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Opposing effects of pre-encoding stress on neural substrates of item and emotional contextual source memory retrieval

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A R T I C L E I N F O

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A B S T R A C T

Although the mediating role of the stress hormone systems in memory for single— especially emotional— events is well-stablished, less is known about the influence of stress on memory for associated contextual information (source memory). Here, we investigated the impact of acute stress on the neural underpinnings of emotional contextual source memory. Participants underwent a stress or a control manipulation before they encoded objects paired with pleasant, neutral, or unpleasant backgrounds. One week later, item and contextual source memory were tested. Acute stress modulated the neural signature of item and contextual source memory in an opposite fashion: stressed participants showed larger activation in the precuneus and the medial prefrontal cortex (mPFC) during the retrieval of items, while the retrieval of contextual unpleasant information was associated with lower activation in the angular gyrus (AG) and mPFC. Furthermore, as revealed by cross-region representational similarity analyses, stress also reduced the memory reinstatement of the previously encoded visual cortex representations of object/unpleasant background pairings in the AG and mPFC. These results suggest that pre-encoding stress induction increases the activity of memory-related regions for single items but reduces the activity of these regions during the retrieval of contextual unpleasant information. Our findings provide new insights into the dissociative effects of stress on item and contextual source memory which could have clinical relevance for stress-related disorders.

1. Introduction

Recent research indicates that the memory-enhancing effects of emotion for single emotional items (e.g., words, images, sounds; Bradley et al., 1992; Dolcos et al., 2004, 2005, 2017, 2020; Weymar et al., 2009; Weymar and Hamm, 2013) may extend to contextual details related to these events (i.e., emotional source or relational memory; for reviews see, Chiu et al., 2013; Dolcos et al., 2017, 2020; Mather et al., 2016; Murray and Kensinger, 2013), particularly if the association between the two pieces of information (item and context) is prioritized (Mather et al., 2016; Mather and Sutherland, 2011). For instance, when neutral objects are integrated into emotional and neutral background scenes (e.g., Ventura-Bort et al., 2016a; 2020a; 2020b), enhanced source memory for emotional contextual backgrounds and associated neutral objects have been found (Smith et al., 2004, 2005; Ventura-Bort et al., 2016; Symeonidou et al., 2022). The memory-enhancing effects are not associated with a familiarity-based (i.e., retrieval of an event without specifics) but with a recollection-based experience (i.e., an elaborate process that includes the retrieval of specific details of the encoding event; Ventura-Bort et al., 2020a, 2020b). Relatedly, the correct recognition of emotional scenes and associated items produced enhanced parietal Old/New differences - an event-related potential (ERP) indexing recollection-based retrieval (Rugg and Curran, 2007; Ventura-Bort et al., 2016a; Ventura-Bort et al., 2019, 2020b; Weymar et al., 2009) - as well

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as larger activation in brain regions associated with recollection processes (Ventura-Bort et al., 2020a), including regions of the posterior parietal and prefrontal cortices (c.f., Gilmore et al., 2015; Rugg and Vilberg, 2013). Altogether these results indicate that, as for item memory (Bogdan et al., 2024; Dolcos et al., 2005, 2020; Ochsner, 2000; Sharot et al., 2004; Tulving, 1985; Weymar et al., 2010; Ventura-Bort et al., 2020a; 2021), emotional relevance also increases the recollection of contextual details and associated neutral information.

Animal and human research suggests that the modulatory effect of emotional relevance on memory, especially for single events, is related to the release of adrenal stress hormones (epinephrine and glucocorticoids) in response to emotionally arousing or stressful events (Schönfeld et al., 2014; Schwabe, 2017). However, how stress hormone release influences source emotional memory is less well understood. The current study therefore aims at providing more insights into the role of stress on source memory by investigating how acute stress exposure prior to encoding of object-scene pairings modulates the neural correlates of emotional contextual source memory retrieval.

Previous studies have shown that the peripheral hormonal release influences central noradrenaline and corticosteroids levels in medial-temporal lobe regions implicated in emotional episodic memory, including amygdala and hippocampus (Henckens et al., 2009; McGaugh, 2000; McGaugh, 2004; McIntyre et al., 2012; Schwabe, 2017; Strange and Dolan, 2004). Consistent with this, pharmacological elevations of adrenaline and cortisol (Cahill and Alkire, 2003), transcutaneous auricular vagus nerve stimulation (Giraudier et al., 2022; Ventura-Bort et al., 2018; Ventura-Bort & Weymar, 2024), or stress induction (Schwabe et al., 2008; Kalbe et al., 2020; Sandi and Pinelo-Nava, 2007) before or during encoding improves recollection-based, long-term memory retrieval for emotionally relevant items (Segal and Cahill, 2009; Ventura-Bort et al., 2021; Weymar et al., 2012; Wirkner et al., 2013). Moreover, the administration of drugs that block adrenergic receptors (e.g., propranolol), prevents the enhanced memory for emotionally arousing events (Cahill et al., 1994), particularly by diminishing the recollective experience of emotional items (Cahill et al., 1994; Cahill and Alkire, 2003; Schwabe et al., 2013; van Stegeren, 2008; Weymar et al., 2010). Neuroimaging studies have further confirmed that the amygdala, in interaction with the hippocampus appears to be primarily responsible for the modulatory effects of glucocorticoids and catecholamines in emotional episodic memory (Henckens et al., 2009; Krenz et al., 2021; Strange and Dolan, 2004).

Extending these findings, it has recently been proposed that the modulatory influence of norepinephrine and corticosteroids expands to broader neurocognitive networks (Hermans et al., 2014; Schwabe et al., 2022), which include medial temporal regions. One of these networks is the ‘salience network’ which is implicated in the processing of salient, and relevant stimuli (Menon, 2011; Seeley et al., 2007) and involves the co-activation of the amygdala, the dorsal anterior cingulate, the hypothalamus, the anterior insula, the striatum, the thalamus, the inferotemporal and temporoparietal regions (Corbetta et al., 2008). In line, Hermans et al. (2011) observed that during the experience of stressful events, activation of the salience network increased, but disappeared after the intake of the beta-adrenergic receptor antagonist propranolol. Together with the activation of the salience network, stress also simultaneously produces changes in the so-called ‘executive control network’ (Hermans et al., 2014). This network has been related to cognitive control and contextual integration processes (Menon, 2011; Seeley et al., 2007) and encompasses the dorsomedial and dorsolateral prefrontal cortex and dorsal parietal regions. It has been suggested that stress – in parallel to an upregulation of the salience network – leads to a downregulation of this executive control network (Hermans et al., 2014). The opposing effects of stress hormones on the salience and executive networks may, thus, on the one hand, facilitate better learning and memory formation for stress-related information (Hermans et al., 2014). On the other hand, it may also come with cognitive costs, hampering the integration of the encoded information and its subsequent source memory retrieval (Schwabe, 2017; Schwabe et al., 2022; van Ast et al., 2013). Supporting this interpretation, earlier studies reported detrimental effects of stress hormone release on contextual source memory. For instance, in one study, stress induction before encoding impaired the beneficial effects of identical context on subsequent memory performance, suggesting a reduced integration of contextual cues under stress (Schwabe et al., 2009). Another study (van Ast et al., 2013) manipulated cortisol levels (via hydrocortisone intake) prior to the encoding of emotional and neutral words with specific background pictures and tested recognition memory for these words using the same or rearranged background scenes. This study found that cortisol abolished the context dependency for emotional words, suggesting that cortisol impaired contextual source memory for emotional events. However, more recent studies have partly yielded inconsistent results (Schwabe et al., 2009; Sep et al., 2019, 2022; Simon-Kutscher et al., 2019; van Ast et al., 2013; van Ast et al., 2013). For example, van Ast, and colleagues (2014), investigated whether similar cortisol effects on source memory after drug administration (van Ast et al., 2014) could also be observed when stress hormone release was promoted via acute stress. Contrary to their prior findings, a positive association between cortisol release before encoding and source memory for both emotional and neutral material was found (see also, Goldfarb, 2019). Other studies further reported no effects of stress prior to encoding (Kamp et al., 2019; Sep et al., 2019) or moderating effects of anxiety and life adversity on the relationship between stress hormone release (both catecholamines and glucocorticoids) and emotional source memory (Sep et al., 2022).

Although, the existing behavioral findings are rather mixed, understanding the role of stress on source memory is highly important not only for basic memory research but also for clinical conditions because dysfunctional integration of item-context information may play a critical role in mental disorders (e.g., intrusive and/or fragmented memory reactivations and overgeneralization in post-traumatic stress disorder, PTSD; Astur et al., 2006; Dolcos, 2013; Hayes et al., 2011; Kitayama et al., 2005; Maren et al., 2013). Given previous inconsistent findings and the importance of providing more insights into potential, clinically relevant (e.g., PTSD) neurobiological alterations related to stress hormones, the current fMRI study therefore aimed at investigating the neural mechanisms underlying the effects of acute stress on emotional contextual source memory retrieval in healthy subjects. Participants underwent either a socially evaluated cold pressor stress or a control test before the incidental encoding task. The task consisted of neutral objects associated with pleasant, neutral, or unpleasant scenes. We used an encoding task identical to our previous emotional source memory studies (Ventura-Bort et al., 2016, 2020a) to favor the comparability of the results. Because long retention intervals favor consolidation processes, which have a positive impact on the memory-enhancing effects of emotion for both items (McGaugh, 2004; Schümann et al., 2017; Weymar et al., 2009, 2011) and source information (Pierce and Kensinger, 2011), contextual source memory was tested one week later. In the memory task, the same encoded objects were intermixed with new ones, and participants were instructed to indicate whether objects were seen during encoding (item memory) and which background category (pleasant, unpleasant, or neutral) they were paired with (contextual source memory). To test the contribution of familiarity and recollection-based memory processes, we used the Remember/Know paradigm (Tulving, 1985). Because previous studies have shown that pre-encoding stress may facilitate the recollection of emotional item information (e.g., Weymar et al., 2012), we expected a recollection-based advantage for items embedded in emotional contexts, particularly in the stress group. At the neural level, we expected that correctly retrieved objects from pleasant and unpleasant scenes would show a larger engagement of brain areas previously linked to the recollection network (e.g., regions of the prefrontal cortex, posterior parietal cortex, and medial temporal cortex), especially in participants from the stress group. Given that previous studies have shown that stress may facilitate, decrease, or have no influence on contextual source memory retrieval, we made no a priori prediction about the modulatory effects of stress on the retrieval of contextual details. Similarly, considering the inconsistent behavioral effects, no specific predictions were made regarding the effects of stress on brain activation for contextual source memory details. Additionally, because previous research has shown that activity in the ventral visual stream during encoding of visual representations is reinstated during retrieval (Bowen et al., 2018; Bowen and Kensinger, 2017; Kark and Kensinger, 2019) and associated with memory performance (e.g., Katsumi et al., 2021), the modulatory effects of stress on the cross-region reinstatement of visual representations during retrieval was explored.

2. Methods

2.1. Participants

A total of seventy-seven healthy students (40 women, 37 men; $M_{age} = 22.84$ years, $SD_{age} = 3.39$) from the University of Greifswald participated in this study for course credits or financial compensation. The sample size was chosen based on prior studies investigating emotional episodic memory and its modulation by stress (e.g., Ventura-Bort et al., 2020a; Weymar et al., 2012; Wirkner et al., 2013). All participants had normal or corrected-to-normal vision and were native German speakers. Exclusion criteria for participating included smoking, current or lifetime diagnosis of mental disorders, medical conditions and medication intake within the prior three weeks and during study participation. Participants were instructed to refrain from physical exercise, meals, and caffeine intake within 2 h prior to the experimental sessions. The experiment always took place between 1 p.m. and 5 p.m. to control for the diurnal variation of the stress hormone cortisol. Each individual provided written informed consent for a protocol approved by the Review Board of the German Psychological Society.

2.2. Stimulus material

Stimuli were identical to our previous studies (e.g., Ventura-Bort et al., 2020a; 2020b) and 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-Martínez and Montoro, 2012; see for stimulus section details, Ventura-Bort et al., 2020a). Objects belonged to a heterogeneous variety of semantic categories (e.g., office supplies, electronics, household objects). 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 (see for details, Ventura-Bort et al., 2020a). Normative valence and arousal ratings were as follows: $M = 7.14$ ($SD = 0.48$) and $M = 6$ ($SD = 0.076$) 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.

Object/scene category pairings were counterbalanced across participants, by creating six different lists (for list construction see Ventura-Bort et al., 2020a). In each list, objects were arranged in six sets. Object categories were equally distributed across lists. The object sets were paired with pleasant (e.g., set 1), unpleasant (e.g., set 2), or neutral background scenes (e.g., set 3) or were available as novel object sets for retrieval (e.g., sets 4 to 6). For objects sets paired with background scenes, the object-image pairing within each set was randomly assigned. Each of the six object sets was equally assigned to each of the experimental conditions across lists (Ventura-Bort et al., 2020a). Each participant was randomly assigned to one of the six lists.

2.3. Design and procedures

The experimental design is displayed in Fig. 1.

2.3.1. General procedures

This experiment included two experimental sessions (encoding and retrieval). In the first session, after arrival, participants rested in a quiet room for 30 min to avoid any confounding baseline effects on physiological and neuroendocrine measures. After collecting the physiological and neuroendocrine measures at baseline, the stress or control induction protocol was applied, which lasted for approx. 15 min (about 20 min prior to the encoding task to optimally assess rapid corticosteroid effects). After the stress/control induction, participants were accompanied to the scanner room and received the instructions for the encoding task. Subjective, physiological, and neuroendocrine measures were collected immediately before and after the task. Approximately one week (8 ± 1 days) after the first session, participants returned to the scanner. We decided to use a one-week consolidation period to be in line with our previous emotional item and contextual source memory studies (e.g., Weymar et al., 2009; Ventura-Bort et al., 2016) that showed reliable memory enhancing effects of emotion. During the first 30 min participants underwent a resting state MRI scan (data are not reported here). Afterward, participants were informed about the surprise retrieval task. Before and after the retrieval task, physiological and neuroendocrine samples were collected.

2.3.2. Stress protocol and control condition

Participants were randomly assigned to the stress ($N = 43$, 25 women, $M_{age} = 22.59$ years, $SD_{age} = 3.24$) or control ($N = 34$, 15 women, $M_{age} = 23.18$ years, $SD_{age} = 3.6$) conditions. In general, the stress protocol used in the present study has reliably and successfully shown to produce acute stress responses, such as an increase in autonomic reactivity, salivary cortisol, and subjective ratings (Schwabe et al., 2008; Schwabe and Schächinger, 2018). However, not all participants may show the expected stress response, especially in hormonal indexes, after stress induction (i.e. cortisol non-responders; Schwabe et al., 2008). We therefore decided to include more participants in the stress than the control group to ensure inclusion of sufficient cortisol responders (see section S3 of the supplementary material for the item and contextual source memory results considering only cortisol stress responders).

In the stress condition, participants were exposed to the Socially Evaluated Cold Pressure Test (SECPT; Schwabe et al., 2008) followed by a difficult mental arithmetic (MA) test, similar to the Maastricht Acute Stress Test (MAST; Smeets et al., 2012). The stress induction lasted 15 min in total. In the first part, participants were asked to immerse their right hand, including the wrist, into ice water (temperature: 0–3 °C) for 3 min (or until they could no longer tolerate it). During hand immersion, participants were instructed to look straight into a camera because their faces were videotaped. They were told that video recordings would later be analyzed for facial expressions. Participants were also monitored by a non-supportive experimenter. Thereafter, participants performed the second part of the stress condition protocol consisting of a difficult 5-min mental arithmetic test, in which they had to count backward as fast and accurately as possible (in steps of 17 starting at 2043). Whenever participants counted too slowly or made mistakes, they received negative feedback (i.e., to count faster or start over again at 2043).

The control condition also consisted of two parts. After being informed about the protocol by a friendly and socially interacting experimenter, participants performed the first part of the protocol in which they immersed their right hand including the wrist for 3 min in warm water (35–37 °C). They were neither videotaped nor monitored by an unfamiliar experimenter. In the second part of the control condition protocol, they performed a simple arithmetic task, in which they had to count consecutively from 1 to 25 at their own pace and had to start anew at 1 when having reached the number 25.

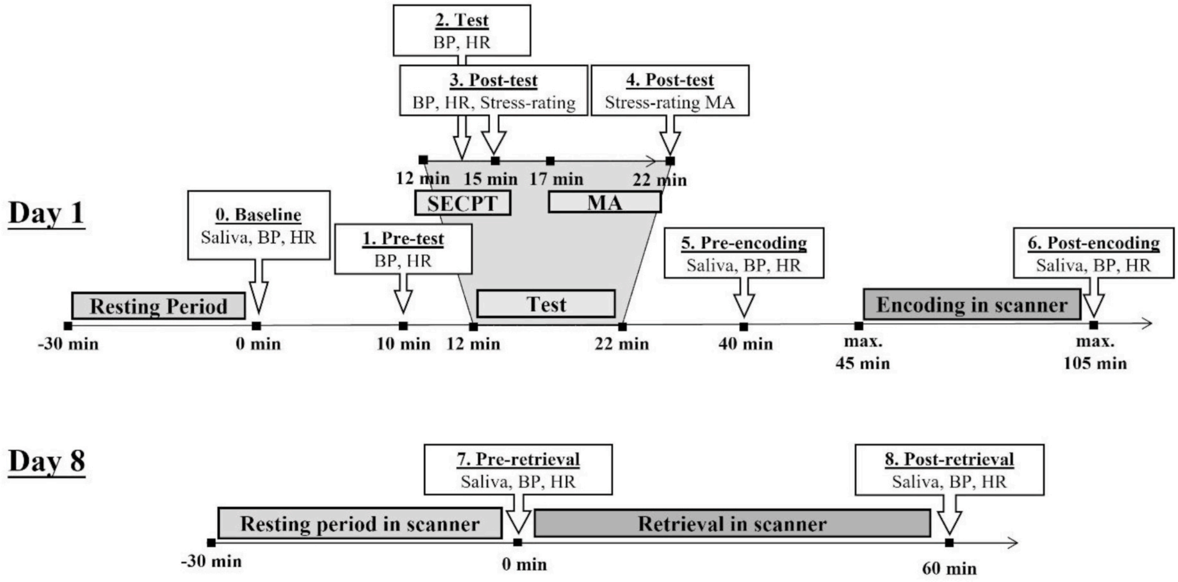

Fig. 1. Schematic representation of the two-session procedure. In the first session (Day 1), after arrival, participants rested in a quiet room for 30 min to avoid any confounding baseline effects on physiological and neuroendocrine measures. After collecting saliva samples, blood pressure (BP), and heart rate (HR) at baseline (0. Baseline), the stress or control induction protocol was applied, which lasted for approx. 15 min. The stress protocol consisted of the Socially Evaluated Cold Pressor Test (SECPT) and a difficult mental arithmetic (MA) test, whereas in the control protocol, participants had to immerse their hands in warm water and do a simple MA test. BP and HR measures were also collected 2 min prior (1. Pre-test) during (2. Test) and right after (3. Post-test) the first part of the stress/control protocol. Additionally, participants were asked to report the difficulty to keep their hand in the water and how unpleasant, painful, and stressful the test was (3. Post-test). Thereafter, the MA test was carried out for 5 min and at the end participants indicated again how difficult, unpleasant, and stressful the MA test was (4. Post-test). After the stress/control protocol, participants were accompanied to the scanner room and received the instructions for the encoding task. Approximately 15–20 min after the stress/control induction, to optimally assess rapid corticosteroid effects, saliva samples, as well as BP and HR, were collected (5. Pre-encoding). Thereafter, the encoding session took place, and afterward, saliva samples, BP, and HR were further gathered (6. Post-encoding). One week after the first session, participants returned to the scanner (Day 8). During the first 30 min participants underwent a resting state MRI scan. Afterward, participants were informed about the surprise memory task. Before (7. Pre-retrieval) and after (8. Post-retrieval) the memory retrieval task, saliva samples, BP, and HR measures were collected.

2.3.3. *Subjective, physiological, and neuroendocrine stress responses*

To test the efficacy of the stress induction protocol, subjective, physiological, and neuroendocrine measures were collected. To test the subjective effects of the stress condition, participants in both the stress and control group were asked to rate on a scale from 0 (“not at all”) to 10 (“very much”) how stressful and unpleasant the SECPT and the MA test were experienced (Steps 3. Post-test and 4. Post-test in Fig. 1). Following the SECPT, participants also rated how painful the procedure was and how difficult it was to keep the hand immersed in the water (tolerance difficulty). In the MA test, task difficulty was also tested. Cardiovascular measures (heart rate, and blood pressure) were recorded, using the Intelli Wrap Manschette M500 device (Omron Healthcare, 198 Medizintechnik Handelsgesellschaft mbH, Mannheim, Germany), immediately before (Step 1. Pre-test, in Fig. 1), during (Step 2. Test in Fig. 1) and right after the SECPT (Step 3. Post-test in Fig. 1). Neuroendocrine stress-related measures (salivary cortisol and alpha-amylase levels) associated with catecholaminergic (sympathetic nervous system) and cortisol stress system (hypothalamus-adrenal axis) were also obtained before and after stress induction using cotton Salivette samples (Sarstedt, Nümbrecht, Germany). Measures were taken before the stress induction protocol (Step 0. Baseline in Fig. 1), around 20 min after the stress induction (Step 5. Pre-encoding in Fig. 1), and about 85 min (Step 6. Post-encoding) after the end of the stress or control protocol. In the retrieval session, physiological, and neuroendocrine measures were collected immediately before (Step 7. Pre-retrieval) and after the memory task (Step 8. Post-retrieval; S2 of the supplementary material). Saliva samples were stored at −20 °C and analyzed by the Dresden LabService GmbH (Thoma et al., 2012) using an enzyme kinetic method.

2.3.4. *Encoding task*

During encoding, 132 objects were superimposed on 132 background scenes. Objects and background scenes were back-projected on a translucent screen, which participants could see through a mirror affixed to the head coil. The distance between the mirror and the participant’s eyes was 18 cm. The size of the stimuli was adapted to maintain a similar visual angle to our previous studies (Ventura-Bort et al., 2016). For each trial, objects were presented first on a black background in one of the four quadrants of the screen. After 3000ms, an emotional or neutral scene was presented as background. During the presentation of the object/background pairings for 5000ms, participants were instructed to imagine that the object is a part of the scene (to enhance object/background integration). No mention of a later memory test was made (i.e., incidental encoding). After a 2000 or 4000ms blank screen following object-background offset, a question mark was presented in the middle of the screen for 2000ms to which participants had to respond by pressing a ‘yes’ or ‘no’ button (on a response pad) whether the imagination was successful or not. Inter-trial intervals jittered between 6000 and 8000ms. A fixation cross was continuously presented in the center of the screen during all object/background trials and participants were instructed to fixate on it.

2.3.5. *Retrieval task*

During the retrieval task, each participant viewed 198 objects (132 old objects and 66 new objects). Object presentation was pseudo-randomized, with the restriction that no more than six objects of the same condition (old or new) were presented consecutively. We used Tulving’s Remember/Know paradigm (Tulving, 1985) to directly assess the contribution of recollection-based (remembering specific spatial, temporal, or other contextual details of events) and familiarity-based memory (knowing that an event occurred but not being able to remember specific contextual details). In each recognition trial, an object was presented in the center of the screen without scene context for 3000ms. After a 3000 or 5000ms blank screen following object offset, the question “Remember/Know/New?” was presented on the screen for

2000ms, and participants were asked to make a ‘Remember’, ‘Know’, or ‘New’ judgment. Participants were instructed to press the ‘Remember’ button on the response pad when they recognized the object as shown during encoding and when they could bring back specific associated information that occurred during encoding (e.g., thoughts evoked by the object when seen for the first time; recollection-based judgment). The ‘Know’ button was required when the object was recognized as presented during encoding but without specific associated information (familiarity-based judgment), and participants were instructed to press the ‘New’ button when the object was not seen (novel) during encoding. If participants made ‘Remember’ or ‘Know’ judgments, the question “Unpleasant/Neutral/Pleasant?” was displayed for 2000ms, and participants were instructed to select the correct emotional category of the contextual background scene that was paired with the object during encoding. Inter-trial intervals were jittered between 6000 and 8000ms. All encoding and recognition procedures were programmed using Presentation v. 16.5 (Neurobehavioral Systems Inc., Albany, CA, USA).

2.4. Analysis of stress-related subjective, physiological, and neuroendocrine measures

Data related to some of the variables of interest could not be analyzed due to technical problems (see S1 of supplementary material for details).

To compare the stress and control groups, subjective ratings of stress, unpleasantness, tolerance, task difficulty, and pain on the SECPT and MA test were separately analyzed using an unpaired *t*-test. To test the effects of the SECPT on heart rate and blood pressure a 3x2 mixed ANOVA was performed with the within-subject factor *Time* (2 min before SECPT vs 2 min-after the beginning of SECPT vs after extracting the hand from water; 1. Pre-test vs 2. Test vs 3. Post-test in Fig. 1) and the between-subject factor *Group* (stress vs control). The effects of stress induction on stress-related cortisol and alpha-amylase levels were tested separately using a 3x2 mixed ANOVA with the within-subject factor *Time* (10 min before stress induction vs 20 min after stress induction vs 85 min after stress induction; 0. Baseline vs 5. Pre-encoding vs 6. Post-encoding in Fig. 1) and the between-subject factor *Group* (stress vs control). For all analyses, significant interaction effects were followed up with t-tests using Bonferroni correction (α/n comparisons). For effects involving repeated measures, the Greenhouse-Geisser correction for non-sphericity was applied when necessary.

2.5. Behavioral data recording and analysis

2.5.1. Item memory

Behavioral performance for objects and contexts was recorded using Presentation (v. 16.5; (Neurobehavioral Systems Inc., Albany, CA, USA). Memory performance for items (i.e., objects) and source (i.e., contexts) was analyzed separately, using MATLAB 2019a, RStudio, and JMP 5.0. First, we analyzed the effects of emotion on overall item memory performance irrespective of memory quality. A mixed ANOVA was therefore conducted involving the within-subject factor *Context* (pleasant vs unpleasant vs neutral) and the between-subject factor *Group* (stress vs control) on d’ scores over all trials (collapsing across Remember and Know judgments). Interactions were followed up with post-hoc t-tests using Bonferroni correction (α/n comparisons). We, then, analyzed the effects of pleasant, unpleasant, and neutral contexts on item memory as indexed by d’ scores for each memory judgment (Remember vs Know: recollection vs familiarity processes) and context category, using a mixed ANOVA, involving the within-subject factors *Memory Type* (Remember vs Know) and *Context (*pleasant vs unpleasant vs neutral) and the between-subject factor *Group* (stress vs control). Interactions were followed up with post-hoc t-tests using Bonferroni correction (α/n comparisons). For effects involving repeated measures, the Greenhouse-Geisser correction for non-sphericity was applied when necessary.

Of note, 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 Ritchey, 2015). 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 based on both familiarity and recollection. Given the characteristics of the current task, it is expected that for these items, participants will use remember judgments, even though the items were also, to some extent, retrieved based on familiarity. Consequently, the probability that an item is familiar will be underestimated by the proportion of know responses over the total number of items presented. To determine the probability that an item is familiar, the proportion of know judgements should be calculated based on the opportunity to make Know judgments (Yonelinas and Ritchey, 2015). Theoretical proposals and empirical data clearly support the independence assumption as a more appropriate index to differentiate between recollection and familiarity processes (Yonelinas and Ritchey, 2015; Yonelinas and Ritchey, 2015). Thus, we decided to control for dependency (see for details Ventura-Bort et al., 2020a). d’ was therefore calculated under the independence assumption for both Remember (d' Recollection $= z(\text{P Remember}) - z(\text{P False Alarm Remember})$ and Familiarity:

$$z\left(\frac{P\ Know\ Hit\ Rate}{1 - P\ Remember\ Hit\ Rate}\right) - z\left(\frac{P\ Know\ False\ Alarm}{1 - P\ Remember\ False\ Alarm}\right)$$

2.5.2. Contextual source memory

Contextual source memory indexes were extracted from participants’ responses to the emotional category of the contextual background scene that was paired with the object during encoding. One potential index to assess contextual memory is the hit rate (e.g., probability of choosing a neutral category when the context was neutral). However, the hit rate does not take into consideration the existence of potential response biases (e.g., a tendency to response ‘neutral’ over and over again). To overcome this limitation, the unbiased hit rate (*Hu*) has been proposed (Ventura-Bort et al., 2020b; 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; see for details Ventura-Bort et al., 2020b). For instance, for neutral contexts of objects restricted to Know judgments, the Hu is calculated as follows:

$$\frac{Hit\ Know\ Neutral\ Context}{(Hit\ Know\ Neutral\ Context + Incorrect\ Know\ Neutral\ Context)} {}^{*} \frac{Hit\ Know\ Neutral\ Context}{N^{\circ}\ of\ times\ Neutral\ Context\ is\ chosen\ under\ Know\ judgements}$$

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.

The effects of emotion on overall contextual source memory performance were analyzed by calculating the Hu index on overall hits (collapsing Know and Remember judgments in one “old” category) for pleasant, unpleasant, and neutral contexts, separately. Differences in overall contextual source memory for emotional and neutral contexts were calculated using a mixed ANOVA, involving the within-subject factor *Context* (pleasant vs unpleasant vs neutral) and the between-subject factor *Group* (stress vs control).

The interaction effects of context and memory processes were analyzed by calculating the Hu indexes for each affective category and memory judgment, separately. Specifically, the Hu indexes for Remember and Know judgments, were calculated by only taking into consideration items that were judged as remembered or known, respectively. A mixed ANOVA was conducted involving the within-subject factors *Memory Type* (remember vs know) and *Context* (pleasant vs unpleasant vs neutral) and the between-subjects factor *Group* (stress vs group). Interactions were followed up with post-hoc t-tests using Bonferroni correction (α/n comparisons; see S4 of supplementary material for exploratory correlational analysis between behavioral performance and stress-related cortisol and physiological changes). For effects involving repeated measures, the Greenhouse-Geisser correction for non-sphericity was applied when necessary.

2.6. *Functional imaging data recording, preprocessing, and analysis*

Functional and anatomical images were recorded using a 3 T S 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 × 4 mm, 1 mm gap, TR 2000ms, TE 30ms, matrix 64 x 64, flip angle 90°). A T1-weighted anatomical volume (MP-RAGE, 176 sagittal slices, voxel size 1 x 1 × 1 mm, TR 1690ms, TE 2.52ms, matrix 256 × 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. Afterward, images were co-registered with the anatomical T1 volume, spatially normalized using segmentation, and spatially smoothed (8 mm FWHM Gaussian kernel). Preprocessed volumes from the retrieval were entered into different 1st level general linear models (GLM) for analysis of item and contextual source memory, as follows.

2.6.1. *GLM for item memory*

For item memory, a total of 21 regressors were entered: 11 regressors modeled the object onsets (correctly retrieved objects (hits) from pleasant, neutral, and unpleasant contexts based on remember judgments, correctly retrieved objects (hits) from pleasant, neutral, and unpleasant contexts based on "Know"-judgments, incorrectly retrieved objects (identified as new, i.e., misses) from pleasant, neutral, and unpleasant contexts, false alarms, and correct rejections; two regressors modeled the onset of the item (i.e., "Remember, Know, New") or contextual source memory questions (i.e., "Pleasant, Neutral, Unpleasant"); one regressor modeled the button press, and one regressor modeled the 60-s break in the middle of the task. Furthermore, six regressors (of non-interest) modeled movement-related noise.

2.6.2. *GLM for contextual source memory*

For contextual source memory, due to the low number of trials per condition, correctly retrieved objects based on remember and know judgments were collapsed together into one hit condition, resulting in a total of 21 regressors. Eleven regressors modeled the object onset. Trials related to contextual source memory were modeled depending on participants' response and context category. Trials in which the context was correctly chosen were modeled as 'correct'. Trials in which the context was incorrectly selected were modeled as 'incorrect'. Trials that were incorrectly categorized as new were modeled as 'miss'. Altogether, the eleven regressors were labeled as follows: 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 two regressors for the onset of the item and contextual source memory questions, one for the button press, one for the 60-sec break, and six as motion parameters.

Analyses were performed using a Region-of-Interest (ROI) approach. ROIs were defined based on prior brain imaging studies showing that successful episodic retrieval is associated with greater activation in regions, including the hippocampus (HC), parahippocampal cortex (PHC), medial and orbital prefrontal cortex (mPFC and OFC), 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 and Ritchey, 2012). All of these regions have been tightly linked to the so-called recollection network that promotes the representation of previously encoded events (Gilmore et al., 2015; Rugg and Vilberg, 2013).

At the whole-brain level, clusters with a minimum size of 5 voxels that surpassed a significance threshold of $p < 0.005$ (uncorrected for multiple comparisons) were detected first. Then, the significance of each cluster was compared to a threshold of $p < 0.05$ corrected for multiple comparisons (family-wise error rate, FWE). Although in ROI analysis the correction for multiple comparisons is commonly performed for each ROI, separately, here we used a more conservative strategy. We used a mask of all ROIs (16 ROIs in total; see Ventura-Bort et al., 2020a for details) consisting of 55,843 voxels to apply the multiple comparison correction. ROI analyses were conducted for regions embedded in the recollection network (Vilberg & Rugg, 2013), including the HC, PHC, PCUN, PCC, AG, mPFC, and OFC. The mask for the HC created based on published guidelines for manual tracing of the MTL (Moore et al., 2014), was obtained from FD's lab, the masks for PHC, medial PFC (mPFC), orbital PFC, PCC, PCUN, and cuneus, were derived from the Wake Forest University Pick Atlas (Maldjian et al., 2003).

2.6.3. *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 used. The RS describes the retrieval-related difference in activity in response to items that were successfully retrieved (hits) from items that were unsuccessfully retrieved (misses). The RS (hits vs misses) was extracted for each participant and tested at a second level using a one-sample *t*-test. To investigate the effects of stress on retrieval success, the RS contrast was compared between groups, using a two-sample *t*-test. Interaction effects between affective category and item memory were tested by comparing the RS of each affective category. A contrast for each comparison was calculated at a first level using the *Imcalc* function from SPM12 (e.g., RS Pleasant > RS Neutral) and tested at a second level using a one-sample *t*-test. Stress effects on RS for unpleasant, pleasant, and neutral objects were tested using two-sample t-tests. Exploratory correlational analysis was conducted to test the relation between the brain activity and behavioral performance. Specifically, the averaged activity of the significant clusters was correlated to memory indexes of item memory. Furthermore, the effects of cortisol on RS were investigated by including the increase of cortisol as a covariate in the analysis.

2.6.4. *Functional activity related to contextual source memory*

To examine the functional activity of contextual source memory (SoM), the difference between context hits (i.e., correctly retrieved item and context) and context errors (i.e., correct item but incorrect context) was calculated. For overall contextual source memory effects, SoM contrasts were performed for each participant, independently of background category, and tested at the second level using one-sample t-tests. To investigate the effects of stress on contextual source memory, the SoM contrast was compared between groups, using a two-sample *t*-test.

For the effect of valence on contextual source memory, SoM contrasts were extracted for each participant and affective category. Thereafter, the SoM effects of each affective category were compared with each other at the first level and tested at the second level, using one-sample t-tests. Stress effects on SoM for objects from unpleasant, pleasant, and neutral contexts were tested using two-sample t-tests. Exploratory correlational analysis was carried out to examine the relation between brain activity and behavioral performance. The averaged activity of the significant clusters was therefore correlated to memory indexes of contextual source memory. Moreover, the effects of cortisol on SoM were examined by including the increase of cortisol as a covariate in the analysis.

2.6.5. Representational similarity analysis (RSA) to test for the effects of stress during encoding on reinstatement of visual memory representations during retrieval

The release of stress hormones may further promote the connectivity between the amygdala and visual regions (Bowen et al., 2018), modulating the initial processing and subsequent retrieval of visual material. In this sense, it has been shown that activity in the ventral visual stream during encoding is associated with subsequent memory retrieval, especially for emotionally relevant information (Dolcos et al., 2017, 2020b; Ritchey et al., 2008). This relationship seems to be associated with the reinstatement of encoded visual representations during retrieval (Katsumi et al., 2021) in both visual areas (Bowen et al., 2018; Bowen and Kensinger, 2017; Kark and Kensinger, 2019) and, cross-regionally, in memory-related areas, including hippocampal regions (Takashima et al., 2006, 2009) and posterior parietal and prefrontal regions (Xiao et al., 2017, 2020).

To test whether the stress effects observed in contextual source memory contrasts were related to variations in the reinstatement of visual representations in both neocortical and medial temporal regions we used representational similarity analysis (RSA; Dandolo and Schwabe, 2018; Krenz et al., 2021; Kriegeskorte et al., 2008; Nili et al., 2014). RSA is a suitable multivariate approach that tests for the similarities between two independent conditions (i.e., activity during encoding and retrieval) by comparing their representational dissimilarity matrices (RDMs; pairwise dissimilarity patterns across stimuli). In the first step, normalized, unsmoothed echoplanar imaging data of individual trials were modeled using GLMs. Each object/scene trial of the encoding session and every single old object of the retrieval session were modeled as individual regressors together with two regressors for the onset of the item and contextual source memory questions, one for the button press, one for the 60-s break, and six as motion parameters. In addition, for the encoding session, the onset of all objects was modeled as one single regressor. Similarly, for the retrieval session, all new objects were modeled as one regressor. Thereafter, we adapted the RSA toolbox (Nili et al., 2014) to construct separate RDMs (44x44) for each participant, context condition (i.e., pleasant, unpleasant, or neutral), and ROI. Considering the existing evidence highlighting the contribution of occipital regions in memory reinstatement (e.g., Bowen et al., 2018), RSMs during encoding were extracted from the left and right occipital cortices, separately. The occipital cortex masks were derived from the Wake Forest University Pick Atlas (Maldjian et al., 2003). The masks consisted of the combination of three subregions of the occipital cortex (superior, middle and inferior occipital gyri). During retrieval, we defined our ROIs, based on the univariate analysis. ROIs were limited to clusters showing significant interacting effects of stress and context, which were uniquely observed in the SoM contrast (i.e. mPFC, left and right Angular gyrus, and left hippocampus; see Fig. 7). RDMs were calculated based on Euclidean distances. Subsequently, the correspondence between encoding- and retrieval-based RDMs was examined, using spearman's correlations for each condition and participant, separately. Given that the interacting effects of stress and context category were specifically related to neutral and unpleasant categories, we used a 2x2 ANOVA with the factors *Group* (stress vs control) and *Context* (neutral vs unpleasant) to test for the modulatory effects of group (stress vs control) and condition (vs neutral vs unpleasant) on memory reinstatement. Interactions were followed up with post-hoc t-tests using Bonferroni correction (α/n comparisons).

3. Results

3.1. Subjective, physiological, and neuroendocrine responses to the SECPT and MA test

Overall, participant's subjective ratings and physiological and neuroendocrine changes indicated that acute stress was successfully induced (descriptive values for each measure are summarized in section S2 of the supplementary material). Fig. 2 depicts the main differences between groups.

3.1.1. Effects of stress on subjective experience

Participants in the stress group rated the SECPT as significantly more stressful, $t_{75} = 9.06$, $p < .001$, unpleasant, $t_{75} = 12.2$, $p < .001$, and painful, $t_{75} = 13.7$, $p < .001$, than participants in the warm water, control condition. In addition, hand immersion in the stress group was harder to tolerate, $t_{75} = 9.16$, $p < .001$, than in the control group. Similarly, the MA test was rated as significantly more stressful, $t_{75} = 13$, $p < .001$, unpleasant, $t_{75} = 8.57$, $p < .001$, and difficult, $t_{75} = 27.6$, $p < .001$, by the stress compared to the control group.

3.1.2. Effects of stress on physiological changes

To test the effects of the SECPT on cardiovascular changes, heart rate and blood pressure values before during, and after the test were compared separately across groups. For heart rate, a mixed ANOVA showed a main effect of *Time,* $F_{1.73,126} = 15.02$, $p < .001$, $\eta^2 = 0.17$, but no main effect of *Group,* $F_{1,73} = 0.07$, $p = .78$, $\eta^2 = 0.001$. Importantly, the *Time* × *Group* interaction was significant, $F_{1.73,126} = 6.28$, $p = .001$, $\eta^2 = 0.08$. Although, subsequent post-hoc t-tests (Bonferroni-corrected threshold: 0.05/3 = 0.016) did not reveal any significant difference between groups at any of the three time points: before the test: $t_{73} = 0.35$, $p = .72$; during the test: $t_{75} = 1.31$, $p = .19$; after the test: $t_{75} = -0.98$, $p = .33$, we could observe the expected heart rate increase during stress induction (*Time:* $F_{1.57,64.54} = 16.12$, $p < .001$, $\eta^2 = 0.28$) as demonstrated by higher heart rate during the hand immersion than before the hand immersion ($t_{41} = -3.35$, $p = .002$). Such an increase in heart rate was, however, not observed in the control group (*Time:* $F_{2,64} = 2.37$, $p = .101$, $\eta^2 = 0.07$).

For systolic blood pressure, a main effect of *Time* was observed, $F_{1.72,125.44} = 11.23$, $p < .001$, $\eta^2 = 0.13$, but no main effect of *Group* was found, $F_{1,72} = 3.36$, $p = .072$, $\eta^2 = 0.04$. Critically, the *Time* × *Group* interaction was significant, $F_{1.72,125.44} = 34.53$, $p < .001$, $\eta^2 = 0.32$. Follow-up t-tests (Bonferroni-corrected threshold: 0.05/3 = 0.016), revealed elevated systolic blood pressure during the SECPT relative to the control manipulation, $t_{75} = 4.83$, $p < .001$, but no differences between groups before, $t_{73} = -0.07$, $p = .93$, and after the test, $t_{75} = 0.83$, $p = .41$.

For diastolic blood pressure, a main effect of *Time,* $F_{1.77,128.98} = 10.78$, $p < .001$, $\eta^2 = 0.13$, and *Group* were found, $F_{1,73} = 4.28$, $p = .04$, $\eta^2 = 0.05$, as well as a significant *Time* × *Group* interaction, $F_{1.77,128.98} = 27.35$, $p < .001$, $\eta^2 = 0.27$. Follow-up t-tests (Bonferroni-corrected threshold: 0.05/3 = 0.016), revealed no differences in diastolic blood pressure between groups before, $t_{73} = -0.97$, $p = .34$, and after the test, $t_{75} = 1.33$, $p = .18$, but again a significant increase during the SECPT, $t_{75} = 5.54$, $p < .001$, compared to the control condition.

3.1.3. Effects of stress on neuroendocrine changes

Salivary alpha-amylase and cortisol levels were log-transformed to normalize the skewed data.

For salivary alpha-amylase levels, a mixed ANOVA revealed a main effect of *Time,* $F_{2,144} = 8.24$, $p < .001$, $\eta^2 = 0.1$, but neither a main effect

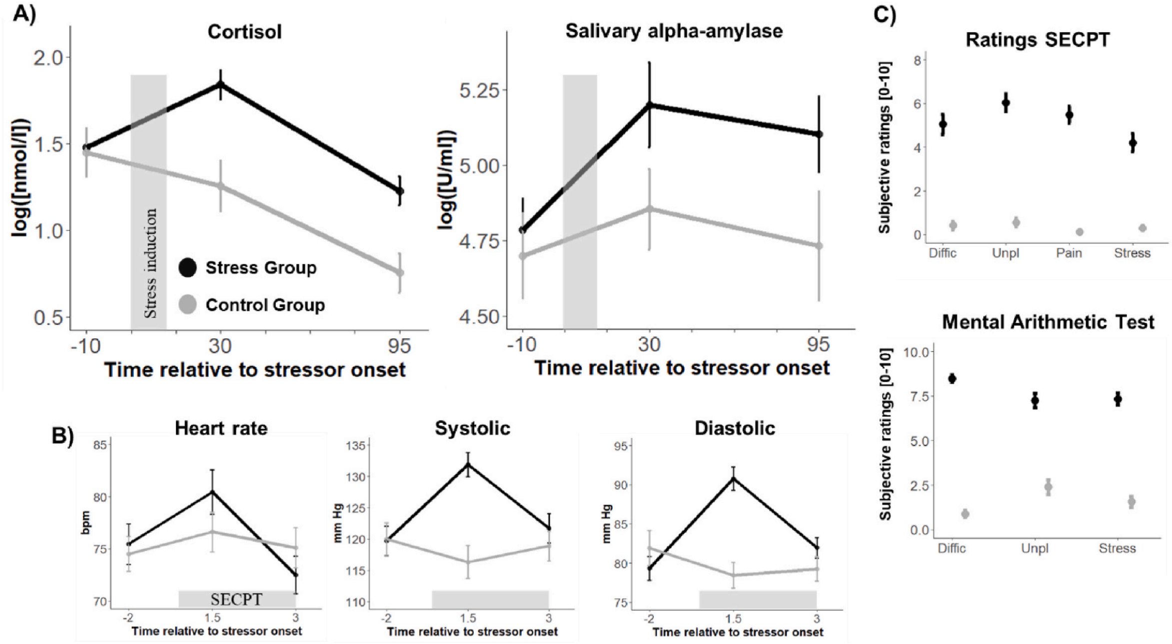

Fig. 2. Neuroendocrine (A), physiological (B), and subjective (C) responses to the stress induction protocol. A) Changes in salivary cortisol (left) and salivary alpha-amylase (right) following the stress or the control protocol. B) Physiological changes during the SECPT as measured by heart rate (left) and systolic (middle) and diastolic (right) blood pressure. C) Subjective stress ratings during stress and control conditions. After the SECPT, subjective ratings about the difficulty to keep the hand in water (Diffic), the unpleasantness (Unpl), pain, and stress were collected. After the mental arithmetic test, participants indicated how difficult (Diffic), unpleasant (Unpl), and stressful (Stress) the task was. Both tasks were rated on a scale from 0 to 10.

of *Group* $F_{1,72} = 2.46$, $p = .12$, $\eta^2 = 0.03$, nor a *Time* × *Group* interaction, $F_{2,144} = 2.23$, $p = .11$, $\eta^2 = 0.03$, was found. Subsequent exploratory analyses were performed to examine group differences at each time point, separately (Bonferroni-corrected threshold: 0.05/3 = 0.016). Results revealed a stronger increase in sAA following the stress induction, however, group differences between the stress and control group were not significant in the *t*-test before, $t_{73} = 0.19$, $p = .85$, 20 min after, $t_{73} = 1.62$, $p = .11$, and 85 min after stress induction, $t_{73} = 1.53$, $p = .13$. Despite that, we observed the expected increase in sAA levels after stress induction (*Time:* $F_{2,82} = 11.45$, $p < .001$, $\eta^2 = 0.22$) as demonstrated by higher sAA levels 20 min ($t_{43} = -4.49$ $p < .001$) and 85 min after treatment ($t_{43} = -2.94$, $p = .006$). Such increase was, however, not observed in the control condition (*Time:* $F_{2,82} = 1.01$, $p = .35$, $\eta^2 = 0.03$).

For cortisol levels, mixed ANOVA showed a main effect of *Time,* $F_{2,144} = 42.33$, $p < .001$ $\eta^2 = 0.37$, a main effect of *Group*, $F_{1,72} = 5.97$, $p = .017$, $\eta^2 = 0.08$, and crucially, an interaction effect between *Time* and *Group*, $F_{2,144} = 11.02$, $p < .001$, $\eta^2 = 0.13$. Follow-up unpaired t-tests revealed no significant differences (Bonferroni-corrected threshold: 0.05/3 = 0.016) between the stress and control group prior to the stress induction, $t_{73} = 0.15$, $p = .88$, but increased cortisol levels in the stress group 20 min after the treatment, $t_{73} = 3.59$, $p < .001$, that still remained significantly elevated 85 min after the stress induction, $t_{73} = 3.37$, $p = .001$.

3.2. Memory performance

Fig. 3 shows the main behavioral findings for item and contextual source memory (descriptive values of memory performance are summarized in Table 1).

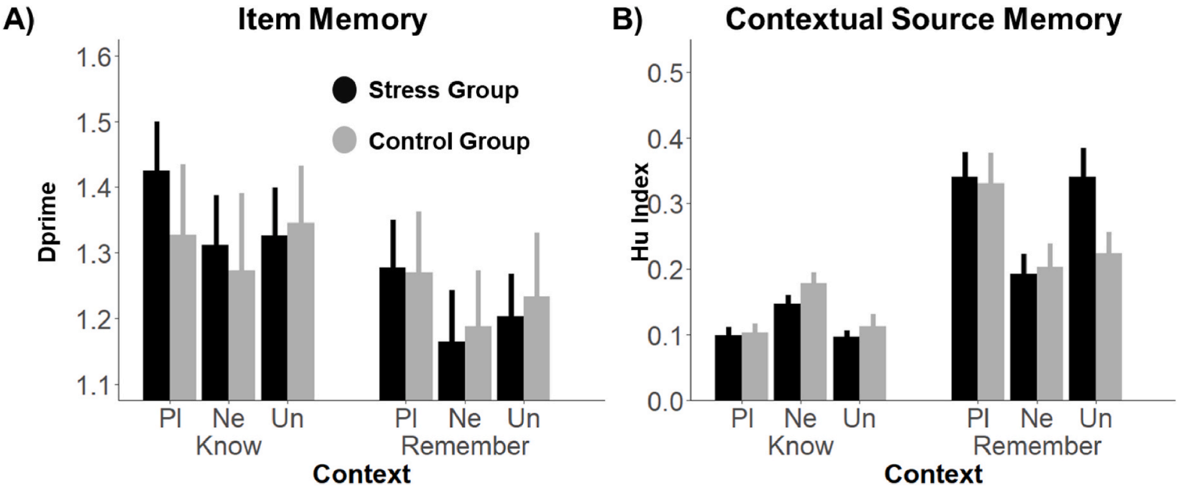

Fig. 3. Memory performance in the Remember/Know task. Depiction of behavioral performance for item (A) and contextual source memory (B) split based on familiarity-driven, know judgments and recollection-driven remember judgments. Error bars represent standard error. Pl = Pleasant, Ne= Neutral, Un = Unpleasant.

Table 1

Item and Contextual Source Memory: Mean values (standard deviation) of hit rates, false alarm rates, d' for old objects originally encoded with pleasant, neutral and unpleasant scenes (context) and Hu index for background scenes, both overall and split by memory type (remember vs. know). S= Stress group, C= Control Group.

	Memory Performance					
	Pleasant Contexts		*Neutral Contexts*		*Unpleasant Contexts*	
	S	*C*	*S*	*C*	*S*	*C*
Item memory						
Overall HR	0.70 (0.16)	0.65 (0.15)	0.66 (0.17)	0.62 (0.16)	0.66 (0.17)	0.62 (0.18)
Overall FA	0.21 (0.15)	0.17 (0.14)	0.21 (0.15)	0.17 (0.14)	0.21 (0.15)	0.17 (0.14)
Overall d'	1.56 (0.52)	1.5 (0.57)	1.44 (0.51)	1.43 (0.62)	1.45 (0.49)	1.44 (0.52)
HR Remember	0.22 (0.17)	0.26 (0.20)	0.19 (0.17)	0.24 (0.19)	0.21 (0.18)	0.23 (0.20)
FA Remember	0.04 (0.09)	0.05 (0.08)	0.04 (0.09)	0.05 (0.08)	0.04 (0.09)	0.05 (0.08)
d' Remember	1.29 (0.47)	1.16 (0.51)	1.18 (0.54)	1.18 (0.5)	1.21 (0.42)	1.22 (0.57)
HR Know Corrected for Dependency	0.61 (0.21)	0.51 (0.18)	0.57 (0.20)	0.51 (0.19)	0.57 (0.20)	0.54 (0.19)
FA Know Corrected for Dependency	0.18 (0.14)	0.14 (0.11)	0.18 (0.14)	0.14 (0.11)	0.18 (0.14)	0.14 (0.11)
d' Know Corrected for Dependency	1.43 (0.48)	1.31 (0.63)	1.32 (0.48)	1.26 (0.68)	1.33 (0.47)	1.33 (0.51)
Contextual source memory						
Overall Hu	0.15 (0.09)	0.14 (0.10)	0.16 (0.07)	0.19 (0.08)	0.15 (0.09)	0.12 (0.09)
Hu Remember	0.34 (0.25)	0.33 (0.27)	0.2 (0.19)	0.2 (0.2)	0.35 (0.29)	0.21 (0.17)
Hu Know	0.1 (0.09)	0.1 (0.09)	0.15 (0.08)	0.18 (0.09)	0.11 (0.07)	0.11 (0.1)

3.2.1. *Item memory*

For overall d', the mixed ANOVA revealed a main effect of *Context*, $F_{2,140} = 5.81$, $p = .004$, $\eta^2 = 0.08$, but neither a main effect of *Group*, $F_{1,70} = 0.3$, $p = .87$, $\eta^2 = 0$, nor a *Context* × *Group* interaction effect, $F_{2,140} = 0.43$, $p = .65$, $\eta^2 = 0.01$, was observed. A follow-up paired *t*-test showed that item memory was higher for objects previously paired with pleasant backgrounds than with unpleasant, $t_{73} = 2.83$, $p = .006$, and neutral backgrounds, $t_{71} = 3.39$, $p = .001$. No difference was observed in memory performance for objects encoded with neutral and unpleasant backgrounds, $t_{71} = 0.45$, $p = .66$.

When memory quality was considered (see Fig. 3A), mixed ANOVA revealed a main effect of *Context*, $F_{2,120} = 7.69$, $p < .001$, $\eta^2 = 0.11$, but no main effect of *Memory*, $F_{1,60} = 0.22$ $p = .64$, $\eta^2 = 0.004$, or *Group*, $F_{1,60} = 0.73$, $p = .39$, $\eta^2 = 0.01$. Furthermore, no interactions were significant (*Context* x *Memory*, $F_{2,120} = 0.4$, $p = .67$, $\eta^2 = 0.01$, *Context* x *Group*, $F_{2,120} = 1.10$, $p = .33$, $\eta^2 = 0.02$, *Memory* x *Group*, $F_{1,60} = 1.12$, $p = .30$, $\eta^2 = 0.02$, *Context* x *Memory* x *Group*, $F_{2,140} = 1.12$, $p = .33$, $\eta^2 = 0.02$.

3.2.2. *Contextual source memory*

The 3x2 mixed ANOVA for the overall Hu index showed a main effect of *Context*, $F_{2,140} = 6.13$, $p = .003$, $\eta^2 = 0.04$, but no main effect of *Group*, $F_{1,70} = 0.1$, $p = .75$, $\eta^2 = 0.001$. The *Context* × *Group* interaction was significant at the trend level, $F_{2,140} = 2.93$, $p = .057$, $\eta^2 = 0.02$. Subsequent t-tests (Bonferroni-corrected threshold: 0.05/3 = 0.016) revealed that contextual source memory (reflected by Hu index) was enhanced for neutral compared to pleasant, $t_{71} = 2.58$, $p = .012$, and unpleasant contexts, $t_{71} = 2.74$, $p = .007$. No difference in contextual source memory was found between pleasant and unpleasant contexts, $t_{71} = 0.40$, $p = .68$. Due to the trend *Context* × *Group* interaction, we performed exploratory analysis (Bonferroni-corrected), comparing contextual source memory for both groups for each category, separately. The group comparison, however, revealed no differences for pleasant, $t_{70} = 0.37$, $p = .71$, unpleasant, $t_{70} = 1.51$, $p = .13$, and neutral contexts, $t_{70} = -1.43$, $p = .16$.

When memory type was considered (see Fig. 3B), we obtained a main effect of *Memory*, $F_{1,67} = 75.71$, $p < .001$, $\eta^2 = 0.15$, but no main effect of *Context*, $F_{2,134} = 2.02$, $p = .13$, $\eta^2 = 0.01$, or *Group*, $F_{1,67} = 0.62$, $p = .43$, $\eta^2 = 0.003$. Only the *Context* × *Memory* interaction was significant, $F_{2,134} = 12.62$, $p < .001$, $\eta^2 = 0.05$, (other non-significant interactions: Context x *Group*, $F_{2,134} = 1.42$ $p = .24$, $\eta^2 = 0.006$; *Memory* x *Group*, $F_{2,140} = 3.14$, $p = .081$, $\eta^2 = 0.07$; *Context* x *Memory* x *Group*, $F_{2,140} = 0.81$, $p = .47$, $\eta^2 = 0.01$), which was followed up by separate 3x2 ANOVAs for recollection- and familiarity-based contextual source memory judgments.

For familiarity-based judgments, the main effect of *Context* reached significance, $F_{2,140} = 11.86$, $p < .001$, $\eta^2 = 0.1$, but no main effect of *Group*, $F_{1,70} = 1.30$, $p = .26$, $\eta^2 = 0.01$, or interaction emerged, $F_{2,140} = 0.71$, $p = .49$, $\eta^2 = 0.01$. When contextual source memory for each context category was compared (Bonferroni-corrected threshold: 0.05/3 = 0.016), the Hu index was higher for neutral than for pleasant, $t_{71} = 2.58$, $p = .012$, and unpleasant contexts, $t_{71} = 2.73$, $p = .007$. No differences were observed between pleasant and unpleasant contexts, $t_{71} = 0.41$, $p = .68$.

For recollection-based judgments, a main effect of *Context* was found, $F_{2,134} = 6.85$, $p = .001$, $\eta^2 = 0.05$, but no main effect of *Group*, $F_{1,67} = 1.61$, $p = .21$, $\eta^2 = 0.01$, or interaction, $F_{2,134} = 1.19$, $p = .31$, $\eta^2 = 0.01$. Paired comparisons for each affective category (Bonferroni-corrected threshold: 0.05/3 = 0.016) revealed enhanced contextual source memory for pleasant, $t_{68} = 3.72$, $p < .001$, and unpleasant contexts, $t_{71} = 2.57$, $p = .013$, compared to neutral ones. No differences were found between pleasant and unpleasant contexts, $t_{68} = 1.69$, $p = .094$. Although the interaction was not significant, visual inspection of the data pointed to group differences in recollection-based contextual source memory for unpleasant contexts. The direct group comparison, however, did not show significant differences when applying the Bonferroni-corrected threshold ($p = .01$): $t_{68} = 2.07$, $p = .04$.

In summary, we observed a general memory advantage for objects encoded in pleasant contexts. For contextual source memory, a recollection advantage for emotional (both pleasant and unpleasant) compared to neutral contexts was found. The modulating effects of emotion on item and contextual source memory were observed for both the stress and control groups.

3.3. *fMRI results*

3.3.1. *Item memory*

Retrieval success for objects. As expected, correctly retrieved old objects, compared to forgotten ones, generated larger activity in a variety of brain regions associated with the recollection network, including the medial and orbital PFC, AG, PCC, Cuneus, and PCUN (main findings are summarized in Table 2; see also S5 of supplementary material). Importantly, acute stress modulated memory retrieval success, as indicated by larger activation in the PCUN and medial PFC (at a trend level) for the stress compared to the control group (See Fig. 4).

When RS was investigated separately for each affective context, comparable RS was observed across categories. No interactions with context and group were observed in regions of the recollection network. No clusters showing main RS effects or clusters showing group effects were significantly related to item memory performance ($rs < |0.21|$, $ps > 0.11$)

Cortisol effects on Item Memory. The increase of cortisol before encoding was related to larger activation in the left AG (coordinates: 42, −69, 27; t = 4.15, cluster p-value (uncorrected) = 0.03), in the RS contrast, irrespective of encoding context. This effect, however, did not reach significance after applying the FWE correction (cluster p-value

Table 2

Brain regions showing overall (collapsed across affective categories) item memory retrieval success (RS; hits vs misses) and the RS contrast comparing the stress and control groups. PFC: prefrontal cortex, PCUN: precuneus, PCC: posterior cingulate cortex, AG: angular gyrus, PHC: parahippocampal cortex, HC: hippocampus. L = Left, R = Right. n.s. = non-significant.

Region	Side	MNI Coordinates			t-values	Cluster level $P_{FWE} < 0.05$	Cluster level (uncorrected)	Cluster size (*k*) $P_{unc} < 0.005$
		x	y	z				
RS: Hit > Miss								
mPFC	LR	−6	24	42	9.39	**.005**	**.001**	306
PCUN	LR	−6	−66	42	8.93	**<.001**	**<.001**	1247
AG	L	−36	−63	45	7.68	**.02**	**<.001**	278
	R	36	−69	42	6.67	*.06*	**.005**	205
PCC	LR	−6	−45	15	7.55	**.02**	**.004**	219
Cuneus	LR	−12	−63	27	7.51	0.15	**.04**	104
Orbital PFC	L	−36	21	−6	6.20	*.07*	**.002**	219
	R	33	27	−6	5.30	0.79	0.16	57
PHC	L	−56	−30	−21	4.44	0.81	0.1	56
HC	R	21	−27	−9	3.07	0.99	0.32	21
RS Stress > Control								
PCUN	LR	9	−69	48	4.04	**.03**	**006**	194
Medial PFC	LR	−3	36	42	3.60	*.10*	**.02**	124
RS Control > Stress								
n.s.								

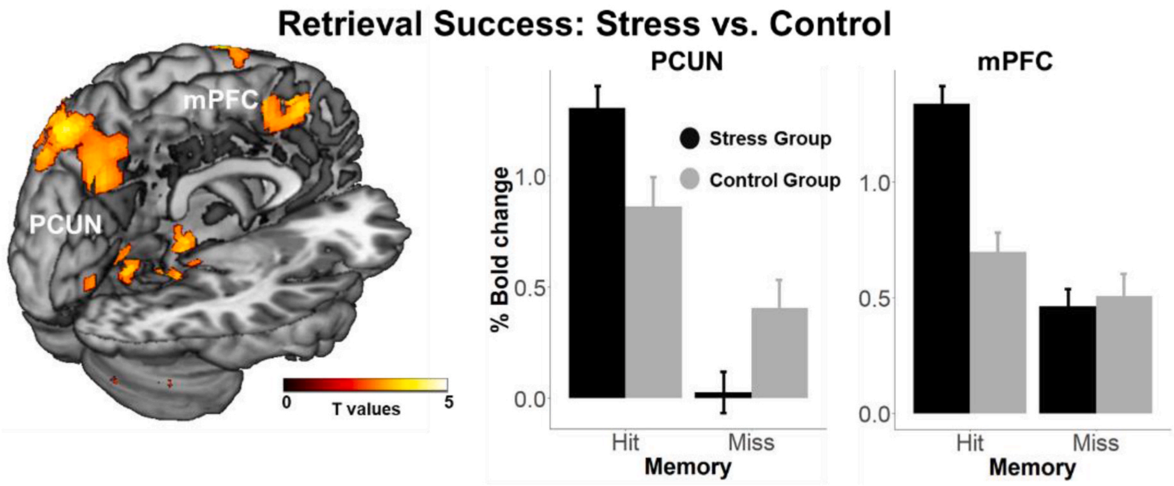

Fig. 4. Larger brain activation related to retrieval success (RS) for Stress compared to Control Group. RS refers to the difference in activity in response to items that were successfully retrieved (hits) from items that were unsuccessfully retrieved (misses). In the stress compared to the control group, correctly retrieved objects (hits) compared to forgotten ones (misses) produced larger activity in the precuneus (PCUN), and medial prefrontal cortex (mPFC; at a trend level) ($p < .005$ uncorrected for the purpose of visualization). Error bars represent standard error.

(FWE-corrected) = 0.129; cluster size = 113).

3.3.2. *Contextual source memory*

When overall contextual source memory retrieval (SoM; hit vs error contexts) was considered, correctly retrieved objects produced larger activation in various regions of the recollection network. However, the functional activation did not survive the correction for multiple comparisons (see Table 3; see also S6 of supplementary material). Furthermore, no group differences were observed in the SoM contrast. When SoM was separately investigated for each affective category, no significant effects were observed for neutral or pleasant contexts. However, the SoM contrasts for unpleasant contexts showed higher activity in PCUN and mPFC (see Fig. 5A). A group interaction also revealed larger activation in mPFC and AG for the control, compared to the stress group (see Fig. 5B).

Finally, the SoM comparison between unpleasant and neutral contexts revealed interacting group and context effects in mPFC and AG (see Table 3), showing larger SoM activation for unpleasant compared to neutral contexts in the control group, which was reversed in the stress group (see Fig. 6).

Exploratory correlational analysis showed that the neural activity of the SoM contrasts for unpleasant contexts was positively related to recollection-based contextual source memory performance for unpleasant contexts, PCUN: $\rho = 0.3$, $p = .02$, mPFC: $\rho = 0.4$, $p = .002$, but not for neutral ones, PCUN: $\rho = 0.05$, $p = .69$, mPFC: $\rho = -0.7$, $p = .57$. No association was found between brain activity and familiarity-based contextual source memory performance either for unpleasant, PCUN: $\rho = 0.01$, $p = .97$, mPFC: $\rho = 0.16$, $p = .22$, or for neutral contexts, PCUN: $\rho = -0.04$, $p = .79$, mPFC: $\rho = 0.20$, $p = .17$. However, clusters showing group effects for unpleasant contexts were unrelated to contextual source memory performance for unpleasant (recollection-based: $rs < |0.24|$, $ps > 0.06$, familiarity-based: $rs < |0.14|$, $ps > 0.18$) and neutral contexts (recollection-based: $rs < |0.07|$, $ps > 0.57$, familiarity-based: $rs < |0.17|$, $ps > 0.18$)

Table 3
Brain regions showing contextual source memory (SoM: correct vs incorrect context) for unpleasant backgrounds overall and between groups. PFC: prefrontal cortex, PCUN: precuneus, PCC: posterior cingulate cortex, AG: angular gyrus, HC: hippocampus. L = Left, R = Right. n.s. = non-significant.

Region	Side	MNI Coordinates			t-values	Cluster level $P_{FWE} < 0.05$	Cluster level (uncorrected)	Cluster size (*k*) $P_{unc} < 0.005$
		x	y	z				
SoM: Hit vs Error Contexts								
mPFC	LR	−9	30	39	4.01	0.18	**.03**	77
PCUN	L	−6	−63	33	3.40	0.26	*.05*	62
	R	9	−63	33	3.79	0.50	0.12	38
AG	L	−54	−57	27	3.79	0.62	0.16	30
HC	R	27	−39	−12	3.56	0.96	0.54	6
SoM Stress > Control								
n.s.								
SoM Control vs Stress								
n.s.								
SoM for Neutral Contexts								
mPFC	L	3	36	39	3.39	0.65	0.18	28
	R	9	60	0	3.90	0.90	0.39	11
SoM for Neutral Contexts: Stress > Control								
mPFC	LR	6	51	30	3.51	0.34	*.07*	53
AG	L	−42	−54	33	3.30	0.32	*.07*	55
	R	54	−54	36	2.88	0.96	0.54	6
SoM for Neutral Contexts Control > Stress								
n.s.								
SoM for Pleasant Contexts								
n.s.								
SoM for Pleasant contexts Stress > Control								
n.s.								
SoM for Pleasant contexts Control > Stress								
n.s.								
SoM for Unpleasant Contexts								
PCC	LR	0	−51	30	3.71	0.26	*.06*	66
PCUN	LR	−3	−60	33	3.55	**.03**	**.005**	159
MPFC	LR	−6	57	15	3.55	**.046**	**.009**	139
AG	L	−45	−63	42	2.96	0.85	0.34	15
	R	45	−48	21	3.09	0.95	0.52	7
HC	R	21	−33	−6	3.06	0.95	0.52	7
SoM for Unpleasant Contexts Stress > Control								
n.s.								
SoM for Unpleasant Contexts Control > Stress								
AG	R	45	−60	27	4.28	**.007**	**.001**	231
	L	−42	−69	42	3.33	0.31	*.07*	60
HC	L	−21	−36	0	4.14	0.75	0.25	22
	R	33	−30	−12	3.03	0.88	0.38	13
MPFC	LR	6	51	27	3.96	**.014**	**.003**	195
PCUN	L	−6	−48	24	3.40	0.47	0.11	43
	R	24	−57	24	3.48	0.36	*.08*	53
PCC	L	−6	−48	24	3.40	0.79	0.28	19
	R	9	−51	30	3.14	0.82	0.31	17
Orbital PFC	L	−9	30	54	2.84	0.96	0.56	5
	R	42	42	−9	3.07	0.89	0.39	12

(*continued on next page*)

Table 3 (*continued*)

Region	Side	MNI Coordinates			t-values	Cluster level $P_{FWE} < 0.05$	Cluster level (uncorrected)	Cluster size (*k*) $P_{unc} < 0.005$
		x	y	z				
SoM for Unpleasant vs Neutral Contexts								
PCC	LR	0	−51	30	3.33	0.537	0.15	39
MPFC	L	−6	57	15	3.15	0.919	0.489	9
SoM for Unpleasant vs Neutral Contexts: Control > Stress								
MPFC	LR	6	51	27	4.62	**<.001**	**<.001**	427
AG	L	−39	−63	42	3.75	0.119	*.025*	106
	R	48	−60	39	4.43	**.005**	**.001**	273
HC	L	−21	−36	0	4.09	0.255	*.057*	72
PCUN	L	−9	−48	12	3.30	0.82	0.355	17
	R	15	−45	3	3.95	0.796	0.308	19
Orbital PFC	L	−48	27	−9	3.25	0.742	0.263	23
	R	42	27	−12	3.43	0.561	0.16	37
PCC	L	−9	−45	9	3.1	0.848	0.366	15
	R	6	−42	30	3.05	0.958	0.617	5

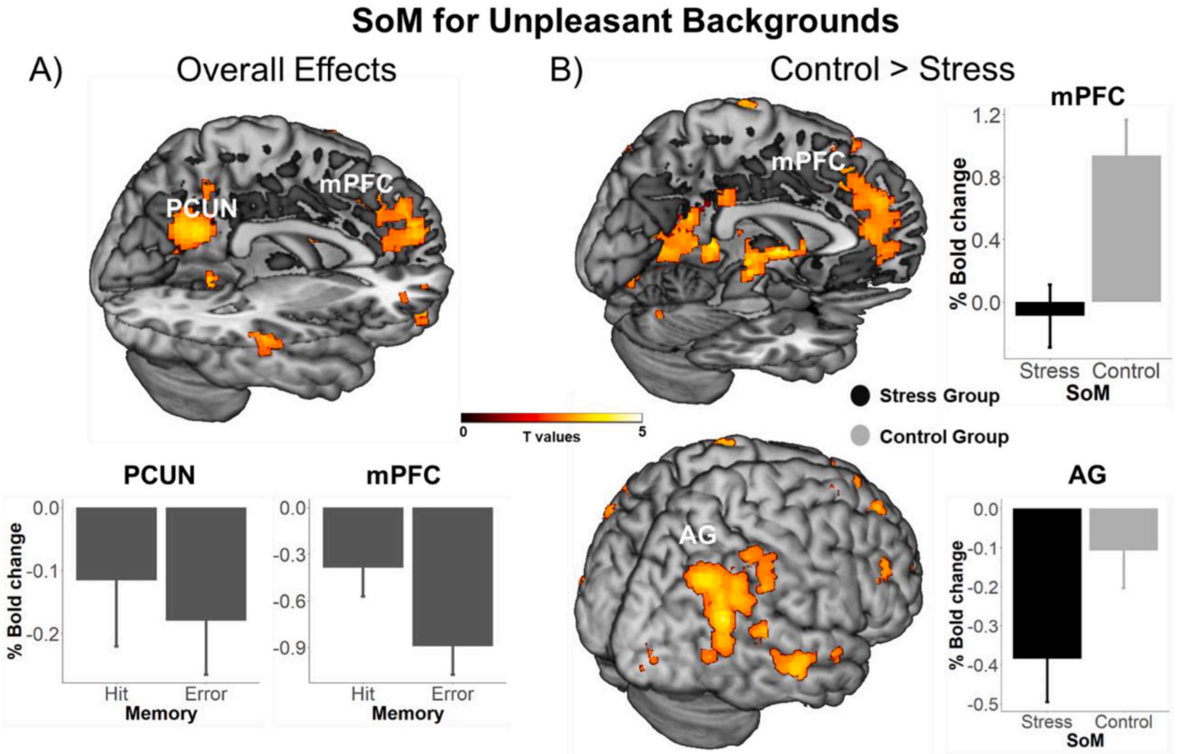

Fig. 5. Brain activation associated with contextual source memory for unpleasant contexts. Source memory refers to the difference between context hits (i.e., correctly retrieved item and context) and context errors (i.e., correct item but incorrect context). **A**) Correctly identified contexts (hits) compared to wrongly identified ones (error) elicited larger activity in the precuneus (PCUN), and medial prefrontal cortex (mPFC). B) When groups were compared, larger SoM activation was found in the control compared to the stress group in mPFC and AG. ($p < .005$ uncorrected for visualization only). Error bars represent standard error.

With regard to the significant group x emotion interacting effects, we observed a positive associations between the mPFC and recollection-based contextual source memory performance for unpleasant contexts (right AG: r = −0.18, p = .17, left AG: r = −0.19, p = .14, mPFC: r = 0.27, p = .038, left HC: r = 0.22, p = .09) whereas non-significant associations were found with familiarity-based, contextual source memory performance for unpleasant contexts (right AG: r = −0.25, p = .05, left AG: r = −0.06, p = .64, mPFC: r = 0.19, p = .15, left HC: r = 0.12, p = .36). Although brain activity was unrelated to recollection-based contextual source memory performance for neutral contexts (right AG: r = 0.15, p = .27, left AG: r = 0.09, p = .49, mPFC: r = 0.1, p = .46, left HC: r = 0.06, p = .46) positive associations were found with familiarity-based contextual source memory performance for neutral ones (right AG: r = 0.25, p = .05, left AG: r = 0.17, p = .18, mPFC: r = 0.29, p = .02, left HC: r = 0.18, p = .16).

Cortisol effects on contextual source memory

Overall SoM activation was not modulated by the stress-induced cortisol increase prior to encoding. However, cortisol increase during encoding was negatively related to left AG activation during source retrieval of unpleasant contexts: coordinates: 45, −69, 39; t = 4.55, cluster p-value (uncorrected) = 0.006; cluster p-value (FWE-corrected) = 0.030; cluster size = 159. Furthermore, context category interacting effects between unpleasant and neutral contexts were modulated by the cortisol increase. Specifically, lower cortisol increase was related to a larger activity for unpleasant compared to neutral SoM in the left and right AG. Left AG: coordinates: 45, −69, 42; t = 4.62, cluster p-value

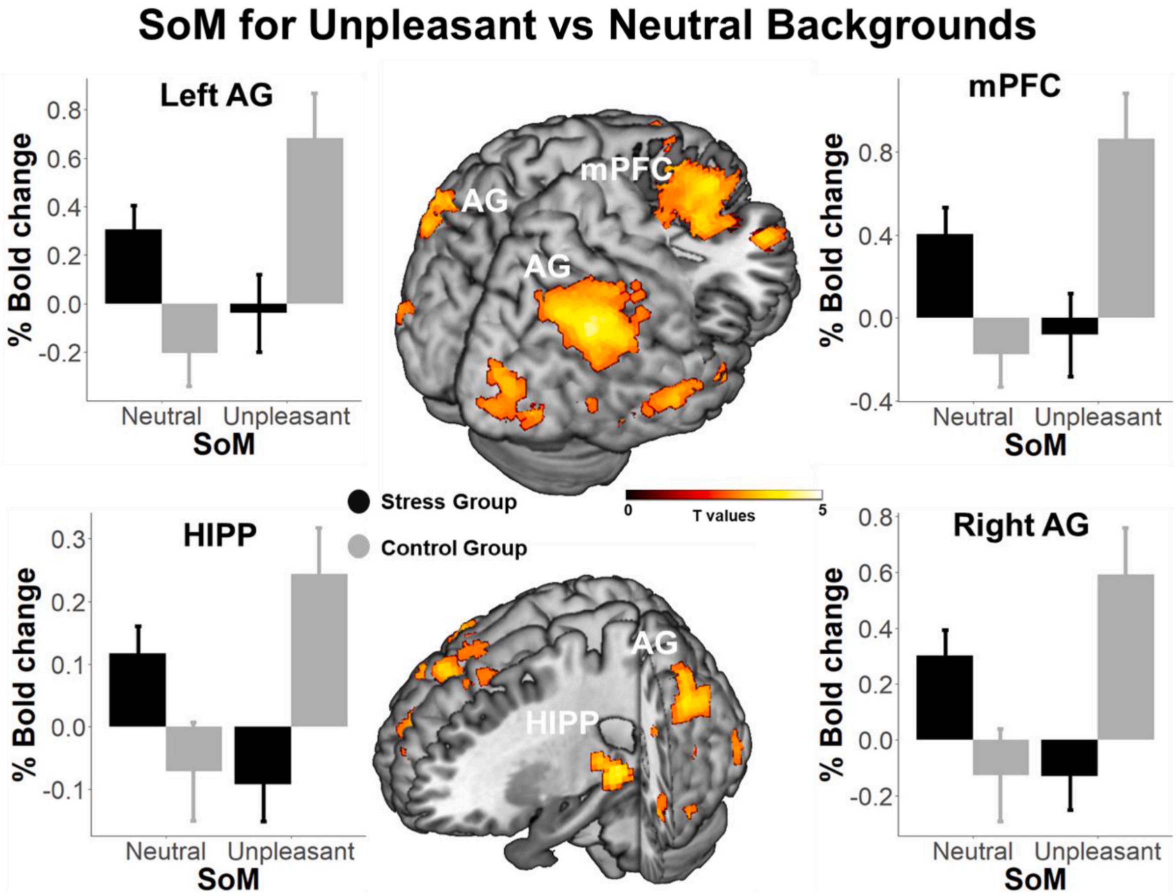

Fig. 6. Brain activation associated with interacting effects of Group in contextual source memory for unpleasant vs neutral contexts. Source memory refers to the difference between context hits (i.e., correctly retrieved item and context) and context errors (i.e., correct item but incorrect context). In comparison to the stress group, the control group showed larger SoM for unpleasant vs neutral contexts activation in the angular gyrus (AG) and medial prefrontal cortex (mPFC). ($p <$ .005 uncorrected for visualization only). Error bars represent standard error.

(uncorrected) = 0.003; cluster p-value (FWE-corrected) = 0.016; cluster size = 209. Right AG: coordinates: 51, −60, 45; t = 4.40, cluster p-value (uncorrected) = 0.006; cluster p-value (FWE-corrected) = 0.03; cluster size = 175.

3.3.3. Effects of stress during encoding on reinstatement of visual representations during retrieval

To follow up on the interaction effects of context and stress in the SoM contrast and based on prior findings pointing toward the cross-regional reinstatement of visual representations of the encoded events in cortical regions during memory retrieval (the so-called cross-region reinstatement effect; e.g., Xiao et al., 2017, 2020), we used RSA to compare the activation pattern of object/scene pairings of unpleasant and neutral contexts in visual regions (occipital cortices) during encoding with the activation pattern of objects from unpleasant and neutral contexts in brain clusters showing significant interaction effects of context and stress during retrieval (see Fig. 7A; see S7 of supplementary material for exploratory analysis on the relation between the cross-region reinstatement and memory performance).

3.3.3.1. Right occipital cortex. In the left AG, the memory reinstatement of visual representations was not modulated by *Group*, $F_{1,47} = 2.31$, p = 0.14, $\eta^2 = 0.05$, or *Context*, $F_{1,47} = 0.035$, p = .85, $\eta^2 = 0.00$, however, the interaction *Group* x *Context* reached significance, $F_{1,47} = 4.189$, p = .046, $\eta^2 = 0.082$. Post-hoc testing (Bonferroni-corrected threshold: 0.05/2 = 0.025) showed no group differences for neutral contexts: $t_{47} = -0.16$, p = .87, but stronger reinstatement for unpleasant contexts in the control group compared to the stress group: $t_{47} = 2.64$, p = .011.

In the right AG, a main effect of *Group* was observed, $F_{1,47} = 5.76$, p = .02, $\eta^2 = 0.11$, but neither the main effect of *Context*, $F_{1,47} = 0.38$, p = .54, $\eta^2 = 0.01$ nor the *Group* × *Context* interaction reached significance, $F_{1,47} = 0.72$, p = .4, $\eta^2 = 0.01$. Based on visual inspection of the data, subsequent testing (Bonferroni-corrected threshold: 0.05/2 = 0.025), comparing both groups for each condition, separately, revealed again, significant differences in the control, compared to the stress group, in the unpleasant, $t_{47.6} = 2.55$, p = .014, but not in the neutral condition, $t_{47} = 1.09$, p = .29.

In the right mPFC, no main effects of *Group*, $F_{1,47} = 1.96$, p = .17, $\eta^2 = 0.04$ or *Context* were observed, $F_{1,47} = 0.69$, p = .41, $\eta^2 = 0.01$ but a significant *Group* × *Context* interaction was found, $F_{1,47} = 4.44$, p = .04, $\eta^2 = 0.09$. Post-hoc testing (Bonferroni-corrected threshold: 0.05/2 = 0.025) revealed no group differences for neutral contexts, $t_{45.9} = -0.49$, p = .62. However, for unpleasant contexts, stronger visual recapitulation was found for the control, compared to the stress group: $t_{47} = 2.51$, p = .016.

In the left hippocampus cluster, no significant effects of *Group* $F_{47} = 0.004$, p = .95, $\eta^2 = 0.00$, *Context*, $F_{1,47} = 0.42$, p = .52, $\eta^2 = 0.00$ or *Group* × *Context* interaction were found, $F_{1,47} = 0.01$, p = .91, $\eta^2 = 0.00$.

3.3.3.2. Left occipital cortex. In the left AG, the memory reinstatement of visual representations was not modulated by *Group*, $F_{1,47} = 0.81$, p = 0.37, $\eta^2 = 0.02$, or *Context*, $F_{1,47} = 0.1$, p = .75, $\eta^2 = 0.002$, however the interaction *Group* x *Context* approached significance, $F_{1,47} = 3.057$, p = .087, $\eta^2 = 0.06$. To follow-up on the trending interaction effect, both groups were compared for unpleasant and neutral contexts, separately (Bonferroni-corrected threshold: 0.05/2 = 0.025). No group differences

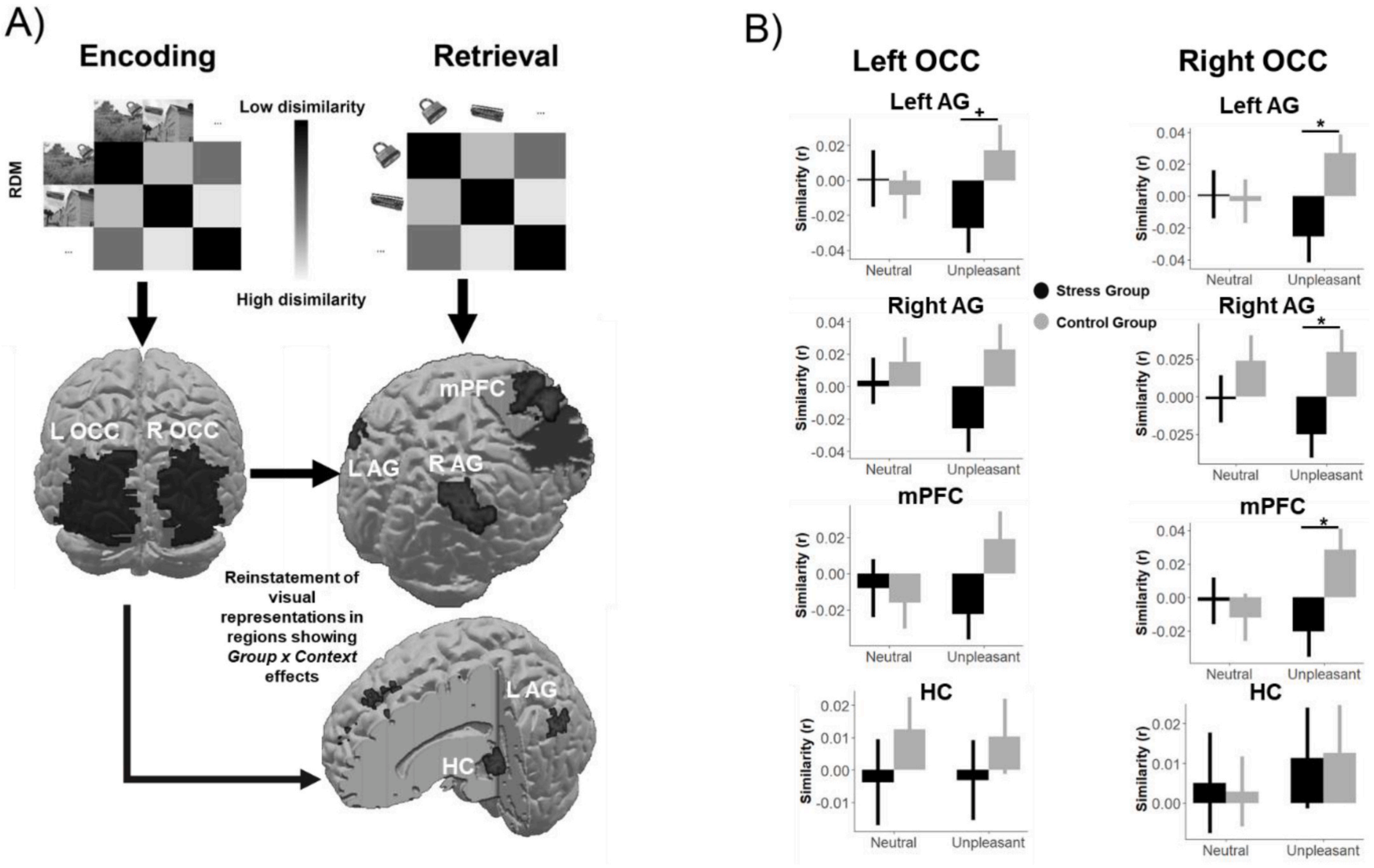

Fig. 7. Reinstatement of visual representations in regions showing Group x Context effects. A) Schematic representation of the procedure. In the first step, representational dissimilarity matrices (RDMs) of object/scene pairings presented during encoding for each condition (i.e., pleasant, unpleasant, and neutral) and participant were extracted in the predefined ROIs, which were the left and right occipital cortices (OCC). Additionally, for the retrieval sequence, RDMs of old objects for each condition and participant were extracted from the clusters showing significant interacting *Group* x *Context* effects in the SoM contrasts. Based on the significant interacting effects observed in SoM, similarities between encoding and retrieval RSMs were submitted to ANOVAs with the within-subject factors *Group* (i.e., control vs stress) and *Context* (i.e., unpleasant and neutral). B) Results of the RSA analysis. Interacting *Context* x *Group* effects were observed in cortical regions, including the angular gyrus (AG) and medial prefrontal cortex (mPFC) —but not in the hippocampus (HC), indicating weaker memory reinstatement of visual representations in the stress group, particularly for unpleasant material. *p ≤ .016 (Bonferroni-corrected significant threshold), + p < .05. Error bars represent standard error.

were found for neutral contexts: $t_{47} = -0.38$, $p = .704$. Stronger memory reinstatement, however, was found for unpleasant contexts, in the control group than the stress group: $t_{47} = 2.19$, $p = .033$ (trend level).

In the right AG, the main effect of *Group* approached significance, $F_{1,47} = 2.99$, $p = .09$, $\eta^2 = 0.06$, but no main effect of Context, $F_{1,47} = 0.89$, $p = .35$, $\eta^2 = 0.02$ or *Group* × *Context* interaction reached significance, $F_{1,47} = 1.16$, $p = .287$, $\eta^2 = 0.024$.

In the right mPFC, neither the main effect of *Group*, $F_{1,47} = 0.78$, $p = .38$, $\eta^2 = 0.01$, *Context*, $F_{1,47} = 0.32$, $p = .58$, $\eta^2 = 0.007$ nor *Group* × *Context* interaction reached significance, $F_{1,47} = 2.43$, $p = .126$, $\eta^2 = 0.05$. Similarly, in the left hippocampus cluster, no significant effects of *Group* $F_{47} = 1{,}15$, $p = .21$, $\eta^2 = 0.03$, Context, $F_{1,47} = 0.006$, $p = .93$, $\eta^2 = 0.0$ or *Group* × *Context* interaction were found, $F_{1,47} = 0.018$, $p = .89$, $\eta^2 = 0.00$.

4. Discussion

In the current study, we investigated the behavioral and neural effects of acute stress on emotional contextual source memory. We observed that, despite the absence of stress effects in memory performance, stress modulated the neural signature of item and contextual source memory, oppositely. Specifically, stressed participants compared to the no stress control group showed larger activation in regions associated with recollection-based memory during the retrieval of items from both emotional and neutral contexts. The retrieval of contextual unpleasant information, however, was associated with lower activation in recollection-related brain areas in the stress compared to the control group. Subsequent analysis revealed that stressed participants also showed weaker cross-region memory reinstatement of visual representations of the object/unpleasant scene pairings in these regions. These results suggest that stress induction before encoding may have differential effects on the neural substrates of item and contextual source memory: stress can facilitate the recollection-related activity of single items, but, at the same time, reduces the recollection-related activation associated with specific contextual, particularly unpleasant, details.

For item memory performance, we observed a general advantage for items encoded in pleasant contexts. These results partly replicate previous findings showing higher memory performance for neutral information encoded in pleasant contexts (Madan et al., 2019; Smith et al., 2004). In terms of stress, we expected a more prominent recollection-based emotional advantage for participants of the stress, compared to the control group (e.g., Weymar et al., 2012). However, the observed advantage for objects from pleasant scenes was found in the stress and control groups alike. Although, these findings are not in line with our prediction, they are nevertheless not at odds with the existing literature, as it has been observed that the recollection-based memory advantage of stress for emotionally relevant material (Weymar et al., 2012; Zoladz et al., 2011) is not always found (Meier et al., 2020;

Quaedflieg et al., 2013), which could be caused by methodological differences (i.e., stimuli used, paradigm length, timing of the stressor) or sample characteristics (Quaedflieg et al., 2013).

For contextual source memory performance, a recollection-based advantage for emotionally relevant contexts (both pleasant and unpleasant) was observed, replicating our previous results (Ventura-Bort et al., 2020a; 2020b). As shown for item memory, no stress effects were found in source emotional memory (e.g., Sep et al., 2019).

Despite the lack of effects at the behavioral level, acute stress prior to encoding modulated the brain activation associated with item and contextual source memory retrieval. When retrieval success was investigated (i.e., item memory), participants from the stress group showed larger activation in regions associated with recollection-based memory retrieval (Rugg and Vilberg, 2013), including the PCUN and mPFC. No interacting effects of contexts and group were observed, indicating that the effects of stress were independent of the emotional context in which the objects were encoded. As part of the so-called recollection network (Rugg and Vilberg, 2013), the PCUN (Vilberg and Rugg, 2007, 2009a, 2009b; see for reviews, Cabeza et al., 2008; Rugg and King, 2018; Sestieri et al., 2017; Vilberg and Rugg, 2008; Wagner et al., 2005; Wheeler and Buckner, 2004), and the mPFC (e.g., Schlichting and Preston, 2015) have shown strong activation during retrieval (c.f., Weymar et al., 2018), particularly when memory was based on recollection-rather than familiarity-driven processes, suggesting that these regions participate in the recollective experience of memories. In line with this view, enhanced functional connectivity between these areas has been associated with recollection-based memory (King et al., 2015). Our results, thus, suggest that exposure to acute stress before encoding may facilitate the memory encoding and/or subsequent consolidation of item information, resulting in a more prominent long-term recollection of previously encoded neutral items, irrespective of encoding context.

In contrast to item memory, stress was associated with decreased activity in areas of the recollection network during contextual source memory retrieval, particularly when unpleasant context information was retrieved. Compared to the neutral condition, the correct retrieval of unpleasant contexts was associated with lower activation in the AG, and mPFC (and HC when using a more lenient threshold). Subsequent analysis revealed that these interacting effects were in part reflecting differences in memory reinstatement of visual representations. While no group differences were observed for object/neutral background scene pairings, the encoded visual representation (i.e., the activity of occipital cortices) of unpleasant events was reinstated in the left and right AG, and mPFC (but not in the HC) during retrieval in the control group but not the stress group. These cross-region reactivation effects are in accord with recent studies showing a cross region correspondence between encoding and retrieval. For instance, Xiao et al. (2017, 2020) found that activity from the visual cortex during encoding was reinstated in parietal and prefrontal regions during retrieval. Sensory processing at the time of encoding, as reflected by activity in occipital cortices, has been previously related to subsequent memory retrieval, particularly for unpleasant information (Bowen and Kensinger, 2017; Kark and Kensinger, 2019). It is hypothesized that during encoding, the activity of the visual cortex interacts with key regions of the salience network such as the AMY (Bowen et al., 2018), modulating the sensory processing of such material. It was shown that this connection is strengthened by the release of stress hormones (Hermans et al., 2014; van Oort et al., 2017) that boost the activity in the salient network, increasing in turn, sensory processing (Schwabe et al., 2011). The increase of activity of the salience network, however, occurs at the expense of a decreased activation of regions from the executive control network important for higher-order cognitive functions (e.g., working memory processes, goal-directed planning), which likely also supports successful object/scene integration during encoding (Dulas and Duarte, 2011; Mather et al., 2006; Uncapher et al., 2006). Our current findings thus suggest that stress hormones (likely cortisol) release may reduce the item/context binding of unpleasant events during encoding, potentially due to its modulatory effects on large-scale network interactions (Schwabe et al., 2022), leading to reduced recollection-related activation for unpleasant contextual details and weaker memory reinstatement of the visual representations of the encoded unpleasant events in the mPFC and AG.[1] This tentative interpretation, however, needs future investigations directly testing how the modulatory effects of stress on large-scale networks are related to a reduced recollection-related activity for unpleasant contextual information. Because the current design was not optimal for applying multivariate representational analysis during encoding/retrieval,[2] future studies investigating changes in memory-related (e.g., contrasting correctly identified vs forgotten information) neural representations during encoding would further help shed light onto the stress effects on the connectivity between memory-related regions (AMY, HC) and visual areas.

The fact that the reinstatement of unpleasant visual representations, particularly in the control group, were only observed in neocortical (but not medial temporal) regions, may be related to the time-dependent transfer of consolidated memories from medial temporal (e.g., HC) to neocortical areas (Takashima et al., 2006). It has been shown that neural representations of encoded memories are stored in medial temporal regions, but over time, they are transferred to more neocortical regions, including the mPFC (Krenz et al., 2021, 2023; Takashima et al., 2006, 2009). Future studies testing the effects of time (1 vs 8/28 days) on the cross-region reinstatement of visual representations would help corroborate this interpretation.

Our fMRI findings are in line with recent evidence showing that stress may have specific long-lasting impairing effects on aversive contextual learning. For instance, Dunsmoor et al. (2017) observed that acute stress (induced via a cold pressor test) before an aversive learning phase promotes the overgeneralization of aversively conditioned stimuli one day later, suggesting that stress may impair the consolidation of contextual details, leading to a loss in memory precision. Similarly, Simon-Kutscher et al. (2019) observed that participants who underwent a social stress test before performing an aversive contextual learning task, showed reduced context-, but not cue-dependent, aversive conditioning, indicating that stress specifically impairs contextual aversive learning. Our study extends this initial evidence by showing that stress-related reduced retrieval of unpleasant episodic contextual information (van Ast et al., 2013; Schwabe et al., 2009; Simon-Kutscher et al., 2019; but see Sep et al., 2019) is also related to lower activation of memory-related brain areas and decreased reinstatement of visual representations during retrieval. Our neural findings are also in line with

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[1] Our results suggest the possibility that stress hormones may mediate brain activation and consequently affect memory performance. We further performed mediation analysis to test whether the effects of stress on brain activation mediated the relationship between cortisol increase and memory performance. These results are reported in section S8 of the Supplementary Material. Overall, we observed no mediation effects of brain activity on the effects of cortisol release on memory performance, suggesting that the association between cortisol changes and memory performance were not explained by changes in brain activity during retrieval. It may thus be that the other factors related to the encoding or consolidation periods have a stronger mediation effect on memory performance. It should further be noticed that these negative findings might be related to lacking behavioral differences between groups. As outlined in the discussion, the lack of differences in memory performance might be attributed to the characteristics of the design.

[2] Although multivariate representational analysis for testing the stress effects on the memory-related representations during encoding would have helped to substantiate some of our assumptions. However, the current design was not ideal for several reasons: (1) we could not disentangle between brain activation for contexts and items, as both were presented together. (2) We did not continuously track the concentration of stress hormones during encoding, which may be crucial to understand their effects on encoding, particularly, for longer periods. (3) Furthermore, the complexity of the imagination task thought to promote object-scene binding may have added extra source of variance to the brain activity associated with object-scene processing from trial to trial.

the assumption that stress during memory encoding produces a shift towards more habitual and less demanding forms of learning—focusing on the prioritized information, i.e., item — (Wirz et al., 2018) at the cost of more flexible, cognitive-demanding learning (object/scene binding), leading to a gist-based memory formation that reduces memory specificity of contextual information (Nadel et al., 2002; Quaedflieg and Schwabe, 2017).

One important limitation of the current study is, however, that the observed neural effects of stress on memory were not reflected at the behavioral level. Although exploratory correlational analysis revealed that some of the fMRI findings were related to recollection-based contextual source memory performance, the group differences found in the brain data were not mirrored in the behavioral performance, which warrants further investigation. The observed brain-behavior discrepancy may lie on methodological variations linked to the adaptation of the current design to the scanner environment. One potential factor could be the length of the encoding session. It has been shown that the effects of stress hormones on memory are time-sensitive (Sep et al., 2019, 2022; Schwabe et al., 2012), and may be specially pronounced 25–30 min after stress induction. Although the start of the encoding session temporally matched with the expected peak concentration of the stress hormones, our task was considerably long, lasting up to 60 min (85 min after stress induction). It may thus be that the modulatory effects of stress hormones on memory are particularly observed when the encoding sessions occur within the time of maximum cortisol release, and less at the end of the encoding session when stress hormone levels are low. In our experiment, we could observe that cortisol levels decreased at the end compared to the beginning of the encoding session in both the stress and control group which may in part support this assumption. In addition, the use of a rather lengthy object-context encoding period (8 s), which was initially chosen to ensure effective binding, might have also contributed to the lack of stress effects on behavioral performance. It has been shown that the duration of encoding plays a relevant role for contextual source memory (e.g., Murray and Kensinger, 2013), with shorter encoding times significantly reducing the binding of information (e.g., word pairs). Thus, it could be that the longer encoding period used in the present study allowed participants in the stress group to counteract the potential detrimental effects of stress on binding. Future studies systematically testing the optimal time window of the encoding task and the modulatory effects of the stress hormones on memory would help to shed more light on this matter. Similar trade-off effects might also have occurred during retrieval. In the current task, the time between stimulus offset and memory judgments (3–5 s) may have allowed participants to use additional strategies to retrieve the target information, further reducing the potential effects of stress. Avoiding such delays in future studies may thus help delineate the effects of stress on emotional item and contextual source memory performance. Another caveat of the current study is related to the specificity of the effects of stress on memory. The characteristics of the current study do not allow to determine whether the findings are more strongly influenced by the effects of stress during memory encoding, consolidation or both.[3] Future studies in which the effects of stress on emotional contextual source memory are tested immediately (not allowing consolidation processes) and after a delay (allowing consolidation processes to take place) would bring insights in this regard.

Although moderate and temporally limited stress responses are highly adaptive (Schwabe et al., 2022), aberrant stress reactions might have dramatic consequences and contribute to the development of stress-related disorders, such as post-traumatic stress disorder (PTSD) or anxiety disorders (De Quervain et al., 2016). The current results may foster our understanding of the effects of stress on memory formation in clinical settings. Indeed, our neural findings are in accordance with recent proposals suggesting that patients suffering from PTSD show a memory pattern that is characterized by an enhanced memory for items, particularly negative ones (Durand et al., 2019; Imbriano et al., 2022), but reduced memory for unpleasant context information (Bisby and Burgess, 2017; Durand et al., 2019; Noriega et al., 2021). For instance, it is commonly observed that some trauma-related memories are overly general and gist-based rather than detailed and context-specific, leading to what is known as fragmented trauma memories (Dolcos, 2013; Ehlers and Clark, 2000; Kaouane et al., 2012; Oyarzún and Packard, 2012). This fragmentation may lead to various PTSD symptoms, such as retrieval distortions of trauma-related information, overgeneralization, and the easy triggering of trauma-related and physically similar neutral cues (Ehlers and Clark, 2000). Our results showing enhanced retrieval activity for items but reduced retrieval activity and reinstatement for unpleasant contextual information following stress exposure may provide initial evidence for the specific role of stress on formation of fragmented, decontextualized trauma-related memories, extending recent findings showing that stress induction prior encoding results in less integrated memories (Grob et al., 2023). Future studies focusing on the neural substrates of emotional contextual source memory in patients suffering from stressor- and trauma-related disorders may shed further light on the clinical relevance of stress-related changes in the neural signature of emotional contextual source memory.

5. Conclusion

In the current study, we observed opposing effects of stress on brain correlates of item and contextual source memory retrieval. Stress prior to encoding produced higher activation in regions associated with recollection-based memory during the retrieval of items from both emotional and neutral contexts but, at the same time, it was associated with lower activation in such brain regions during the retrieval of unpleasant contexts. These findings suggest that acute stress prior to encoding increases memory-related activity for single items, but impairs the retrieval activation of contextual, particularly unpleasant, details. This reduced activation may be related to a dampened reinstatement of visual representations of unpleasant contexts. The present findings provide new neuroscientific insights into the binding mechanism of emotional and neutral context information under stress, which could also be important for better understanding memory abnormalities and neural changes that are typically observed in individuals suffering from stressor- and trauma-related disorders (Bisby and Burgess, 2017; Durand et al., 2019; Noriega et al., 2021).

CRediT authorship contribution statement

Carlos Ventura-Bort: Writing – original draft, Methodology, Formal analysis. **Janine Wirkner:** Writing – review & editing, Supervision. **Julia Wendt:** Writing – review & editing, Software. **Lars Schwabe:** Writing – review & editing. **Florin Dolcos:** Writing – review & editing. **Alfons O. Hamm:** Writing – review & editing. **Mathias Weymar:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial

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[3] We exploratively tested for group differences on brain activity during encoding, assuming that the emergence of group differences would indicate that stress at least affected immediate encoding, whereas the absence of such group effects would suggest that stress may more likely affect consolidation processes. At the whole brain level, we therefore compared the brain activation between groups when processing neutral, pleasant and unpleasant scenes. We also explored whether the group effects emerged for the emotional versus neutral contrast (unpleasant vs neutral; pleasant vs neutral). We, however, did not observe any cluster that surpassed the significant threshold $p < .005$ uncorrected. The lack of group differences during encoding may, thus, indicate that the acute stress effects on memory observed during retrieval on the neural level might be rather related to consolidation processes.

interests or personal relationships that could have appeared to influence the work reported in this article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ynstr.2024.100691.

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