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

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ABSTRACT
Since Tulving’s influential work on the distinction between familiarity and recollection-based retrieval, numerous studies have found evidence for differential contribution of these retrieval mechanisms on emotional episodic memory. Particularly, retrieval advantage for emotional, compared to neutral, information has been related to recollection-, but not familiarity-mediated processes. Neuroimaging studies suggest that this recollection-based retrieval for emotional information is related to stronger engagement of regions in the medial temporal lobe (MTL), posterior parietal cortex (PPC), and prefrontal cortex (PFC). In the present study, we investigated neural correlates related to long-term memory of neutral information that has been associated with emotional and neutral 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 intermixed with new ones and participants had to indicate whether the objects were previously seen or not, using the Remember/Know procedure (item memory). Furthermore, memory for the correct scene background category was also tested (contextual source memory). First, replicating previous findings, we observed a preference for recollection-dependent memory retrieval versus familiarity-dependent memory retrieval for those neutral objects encoded in emotional compared to neutral contexts. Second, consistent with these behavioral effects, objects encoded with emotional, compared to neutral scenes were presented. One week later, the encoded objects were intermixed with new ones and participants had to indicate whether the objects were previously seen or not, using the Remember/Know procedure (item memory). Furthermore, memory for the correct scene background category was also tested (contextual source memory). First, replicating previous findings, we observed a preference for recollection-dependent memory retrieval versus familiarity-dependent memory retrieval for those neutral objects encoded in emotional compared to neutral contexts. Second, consistent with these behavioral effects, objects encoded with emotional, compared to neutral, scenes produced larger memory-related activity in recollection-sensitive brain regions, including PPC and PFC regions. Third, correctly retrieved emotional compared to neutral contextual information was associated with increased activity in these brain areas. Together, these results suggest that memory for information encoded in emotional contexts is remarkably robust over time and mediated by recollection-based processes.

1. Introduction
A large amount of empirical evidence has robustly confirmed that there is a memory advantage for emotional events (Bradley et al., 1992; Dolcos et al., 2017; Dolcos et al., 2004, 2005; Weymar et al., 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. This effect is found for free recall and recognition memory tasks (Bradley et al., 1992; Dolcos et al., 2004; Dolcos et al., 2005; Weymar et al., 2009), for different retention intervals (immediate and delayed; Ritchey et al., 2008; Wirkner et al., 2018; Schümann et al., 2017), and various stimulus materials (images, faces, sounds; Weymar et al., 2009; Maratos and Rugg, 2001; Righi et al., 2012; see for reviews, Dolcos et al., 2017, 2020; Weymar and 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 (Ochsner, 2000; LaBar and Cabeza, 2006). According to Tulving’s seminal work (Tulving, 1985), this

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mnemonic advantage is related to autonoetic consciousness which is expressed by means of recollection- (remembering specific spatial, temporal, or other contextual details of events), rather than familiarity-based retrieval (knowing that an event occurred but not being able to remember specific contextual details) (Dolcos et al., 2005; Ochser, 2000; Sharot et al., 2004; Tulving, 1985; Weymar et al., 2010).

Whether emotional information facilitates memory when perceived in the context of a more complex event or in relation to other pieces of information and/or source details, also termed source or relational memory, is less clear (see for reviews, Chiù et al., 2013; Dolcos et al., 2017; Mather and Sutherland, 2011; Mather et al., 2016; Murray and 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 and Van der Linden, 2005; D’Argembeau and Van der Linden, 2005; Doeksen and Shimamura, 2001; MacKay & Ahmet-zanov, 2005; Mather et al., 2009; Mather and Knight, 2008; Nashiro and Mather, 2011; Rimmele et al., 2011; but see Koenig & Mckelgin, 2008; Mather and 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 and Arndt, 2009; Luck et al., 2014; Maratos and Rugg, 2001; Pierce and Kensinger, 2011; Smith et al., 2004, 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, compared to neutral, material (Bisby and Burgess, 2014; Bisby and Burgess, 2014; Ferré et al., 2019; Kensinger et al., 2007; Madan et al., 2017; Madan et al., 2012; Mather et al., 2006, 2009; Mather and Knight, 2008; Murray and Kensinger, 2012; Nashiro and Mather, 2011; Rimmele et al., 2011; Touryan et al., 2007). Altogether, these findings point to divergent effects of emotion on source memory, in some cases enhancing and in others decrementing memory retrieval.

The Arousal-Biased Competition (ABC) Theory (Mather et al., 2016; Mather and 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 and 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 and 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 and Sharot, 2008; Schümann et al., 2017; Sharot et al., 2004; Yonelinas and Ritchey, 2015). In line with this, longer retention intervals favor memory retrieval for items paired with emotional (particularly unpleasant) information, rather than recollection-based memory consolidation processes (Pierce and 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., 2016a), but also facilitate long-term memory storage (Ventura-Bort et al., 2016b). 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 exclusively found for objects encoded in emotional background scenes (Ventura-Bort et al., 2016b; Ventura-Bort et al., 2017; see for similar results, Martinez-Galindo & Cansino, 2016; Maratos and Rugg, 2001; Meng et al., 2017). This effect was also observed during a long-term spontaneous retrieval task, suggesting that the memory enhancement is driven by the acquired relevance of the triggering event due to its association with emotional contextual information (background scene) at encoding (Ventura-Bort et al., 2019). Given that the late ERP Old/New effect has been associated with recollection-based retrieval (Rugg and Curran, 2007; MacLeod and Donaldson, 2017), our findings extended prior emotional item memory studies (Weymar et al., 2009; Weymar and Hamm, 2013), indicating that the long-term memory retrieval for emotional associates is also mediated by the process of recollection (Curran, 2000; Duarte et al., 2004; Rugg and Curran, 2007; Düzel et al., 2003; MacLeod and Donaldson, 2017).

In the present study, we followed up on this ERP research and used functional magnetic resonance imaging (fMRI) to identify the associated brain substrates related to the long-term memory enhancing effects of emotional contextual information, and their link to recollective 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 precuneus (PCUN)/cuneus (see reviews by Davachi, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Ranganath, 2010; Ranganath and Ritchey, 2012). These anatomical regions seem to have both specific and shared (or complementary) functions, including their involvement in recollection- and familiarity-based processes. Within the MTL, activity in the PrC may be crucial for familiarity-based memory, whereas activity in the HC and PHC may be necessary for recollection-based retrieval (Diana et al., 2007; Charan Ranganath and Ritchey, 2012; Michael D. Rugg and Vilberg, 2013). For instance, in a detailed review of eight studies from their own group, Rugg et al. (2012) found that 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 (i.e. recollection processes). Furthermore, the successful retrieval of associated source information has been not only related to HC but also to PFC activity (Düzel et al., 2003; see for review Diana et al., 2007).

Other regions beyond the MTL, such as the AG, PCC, PCUN (Vilberg and Rugg, 2007, 2009a, 2009b; see for reviews, Cabeza et al., 2008; Rugg and King, 2013; Sestieri et al., 2017; Vilberg and Rugg, 2008; Wagner et al., 2005; Wheeler and Buckner, 2004), and medial PFC (e.g., Schlichting and Preston, 2015) have also showed strong activation during retrieval, particularly when memory was based on recollection rather than familiarity-related processes. Supporting the joint participation of these regions in recollection-based retrieval, it has recently been observed that functional connectivity between these areas is associated with recollection-based memory (King et al., 2015), providing evidence for the existence of the so-called recollection-sensitive network (Rugg and Vilberg, 2013).

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 (Hoppstädt et al.,
from three participants (all women) could not be analyzed due to the Review Board of the German Psychological Society. Retrieval data been associated with greater activation in regions of the recollection guided by recollection processes (Ventura-Bort et al., 2017) and has for successfully retrieved items. As in prior imaging studies testing expected larger activation in regions of the recollection memory network (Rugg et al., 2012; Rugg and Vilberg, 2013; Rugg and Keightley et al., 2011; Dolcos et al., 2005; Sterpenich et al., 2009; see for review LaBar and Cabeza, 2006), as part of a putative recollection network (Gilmore et al., 2015; Rugg and 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 PPC activation than objects encoded in neutral background scenes (Smith et al., 2004, 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 (Murray and Kensinger, 2014). Similarly, memory for information paired with emotional cues was related to a decreased 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, PPC, 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 seen during encoding (item memory), and which background category each 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., 2016b, 2017, 2019), 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, PPC, 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 and Vilberg, 2013; Rugg and King, 2018), we expected increased activation of MTL, PPC, 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 in this study 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. Retrieval data from three participants (all women) 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 (>3 mm displacement from each scan in relation to a reference [first scan] in translation parameters in any direction), leaving a final sample of 23 (21 women; mean age = 22.8) 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 et al., 2014) and the Ecological Adaptation of Snodgrass and Vanderwart set (Moreno-Martinez and 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., 2016b). 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; see section S1 of the supplementary material for mean and standard deviation scores). The background scenes were selected from the International Affective Picture System (IAPS; Lang et al., 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; see section S1 of the supplementary material for separate mean and standard deviation scores). Normative valence and arousal ratings were as follows: M = 7.14 (SD = 0.48) and M = 6 (SD = 0.07) for pleasant; M = 5.13 (SD = 0.36) and M = 3.25 (SD = 0.35) for neutral; and M = 2.34 (SD = 0.6) and M = 6.06 (SD = 0.56) for unpleasant scenes. The three picture categories did not overlap in the valence x arousal space (see for similar approach, Jordan et al., 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 (p < 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 (see Figure S1 in section S1 of the supplementary material for more detailed information). Each participant was randomly assigned to one of the six lists across experimental sessions (i.e. encoding and retrieval).

2.3. Procedure and design

The experimental design is displayed in Fig. 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. 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 binding). No mention of a later memory.

1 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.
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). The current manuscript focused on the brain activation during retrieval. For results on the brain activation during encoding, see section S6 of the supplementary material.

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. 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 consecutively. 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. A blank screen followed after object-offset for 3000 or 5000 ms, the question “Remember/Know/New?” was presented for 2000 ms, and participants were asked to make ‘Remember’, ‘Know’, or ‘New’ judgments (Fig. 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 recognized as 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. All encoding and recognition procedures were programmed using Presentation v. 16.5 (Neurobehavioral Systems Inc., Albany, CA, USA).

2 Although it has typically been suggested that the retrieval of contextual source information is a clear indication of recollection-based processes (Wilding & Rugg, 1996), some evidence suggests that under familiarity processes the recognition of contextual information may also occur, especially when source and item information are unitized. Unitization is understood as the process by which two separate components of an event (e.g. an object and contextual background) are integrated as a single unit (Graf & Schacter, 1989). Behavioral, electrophysiological, and neuroimaging studies have provided support for familiarity-based retrieval of source information when source and item were unitized during encoding (e.g. Diana et al., 2007; 2010, 2011; Tu et al., 2017). We believe that in current design, where the integration of item and background scenes was promoted — by presenting objects frameless and with transparent backgrounds and by instructing the participants to imagine that objects are a part of the scene — unitization processes may have been taken place during encoding, by means of which background and objects were encoded as a single entity. As a result, the retrieval of contextual sources could be driven by familiarity-based processes. Therefore, we decided to keep the question about the emotional category of the contextual background scene for both ‘Remember’ and ‘Know’ judgments.
contribution of recollection and familiarity by analyzing differences between Remember and Know judgments. Analysis of familiarity and recollection processes in explicit memory retrieval is constrained by the assumption that both processes are interrelated. However, this relation can be exclusive or independent (Yonelinas and Jacoby, 1995). Under the exclusivity assumption, familiarity and recollection processes cannot take place simultaneously, the occurrence of one process (e.g., recollection) implies the non-occurrence of the other process (e.g. familiarity), and vice versa. Using the Remember/Know procedure, this assumption entails that familiarity-based memory can be calculated as the proportion of Know judgements in relation to the total number of items presented, whereas recollection-based memory can be indexed as the proportion of Remember judgements in relation to the total number of items presented. On the other hand, under the assumption of independency, recollection and familiarity judgments can co-occur. Thus, a proportion of the retrieved events can be recognized both as familiar and as recollected. Given the characteristics of the current task, it is expected that for these items, participants will use remember judgments, even though the items are also, to some extent, retrieved based on familiarity. Consequently, the probability that an item is familiar will be underdetermined as a more appropriate index to differentiate between recollection and familiarity processes (Yonelinas and Jacoby, 1995; Yonelinas, 2002). Thus, we decided to use these parameters (i.e. corrected for dependency) as indexes of familiarity- and recollection-based memory retrieval (for descriptive memory performance scores derived under the exclusivity assumption, see section S3 of the supplementary material). Remember hit rates were indexed as: \( P \text{ Remember Hit Rate} \). 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:

\[
P \text{ Know Hit Rate} = \frac{1}{P \text{ Remember Hit Rate}} - 1
\]

In addition, d’prime (d’), derived from signal detection theory, \(^3\) was further calculated under the independence assumption for both Remember (d’Recollection = \( z(P \text{ Remember}) - z(P \text{ False Alarm Remember}) \)) and Familiarity:

\[
Z\left( \frac{P \text{ Know Hit Rate}}{1 - P \text{ Remember Hit Rate}} \right) = z\left( \frac{P \text{ Know False Alarm}}{1 - P \text{ Remember False Alarm}} \right)
\]

In a second step, we analyzed the effects of emotion on overall item memory performance, independently of memory quality. To do so, we calculated d’ scores over all trials (collapsing across Remember and Know judgments) for emotional and neutral associates. In preliminary analyses, we explored possible valence effects on all of these memory indices for objects from pleasant and unpleasant scene contexts (see supplementary material section S5). Because no differences were observed \((ts < 1)\), the Hu index scores for unpleasant and pleasant contexts were first individually calculated, and then averaged together to one emotional category. Firstly, the effects of emotion on overall source memory performance were analyzed by calculating the Hu index on overall hits (collapsing Know and Remember judgments in one “old” category) for emotional and neutral contexts, separately. Differences on overall source memory for emotional and neutral contexts was calculated using a \(t\)-test. Secondly, we analyzed the interacting effects of emotion and memory processes by calculating the Hu indexes for each emotion and memory judgment, separately. The interacting effects of emotion and memory were 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 \((\alpha/n\) comparisons).

For contextual source memory performance, the unbiased hit rate \((H_u)\) was calculated (Wagner, 1993; Ventura-Bort et al., 2017). The \(H_u\) 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 \(H_u\) is calculated as follows:

\[
H_u = \frac{\text{Hit Know Neutral Context}}{N' \text{ of times Neutral Context is chosen under Know judgments}}
\]

where \( \text{Hit Know Neutral Context} = \text{Number of objects paired with neutral contexts retrieved based on Know judgments and whose background category was correctly identified; Incorrect Know Neutral Context} = \text{Number of objects paired with neutral contexts retrieved based on Know judgments and whose background category was not correctly identified; } N' \text{ of times Neutral Context is chosen under Know judgments} = \text{Number of objects whose background was labeled as “Neutral”, including those whose background was mistakenly misclassified.}

In the context of an explicit memory task, a particular contextual source selection is primarily driven by mnemonic processes. When no contextual information is retrieved, such selection tends to be random, although, a bias could exist toward a specific option (context category). We cannot elucidate, based on the memory performance, when a selection of a response was driven by mnemonic processes or by biased preferences. To overcome the possibility of a possible response bias, we applied the Hu index. Similar to item memory, in a preliminary analysis (see section S5 of the supplementary material), we explored possible valence differences between pleasant and unpleasant contexts. Because no differences were observed \((ts < 1)\), the Hu index scores for unpleasant and pleasant contexts were first individually calculated, and then averaged together to one emotional category. Firstly, the effects of emotion on overall source memory performance were analyzed by calculating the Hu index on overall hits (collapsing Know and Remember judgments in one “old” category) for emotional and neutral contexts, separately. Differences on overall source memory for emotional and neutral contexts was calculated using a \(t\)-test. Secondly, we analyzed the interacting effects of emotion and memory processes by calculating the Hu indexes for each emotion and memory judgment, separately. The interacting effects of emotion and memory were 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 \((\alpha/n\) 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 $3 \times 3 \times 4$ mm, 1 mm gap, TR 2000 ms, TE 30 ms, matrix $64 \times 64$, flip angle 90°). A T1-weighted anatomical volume (MP-RAGE, 176 sagittal slices, voxel size $1 \times 1 \times 1$ mm, TR 1690 ms, TE 2.52 ms, matrix $256 \times 256$ mm, flip angle 9°) was also recorded. MRI data were preprocessed and analyzed with SPM12 (Functional Imaging Laboratory, Wellcome Center for Human Neuro-imaging, 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). Pre-processed volumes from the retrieval session (for fMRI encoding results, see section S6 in the supplementary material) 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. Firstly, at a whole-brain level, clusters with a minimum size of 5 voxels, that surpassed a significant threshold-level of p < .001 (uncorrected for multiple comparisons) were detected. Secondly, the significance of each cluster was compared to a threshold of p < .05 corrected for multiple comparisons (family wise error rate, FWE) using a mask formed by all ROIs (16 ROIs in total; see section S7 of the supplementary material for visualization of the ROIs). 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 et al., 2003). We decided to collapse all ROIs in a mask for correcting for multiple comparisons because, although the regions embedded in the recollection network may have specific functions within the retrieval processes, the high correlation across these regions (e.g. King et al., 2015) suggest that they may act to some extent in concert. Thus, given its interrelation, this procedure seems appropriate to carry out our analysis.

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 and 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 a 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 RS activity for objects paired with unpleasant and pleasant backgrounds showed similar differences to objects from neutral backgrounds in the ROIs of the recollection network, both conditions were considered as one emotional category in the fMRI analysis (as in behavioral analysis). Specific valence specific differences are included in S9 of the supplementary material. 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), using paired t-tests.

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, both conditions (pleasant and unpleasant contexts) were collapsed together into one emotional category (see section S9 of the supplementary material for specific valence differences in SoM). 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 paired t-tests contrasts: Emotional SoM > Neutral SoM, and Neutral SoM > Emotional SoM.

3. Results
3.1. Behavioral results
3.1.1. Item memory
Table 1 summarizes the mean (standard deviation) memory accuracy

<table>
<thead>
<tr>
<th>Memory Performance</th>
<th>New Objects</th>
<th>Total Old Objects</th>
<th>Neutral Contexts</th>
<th>Emotional Contexts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall CR/HR</td>
<td>.81 (.16)</td>
<td>.64 (.18)</td>
<td>.64 (.19)</td>
<td>.64 (.18)</td>
</tr>
<tr>
<td>Overall d’</td>
<td>1.49 (.54)</td>
<td>1.50 (.51)</td>
<td>.35 (.19)</td>
<td>.35 (.18)</td>
</tr>
<tr>
<td>Overall FA/misses</td>
<td>.18 (.15)</td>
<td>.26 (.24)</td>
<td>.23 (.24)</td>
<td>.27 (.24)</td>
</tr>
<tr>
<td>FA/HR Remember</td>
<td>.05 (.09)</td>
<td>.53 (.18)</td>
<td>.54 (.2)</td>
<td>.53 (.2)</td>
</tr>
<tr>
<td>FA/HR Know Corrected for Dependency</td>
<td>.15 (.13)</td>
<td>.31 (.45)</td>
<td>.33 (.53)</td>
<td>.31 (.44)</td>
</tr>
<tr>
<td>d’ Remember</td>
<td>1.23 (.53)</td>
<td>.98 (.67)</td>
<td>1.25 (.56)</td>
<td>1.23 (.56)</td>
</tr>
<tr>
<td>d’ Know Corrected for Dependency</td>
<td>1.31 (.45)</td>
<td>1.33 (.53)</td>
<td>1.31 (.44)</td>
<td>1.31 (.44)</td>
</tr>
<tr>
<td>Hu Index</td>
<td>.16 (.09)</td>
<td>.13 (.09)</td>
<td>.17 (.23)</td>
<td>.26 (.18)</td>
</tr>
<tr>
<td>Hu Remember</td>
<td>.15 (.11)</td>
<td>.10 (.11)</td>
<td>.15 (.11)</td>
<td>.10 (.11)</td>
</tr>
</tbody>
</table>
for item and source memory as a function of context category.

After assuming independence of redundancy (Yonelinas and Jacoby, 1995), significant differences in item memory were found, showing larger hits for Know than for Remember judgments, \( t(28) = 4.45, p < 0.001, d = 0.82 \) (see Table 1). This difference, however, was not found for d’ indices, (d’ Know vs. d’ Remember: \( t < 1 \)).

### 3.1.1. Effects of emotional content on item memory.

A paired t-test was performed to compare memory performance, as indexed by d’. Emotional (M = 1.50, SD = 0.51) and neutral associates (M = 1.49, SD = 0.54). Results showed no differences on memory performance between emotional and neutral associates (t < 1).

#### 3.1.1.1. Interacting effects of emotion and memory.

Analyses of d’ revealed a main effect of Emotion, \( F(1,28) = 8.90, p < .001, \eta^2_p = 0.24 \), and a trend for Memory \( F(1,28) = 2.9, p = .098, \eta^2_p = 0.09 \). Most interestingly, an interaction Emotion x Memory effect was found, \( F(1,28) = 13.8, p < .001, \eta^2_p = 0.33 \). Post-hoc testing after correcting for multiple comparisons (p value after Bonferroni correction: 0.05/6 = 0.008) revealed that objects paired with emotional backgrounds showed larger d’ Remember, \( t(28) = 4.56, p < .001, d = 0.84 \), but comparable d’ Know \( t < 1 \), relative to their neutral counterparts. Furthermore, across both emotional and neutral contexts, total d’ Know and d’ Remember was comparable (ps > .02).

### 3.1.2. Source memory

#### 3.1.2.1. Effects of emotional content on overall source memory.

A paired t-test comparing overall source memory for neutral and emotional contexts revealed that source memory for neutral contexts (M = 0.16, SD = 0.09) was larger than for emotional ones (M = 0.13, SD = 0.09): \( t(28) = 2.87, p = .008, d = 0.53 \).

#### 3.1.2.2. Interacting effects of emotion and memory.

Results showed a main effect of Memory, \( F(1,28) = 12.26, p = .002, \eta^2_p = 0.31 \), but no effect of Emotion, \( F < 1 \). Most interestingly, an interaction Memory x Emotion approached significance, \( F(1,28) = 3.39, p = .076, \eta^2_p = 0.11 \). Post-hoc, exploratory analyses were performed to unfold the interaction effect (p value after Bonferroni correction: 0.05/6 = 0.008). 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 = .154, d = 0.29), correct source memory for emotional scenes was higher when memory was based on Remember rather than Know judgments (t [28] = 3.61, p = .001, d = 0.067). No such differences were observed for correct source memory for neutral scenes, \( t < 1 \) (see Fig. 2).

In summary, in line with our hypothesis, recollection-based memory (as indexed by d’ Remember) was higher for objects encoded in emotional compared to neutral contexts, whereas no differences were observed when memory was based on familiarity (i.e., d’ Know). Contextual source memory for backgrounds was also enhanced when item memory was based on Remember judgments, indicating that item and source memory performance for emotionally relevant events was especially pronounced when memory was based on recollection.

### 3.2. fMRI results

#### 3.2.1. Item memory

#### 3.2.1.1. Retrieval success for objects.

Fig. 3 represents the brain activation related to retrieval success (correctly retrieved neutral objects, collapsed across context categories, 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, and PCUN (Table 2).

#### 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 PCC, PCUN, and medial PFC, and at a trend level in the AG and orbital PFC (Fig. 4). RS for neutral associates, however, did not show any increased functional activity in comparison to emotional associates (Neutral RS > Emotional RS). Results are presented in Table 2.

#### 3.2.2. Contextual source memory

#### 3.2.2.1. Correct vs. incorrect contextual source memory.

As shown in Fig. 5, objects with correctly recognized background scenes elicited larger BOLD responses in the PCUN than objects from which memory for background scenes was not accessible (Table 3).

#### 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 the PCC, medial PFC, and orbital PFC (Fig. 6). However, correct memory for neutral contextual backgrounds relative to emotional backgrounds was not reflected in enhanced activity in any brain region (Neutral SoM > Emotional SoM) (see Table 3).

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**Fig. 2. Memory performance in the Remember/Know task.** A: Item memory performance as indexed by d prime (d’) as a function of Know and Remember judgments for objects encoded with emotional and neutral scenes. B: Source memory performance as indexed by unbiased hit rate (Hu) as a function of Know and Remember judgments for objects encoded in emotional and neutral backgrounds.
In the present study, we investigated long-term item and source recognition memory for neutral objects encoded with emotional and neutral scenes. Overall, we observed similar item memory performance for emotional and neutral associates. However, when memory quality was considered, memory for emotional, compared to neutral, associates was more dependent on recollection-based memory. Similarly, correct source memory was more likely driven by recollection processes, particularly for emotional cues. These results extend previous findings showing an increased long-term, recollection-based memory 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 previously associated with an emotional context.

At a neural level, replicating previous work, we observed a stronger engagement of regions embedded in a network related to recollection-based memory, including PPC, and PFC regions (Rugg and Vilberg, 2013; Gilmore et al., 2015). Critically, retrieval of emotional associates activated these regions more strongly, a pattern that was not only

**Table 2**

<table>
<thead>
<tr>
<th>Region</th>
<th>Side</th>
<th>MNI Coordinates x y z</th>
<th>t-values</th>
<th>Cluster level P_{FWE} &lt; .05</th>
<th>Cluster size (k) P_{unc} &lt; .001</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>RS: Hit &gt; Miss</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Medial PFC</td>
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<td>207</td>
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<tr>
<td></td>
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<td>.017</td>
<td>61</td>
</tr>
<tr>
<td>Orbital PFC</td>
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<td>−42 42 −6</td>
<td>7.53</td>
<td>&lt;.017</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>R</td>
<td>24 −6 −12</td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Emotional RS &gt; Neutral RS</strong></td>
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<td></td>
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<td>12</td>
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<td></td>
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<tr>
<td>AG</td>
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<td>271</td>
</tr>
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<td></td>
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<tr>
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<tr>
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<tr>
<td><strong>Neutral RS &gt; Emotional RS</strong></td>
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<tr>
<td>Posterior cingulate cortex</td>
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<tr>
<td></td>
<td>R</td>
<td>−3 −69 42</td>
<td></td>
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<tr>
<td>Orbital PFC</td>
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<td>.077</td>
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<td></td>
<td>R</td>
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<tr>
<td>AG</td>
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<td></td>
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<td></td>
<td>R</td>
<td>−6 −69 42</td>
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</table>

4. Discussion

In the present study, we investigated long-term item and source recognition memory for neutral objects encoded with emotional and neutral scenes. Overall, we observed similar item memory performance for emotional and neutral associates. However, when memory quality was considered, memory for emotional, compared to neutral, associates was more dependent on recollection-based memory. Similarly, correct source memory was more likely driven by recollection processes, particularly for emotional cues. These results extend previous findings showing an increased long-term, recollection-based memory 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 previously associated with an emotional context.

At a neural level, replicating previous work, we observed a stronger engagement of regions embedded in a network related to recollection-based memory, including PPC, and PFC regions (Rugg and 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,4 but also for source recognition memory. Altogether, we provide converging behavioral and neural evidence indicating that item and source memory for emotional, compared to neutral, associates was preferentially mediated by networks supporting recollection-based processes. Recollection-based retrieval has been associated with stronger feelings of vividness and re-experience of spatial, temporal or other contextual information of the encoding episode (Ochsner, 2000; Sharot et al., 2004; Yonelinas, 2002; Dolcos et al., 2005). In turn, a recollection-related preference for emotional associates and contextual information may indicate that, in the absence of an overall increase in memory performance, items associated with emotional contexts are more richly re-experienced during retrieval. Moreover, our results provide more information about the specific involvement of different anatomical areas in these processes. Below, we discuss the critical brain regions in more details.

4.1. Medial temporal lobe

We did not find any significant activation in MTL regions (but see section S10 and S11 of supplementary material for results using a more liberal threshold). The reduced differential activation in the MTL may in some way be caused by the delayed testing (one-week retention interval). Recent consolidation theories suggest that, although the MTL is necessary for the initial storage and recall of memories, with the passage of time and due to (sleep-related) consolidation, these memories are stored elsewhere in the neocortex, becoming less dependent on MTL activation (Dudai et al., 2015; Squire et al., 2007). Supporting this assumption, neuroimaging studies have shown increased functional connectivity between HC and mPFC during a recall task, if participants slept after the encoding session compared to when they did not (Gais et al., 2007). Similarly, hippocampal activation during retrieval has been shown to decrease with an increased amount of time passed from encoding, while the opposite pattern has been shown in PFC regions (C. N. Smith and Squire, 2009; Takashima et al., 2006), as well as in PPC regions (C. N. Smith and Squire, 2009). In line with these findings, the reduced effects in MTL may be due to the transference of information from MTL to neocortical regions after a long-term consolidation period. Supporting this view, areas of PPC and PFC showed much stronger activation during retrieval, surviving more conservative significant thresholds (see section S8 of the supplemental material).

4.2. Posterior parietal cortex (PPC)

Regions in the PPC (posterior cingulate cortex, angular gyrus, and precuneus/cuneus) typically involved in recognition memory (Rugg and Vilberg, 2013; Gilmore et al., 2015; King et al., 2015), showed larger activation during item and context memory retrieval of neutral objects. Activation of these regions was particularly pronounced for emotional, compared to neutral, 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 and King, 2018; Sestieri et al., 2017; Vilberg and 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 et al., 2014), indicating that the AG is linked to the vividness of the experience of the retrieved episode (Rugg and King, 2018). Others found that the AG is linked to processes such as semantic processing (Binder et al., 2009), number processing (Dehaene et al., 2003), attentional processing (Ciaramelli et al., 2008), or theory-of-mind (Decety and 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 and 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 and Rugg, 2012; Vilberg and Rugg, 2008) until the prominent task is finally executed. We observed that AG was more activated (at trend level) during the retrieval of emotional associates and contextual information, compared to their neutral counterpart. Given the role of emotion in generating more vivid recollective experiences (Dolcos et al., 2005; Weymar et al., 2009; Sharot et al., 2004), these findings suggest that emotional contextual information enhances the vividness and integration of the retrieved, associated representation.

The precuneus/cuneus has also been reliably related to episodic retrieval (Cavanna and Trimble, 2006; Rugg et al., 2002; Wagner et al., 2005). Although PCUN activity strongly covaries with other regions of the PPC (Gilmore et al., 2015; Hassabis et al., 2007; Weymar et al., 2018), the functional roles of these regions seem to differ. It has been

![Fig. 5. Brain activation associated with contextual source memory (item and background). Correctly compared to incorrectly retrieved source information evoked larger activity in the Precuneus (PCUN) (p < .001 uncorrected for the purpose of visualization), but not medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC) and Hippocampus (HC). ROI masks are displayed for each region for better illustration.](image-url)

<table>
<thead>
<tr>
<th>Region</th>
<th>Side</th>
<th>MNI Coordinates</th>
<th>t-values</th>
<th>Cluster level</th>
<th>Cluster size (k)</th>
<th>P_FWE</th>
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<tbody>
<tr>
<td>Correct &gt; Incorrect Context</td>
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<td>Angular gyrus</td>
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<tr>
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</table>
suggested that the PCUN, as part of the dorsal parietal cortex, is involved in top-down, goal-directed attentional processes during memory retrieval (Cabeza et al., 2008). However, recent evidence also found similar activations during undeliberate retrieval, when old stimuli were merely presented without explicit recognition instructions (Bradley et al., 2015; Weymar et al., 2018), suggesting that the PCUN region may be involved in both top-down and bottom-up attentional mechanisms (Gilmore et al., 2015). In our data, this region showed stronger activation during item and source memory retrieval, particularly for emotional associates. This finding extends a recognition memory study by Keightley et al. (2011) using emotional scenes and faces and suggests 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 and Vilberg, 2013). The PCC, among other regions, such as PCUN and AG, has been suggested to play a pivotal role in scene construction (Irish et al., 2015) during retrieval episodes (Hassabis et al., 2007). Furthermore, PCC activation has been related to representations of self-relevant information (Summerfield et al., 2009). In this vein, strong activation in the PCC is related to retrieval of self-relevant (autobiographical) memories (Maddock et al., 2001) and emotionally salient information (Maddock et al., 2003; Maratos et al., 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 et al., 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 is perceived as 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 et al., 2012). The medial PFC is particularly important for memory retrieval and is thought to guide behavior through the integration of current information with prior experiences. This region 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 and Preston, 2015). Furthermore, emotional relevance seems to enhance the integrative role of the medial PFC (Barron et al., 2013; Maratos et al., 2001; Smith et al., 2004). Regarding our data, greater involvement of the medial PFC during successful retrieval may indicate updating of the information from the reinstated events. Most interestingly, we found that medial PFC activity was specifically related to item and source memory for emotional associates, suggesting that the ongoing integration between previous and current encounters with an event may be particularly enhanced by the emotional relevance of the event (Schlichting and 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 and Northoff, 2009). Also, 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 associates (at trend level) and source cues, suggesting that the orbital PFC may be signaling the significance of the to-be-retrieved stimulus.

4.4. Limitations

Some limitations of the present study also need to be discussed. One limitation is related to source selection during the source memory retrieval. Participants were instructed to select the emotional category of the encoded background scene. It might be, however, that the scenes

![SoM for emotional vs neutral contexts](image-url)
were perceived differently by the participants. For instance, a participant might have evaluated a sport-related scene (preassigned to the pleasant category) as neutral or even unpleasant. We took some precautions to counteract this limitation. We made sure that valence and arousal ratings for the emotional and neutral images did not overlap in the valence and arousal dimension (cf. Jordan et al., 2015). We also used a heterogeneous variety of contents for each of the emotional category with a moderate number of trials, in order to minimize the distortion of the averaged patterns by outlier responses. In addition, we constrained the sample to healthy young individuals who did not suffer any mental disorder associated with deficits in emotional processing. Future studies may consider the assessment of the subjective value assigned to each of the background scenes, or the usage of a set of mixed lures and encoded background scenes as cues for participants during recognition. It must further be noted that, although we focused on the modulatory effects of emotion on the recollection network, there are other brain regions also involved in memory retrieval (e.g. thalamus, locus-coeruleus; Carlesimo et al., 2015; Clewett et al., 2018; Spaniol et al., 2009; Virginie Sterpenich et al., 2006). Thus, investigating how emotion modulates other brain areas beyond and/or in interaction with the recollection network may also be relevant for the field. Furthermore, in the current study, we directly tested for differences in memory retrieval between emotionally arousing (valence-ungspecific) and neutral associates (see supplementary material S9 for valence specific differences between pleasant and unpleasant categories). We rationalized this approach based on our and others’ prior studies, in which pleasant and unpleasant material produced memory enhancing effects in a similar fashion compared to neutral stimuli (e.g. Dolcos et al., 2005; Hamann et al., 1999; Ritchey et al., 2008; Ventura-Bort et al., 2016, 2017; 2019; Weymar et al., 2009), as well as on theoretical proposals stating that the increase of the arousal levels, produced by both pleasant and unpleasant stimuli play a critical role in the memory enhancing effect of emotion (McGaugh, 2004; Mather and Sutherland, 2011; Mather et al., 2016). However, future studies examining potential (individual) differences in relation to the retrieval of pleasant and unpleasant-related information, may help identify valence-dependent, memory mechanisms (Dolcos et al., 2004, 2017). Another limitation of the present study involves the unbalanced sex ratio of the participants. Although both females and males were included in the current study, the proportion of females was notably larger, which constrains the generalizability of our result.

4.5. Conclusion

In the present study, we found behavioral and neural evidence for preferential long-term recollection of neutral objects that have been associated with emotional scenes during encoding. Our findings suggest that emotional contexts enhance the recollective experience for neutral associated information by engaging different mechanisms involved in bottom-up and top-down processes (Dolcos et al., 2017, 2020). 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 and Clark, 2000; Robinson and Berridge, 1993).

Credit author statement

MW conceived the present idea. All authors contributed to the design. CV-B programmed the experiment and analyzed the data. All authors discussed the results and contributed to the final manuscript

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Appendix A. Supplementary data

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References


