.

Word count abstract: 252 words.

Introduction

When past events are intentionally retrieved, memory is usually better for events that are emotionally significant (Bradley, Greenwald, Petry, & Lang, 1992; Dolcos et al., 2017; Dolcos, LaBar, & Cabeza, 2005; Weymar, Löw, Melzig, & Hamm, 2009). This mnemonic advantage is not exclusively observed for emotional events, but also for neutral cues that have been stored as a part of the emotional event at the time of encoding (Anderson, Wais, & Gabrieli, 2006; Guillet & Arndt, 2009; Maratos & Rugg, 2001; Pierce & Kensinger, 2011; Smith, Dolan, & Rugg, 2004; Ventura-Bort et al., 2016; see for reviews Chiu, Dolcos, Gonsalves, & Cohen, 2013; Mather, Clewett, Sakaki, & Harley, 2016). For instance, when neutral items (i.e. words, objects or faces) are encoded in different contexts, memory for such items is enhanced if associated with emotional contextual cues, compared to neutral contexts (e.g. Bayer, Grass, & Schacht, in press; Galindo, & Cansino, 2016; Maratos & Rugg, 2001; Schacht, Adler, Chen, Guo, & Sommer, 2012; Ventura-Bort et al., 2016).

Further support comes from research using electrophysiological correlates of recognition memory. Studies using event-related potential (ERP) recordings during recognition memory testing (i.e., explicit retrieval) typically find larger ERP positivity for correctly recognized old items compared to correctly identified new ones, the so-called ERP Old/New effect (for reviews, Rugg & Curran, 2007; Wilding & Ranganath, 2012). Two temporally and spatially dissociable Old/New ERP effects have been identified: (1) an early Old/New effect (also labeled FN400; Curran, 1999), maximal over fronto-central (Rugg & Curran, 2007) or left-frontal sites (Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010), peaking around 300-500 ms following stimulus onset, and (2) a late ERP Old/New effect (also labeled late posterior complex, LPC; Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000), typically evident over centro-parietal (Weymar & Hamm, 2013) or left-parietal regions (Rugg & Curran, 2007), starting around 400 ms after stimulus presentation. Functionally, the early and late Old/New effects have also been linked to different processes. The early Old/New effect has been associated with memory processes related to the subjective experience of *familiarity*, that is, the retrieval of an event without specific contextual details (but also see other literature linking the early Old/New effect to implicit memory processes; Leynes, Bruett, Krizan, & Veloso, 2017; Paller, Voss, & Boehm, 2007; Voss, Lucas, & Paller, 2012; Voss & Paller, 2006, 2007).

The late Old/New effect has been related to the subjective experience of *recollection*, understood as the retrieval of an event and the specific contextual information about the learning episode (Curran, 2000; Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Rugg & Curran, 2007), as it is modulated by depth of processing (Rugg et al., 1998), amount of information recollected (Vilberg, Moosavi, & Rugg, 2006), correct source judgments (Wilding & Rugg, 1996), retrieval of associative information (MacLeod & Donaldson, 2017), high confidence ratings (Weymar et al., 2009), and the report of Remember judgements (MacLeod & Donaldson, 2017).

In the emotion memory literature, larger late ERP Old/New differences have been observed for emotionally arousing stimuli in comparison to neutral information (Weymar et al., 2009; Weymar, Löw, Schwabe, & Hamm, 2010; see for reviews, Dolcos et al., 2017; Weymar & Hamm, 2013), suggesting that memory enhancement for emotional information is mediated by the process of recollection rather than familiarity. Recent ERP work by our group also found that neutral objects encoded in emotional, but not in neutral, background scenes elicited larger late Old/New effects (Ventura-Bort et al., 2016; Ventura-Bort et al., 2017), suggesting that memory for emotional associates also relies more on recollection processes.

Although the extant literature points to converging evidence regarding recollection-based explicit retrieval for emotional events and associates, little is known about how emotion may modulate less controlled forms of memory, namely involuntary or spontaneous memories. Spontaneous memories are understood as memories that are retrieved without a deliberate intention (Berntsen, 2009). Typically, these memories are evoked by highly salient past events and/or by the presence of a specific feature matching with previously stored information

(Berntsen, 2010; Hintzman, 2011). Spontaneous memories are as recurrent in daily life as voluntary memories (Rubin & Berntsen, 2009), and such recurrence may be an advantageous mechanism by means of which effortless retrieval of relevant information can facilitate adaptive responses (Berntsen, 2009). However, spontaneous memories can also become maladaptive as it is the case in different mental disorders like depression, social anxiety disorder, or posttraumatic stress disorder (American Psychiatric Association, 2013; Horowitz, 1986).

Despite its relevance, to date only a few studies examined emotional spontaneous memory using ERPs (Ferrari, Bradley, Codispoti, Karlsson, & Lang, 2013; Jaworek, Weymar, Löw, & Hamm, 2014; Weymar, Bradley, El-Hinnawi, & Lang, 2013). In these studies, spontaneous memory was tested in a non-memory-related task, involving free viewing (Weymar et al., 2013) or an active decision task (Ferrari et al., 2013a; Jaworek et al., 2014), in which previously encoded images were presented along with new ones. Results showed enhanced parietal Old/New effects exclusively for emotional images during immediate recognition (Ferrari et al., 2013a; Weymar et al., 2013), suggesting that the mere exposure to previously seen emotionally relevant information triggered spontaneous recollection. However, when spontaneous memory was prompted one week after encoding, emotional images generated larger ERP Old/New differences over frontal regions, suggesting that for long-term delays, implicitly remembered emotional scenes were mediated by familiarity-based processes (Jaworek et al., 2014).

In the current study, we followed up on these results and investigated whether the emotional enhancing effect on spontaneous memory is also evident for neutral information previously encoded with emotional events, as indicated by ERPs. As in our previous studies (Ventura-Bort et al., 2016, 2017), participants viewed neutral objects together with emotionally arousing (pleasant or unpleasant) or neutral scenes. One week later, all previously encoded neutral items were presented again intermixed with novel ones. During retrieval, participants were instructed to attentively watch the presented material (i.e. free viewing procedure). Based on prior findings, we expected that cues paired with emotional events would more likely attract attention (Ventura-Bort et al., 2016), and thus undergo deeper memory storage, which would increase the probability of being spontaneously retrieved when re-encountered one week later. As an index for episodic retrieval, we expected to observe Old/New ERP differences, even when no explicit memory search was required, which would be particularly enhanced for neutral cues associated with emotional events.

Methods

Participants

Based on our previous results (Ventura-Bort et al., 2016, 2017), the initial sample consisted of 27 healthy students (24 women, 3 men) from the University of Greifswald, who participated for course credits or financial compensation. All participants had normal or corrected-to-normal vision. Each individual provided written informed consent for a protocol approved by the Review Board of the German Psychological Society. Two participants were excluded from the analyses due to poor EEG quality and technical problems during recording that did not allow recording during the retrieval session, leaving a final sample of 25 participants (22 women; 3 men; mean age = 23.58; SD = 3.07).

Stimulus Materials and Procedure

Stimuli consisted of 360 neutral objects and 180 background scenes. Neutral objects (e.g. office supplies, electronics, household objects) were mainly selected from *The Bank of Standardized Stimuli* (BOSS; Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010; Brodeur, Guérard, & Bouras, 2014) and the *Ecological Adaptation of Snodgrass and Vanderwart* set (Moreno-Martínez & Montoro, 2012; see for specific stimuli Ventura-Bort et al. 2017). Background scenes were selected from the *International Affective Picture System* (IAPS; Lang, Bradley, & Cuthbert, 2008) and consisted of 60 pleasant (e.g., erotic adventure, babies, animals), 60 neutral (e.g., buildings, neutral views, neutral human faces) and 60 unpleasant pictures (e.g., depicting mutilations, attacks, disgusting content, accidents, etc.; for specific details, see Ventura-Bort et al. 2017). In order to counterbalance object/scene pairings across participants, the six object sets were arranged in six different lists, ensuring that each object was equally presented within each context category.

During encoding, objects (mean vertical and horizontal visual angle of 4.96º) and background scenes (vertical visual angle of 7.73º, horizontal visual angle of 10.93º) were presented on a 20” computer monitor located 150 cm in front of the participant (for specific details, see Ventura-Bort et al., 2017). Objects were randomly presented in one of four quadrants of the screen, with the same probability for each context category, and 3000 ms after the onset of object presentation an emotional or neutral scene was added as background. Each object and scene pairing was presented for 5000 ms, and the inter-trial interval (ITI) varied between 3000, 3500, and 4000 ms. One week later, the 180 old and 180 novel objects were presented for free viewing. Of the 180 old objects, 60 objects had been encoded in the context of unpleasant scenes, 60 objects in the context of pleasant scenes, and 60 objects in the context of neutral scenes. Each object was presented for 3000 ms in the center of the screen (mean vertical and horizontal visual angle of 5.92º), followed by an ITI of 3000, 3500, or 4000 ms. Participants were seated in a comfortable chair in a sound-attenuated, dimly lit room.

During encoding, each participant was instructed to attentively watch the object and the emotional and neutral images displayed on the screen. No mention of an upcoming memory test was made (i.e., incidental encoding). One week after encoding, participants returned to the lab. After the electrode net was attached, old and new objects were presented and participants were instructed to attentively view each object on the screen and to maintain fixation at the center of the screen. Each participant was instructed to avoid eye blinks and body movements during the retrieval recording session.

Apparatus and data analysis

EEG signals were recorded continuously from 257 electrodes using an Electrical Geodesics (EGI) HydroCel high-density EEG system with NetStation software on a Macintosh computer. The EEG recording was digitized at a rate of 250 Hz, using vertex sensor (Cz) as recording reference. Scalp impedance for each sensor was kept below 30 kΩ, as recommended by manufacturer guidelines. All channels were band-pass filtered online from 0.1 to 100 Hz. Offline reduction was performed using *ElectroMagnetic EncephaloGraphy Software* (EMEGS;

Peyk, De Cesarei, & Junghöfer, 2011) a well-suited software for EEG analyses in dense arrays studies (Junghöfer, Elbert, Tucker, & Rockstroh, 2000), which included lowpass filtering at 40 Hz, artefact detection, sensor interpolation, baseline correction, and conversion to the average reference (Junghöfer et al., 2000). The MATLAB-based toolbox BioSig (Vidaurre, Sander, & Schlögl, 2011) was used for eye movement and blink artefact corrections of the extracted epochs. This method is based on linear regression to reliably remove electrooculogram activity from the EEG (Schlögl et al., 2007). If after artefact correction, a sensor within an individual trial was detected as artefact-contaminated, activity on that sensor was replaced by means of spherical spline interpolation, statistically weighted on the basis of the remaining sensors. Stimulus-synchronized epochs were extracted from 100 ms before to 1200 ms after picture onset and baseline corrected (100 ms prior to stimulus onset).

For each participant, separated ERP averages were computed for each sensor and each condition. First, old objects (irrespective of emotional and neutral picture context) were compared to new objects. If significant differences were found, old objects previously encoded with emotional pictures and old objects previously encoded with neutral pictures were compared with new objects, separately. In both analyses, a non-parametric statistical testing procedure that includes correction for multiple comparisons was used (Maris & Oostenveld, 2007), the so-called cluster-based permutation test. This test uses a two-step procedure to identify significant effects between conditions. In a first step (i.e. sensor-level criterion), F-tests are performed for each time point and sensor and those with a significant alpha value of $p = 0.05$ during at least five consecutive time points (i.e. 20 ms), and for at least five neighbor sensors are detected, and their F-values summed in “cluster masses”. In a second step (cluster-level criterion), using Monte Carlo simulations of 1,000 permuted drawings of experimental conditions and participants, random permutation cluster masses are extracted and compared against the original cluster masses with an alpha-level of $p = 0.05$. Only cluster masses that surpassed the conservative alpha-level of $p = 0.05$ in the whole time epoch (i.e. 0 to 1200 ms after stimulus onset) were considered as significant. If significant clusters masses with overlapping sensor and time point were detected, those clusters with a larger mass were considered. Following a first inspection, a cluster-based permutation test was performed, comparing objects paired with pleasant, and unpleasant background scenes to test for valence differences. Because no meaningful spatio-temporal differences were found, we treated both picture categories as one “emotional” category.

Finally, emotion effects were also analyzed (late positive potential - LPP) using the cluster-based permutation test.

Results

Overall Old/New effects

The cluster-based permutation test comparing the overall old object against the new ones, revealed two clusters exceeding the critical cluster mass of 3,664.5. A first cluster with a mass of 13,176.8, was found between 364 and 744 ms, overlapping with the time window of the early Old/New effect (sensors: 7, 8, 9, 15, 16, 17, 22, 23, 24, 30, 36, 40, 41, 42, 43, 44, 45, 48, 49, 50, 51, 52, 53, 57, 58, 59, 60, 64, 65, 66, 72, 77, 78, 79, 80, 81, 88, 89, 90, 99, 100, 101, 110, 119, 128, 129, 130, 131, 132, 143, 144, 184, 185, 186, 198, and 257) followed by a second cluster with a mass of 6,545.2 between 760 and 1148 ms, overlapping with the time window of the late Old/New effect (sensors: 6, 7, 8, 12, 13, 14, 15, 16, 17, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 36, 40, 41, 42, 43, 44, 50, 51, 52, 58, 59, 65 and 257), see Figure 1. Subsequent t-tests showed that for both, the early and late electrode cluster, electrophysiological activity for old objects was larger than for the new ones. Early Old/New effect: *t* (24) = 3.66, *p* = .001, *d* = 0.73, late Old/New effect: *t* (24) = 2.79, *p* = .01, *d* = 0.56.

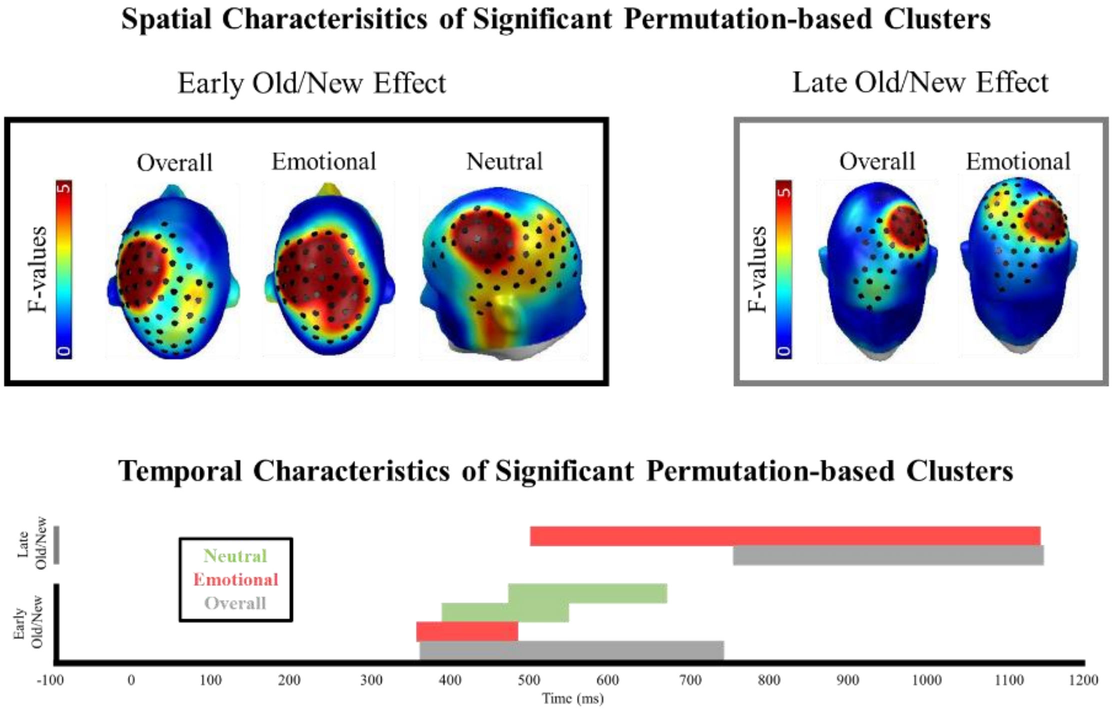


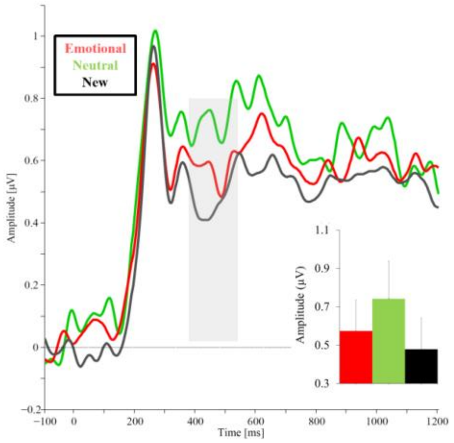
Figure 1. Spatio-temporal characteristics of significant clusters revealed by the cluster-based permutation test. The upper part displays the spatial distribution of the statistically significant sensor clusters showing early (left) and late (right) Old/New effects. The lower part displays the temporal characteristic of significant clusters during the whole epoch from 0 to 1200 ms.

Context-dependent Old/New effects

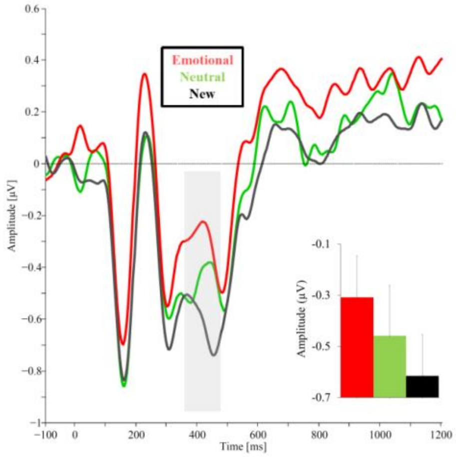
For neutral objects, the cluster-based permutation test showed two clusters with a larger mass than the critical one of 3,397.5. A first cluster with a mass of 5,549.8, was found between 392 and 548 ms (sensors: 17, 24, 30, 35, 36, 39, 40, 41, 42, 43, 44, 50, 51, 52, 53, 58, 59, 60, 62, 63, 64, 65, 66, 68, 69, 70, 71, 72, 75, 76, 77, 78, 79, 85, 86, 87, 88, 89, 96, 97, 98, 99, 100, 101, 107, 108, 109, 110, 116, 117, 118, and 119), and a second cluster with a mass of 4,039.5 was found between 476 and 672 ms (sensors: 17, 24, 30, 42, 43, 44, 50, 51, 52, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 75, 76, 82, 75, 96, 251, 255, and 256), both overlapping with the time window of the early Old/New effect. The strong similarity in time and space of both clusters indicates that they likely reflect the same underlying processes (see Figure 1). Thus, only the first cluster was considered. Subsequent t-test showed that neutral objects elicited a significant early Old/New effect: *t* (24) = 4.33, *p* < .001, *d* = 0.87 (see Figure 2).

For emotional objects, two clusters survived the critical cluster mass of 3,450. A first cluster with a mass of 13,263.5, which was found in a time window overlapping with the late Old/New effect (504-1144 ms; sensors: 5, 6, 7, 8, 9, 12, 13, 14, 15, 16, 17, 19, 20, 21, 22, 23, 24, 27, 28, 29, 30, 36, 41, 42, 43, 44, 50, 51, 52, 53, 58, 59, 60, 65, 66, 81, 90, 131, 132, 143, 144, 155, 184, 185, 186, 197, 198, 206, 207, 215, and 257), and a second cluster with a mass of 6,002.2, in the time window between 360 to 484 ms (sensors: 6, 7, 8, 9, 15, 16, 17, 23, 24, 30, 41, 42, 43, 44, 45, 50, 51, 52, 53, 58, 59, 60, 65, 66, 79, 80, 81, 88, 89, 90, 100, 101, 129, 130, 131, 132, 142, 143, 144, 155, 184, 185, 186, 197, 198, 207, and 257), overlapping with the temporal characteristic of the early Old/New effect (Figure 1). Subsequent t-test revealed larger ERP positivity for old objects from emotional contexts compared to new objects in the early, t (24) = 3.41, p = .002, d = 0.68, and late cluster, t (24) = 3.43, p = .002, d = 0.69, (Figure 2).

Early Neutral Old/New Effect



Early Emotional Old/New Effect



Late Emotional Old/New Effect

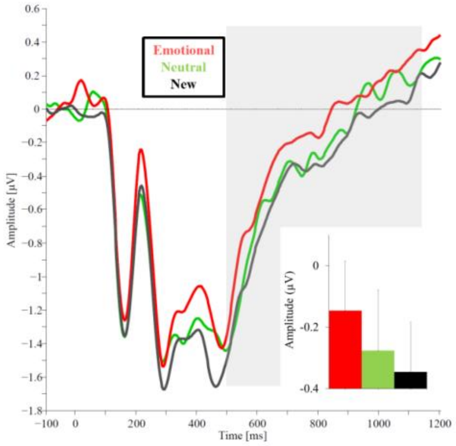


Figure 2. Grand-averaged memory related ERPs extracted from cluster-based permutation test. Grand-averaged ERPs in response to new (black) objects, and old objects encoded with neutral (green) and emotional (red) backgrounds. ERPs are presented across electrodes of the significant clusters that were found by the cluster-based permutation tests. The significant time window is shaded gray. The insets show mean amplitude of each condition (for specific cluster and time window).

Emotion effects.

We also explored whether emotion differences between objects from emotional and neutral contexts were evident in the LPP time window (400-1200 ms). Result showed that during 484-580 ms after onset, emotional associates showed larger activity over right-central electrodes than their neutral counterparts (cluster mass: 2,901.1, critical cluster mass: 2,775.5; sensors: 3, 4, 5, 6, 7, 8, 14, 15, 131, 132, 144, 155, 164, 173, 181, 182, 183, 184, 185, 193, 194, 195, 196, 197, 198, 202, 203, 204, 205, 206, 207, 210, 211, 212, 213, 214, 215, 221, 222, 223, 224; *t* [24] = 3.058, *p*= .005, *d*= 0.61; See Figure 3).

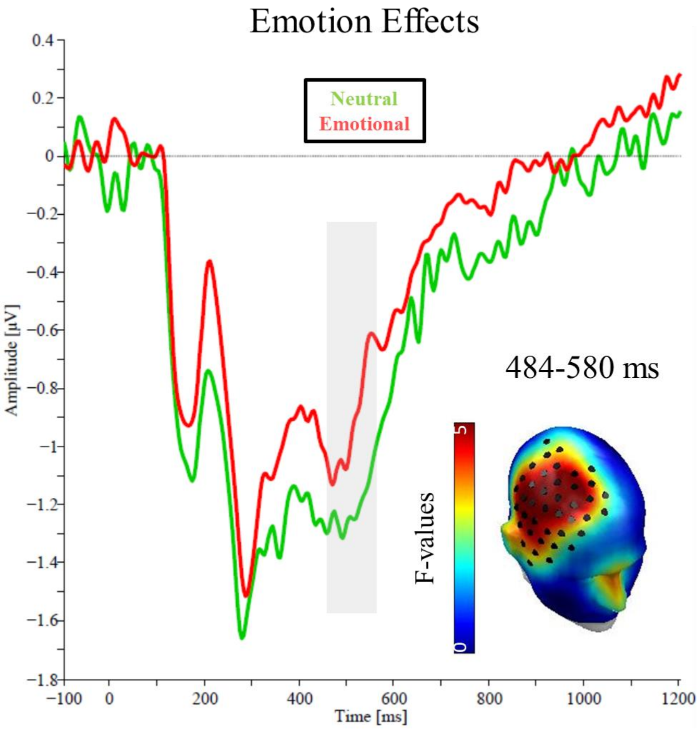


Figure 3. Emotion effects. Grand-averaged ERPs in response to old objects encoded in neutral (green) and emotional (red) backgrounds. ERPs are represented across electrodes of the significant clusters that were found by the cluster-based permutation tests. The significant time window is shaded gray. The inset represents the spatial distribution of the significant sensor cluster.

In summary, early Old/New effects were observed across different encoding context categories, whereas the late Old/New effects were exclusively found for objects encoded in emotional backgrounds.

Discussion

In the present study, we investigated how emotionally arousing contexts modulate long-term spontaneous retrieval for associated neutral information. We found earlier (364-744 ms) and later (760-1148 ms) ERP Old/New differences during mere viewing of old and new objects. Interestingly, in line with prior studies using emotional stimuli (Ferrari et al., 2013; Weymar et al., 2013), only the objects encoded in emotional contexts showed a pronounced late (504-1144 ms) Old/New effect, whereas the early Old/New effect was observed for both neutral (392-548 ms) and emotional (360-484 ms) associates. The present results extend previous findings, demonstrating that spontaneous recollection-based retrieval for emotionally arousing events, as reflected by the late ERP Old/New difference (Weymar et al., 2013), also occurs for neutral stimuli previously associated with emotional events. Our results are in line with the *Arousal-Biased Competition* theory (ABC; Mather & Sutherland, 2011). According to the ABC theory, emotionally arousing information can enhance memory for associated neutral information if, at encoding, both are bound and highly prioritized. Here object-context binding was most likely promoted by presenting the objects first and frameless over background scenes favoring emotional associative processes that led to deeper encoding and later retrieval of emotional associates (Ventura-Bort et al., 2017).

The current findings parallel results of our previous explicit recognition memory study with an identical encoding procedure (Ventura-Bort et al., 2017; see also supplementary material). During explicit recognition, we observed a comparable early Old/New effect for objects paired with emotional and neutral contexts, whereas only correctly recognized neutral objects encoded within emotionally arousing backgrounds generated larger late parietal Old/New differences. The convergence between the current study testing spontaneous memory and prior explicit memory study (Ventura-Bort et al., 2017) may suggest that similar neural processes are involved in spontaneous and explicit emotional retrieval. This assumption is also supported by recent ERP studies testing stimulus repetition effects for pictures that were presented in a massed or distributed fashion together with novel scenes, during a passive viewing procedure (Ferrari et al., 2013; Ferrari, Bradley, Codispoti, & Lang, 2015). The results showed that distributed repetition uniquely prompted a centro-parietal Old/New effect, consistent with the hypothesis of spontaneous retrieval. Further support comes from recent neuroimaging evidence which points towards similar functional activation during spontaneous and explicit retrieval. In one study, Weymar and colleagues (2018) observed that regions associated with recollection processes (Rugg & Vilberg, 2013), such as the lateral and medial posterior parietal cortex and prefrontal cortex (Weymar, Bradley, Sege, & Lang, 2018; see also, Hall et al., 2014), were activated during both spontaneous and explicit retrieval (for parietal activation see also Bradley et al., 2015). Of note, the posterior and lateral parietal cortex have been associated with episodic retrieval (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Cabeza & Nyberg, 2000; Wagner, Shannon, Kahn, & Buckner, 2005), and have been recently embedded within a general "parietal memory network" (Gilmore, Nelson, & McDermott, 2015). Considering that these regions seem to play an important role in the generation of the late Old/New effect (Hoppstädter, Baeuchl, Diener, Flor, & Meyer, 2015; Vilberg et al., 2006; Weymar, Löw, & Hamm, 2011; Weymar, Löw, Modess, et al., 2010), the enhanced Old/New differences for emotional associates across spontaneous and explicit retrieval could reflect a larger involvement of the parietal cortex on memory, independently of task demands.

Using cluster-based permutation tests, the observed early Old/New effect was significant in a central electrode cluster. Although the early Old/New effect is commonly observed over frontal regions (Curran & Rugg, 2007), some studies also reported similar early Old/New differences over posterior regions when recognizing faces (McKenzie & Donaldson, 2007) or unitized words (Bader, Mecklinger, Hoopstädter, & Meyer, 2010; Wiegand, Bader & Mecklinger, 2010). Even though both, frontal and more posterior early Old/New effects have been associated to familiarity-based retrieval, it has been suggested that the frontal Old/New effect reflects relative familiarity, which is interpreted as the increase of familiarity relative to previously encounters. The more posterior Old/New effect, however, has been suggested to reflect absolute familiarity which is the strength of the memory representation after the first encounter (MacKenzie & Donaldson, 2007). Although the objects used in our study were of daily use (e.g. office supplies, electronics, household objects), it might be that due to association with scenes, new characteristics were assigned to objects, promoting the generation of somewhat new concepts. Consequently, when encountered during retrieval, objects might have been matched to the representation formed during encoding and evoked absolute familiarity, leading to a more posterior distribution.

Interestingly, the neutral Old/New effect was left-lateralized, whereas the emotional Old/New effect was found to occur over central electrode locations. The early Old/New effect has been previously identified over central (Rugg & Curran, 2007) and left-lateralized sites (Woodruff et al., 2006; Yu and Rugg, 2010). Although to date, no studies have focused on the nature of the lateralization of the early Old/New effects (see Woodruff et al., 2006; Yu and Rugg, 2010), the fact that in the present and in our previous study (Ventura-Bort et al., 2017; see also supplementary material), a left-lateralized effect was more pronounced for neutral associates, suggest that there might be differences in the nature of the mechanisms involved during retrieval of emotional and neutral associates. Giving support to this possibility, recent neuroimaging evidence has shown that integration during encoding and retrieval of emotional and neutral information follows divergent pathways (Murray & Kensinger, 2014). Whereas the cuneus seems to be particularly involved in the retrieval of integrated emotional information, the parahippocampal cortex is more engaged during retrieval of integrated neutral information. It may thus be that the differential spatial disposition of the early Old/New effect for neutral and emotional associates is somewhat related to the involvement of different neural routes involved in retrieval.

Unlike our previous study (Ventura-Bort et al., 2017; see also supplementary material), in which emotional associates showed larger late positivity (LPP) than neutral associates, in the current study emotional effects were only observed in an earlier time interval of the LPP. The LPP has been associated with flexible, sustained and elaborative processes (Hajcak & Olvet, 2008; Olofsson, Nordin, Sequeira, & Polich, 2008), and modulated by task demands (Dunning & Hajcak, 2009; Hajcak, Dunning, & Foti, 2009). For instance, when attention is explicitly deployed towards emotional characteristics of an event, LPP amplitudes are larger for emotional compared to neutral material, however, this difference vanishes if attention is directed towards non-emotional aspects of the emotional event (Dunning and Hajcak, 2009) or when attentional resources are limited (Schupp, Schmälzle, & Flaisch, 2014). Thus, it may be that differences in LPP latencies between the present and our previous study are related to differential cognitive demands during both tasks. Specifically, explicit retrieval (focus on old and new stimuli attributes), may have limited the resources for emotion processing (Pessoa, McKenna, Gutierrez, & Ungerleider, 2002), delaying the onset of the LPP. Furthermore, methodological differences related to the number of trials included for analyses (only correctly recognized trials in Ventura-Bort et al., 2017 vs. all old trials in the current study) may have also contributed to these discrepancies. Future studies systematically testing the cognitive demands during retrieval on the timing of the LPP may help elucidate the observed discrepancy.

Although, overall, the present study reveals new insights into processes involved in emotional long-term spontaneous retrieval, it should be mentioned that we only provide neural evidence for spontaneous emotional episodic retrieval (in line with Ferrari et al. 2013; Jaworek et al. 2014; Weymar et al. 2013). Future studies should, therefore, also implement behavioral measures of spontaneous retrieval (Hall et al., 2014; Voss et al., 2012)

Conclusion

Taken together, these data indicate that in the absence of explicit retrieval, emotionally arousing contextual information facilitates the spontaneous recollection of the associated neutral cues. Involuntary retrieval of past relevant events may be beneficial to regulate behavior, in accordance with environmental changes (Hintzman, 2011), most importantly for motivationally relevant information. However, such spontaneous retrieval can sometimes become maladaptive and facilitate the development or maintenance of mental disorders, such as depression, social anxiety or PTSD (Ehlers & Clark, 2000). The present results emphasize the use of ERPs to study spontaneous (intrusive) retrieval and its neurobiological alterations in mental disorders. Moreover, consistent with prior findings, the present results indicate that affectively salient cues enhance attentional and mnemonic processes for associated neutral events, which is in accordance with the hypothesis that learning and memory processes have been tuned to facilitate the survival of the individual and of the species (Lang & Bradley, 2010).

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Supplementary Material

To compare brain activity for explicit and implicit retrieval, we re-analysed the dataset from Ventura-Bort et al., (2017), with the help of the cluster-based permutation test. Similar to the current study, we first compared the brain activity for all correctly recognized objects to all correctly identified new objects over all sensors and time epoch (0-1200ms). Following up on this analysis, correctly retrieved emotional and neutral associates were compared to correctly identified new objects, separately. Finally, emotional differences were investigated for the LPP time window (400-1200 ms) over all sensors.

Overall Old/New effects

The cluster-based permutation test which compared the overall old objects with the new ones, revealed two significant clusters exceeding the critical cluster mass of 3,231. A first cluster with a mass of 24,441.4, during 616-1152 ms (sensors: 4, 5, 6, 7, 8, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 42, 43, 44, 45, 51, 52, 53, 58, 59, 60, 64, 65, 66, 70, 71,,72, 75, 76, 77, 78, 79, 81, 86, 132, 144, 184, 185, 186, 195, 196, 197, 198, 204, 205, 206, 207, 214, 215, and 257), was matching the time window of the late Old/New effect (t[27] = 4.11, *p* <.001, *d* = 0.78), and a second cluster with a mass of 6,574.3 during 264-504 ms (sensors: 7, 8, 9, 14, 15, 16, 17, 21, 22, 23, 24, 27, 28, 29, 30, 32, 33, 36, 41, 42, 43, 44, 45, 50, 51, 52, 53, 57, 58, 59, 60 , 62, 63, 64, 65, 66, 69, 70, 71, 72, 185, 186, 196, 197, 198, and 257), was matching the time window of the early Old/New effect (t[27] = 3.22, *p* =.003, *d* = 0.61; see figure 1 and 2 in the supplementary material).

Context-dependent Old/New effects

For neutral objects, the cluster-based permutation test showed one single cluster with a larger mass than the critical one of 2,482. The cluster had a mass of 7,215.8 with the duration of 284-516 ms (sensors: 9, 17, 24, 30, 36, 40, 41, 42, 43 ,44, 45, 49, 50 ,51 ,52, 53, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 68, 69, 70 71, 72, 74, 75, 76, and 77), matching with the time window of the early Old/New effect (t[26] = 2.92, *p* =.007, *d* = 0.56; see figure 1 and 2 in the supplementary material).

For emotional objects, three clusters showing larger Old/New differences survived the critical cluster mass of 2,266. A first cluster with a mass of 24,470.3 in the time window 464-1040 ms (sensors: 4, 5, 6, 7, 8, 9, 12, 13, 14, 15, 16, 17, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 37, 38, 43, 44, 45, 52, 53, 59, 60, 65, 66, 72, 78, 79, 80, 81, 88, 90, 130, 131, 132, 143, 144, 155, 182, 183, 184, 185, 186, 195, 196, 197, 198, 204, 205, 206, 207, 213, 214, 215, 224, and 257), in line with the late Old/New effect (t[27] = 3.55, *p* =.001, *d* = 0.67), a second cluster with a mass of 7,622.8, during 244-408 ms (sensors: 6, 7, 8, 9, 14, 15, 16, 17, 22, 23, 24, 29, 30, 42, 43, 44, 45, 50, 51, 52, 53, 58, 59, 60, 63, 64, 65, 81, 131, 132, 143, 144, 155, 164, 173, 182, 183, 184, 185, 186, 194, 195, 196, 197, 198, 204, 205, 206, 207, 215, and 257) , overlapping with the timing of the early Old/New effect (t[27] = 3.91 *p* <.001, *d* = 0.74), and a third cluster with a cluster mass of 3,907.2, during 1056-1200 ms (sensors: 7, 8, 9 ,15, 16, 17, 43, 44, 45, 52, 53, 60, 66, 78, 79, 88, 13, 132, 143, 144, 155, 183, 184, 185, 186, 195, 196, 197, 198, 204, 205, 206, 207, and 257), likely reflecting the late Old/New effects. (see figure 1 and 2 in the supplementary material).

<u>*Emotion effects.*</u>

Given the differential contribution of emotional and neutral associates in the Old/New effects, we explored whether differences between both categories were also observed in the LPP time window (400-1200 ms). Result showed that during 740-852 ms after onset (sensors: 6, 7, 8, 9, 15, 16, 17, 23, 24, 45, 80, 81, 89, 90, 100, 101, 128, 129, 130, 131, 132, 141, 142, 143, 144, 185, 186, 197, 198, 207, and 257), emotional associates showed larger activity over central electrodes than their neutral counterparts (cluster mass: 3,593.2, critical cluster mass: 2,086; t [26] = 4.69, *p* < .001, *d* = 0.9)

In summary, using cluster-based permutation test, we were able to firmly replicate results from our prior analysis strategy, that is, the early Old/New effects were observed across different context categories, whereas the late Old/New effects were exclusively found for objects encoded in emotional backgrounds, strongly suggesting that objects previously encoded with emotional information triggered enhanced episodic retrieval. Furthermore, emotional differences in the LPP time window were observed between neutral and emotional associates, which suggests that objects previously associated with emotional information acquired emotional properties.

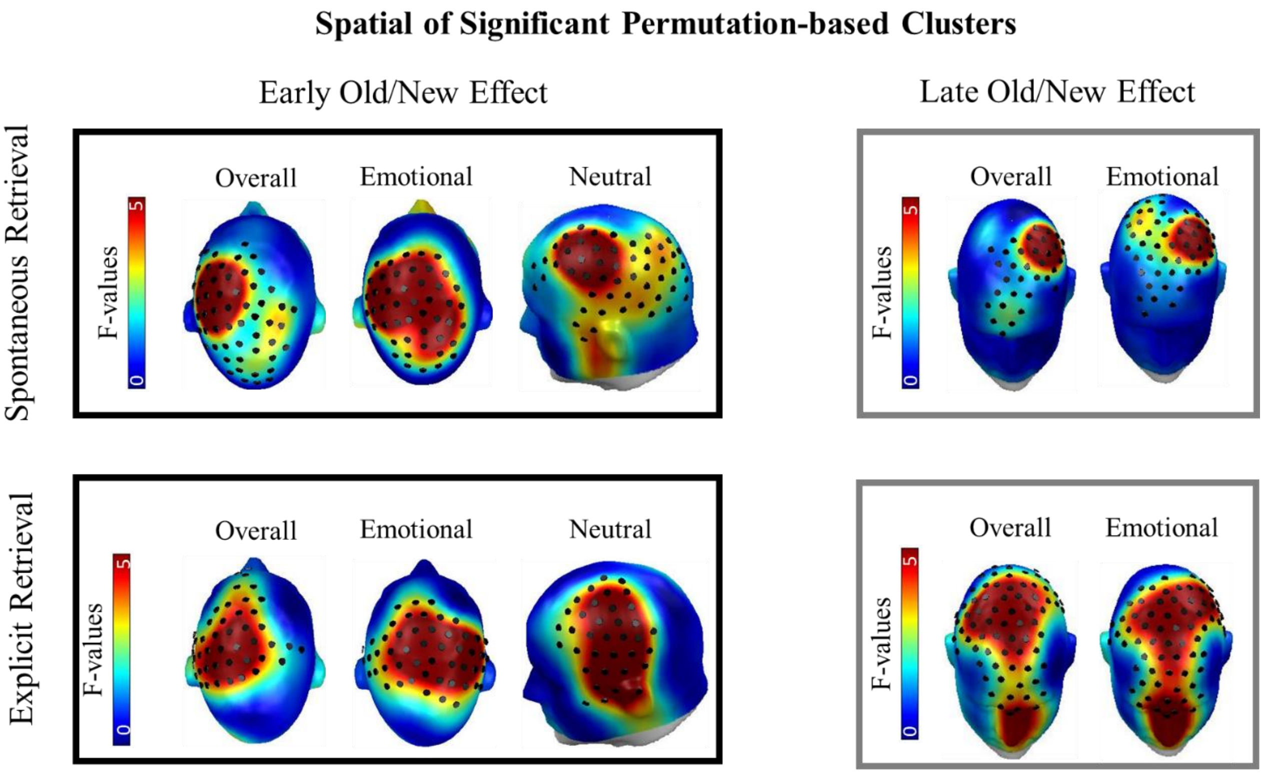

Figure 1. Spatial characteristics of significant the Old/New effects during the present study (upper part) and Ventura-Bort et al., (2017) study (lower part), using cluster-based permutation tests.

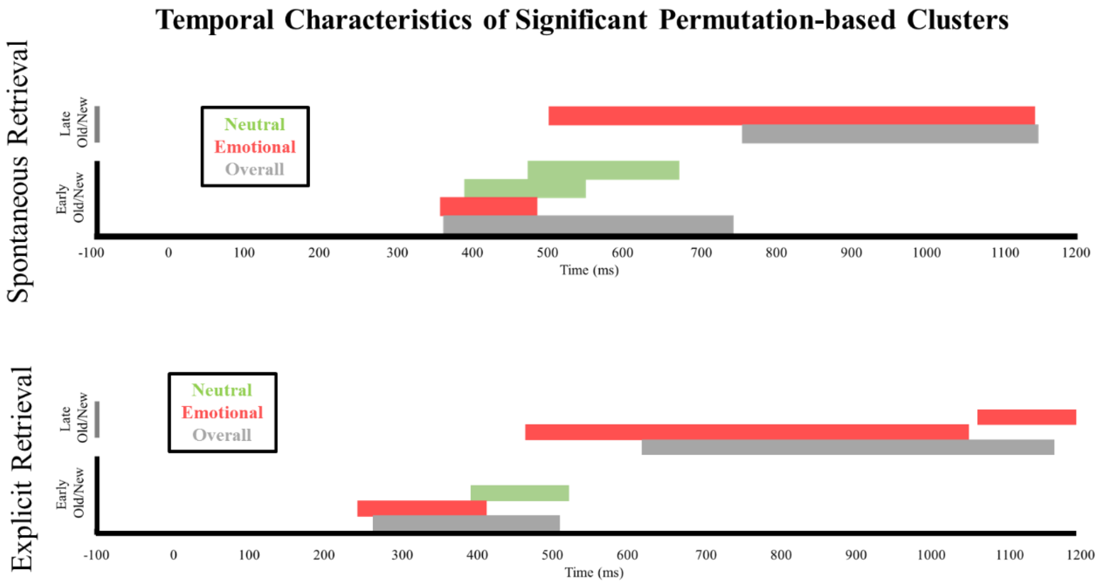

Figure 2. Temporal characteristics of significant the Old/New effects during the present study (upper part) and Ventura-Bort et al., (2017) study (lower part), using cluster-based permutation tests.

8.5. MANUSCRIPT 5

Neural substrates of long-term item and source memory for emotional associates: an fMRI study

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Submitted

Authors contributions:

CVB, FD, MW, JW, JK and AOH design the experiment. CVB supervised the data acquisition. CVB analyzed the data and provided the first draft of the manuscript. All authors contributed to the interpretation of the data and wrote the manuscript

Neural substrates of long-term item and source memory for emotional associates: an fMRI study

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Running title: Long-term Item and Emotional Source Memory

Abstract

Since Tulving's influential work on the distinction between familiarity and recollection-based retrieval, a large number of studies have found a differential contribution of these retrieval mechanisms on emotional episodic memory, being recollection more advantageous during the recognition of emotional items. Extending these findings, recent ERP research found that objects encoded with emotional, but not neutral scenes prompt enhanced long-term, recollection-based memory as evidenced by larger late (> 400ms) ERP Old/New differences. Furthermore, Neuroimaging studies suggest that recollection-based retrieval is related to stronger engagement of regions in the medial temporal lobe (MTL), posterior parietal cortex (PPC) and prefrontal cortex (PFC) regions. In the present study, we investigated for the first time the neural correlates related to long-term, recollection-based enhancement effects of emotional contexts using functional magnetic resonance imaging (fMRI). During encoding, different neutral objects integrated with emotional or neutral scenes were presented. One week later, the encoded objects were presented together with new ones and participants had to indicate whether the objects were old or new (item memory), using Remember/Know/New judgments. Furthermore, memory for the correct scene background category was also tested (contextual source memory), following the item memory judgments. First, emotion enhanced both item and contextual source memory for Remember judgments. Second, consistent with these behavioral effects, there was enhanced retrieval activity for objects encoded with emotional compared to neutral scenes in recollection-sensitive regions, including hippocampus, posterior cingulate cortex, and cuneus. Moreover, enhanced correctly retrieval of emotional compared to neutral contextual information was associated with increased activity in MTL (hippocampal and parahippocampal areas), PPC (posterior cingulate cortex), and PFC regions (both medial and orbital). Together, these results suggest that memory for emotional associates is remarkably robust over time and mediated by recollection-based processes.

Keywords: fMRI, Hippocampus, Parahippocampal Cortex, Emotion, Item Memory, Context Memory, Recollection, Retrieval.

Word count abstract: 283 words.

1. Introduction

Imagine you are walking down the street on the way to work, hands in pockets, listening to the radio, thinking about last weekend's events when suddenly you run into another passerby, fall on the street, and your nose starts bleeding. Will this unfortunate day be better remembered than any other day without such an incidence? And what about contextual information? Will the music you were listening to, the thoughts you were having, or the characteristics of the passerby you bumped into be also better remembered when associated with such an unpleasant event? In regards to the first question, a large amount of empirical evidence has robustly confirmed that there is a memory advantage for emotional events (Bradley, Greenwald, Petry, & Lang, 1992; Dolcos et al., 2017; Dolcos, LaBar, & Cabeza, 2004a, 2005; Weymar, Löw, Melzig, & Hamm, 2009). For instance, when emotional and neutral pictures are presented and memory is subsequently tested, emotionally arousing scenes are better remembered than less arousing, neutral ones, an effect found for free recall and recognition memory tasks (Bradley et al., 1992; Dolcos et al., 2005; Weymar et al., 2009), for different retention intervals (immediate and delayed; Ritchey, Dolcos, & Cabeza, 2008; Weymar, Löw, & Hamm, 2011a; Wirkner, Ventura-Bort, Schulz, Hamm, & Weymar, 2018; Schüman et al., 2018) and various stimulus materials (images, faces, sounds; Weymar et al., 2009; Maratos & Rugg, 2001; Righi et al., 2012; see for reviews, Dolcos et al., 2017; Weymar & Hamm, 2013). Furthermore, remembering an emotionally relevant event does not take place in isolation, but is typically accompanied by rich detailed information of the encoding episode. According to Tulving's seminal work (Tulving, 1985), this mnemonic advantage is related to autonoetic consciousness which is expressed by means of recollection- (remembering of a certain events and related specifics such as time or location), rather than familiarity-based retrieval (remembering an event without details; Dolcos et al., 2005; Ochsner, 2000; Sharot, Delgado, & Phelps, 2004; Tulving, 1985; Weymar, Löw, Schwabe, & Hamm, 2010).

The answer to the second question, whether emotion facilitates memory for contextual details, also termed source or relational memory, is less clear (see for reviews, Chiu, Dolcos, Gonsalves, & Cohen, 2013; Dolcos et al., 2017; Mather & Sutherland, 2011; Mather, Clewett, Sakaki, & Harley, 2016; Murray & Kensinger, 2013). Some studies observed that retrieval of source information is facilitated when associated with an emotional compared to neutral stimulus (e.g., scenes or words). These effects have been shown for the recognition of colors, spatial location and temporal order of the items (D'Argembeau & Van der Linden, 2004; D'Argembeau & Van der Linden, 2005; Doerksen & Shimamura, 2001; MacKay & Ahmetzanov, 2005; Mather, Gorlick, & Nesmith, 2009; Mather & Nesmith, 2008; Nashiro & Mather, 2011; Rimmele, Davachi, & Phelps, 2012; but see Koenig & Mecklinger, 2008; Mather & Knight, 2008; Maddock & Frein, 2009). Several studies also showed that memory for neutral objects or words integrated as a part of emotional cues (e.g. high arousing words or emotional scenes), are better retrieved than when encoded with neutral or less arousing cues (Martinez-Galindo, & Cansino, 2016; Guillet & Arndt, 2009; Luck, Leclerc, & Lepage, 2014; Maratos & Rugg, 2001; Pierce & Kensinger, 2011; Smith, Dolan, & Rugg, 2004; Smith, Henson, Rugg, & Dolan, 2005; Ventura-Bort et al., 2016). However, other studies have reported a negative impact of emotion on memory for neutral or emotional source cues (e.g. objects, words, frames, spatial location or language) presented with emotional information, compared to when encoded together with neutral material (Bisby & Burgess, 2014; Bisby, Horner, Horlyck, & Burgess, 2016; Ferré, Comesaña, & Guasch, 2019; Kensinger, Garoff-Eaton, & Schacter, 2007; Madan, Fujiware, Caplan, & Sommer, 2017; Madan, Caplan, Lau, & Fujiwara, 2012; Mather et al., 2006, 2009; Mather & Knight, 2008; Murray & Kensinger, 2012; Nashiro & Mather, 2011; Rimmele, Davachi, Petrov, Dougal, & Phelps, 2011; Touryan, Marian, & Shimamura, 2007). Altogether, these findings point to divergent effects of emotion on source memory, i.e., in some cases enhancing and in others decrementing memory retrieval.

The Arousal-Biased Competition Theory (Mather et al., 2016; Mather & Sutherland, 2011) integrates these conflicting findings of emotion effects on source memory. According to this model, the modulatory effects of emotion on memory binding depend upon the attentional priority that the critical cue receives during learning (via bottom-up perceptual salience, top-down attentional focus, or via past experience with particular stimuli). Therefore, emotional arousal can have opposing effects on neutral associated cues, enhancing their memory if high-prioritized or integrated in the emotional event, or weakening their memory if low-prioritized or perceived as a competitor for resources against emotional cues (Mather et al., 2016; Mather & Sutherland, 2011).

Along with the priority-dependent effects, the retention interval is another important feature that may exert crucial influence on the effects of emotion on source memory (Mather et al., 2016; Mather & Sutherland, 2011). Indeed, increasing retention interval and thereby memory consolidation has been shown to potentiate the enhancing effect of emotion on episodic memories (McGaugh, 2004; Phelps & Sharot, 2008; Schümann, Bayer, Talmi, & Sommer, 2017; Sharot et al., 2004; Yonelinas & Ritchey, 2015). In line with this, longer retention intervals favor memory retrieval for items paired with emotional (particularly unpleasant) information in comparison to neutral material, likely by facilitating consolidation processes (Pierce & Kensinger, 2011). Thus, memory for neutral information and/or source details may be enhanced if integrated with emotional material, particularly when the retention interval is long enough to allow for consolidation processes to take place.

Findings from our studies using event-related potentials (ERPs) support these assumptions. When neutral objects are presented with emotional and neutral background scenes and participants are instructed to mentally integrate or connect both events (which gives to such associations high "attentional priority"), neutral objects associated with emotional scenes do not only undergo deeper encoding processing (Ventura-Bort et al., 2016), but also facilitate long-term memory storage (Ventura-Bort et al., 2016). Moreover, when ERPs are measured during a 1-week-delay recognition task, a larger late positive-going waveform over centro-parietal regions, compared to correctly identified new objects (ERP Old/New effect) is found for objects encoded in emotional background scenes (Ventura-Bort et al., 2016; Ventura-Bort et al., 2017; see for similar results, Martinez-Galindo & Cansino, 2016; Maratos & Rugg, 2001; Meng et al., 2017; Smith et al., 2004). This effect was also observed during a long-term spontaneous retrieval task, suggesting that the memory enhancement is driven by the acquired motivational relevance of the triggering event (Ventura-Bort et al., in revision). Given that the late ERP Old/New effect has been associated with recollection-based retrieval (Rugg & Curran, 2007; MacLeod & Donaldson, 2017), our findings extended prior emotional item memory studies (Weymar et al., 2009; Weymar & Hamm, 2013), indicating that the long-term memory retrieval for emotional associates is also mediated by the process of recollection (Curran, 2000; Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Rugg & Curran, 2007; Düzel et al., 1997; MacLeod & Donaldson, 2017).

In the present study, we followed up on this ERP research and used functional magnetic resonance imaging (fMRI) to identify the underlying brain substrates related to the long-term memory enhancing effects of emotional contextual information, and their link to recollection processes. As in our ERP studies, we specifically focused on episodic memory retrieval. In brain imaging studies, episodic retrieval is associated with greater activation in various brain regions, including the medial temporal lobe (MTL), which encompasses the hippocampus (HC) and associated parahippocampal cortices (e.g., perirhinal cortex, PrC and parahippocampal, PHC), the prefrontal cortex (PFC), including the medial and orbital areas, and the posterior parietal cortex (PPC), including the angular gyrus (AG), retrosplenial/posterior cingulate cortex (PCC) and cuneus/precuneus (PCUN) (see for reviews, Davachi, 2006; Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Ranganath, 2010; Ranganath & Ritchey, 2012). These anatomical regions seem to have both specific and shared (or complementary) functions within the retrieval network including their involvement in recollection- and familiarity-based processes. For instance, Rugg et al. (2012) found in a detailed review of eight studies from their own group that particularly HC activation consistently increased with the amount of information retrieved, both during item recognition and source recognition tasks, suggesting that HC is modulated by the quantity of retrieved information. Furthermore, the successful retrieval of associated source information has been not only related to HC but also to PHC (Düzel et al., 2003; see for review Diana et al., 2007) medial PFC (e.g., Schlichting & Preston, 2015), and PPC activity (Vilberg & Rugg, 2007, 2009a, 2009b; see for reviews, Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Rugg & King, 2018; Sestieri et al., 2017; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005), particularly when memory retrieval was based on recollection- rather than familiarity-related judgments (Wheeler & Buckner, 2004).

Of note, the activation of PPC regions seems to be closely related to the aforementioned recollection-sensitive late ERP Old/New effect, as suggested by studies using combined fMRI-ERP (Vilberg et al., 2006) and ERP source localization analysis (Weymar, Löw, Modess, et al., 2010; Weymar, Löw, & Hamm, 2011). Along this line, prior brain imaging studies using immediate and long-term retrieval also suggest that —as for the ERP old/new effect (e.g., Weymar et al., 2009; 2011)— the recognition of emotional information (e.g. scenes) is associated with enhanced PPC activity (Keightley, Chiew, Anderson, & Grady, 2011; Sterpenich et al., 2009). Furthermore, emotion-specific retrieval effects have been also observed in MTL and PFC regions (Keightley et al., 2011, Dolcos et al., 2005, Sterpenich et al., 2009; see for review LaBar & Cabeza, 2006) as part of a putative recollection network (Gilmore, Nelson, & McDermott, 2015; King, de Chastelaine, Elward, Wang, & Rugg, 2015; Rugg & Vilberg, 2013). However, the scarce evidence for the emotion effects on the neural substrates underlying immediate source memory retrieval is mixed. Whereas Smith and colleagues observed that the retrieval of neutral objects encoded in emotional backgrounds elicited stronger MTL and PFC activation than objects encoded in neutral background scenes (Smith, Henson, Dolan, & Rugg, 2004; Smith et al., 2005), other studies have found opposing effects. For instance, memory for neutral words integrated with other emotional words, compared to neutral ones, showed larger activation in the PPC regions, but lower in MTL regions. Similarly, memory for information paired with emotional cues was related with a decrease activation of the MTL regions, compared to when paired with neutral cues (Bisby et al., 2015).

Here, we investigate for the first time whether during long-term memory retrieval, in which emotional effects are more prominent (McGaugh, 2000), neutral cues previously associated with emotional arousing events engage brain areas typically associated with episodic memory (i.e. MTL, PFC, and PPC) more strongly than cues previously related to low arousing neutral events. To address this, we presented neutral objects integrated with emotional or neutral scenes and, one week later, the same encoded objects together with new ones were presented to participants who had to indicate whether the objects were old or new (item memory), and which background category the object was paired with (contextual source memory). To directly assess the contribution of recollection- and familiarity-based memory, Tulving's Remember/Know paradigm was used (Tulving, 1985). In line with prior studies (Ventura-Bort et al., 2016, 2017), we expected that emotion would increase recollection-based memory for objects paired with emotional backgrounds as well as for contextual source information. In accordance with the behavioral performance, we expected larger activation in regions of the recollection memory network for successfully retrieved items. As in prior imaging studies testing long-term memory of emotional scenes (i.e. item memory; Sterpenich et al., 2009; Dolcos et al., 2005), we expected to find larger activation in MTL, PFC, and PPC regions for successfully retrieved objects paired with emotional backgrounds compared to their neutral counterparts. Similarly, given that recognition memory for contextual source cues is also guided by recollection processes (Ventura-Bort et al., 2017) and has been associated with greater activation in regions of the recollection memory network (Rugg et al., 2012; Rugg & Vilberg, 2013; Rugg & King, 2017), we expected increased activation of MTL, PFC, and PPC regions during the retrieval of contextual cues, especially for emotional background scenes in comparison to their neutral counterparts.

2. Methods

2.1. Participants

A total of thirty-two healthy students (29 women, 3 men; mean age = 22.68) from the University of Greifswald participated for course credits or financial compensation. All participants had normal or corrected-to-normal vision and were native German speakers. Each individual provided written informed consent for a protocol approved by the Review Board of the German Psychological Society. Data from three participants (all female) could not be analyzed due to technical problems during recording, leaving a total of 29 participants (26 women; mean age = 22.75). For fMRI data, 6 participants were excluded from retrieval analyses due to excessive head movements (> 3mm), leaving a final sample of 23 for fMRI analyses.

2.2. Stimulus material

Stimuli consisted of 264 neutral objects and 132 background scenes. The neutral objects were selected from *The Bank of Standardized Stimuli* (BOSS; Brodeur et al., 2012; Brodeur, Guérard, & Bouras, 2014) and *the Ecological Adaptation of Snodgrass and Vanderwart* set (Moreno-Martínez & Montoro, 2012). Objects belonged to a heterogeneous variety of semantic categories (e.g. office supplies, electronics, household objects) and were distributed in six different sets of forty-four items each (see Ventura-Bort et al., 2016). The sets were carefully matched in terms of semantic category, familiarity, object agreement, and manipulability according to the normative scores of the standard samples (see BOSS and ecological adaptation of Snodgrass and Vanderwart norms). The background scenes were selected from the *International Affective Picture System* (IAPS; Lang, Bradley, & Cuthbert, 2008) and consisted of 44 pleasant (e.g. erotic, adventure, babies, animals), 44 neutral (e.g. buildings, neutral views, neutral human faces), and 44 unpleasant (e.g. mutilation, attack, disgust, accident) pictures. The three categories were matched for complexity, brightness, and contrast (ps > .5). Normative valence and arousal ratings were 7.14 (0.48) and 6 (.076) for pleasant; 5.13 (0.36) and 3.25 (0.35) for neutral; and 2.34 (0.6) and 6.06 (0.56) for unpleasant scenes. The three picture categories did not overlap in the valence x arousal space (see for similar approach, Iordan, Dolcos, & Iordan, 2015; Ventura-Bort et al., 2017). Pleasant, neutral, and unpleasant scenes differed in normative valence ratings (ps< .001). Arousal ratings were higher for emotional (both pleasant and unpleasant) compared to neutral scenes (ps < .001) but did not differ between pleasant and unpleasant pictures (ts < 1). Finally, to counterbalance object/scene pairings across participants, the six object-sets were arranged in six different lists (for list construction see Ventura-Bort et al., 2016b), and each of the six object-sets was assigned to each of the experimental conditions across lists.

2.3. Procedure and design

The experimental design is displayed in Figure 1. During encoding, 132 objects were superimposed on 132 background scenes. Objects (mean vertical and horizontal visual angle of 6.18°) and background scenes (vertical visual angle of 9.27°, horizontal visual angle of 33.1°) were presented on a mirror located 18 cm distance from the eyes of the participant. For each trial, objects were presented on a black background in one of the four quadrants of the screen. The four positions of the objects were randomly selected and balanced across context categories[3]. After 3000 ms, an emotional or neutral scene was added as background for 5000 ms. During presentation of the object-background compound (5s), participants were instructed to imagine the object as a part of the scene (to enhance between-item

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[3] To keep the design as similar to our previous studies as possible, we maintained the object location equiprobable in the four quadrants of the screen across context categories. However, based on the low memory performance for object location previously found (Ventura-Bort et al., 2016b, 2017) and to avoid longer scanner sessions, we decided not to evaluate source memory location during retrieval.

binding). No mention of a later memory test was made (i.e., incidental encoding). After a 2000 or 4000 ms blank screen following object-background offset, a question mark was presented in the middle of the screen for 2000 ms to which participants indicated whether the imagination was successful or not by pressing a ‘yes’ or ‘no’ button on a response pad. Inter-trial intervals jittered between 6000 and 8000 ms. A fixation cross was presented continuously during all object/picture trials to ensure that participants fixated the center of the screen.

One week after the encoding session, participants returned to the scanner for a surprise memory task, in which old and new objects were presented. Each participant viewed 264 objects (i.e., the three sets of old-objects and three sets of novel-objects). To reduce fatigue, the recognition task was split in two experimental blocks (i.e. two different runs). Object presentation was pseudo-randomized, so that an equal number of objects per condition was presented in each block with the restriction that no more than six objects of the same condition (old or new) were presented in consecutive fashion.

For each recognition trial, an object was presented in the center of the screen (mean vertical and horizontal visual angle of 7.73°) without context for 3000 ms. After a 3000 or 5000 ms blank screen following object offset, the question “Remember/Know/New?” was presented on the screen for 2000 ms, and participants were asked to make ‘Remember’, ‘Know’, or ‘New’ judgments (Figure 1). Participants were instructed to press the ‘Remember’ button on the response pad when they recognized the object as shown during encoding and could bring back specific associated information that occurred during encoding (e.g., thoughts evoked by the object when seen for the first time). The ‘Know’ button was required when the object was recognized as presented during encoding but without specific associated information, and participants were instructed to press the ‘New’ button when the object was not seen during encoding. If participants made ‘Remember’ or ‘Know’ judgments, the question “Unpleasant/Neutral/Pleasant?” was displayed for 2000 ms and participants had to indicate the emotional category of the contextual background scene that was paired with the object during encoding. Inter-trial intervals were jittered between 6000 and 8000 ms.

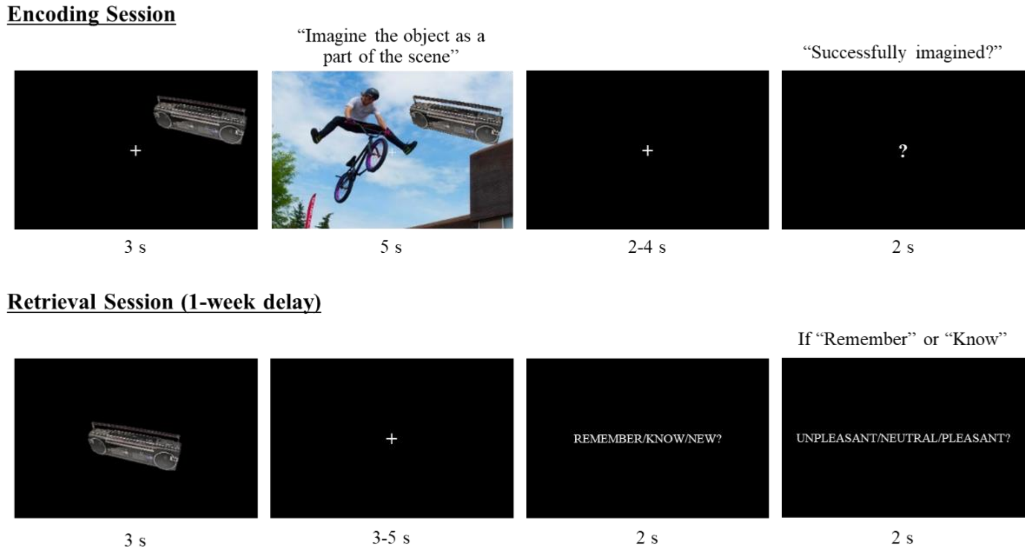

Figure 1. Schematic representation of the task design. During encoding, participants incidentally viewed 132 different everyday objects (office supplies, electronics, household objects) presented in one of the four quadrants of the screen, overlaid on 132 different background scenes that were either pleasant, neutral or unpleasant. Object/background integration was facilitated by presenting the objects frameless and with transparent background, and by instructing participants to imagine that the object is a part of the scene. During retrieval, participants viewed the encoded objects intermixed with new objects and performed a recognition task, using Remember/Know/New judgments. If objects were recognized as old (i.e. Remember or Know), participants were asked to retrieve the associated scene background (pleasant, unpleasant or neutral).

2.4. Behavioral data recording and analysis

Behavioral performance for objects and contexts was recorded using Presentation (v. 16.5; (Neurobehavioral Systems Inc., Albany, CA, USA). Memory performance for item (i.e., objects) and source (i.e. contexts) was analyzed separately, using both IBM SPSS Statistics 24, and JMP 5.0. For item memory, we first investigated the differential contribution of recollection and familiarity by analyzing differences between Remember and Know judgments. Because Know responses are mathematically constrained by Remember responses, hit rates for Remember and Know judgments (irrespective of context category) were scored with respect to the independence-of-redundancy assumption (A P Yonelinas & Jacoby, 1995). Remember responses were indexed by: *P Remember Hit Rate – P Remember False Alarms*. Independent Know responses representing the probability that an old object was recognized as known given that it was not categorized as remembered were scored as:

$$\frac{PKnowHitRate}{1-PRememberHitRate} - \frac{PKnowFalseAlarm}{1-PRememberFalseAlarm}$$

In a second step, we analyzed the effects of emotional and neutral contexts on item memory. In preliminary analyses, we explored possible valence effects on hit rates for objects from pleasant and unpleasant scene contexts. Because no differences were observed (*t*s < 1), they were collapsed into one *emotional* category. Thus, hit rates were individually scored for objects encoded in emotional and neutral backgrounds and analyzed using a repeated-measures ANOVA involving the within-factors *Memory Type* (Remember vs. Know) and *Emotion* (neutral objects encoded in emotional contexts vs. neutral contexts). Interactions were followed up with post-hoc t-tests using Bonferroni correction (α/n comparisons).

For contextual source memory performance, the unbiased hit rate (*Hu*) was calculated (Wagner, 1993; Ventura-Bort et al., 2017). The *Hu* index takes into account not only the stimulus performance, but also the judge performance, and is defined as the conjoint probability of the correct identification of a stimulus and the correct use of a response (Wagner, 1993). For instance, for neutral contexts of objects restricted to Know judgments, the Hu is calculated as follows:

$$\frac{\frac{HitKnowNeutralContext}{(HitKnowNeutralContext + IncorrectKnowNeutralContext)} * HitKnowNeutralContext}{N°of \times NeutralContextischosenunderKnowjudgements}$$

Hit Know Neutral Context: Number of objects paired with neutral contexts retrieved based on Know judgments and whose background category was correctly identified

Incorrect Know Neutral Context: Number of objects paired with neutral contexts retrieved based on Know judgments and whose background category was not correctly identified.

N° of times Neutral Context is chosen under Know judgments: Number of objects whose background was labeled as “Neutral”, including those whose background was mistakenly misclassified.

Similar to item memory, in a preliminary step, we explored possible valence differences between pleasant and unpleasant contexts. Because no differences were observed (*t*s < 1), they were treated as one *emotional* category. Source memory performance was analyzed using a repeated-measures ANOVA involving the factors *Memory Type* and *Emotion*. Interactions were followed up with post-hoc t-tests using Bonferroni correction (α/n comparisons).

2.5. Functional imaging data recording, preprocessing, and analysis

Functional and anatomical images were recorded using a 3 T Siemens Magnetom Verio scanner with a 32-channel head coil. During encoding, 1360 echo-planar images (EPIs) were recorded. During retrieval, a total of 1880 EPIs were acquired in two runs (990 each). For both encoding and retrieval, EPIs were acquired in transversal direction in a 20° angle to the AC-PC-line (34 slices, voxel size 3 x 3 x 4 mm, 1 mm gap, TR 2000 ms, TE 30 ms, matrix 64 x 64, flip angle 90°). A T1-weighted anatomical volume (MP-RAGE, 176 sagittal slices, voxel size 1 x 1 x1 mm, TR 1690 ms, TE 2.52 ms, matrix 256 x 256 mm, flip angle 9°) was also recorded.

MRI data were preprocessed and analyzed with SPM12 (Functional Imaging Laboratory, Wellcome Centre for Human Neuroimaging, London, UK). Functional images were realigned to the first scan to account for head movements and unwarped to correct for magnetic field inhomogeneities. Afterwards, images were co-registered with the anatomical T1 volume, spatially normalized using segmentation and spatially smoothed (8 mm FWHM Gaussian kernel). Preprocessed volumes were entered in different 1st level general linear models (GLM) for analysis of item and source memory, as follows.

2.5.1. *GLM for Item memory*

For item memory, due to a low number of Remember responses per run, Remember and Know judgments were collapsed together into one Hit condition. The model was composed of a total of 17 regressors: 8 regressors modeled the object onsets (pleasant object hits, pleasant object misses, unpleasant object hits, unpleasant object misses, neutral object hits, neutral object misses, false alarms and correct rejections), two regressors modeled the onset of the questions (for item memory and source memory) and one regressor modeled the button press. The remaining six regressors (of non-interest) modeled movement-related noise.

2.5.2. *GLM for contextual source memory*

For contextual source memory, a total of 20 regressors were entered: 11 regressors modeled the object onset (correct pleasant context, incorrect pleasant context, pleasant misses, correct unpleasant context, incorrect unpleasant context, unpleasant misses, correct neutral context, incorrect neutral context, neutral misses, false alarms and correct rejections). The model also included the regressors for the onset of the questions (i.e., two), the button press (i.e., one) and the motion parameters (i.e., six).

Analyses were performed using a Region-of-Interest (ROI) approach with a significance threshold of $p < 0.05$ corrected for multiple comparisons (family wise error rate; FWE) and a minimum cluster size of 5 voxels. ROI analyses were conducted on regions embedded in the recollection network, including the HC, PHC, PCUN, cuneus, PCC, AG, medial and orbital PFC. The mask for the HC, created based on published guidelines for manual tracing of the MTL (Moore et al., 2014), was obtained from FD lab, the masks for PHC, medial PFC, orbital PFC, PCC, PCUN, and cuneus, were derived from the Wake Forest University Pick Atlas (Maldjian, Laurienti, Kraft, & Burdette, 2003).

2.5.3. *Functional activity related to item memory*

To investigate the effects of successful item memory, the retrieval success index (RS; Dolcos et al., 2005; Labar & Cabeza, 2006) was scored. The RS describes the difference in activity in response to items that were successfully retrieved ('hits') from items that were not successfully retrieved ('misses'). The RS was extracted for each participant and tested at a second-level using one-sample t-test. To investigate the effects of emotion on item memory, RS contrasts were obtained for each participant and condition and tested at a second level using one-sample t-tests. Because no differences were observed between RS for objects paired with unpleasant and pleasant backgrounds in the ROIs (see supplementary results), and to comply with the behavioral results, both conditions were considered as one emotional category in the fMRI analysis. RS for objects encoded in emotional backgrounds (hits: mean = 57.90, max = 84 , min = 24; misses: mean = 29.77, max = 68 , min = 4) was compared to RS for objects in neutral backgrounds (hits: mean = 28.68, max = 42 , min = 9 ; misses: mean = 15.32, max = 35, min = 2) in two contrasts: Emotional RS > Neutral RS and Neutral RS > Emotional RS.

2.5.4. *Functional activity related to contextual source memory*

To examine functional activity of source memory (SoM), the difference between contexts hits (i.e., correctly remembered item and context) and context errors (i.e., correct item but incorrect context) was calculated. To study overall contextual source memory effects, SoM contrasts were performed for each participant, independently of background category and tested at a second level using one-sample t-tests. To test emotional effects on contextual source memory, SoM contrasts were extracted for each participant and emotional condition. Similar to item memory, because no differences were observed between SoM for unpleasant and pleasant backgrounds in the ROIs (see supplementary results), both conditions were collapsed together into one emotional category. Emotion effects in SoM were analyzed comparing Emotional SoM (hits: mean = 16.50, max = 33, min = 1; misses: mean = 42.60, max =72, min = 18) with Neutral SoM (hits: mean =13.70, max = 30, min =4 ; misses: mean = 15.82, max =26, min = 4), using two contrasts: Emotional SoM > Neutral SoM, and Neutral SoM> Emotional SoM.

2.5.5. *Brain-Behavior Interaction analyses*

To identify brain regions sensitive to individual memory performance, the relationship between brain functional activity and memory performance was analyzed for item and source memory. For item memory, brain-behavior correlations were carried out by calculating covariations between BOLD activity in response to RS and Remember and Know hit rates, separately for objects paired with emotional and neutral categories. For contextual source memory, covariations were performed between BOLD activity in response to SoM, Know and Remember Hu indexes, separately for emotional and neutral objects. These analyses were restricted to the ROIs specified above.

3. Results

3.1. Behavioral Results

Table 1 summarizes the mean (standard deviation) hit rates for item and source memory as a function of context category.

	Item Recognition				*Contextual Source (Hu)*	
	Correct Rejection	*Total*	*Remember*	*Know*	*Remember*	*Know*
New objects	.81 (.16)	.18 (.15)	.05 (.08)	.14 (.11)		
Old objects						
Emotional context		.64 (.18)	.27 (.24)	.37 (.17)	.26 (.22)	.10 (.11)
Neutral context		.64 (.19)	.23 (.25)	.41 (.18)	.17 (.23)	.15 (.11)
Overall		.64 (.18)	.26 (.24)	.39 (.17)		
Corrected for Dependency			.21 (.2)	.39 (.14)		

Table 1. Averages of recognition judgments (standard deviation) to new and old objects originally encoded with emotional and neutral scenes (context).

3.1.1 Item Memory

After assuming independence of redundancy (Yonelinas & Jacoby, 1995), significant differences in item memory were found, showing larger hits for Familiarity- than for Recollection-related retrieval, t (28) = 4.45, $p < .001$, d = 0.82; see Table 1).

Effects of emotional content on item memory.

Analyses revealed that the effects of *Memory* approached significance, F (1,28) = 4.09, p = .053, $\eta_p^2 = 0.127$, but no effect of *Emotion* was found, $F < 1$. Critically, an interaction was observed, *Memory* x *Emotion:* F (1,28) = 12.36, p = .002, $\eta_p^2 = 0.31$. To reveal the nature of the interaction, post-hoc t-test were conducted comparing hit rates between emotional and neutral objects for Remember and Know judgments, separately (p value after Bonferroni correction: .05/4 = .0125). Whereas hit rates for Know responses did not differ after adjusting for multiple comparisons (t [28]= 2.15, p = .04, d = 0.4), for Remember judgments, hit rates for objects associated with emotional background scenes were significantly larger than for objects associated with neutral background scenes, t (28) = 3.84, $p < .001$,

d = 0.71 (see Figure 2). Furthermore, memory for neutral objects associated with neutral backgrounds was larger for Know than Remember judgments at a trend level (t [28]= 2.38, p = .024, d = 0.44), whereas no differences were found for objects paired with emotional backgrounds (t [28]= 1.6, p = .12, d = 0.3; Figure 2).

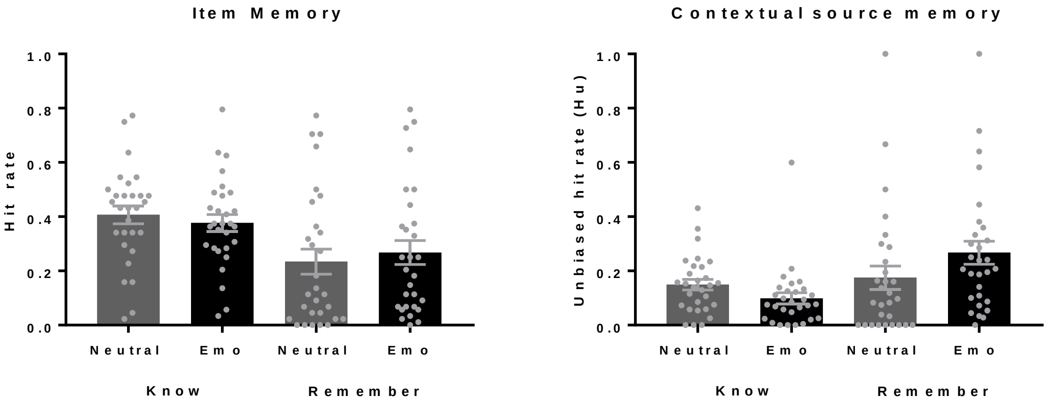

Figure 2. Memory performance in the Remember/Know task. Left: Item memory for objects encoded with neutral (gray) and emotional (black) scenes when memory was based on "Knowing" or "Remembering". Right: Source memory based on Know and Remember judgments for objects encoded in neutral (gray) and emotional (black) backgrounds.

.1.2. Source Memory

Results showed a main effect of *Memory*, F (1,28) = 12.26, p = .002, η_p^2 = 0.31, but no effect of *Emotion*, $F < 1$. Most interestingly, an interaction *Memory* x *Emotion* approached significance, F (1,28) = 3.39, p = .076, η_p^2 = 0.11. Post-hoc, exploratory analyses were performed to unfold the interaction effect (p value after Bonferroni correction: .05/4 = .0125). Although source memory for emotional and neutral contexts did not differ for Know (t [28] = -1.7, p = .098, d = 0.31) and Remember responses (t [28] = 1.54, p = .134, d = 0.29), correct source memory for emotional scenes was larger when memory was based on Remember rather than Know judgments (t [28] = 3.61, p = .001, d = .067). No such differences were observed for correct source memory for neutral scenes, $t < 1$ (Figure 2).

In summary, item memory performance was driven by the subjective experience of familiarity, irrespective of whether the objects were previously encoded in emotional or neutral contexts. Critically and in line with our hypothesis, recollection-based memory was larger for objects encoded in emotional compared to neutral contexts. Contextual source memory for backgrounds was also enhanced when item memory was driven by recollection. Replicating previous results (Ventura-Bort et al., 2017), we observed a differential involvement of familiarity and recollection in item and context memory. Item and source memory performance for emotionally laden events was especially pronounced when memory was based on recollection.

31.2. fMRI Results

.2.1.Item Memory

3.2.1.1. Retrieval success for objects

Figure 3 represents the brain activation related to retrieval success (correctly retrieved neutral objects compared to forgotten objects). Successfully retrieved objects, relative to forgotten ones, generated larger activity in a variety of brain regions associated with the recollection network, including medial and orbital PFC, AG, PCC, PCUN, and HC (Table 2).

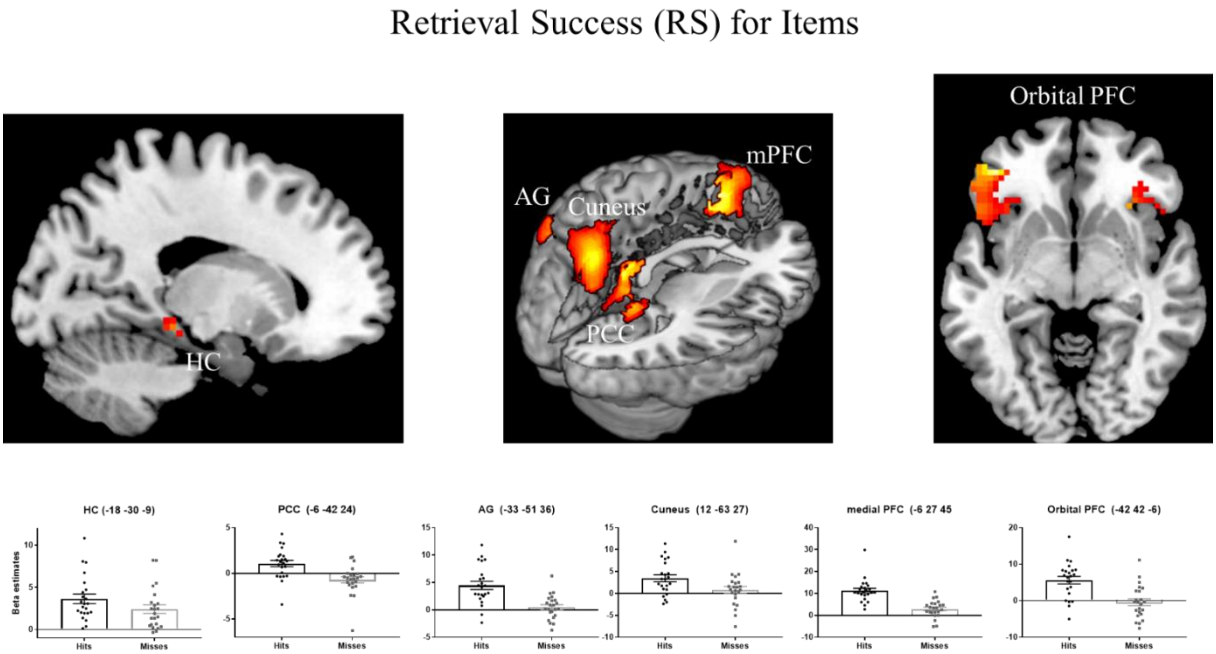
Retrieval Success (RS) for Items

Figure 3. Brain activation associated with retrieval success. Correctly retrieved objects (hits) compared to forgotten ones (misses) elicited larger activity in different brain regions related to recollection: Hippocampus (HC), posterior cingulate cortex (PCC), angular gyrus (AG), cuneus, medial prefrontal cortex (medial PFC), and orbital PFC (p< .005 uncorrected for the purpose of visualization).

Region	Side	MNI Coordinates			t-values	Peak voxel P_{FWE}	Cluster size (*k*) $P_{unc} < .005$
		x	y	z			
RS: Hit>Miss							
Medial PFC	L	-6	27	45	8.37	**<.001**	245
	R	3	27	48	5.75	**.002**	84
Orbital PFC	L	-42	42	-6	7.53	**.001**	107
	R	30	24	-6	5.15	**.005**	42
Posterior cingulate cortex	L	-6	-42	24	7.14	**<.001**	71
	R	6	-45	9	5.45	**.001**	51
AG	L	-33	-51	36	6.93	**<.001**	142
	R	36	-57	42	4.83	**.011**	95
Precuneus	L	-3	-66	51	6.56	**.001**	352
Cuneus	L	-12	-63	27	5.14	**.005**	23
Hippocampus	L	-18	-30	-9	4.66	**.009**	10
Emotional RS> Neutral RS							
Posterior cingulate cortex	L	-6	-36	27	5.41	**.001**	13
	R	9	-39	27	3.32	.062	6
Cuneus	R	9	-84	45	4.35	**.029**	32
Hippocampus	R	36	-27	-9	4.18	**.028**	15
Neutral RS> Emotional RS							
n.s.							

Table 2. Brain regions showing item memory retrieval success (RS; hits vs. misses) for objects encoded with emotional and neutral scenes. L = left, R = right.

3.2.1.2. Retrieval success for objects encoded in emotional vs. neutral background scenes

RS for emotional, compared to neutral associates (Emotional RS> Neutral RS) evoked larger activation particularly in the HC, PCC, and cuneus (Figure 4). RS for neutral associates, however, did not show any increased functional activity in comparison to emotional associates (Neutral RS > Emotional RS).

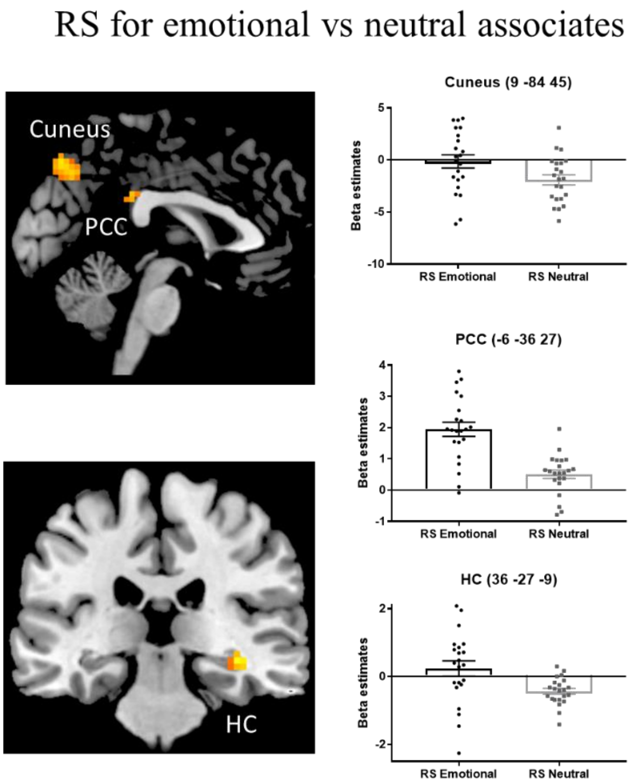

Figure 4. Brain activation associated with retrieval success (RS) for emotional compared to neutral associates in cuneus, hippocampus (HC) and posterior cingulate cortex (PCC) (p< .005 uncorrected for the purpose of visualization).

.2.2.Contextual Source Memory

3.2.2.1. Correct vs. incorrect contextual source memory

As shown in Figure 5, objects with correctly recognized background scenes elicited larger BOLD responses than objects where memory for background scenes was not accessible in brain regions including the PCC, PCUN, AG, as well as in the orbital PFC (Table 3).

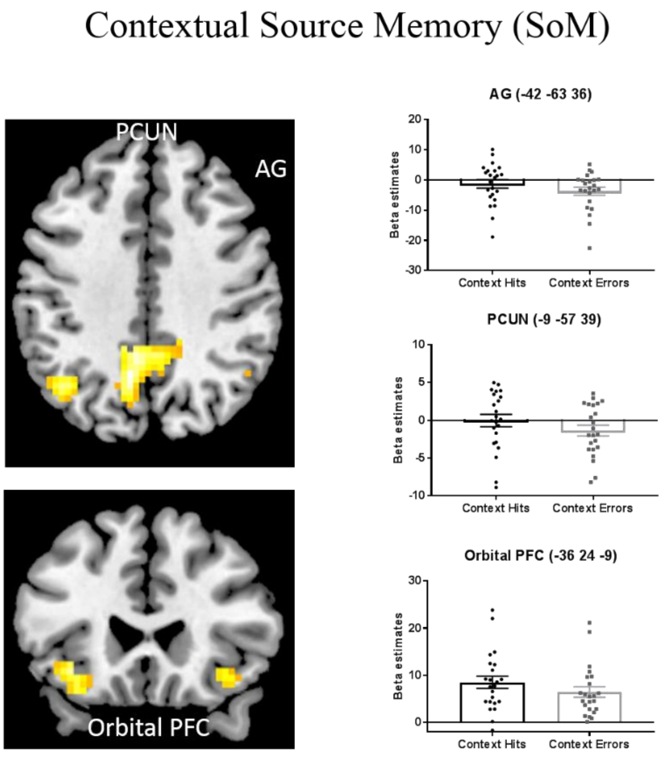

Figure 5. Brain activation associated with contextual source memory (item and background). Correctly compared to incorrectly retrieved source information evoked larger activity in various brain regions related to recollection: Angula gyrus (AG), precuneus (PCUN) and orbital prefrontal cortex (PFC) (p< .005 uncorrected for the purpose of visualization).

Region	Side	MNI Coordinates			t-values	Peak voxel P_{FWE}	Cluster size (*k*) $P_{unc} < .005$
		x	y	z			
Correct> Incorrect Context							
Precuneus	L	-9	-57	39	4.49	**.042**	121
Angular gyrus	L	-42	-63	36	4.2	**.027**	52
Orbital PFC	L	-36	24	-9	4.03	**.050**	52
	R	42	36	-15	4.19	**.038**	34
Emotional SoM> Neutral SoM							
Medial PFC	L	-6	33	48	4.65	**.030**	218
	R	12	45	6	4.1	**.070**	11
Orbital PFC	L	-36	24	-12	4.28	**.040**	37
	R	33	30	-15	4.07	.060	11
Posterior cingulate cortex	L	-3	-45	30	3.53	.057	29
	R	33	30	-15	4.07	.060	11
Hippocampus	L	-27	-39	-6	3.91	**.049**	16
Parahippocampal cortex	L	-24	-33	-12	3.75	**.050**	11
Neutral SoM > Emotional SoM							
n.s.							

Table 3. Brain regions showing source memory (SoM; Correct vs. incorrect context) effects and difference in SoM between emotional and neutral contents. L = left, R = right.

3.2.2.2. Contextual source memory for emotional vs neutral backgrounds

The contrast between correctly retrieved emotional and neutral scene backgrounds (Emotional SoM > Neutral SoM) revealed larger activity in MTL regions, including HC and PHC, as well as in the PCC, and medial PFC and orbital PFC (Figure 6). However, correct memory for neutral contextual backgrounds relative to emotional backgrounds was not reflected in enhanced functional activity in any brain region (Neutral SoM> Emotional SoM) (see Table 3).

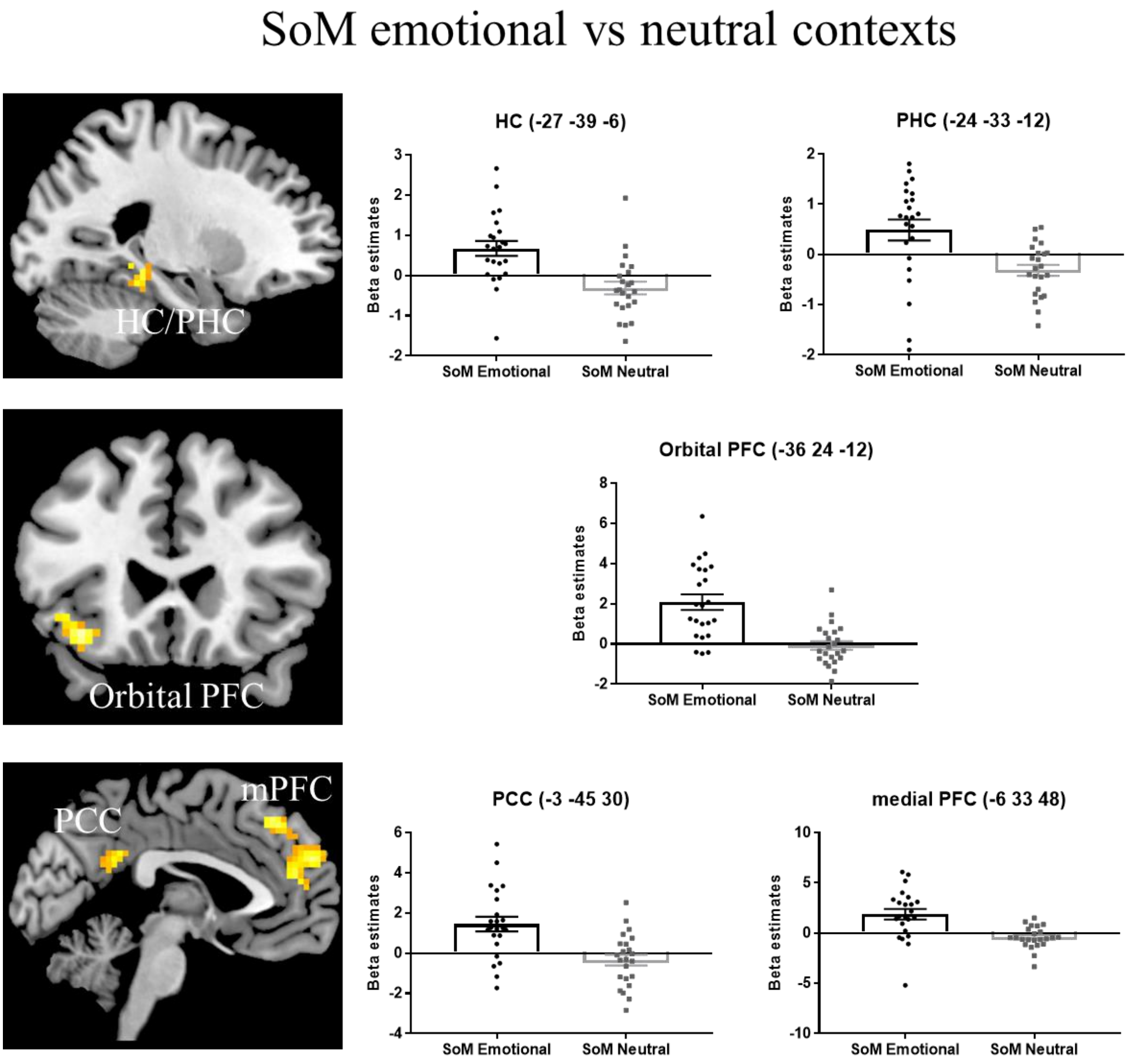

Figure 6. Brain activation related to emotional source memory (SoM) effect (SoM larger for emotional compared to neutral contexts) in the following regions: Parahippocampal cortex (PHC), Hippocampus (HC), Orbital prefrontal cortex (PFC), posterior cingulate cortex (PCC), medial PFC (p< .005 uncorrected for the purpose of visualization).

.2.3.Brain-behavior interaction

3.2.3.1. Item memory

Recollection-based memory performance (i.e. Remember hit rates) was positively associated with RS for emotional associates in various brain regions of the recollection network, including the HC (Figure 7), PCUN, PCC, AG, and medial PFC. For Know judgments, positive correlations were observed in the AG. Retrieval success for neutral associates did not show any positive correlation with memory performance (Table 4).

Region	Side	MNI Coordinates			t-values	Peak voxel P_{FWE}	Cluster size (*k*) $P_{unc} < .005$
		x	y	z			
RS for emotional associates:							
Remember judgments							
Hippocampus	R	39	-21	12	4.98	**.007**	22
posterior cingulate cortex	R	9	-48	24	3.81	**.028**	18
Precuneus	R	15	-42	48	5.19	**.014**	12
Angular gyrus	L	-39	-57	27	3.84	.065	22
	R	45	-54	24	4.3	**.041**	54
Medial PFC	L	-3	51	42	4.29	.064	121
Know judgments							
Angular gyrus	L	-45	-57	24	4.58	**.017**	46
RS for neutral associates:							
n.s.							

Table 4. Brain-behavior co-variation between RS and item memory performance.

3.2.3.2. Contextual source memory

For contextual source memory, the Remember hit unbiased index for emotional contexts correlated positively with emotional SoM in several regions involved in recollection, including the PHC (Figure 7), AG, PCC, PCUN and cuneus, and orbital PFC. A summary of further significant correlations is reported in Table 5.

Region	Side	MNI Coordinates			t-values	Peak voxel P_{FWE}	Cluster size (*k*) $P_{unc} < .005$
		x	y	z			
Emotional contextual SoM:							
Remember Hu							
Parahippocampal cortex	L	-30	-39	-12	4.38	**.013**	14
Angular gyrus	L	-39	-66	45	6.21	**.001**	62
	R	36	-69	42	7.98	**< .001**	207
Poserior cingulate cortex	R	6	-36	30	4.93	.004	11
Precuneus	L	-9	-54	72	6.77	**.001**	247
	R	12	-69	60	4.71	**.041**	140
Cuneus	L	18	-87	42	4.79	**.017**	10
Orbital PFC	R	54	42	-15	7.22	**.001**	49
Know Hu							
Orbital PFC	L	-24	30	-12	4.53	**.027**	8
RS for neutral associates:							
Remember Hu							
n.s.							
Know Hu							
Medial PFC	L	-9	45	18	4.47	**.003**	225
	R	9	39	36	5.	**.006**	267

Table 5. Brain-behavior co-variation between SoM and contextual source memory performance.

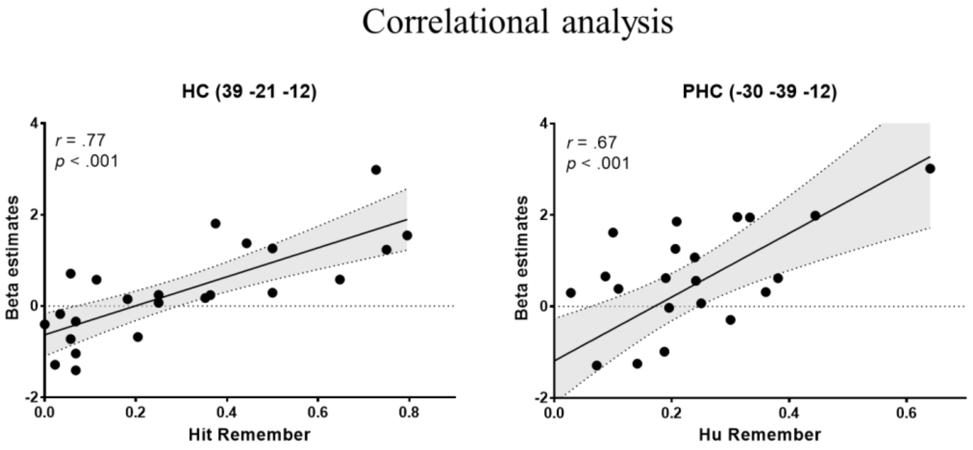

Figure 7. Correlational analyses between brain activation and memory performance. Left: Correlation in the hippocampus (HC) between RS for emotional associates and hit rates for Remember judgments. Right: Correlation between parahippocampal cortex (PHC) between SoM for emotional contexts and Hu index for Remember judgments.

4. Discussion

In the present study, we investigated long-term item and source recognition memory for neutral objects encoded with emotional and neutral scenes. As predicted, memory performance for the emotional compared to neutral associates was enhanced for Remember judgments, which was also observed when the correct emotional context (content of background scene) was remembered. These results extend previous findings showing a long-term, recollection-based memory enhancing effect not only for emotional information (Dolcos et al., 2005; Ochsner, 2000; Sharot et al., 2004; Weymar et al., 2009, 2010), but also for neutral information that was previously associated with an emotional event (Ventura-Bort et al., 2016; Pierce & Kensinger, 2011). At a neural level, replicating previous work, we observed a stronger engagement of regions embedded in a network related to recollection-based memory, including MTL, PPC, and PFC regions (Rugg & Vilberg, 2013; Gilmore et al., 2015). Critically, retrieval of emotional associates activated these regions more strongly, a pattern that was not only observed for item, but also for source recognition memory. Thus, our behavioral and neural findings indicate that item and source memory for emotional associates is remarkably robust over time and mediated by networks supporting recollection-based processes. Moreover, our results provide more information about the specific involvement of different anatomical areas in these processes.

4.1. *Medial Temporal Lobe*

Interestingly, we observed that both the HC and PHC showed differential activation for correctly retrieved objects and associated contextual information: the HC was found to be more activated during successful retrieval of objects, especially for emotional associates. For contextual source memory, both HC and PHC were involved during retrieval of associated emotional information. Within the MTL, the HC and the PHC are discussed to mediate recollection-based memory (Davachi, Mitchell, & Wagner, 2003; Diana et al., 2007; Eichenbaum et al., 2007). Albeit related, HC and PHC have been attributed to different functions supporting episodic memory (Diana et al., 2007). The PHC is thought to process spatial contextual information (i.e., where) of an event (Burgess, Maguire, Spiers, & O'Keefe, 2001; Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011), whereas the HC binds together all aspects of an event (i.e. what, when, how, where), generating compound representations and creating a rich episodic memory trace (Ekstrom et al., 2011; Staresina & Davachi, 2009; see for reviews, Davachi, 2006; Eichenbaum et al., 2007; Ranganath, 2010). The observed larger HC activity for emotional associates suggests that multiple details of the encoding episode were retrieved during recognition, converging with the recollection enhancement observed in the behavioral data.

The involvement of the HC during retrieval of emotional associates is also in line with findings by Dolcos and colleagues, who found enhanced hippocampus activity for emotional scenes during both memory encoding (Dolcos, LaBar, & Cabeza, 2004b) —in interaction with the amygdala (Dolcos et al., 2004b; Keightley et al., 2011; McGaugh, 2004; Ritchey et al., 2008; Smith, Stephan, Rugg, & Dolan, 2006)— and retrieval (Dolcos et al., 2005). In the present study, we also observed stronger hippocampal activation when retrieving emotional associates from long-term memory, which extends prior work by Smith et al. (Smith, Henson, Dolan, & Rugg, 2004), using an immediate recognition task. As in Dolcos et al. (2005), larger hippocampal activation was exclusively related to Remember judgments, suggesting that the long-term memory advantage for emotional associates is mediated by recollection processes.

The enhanced hippocampus activation during retrieval of emotional associates contrasts with a recent study showing a detrimental effect of emotion on source memory (Bisby, et al., 2016). In this study, Bisby and colleagues found that emotional cues (scenes) impair memory for associated scene information by down-regulating hippocampal activation. Despite various methodological differences to our study (i.e. in terms of stimulus materials and recognition interval: immediate vs. delayed recognition), differences in the encoding instructions might have determined the contradicting effects. Whereas Bisby and colleagues instructed participants to merely indicate whether images (emotional cue and associated emotional/neutral information) fit well together or not, in our study an active object-background scene binding instruction was given. According to the ABC theory (Mather & Sutherland, 2011), in Bisby et al.'s study (2016), the non-integrative instruction may have led to a competition for attentional resources between both pieces of information (i.e. emotional cue and emotional/neutral target), resulting in a preferential processing for the emotionally arousing materials. In our study, however, the integration of emotional and neutral information may have prevented such competition, promoting the processing of both pieces of information (see also Smith et al. (2004) for similar results).

However, this explanation remains speculative and future studies are needed which systematically investigate the differences of the encoding instruction on emotional source memory.

41.2. Posterior Parietal Cortex (PPC)

Three regions in the PPC (posterior cingulate cortex, angular gyrus, and precuneus/cuneus) typically involved in recognition memory (Rugg & Vilberg, 2013; Gilmore et al., 2015; King et al., 2015), showed larger activation during item and context memory retrieval of neutral objects and more largely for emotional associates. The AG has consistently been found to be activated during retrieval across a number of studies (see for reviews, Cabeza et al., 2008; Rugg & Kim, 2017; Sestieri et al., 2017; Vilberg & Rugg, 2008; Wagner et al., 2005) but the exact function is largely unknown. Lesion studies have shown that AG damage is associated with lower confidence and Remember judgments (Ciaramelli et al., 2017; Hower, Wixted, Berryhill, & Olson, 2014), indicating that the AG is linked to the vividness of the experience of the retrieved episode (Rugg & King, 2018). Others found that the AG is linked to processes such as semantic processing (Binder, Desai, Graves, & Conant, 2009), number processing (Dehaene, Piazza, Pinel, & Cohen, 2003), attentional processing (Ciaramelli, Grady, & Moscovitch, 2008), or theory-of-mind (Decety & Lamm, 2007). This heterogeneity of findings has therefore led to the assumption that the AG is a core system (Seghier, 2012) or convergence zone (Damasio, 1989) that gathers and structures internally generated information (Ramanan & Bellana, 2019) together with low-level inputs from different multi-modal subsystems in higher-order representations, and actively holds this integrated information (“episodic buffer”, see Vilberg & Rugg, 2012; Vilberg & Rugg, 2008) until the prominent task is finally executed. Although no differential activation between emotional and neutral associates or contextual details was found, the AG activity was positively related to retrieval of both emotional associates and contextual source cues. Given the role of emotion on generating more vivid recollective experiences (Dolcos et al., 2005; Weymar et al., 2009; Sharot et al., 2004), these findings suggest that emotion enhances the vividness and integration of the retrieved, past representations.

The precuneus/cuneus as a part of the memory network has also been reliably related to episodic retrieval (Cavanna & Trimble, 2006; Rugg, Otten, & Henson, 2002; Wagner et al., 2005). Although

PCUN strongly covariates with other regions of the PPC (Gilmore et al., 2015; Hassabis, Kumaran, & Maguire, 2007; Weymar et al., 2018), the functional roles of these regions seem to differ. It has been suggested that the PCUN, as part of the dorsal parietal cortex, is accounted for top-down, goal-directed attentional processes during memory retrieval (Cabeza et al. 2008). However, recent evidence also found similar activations during undeliberated retrieval, when old stimuli were merely presented without an explicit recognition instruction (Bradley et al., 2015; Weymar et al., 2018), suggesting that the precuneus/cuneus region may be involved in both top-down and bottom-up attentional mechanisms (Gilmore et al., 2015). In our data, the precuneus/cuneus region showed stronger activation during item memory retrieval and correlation with memory performance, particularly for emotional associates (cuneus). This extends a recognition memory study by Keightley and colleagues (2011) using emotional scenes and faces, and suggest a generally larger deployment of attentional resources during retrieval of salient memory representations.

Finally, memory retrieval was also associated with activation of the posterior cingulate cortex, which is in accordance with prior studies (Natu et al., 2018; Rugg & Vilberg, 2013). The PCC, among other regions, such as PCUN and AG, has been discussed to play a pivotal role in scene construction (Irish et al., 2015) during the retrieval episode (Hassabis & Maguire, 2007). Furthermore, PCC activation has been related to representations of self-relevant information (Summerfield, Hassabis, & Maguire, 2009). In this vein, strong activation in the PCC is related to retrieval of self-relevant (autobiographical) memories (Maddock, Garrett, & Buonocore, 2001) and emotionally salient information (Maddock, Garrett, & Buonocore, 2003; Maratos, Dolan, Morris, Henson, & Rugg, 2001). This interpretation is also in line with the literature linking the PCC to the default network that is associated with internally directed cognition (Buckner, Andrews-Hanna, & Schacter, 2008). Greater involvement of the PCC during retrieval of emotional associates and emotional contextual source cues observed in the present study may, thus, indicate that the recognized emotionally-laden material have increased motivational relevance, and hence are more self-relevant, than neutral information.

4.3. *Prefrontal Cortex*

Within the PFC, the medial and orbital PFC showed stronger activation during successful retrieval of objects. It has been suggested that the PFC modulates mnemonic processes in an indirect fashion, by means of strategic, semantic, working memory and attentional processes (Roy, Shohamy, & Wager, 2012). One of the PFC regions more important for retrieval is the medial PFC. The medial PFC is thought to guide behavior through the integration of current information with prior experiences. The medial PFC works in interaction with MTL regions (e.g. HC) continuously updating the attributes (i.e., schema) that define an event by means of integrating past and current experiences (Schlichting & Preston, 2015). Furthermore, emotional relevance seems to enhance the integrative role of the medial PFC (Barron, Dolan, & Behrens, 2013; Maratos et al., 2001; Smith et al., 2004). Regarding our data, greater involvement of the medial PFC during successful retrieval may indicate an update of the information from the reinstated event. Most interestingly, we observed that medial PFC activity was specifically related to source memory for emotional associates. Our results suggest that the ongoing integration between previous and current encounters with an event may be particularly enhanced by the emotional relevance of the event (Schlichting & Preston, 2015). Turning to the orbital PFC, this region has been shown to play an important role in decision making (Krawczyk, 2002) and has been associated with affective, reward-related valuation (Heinzel & Northoff, 2009). Emotional relevance has shown to increase orbital PFC activation during retrieval processes (Smith et al., 2004). In this vein, we also found larger orbital PFC activation during the retrieval of emotional source cues, suggesting that the orbital PFC may be signaling the significance of the to-be-retrieved stimulus.

.4.Conclusion

In the present study, we found behavioral and neural evidence for enhanced long-term recollection of neutral objects that have been associated with emotional scenes during encoding. Specifically, enhanced memory performance for emotion-associated information was predicted by stronger activation in regions previously related to episodic retrieval, such as PFC, MTL and PPC. Our findings suggest that emotional contexts seem to enhance longer lasting memory traces for neutral associated information by engaging different mechanisms involved in bottom-up and top-down processes (Dolcos et al., 2017). The ability to remember past events and the surrounding contextual information is crucial for the survival of the individual (McGaugh, 2000). However, in some circumstances, when the contextual cues are bound to traumatic events or to impulsive behaviors, the retrieval of these cues might bring back emotional and motivational states that could facilitate the development and/or maintenance of clinical conditions, such as stress- and trauma-related disorders and addiction (Dolcos, 2013; Ehlers & Clark, 2000; Robinson & Berridge, 1993)

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Supplementary results

In the supplementary results the contrasts between pleasant and unpleasant conditions for both item and source memory are shown. For item memory, Stable 1 contains the results for the contrasts on RS between objects paired with pleasant and unpleasant contexts. For contextual source memory, Stable 2 represents the results for contrasts on SoM between objects paired with pleasant, and unpleasant contexts. Results are restricted to the ROIs (see method section).

Region	Side	MNI Coordinates			t-values	Peak voxel P_{FWE}	Cluster size (*k*) $P_{unc} < .005$
		x	y	z			
Pleasant RS > Unpleasant RS							
Posterior cingulate cortex	R	9	-48	21	3.19	.081	6
Hippocampus	L	15	-12	-15	3.38	.119	2
Precuneus	R	6	-54	33	3.46	.27	12
Unpleasant RS > Pleasant RS							
n. s.							

STable 1. Brain regions showing item memory retrieval success (RS; hits vs. misses) for objects encoded with pleasant and unpleasant scenes. L = left, R = right

Region	Side	MNI Coordinates			t-values	Peak voxel P_{FWE}	Cluster size (*k*) $P_{unc} < .005$
		x	y	z			
Pleasant SoM > Unpleasant RS							
n.s.							
Unpleasant RS > Pleasant RS							
n.s.							

STable 2. Brain regions showing source memory (SoM; Correct vs. incorrect context) effects and difference in SoM between pleasant, unpleasant and neutral contents. L = left, R = right.

9. APPENDIX B: LIST OF PUBLICATIONS

Weymar, M., **Ventura-Bort, C.,** Wendt, J., Lischke, A. (submitted). Trustworthiness shapes long-term memories: Brain potentials indicate enhanced familiarity for untrusworthy faces.

Ventura-Bort, C., Wirkner, J., Dolcos, F., Wendt, J., Hamm, A. O., & Weymar, M. (submitted). Enhanced spontaneous retrieval of cues from emotional events: An ERP study.

Ventura-Bort, C., Wendt, J., Wirkner, J., König, J., Lotze, M., Hamm, A. O., Dolcos, F., & Weymar, M. (submitted) Neural substrates of long-term item and source memory for emotional associates: an fMRI study

Dolcos, F., Katsumi Y., Moore, M., Berggren, N., de Gelder, B., Derakshan, N., Hamm, A. O., Koster, E. H. W., Ladouceur, C. D., Okon-Singer, H., Pegna, A. J., Richter, T., Schweizer, S. Van den Stock, J., **Ventura-Bort**, C., Weymar, M., & Dolcos S. (submitted). Neural correlates of Emotion-Attention Interactions.

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