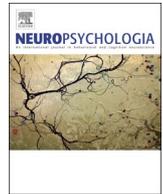




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Suppress to feel and remember less: Neural correlates of explicit and implicit emotional suppression on perception and memory

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ABSTRACT

Available evidence suggests that emotion regulation can modulate both immediate (emotional experience) and long-term (episodic memory) effects of emotion, and that both explicit and implicit forms may be effective. However, neural mechanisms by which explicit and implicit emotional suppression affect these phenomena remain unclear, particularly regarding their effects on memory. In this study, participants rated the emotional content of negative and neutral images, following explicit (verbal instructions) or implicit (priming) induction of emotional suppression goals, during functional magnetic resonance imaging. Participants' memory for the images was tested one week later. Behaviorally, explicit suppression reduced emotional ratings of negative images, whereas both explicit and implicit suppression reduced subsequent memory. At the neural level, the engagement of explicit suppression was uniquely associated with decreased activity in the amygdala (AMY), during emotional ratings, and in the AMY and inferior frontal gyrus (IFG), during successful encoding. Although both explicit and implicit suppression diminished functional connectivity between these regions and the hippocampus (HC) linked to successful encoding, explicit suppression was uniquely associated with interference with AMY-HC interactions, which no longer predicted subsequent memory for the explicitly-suppressed items. Overall, these findings advance our understanding of the common and dissociable mechanisms of explicit and implicit emotional suppression on perception and memory, and suggest their impact on both bottom-up and top-down mechanisms involved in emotion-cognition interactions.

1. Introduction

Research on emotion regulation (ER) – i.e., the processes influencing which, when, and how emotions are experienced and expressed (Gross and John, 2003) – has established that the ability to cope adaptively with emotionally challenging situations is vital for both physical and mental health (Gross, 2008, 2015). ER behaviors that individuals engage in emotional situations are often promoted by the pursuit of various goals, driven by basic (e.g., hedonistic) or more complex social motivations (Gross, 2008; Koole et al., 2015; Tamir, 2009). Although these ER goals may be pursued through effortful and intentional attempts (*explicit* ER), extant evidence suggests that the mental representations of ER goals can also be activated without conscious awareness of the priming stimuli or active intention toward the goal (*implicit* ER) (Bargh et al., 2010; Gyurak et al., 2011; Kobylińska and Karwowska, 2015; Koole and Rothermund, 2011; Sheeran et al., 2013).

Previous studies of ER have shown that the engagement of specific ER strategies can influence not only immediate emotional experience,

but also long-term memory for emotional events after a delay (e.g., Dillon et al., 2007; Kim and Hamann, 2012). However, despite converging evidence suggesting the existence of neural networks involved in the impact of ER on immediate emotional experience (Buhle et al., 2014; Kohn et al., 2014), relatively less is known about the neural correlates of the long-term impact of ER on episodic memory. Moreover, prior studies investigating the effect of ER on episodic memory have focused on the role of explicit ER, and therefore the effect of implicit ER remains unclear. The present study addressed these issues by using an experimental design that assessed both the immediate (emotional ratings) and long-term (episodic memory) effects of ER, with a focus on the explicit and implicit forms of *emotional suppression*. Clarification of these issues is relevant for understanding both healthy functioning and alterations in affective disorders, in which an excessive focus on negative memories and emotion dysregulation are often among the core debilitating features (Dalgleish and Werner-Seidler, 2014; Dolcos, 2013). In this context, forgetting unwanted negative memories may serve an adaptive function (Dunn et al., 2009; Nørby, 2015), and doing so with reduced cognitive costs (e.g., implicitly) may

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prove particularly useful for individuals with limited resources available for information processing (Williams et al., 2009).

1.1. Neural correlates of emotional suppression: immediate vs. long-term effects

Emotional suppression is an ER strategy that typically involves attempts to inhibit the external expression and/or internal experience of emotion (Dunn et al., 2009; Gross, 2008; Webb et al., 2012). Behaviorally, previous laboratory studies examining the immediate impact of instructed emotional suppression have yielded mixed results,¹ with some studies identifying reduced subjective experience of negative emotions (Binder et al., 2012; Dunn et al., 2009; Goldin et al., 2008; Hayes et al., 2010), and others showing no significant changes in emotional experience (Gross, 1998; Gross and Levenson, 1993, 1997; Richards and Gross, 1999, 2000) compared to control conditions with no instructions to engage specific ER strategies (i.e., passive viewing). At the neural level, available evidence from studies using functional magnetic resonance imaging (fMRI) shows that the engagement of emotional suppression compared to passive viewing is associated with increased activity in brain regions typically involved in cognitive control, such as the lateral prefrontal cortex (PFC) and parietal cortex (Dorfel et al., 2014; Goldin et al., 2008; Hayes et al., 2010). Paralleling the behavioral evidence, there is also mixed fMRI evidence concerning the effect of emotional suppression on activity in regions typically involved in basic emotion processing (e.g., amygdala [AMY]), with some studies identifying decreased AMY activity (Dorfel et al., 2014; Hayes et al., 2010; Ohira et al., 2006), and others observing increased AMY activity (Goldin et al., 2008), linked to the engagement of this ER strategy compared to passive viewing.

Although the current evidence regarding the immediate effect of emotional suppression remains inconclusive possibly due to differences in task instructions (Webb et al., 2012), previous laboratory studies examining the long-term impact of emotional suppression on episodic memory have consistently shown that the instructed engagement of this ER strategy during encoding of visual stimuli leads to reduced subsequent memory for the suppressed stimuli (Dillon et al., 2007; Dunn et al., 2009; Richards and Gross, 1999, 2000, 2006). Despite these remarkably consistent behavioral findings, only a few published studies to date have provided evidence concerning the neural correlates of emotional suppression on episodic memory (Binder et al., 2012; Hayes et al., 2010).

In general, available evidence points to the existence of multiple neural routes involved in the impact of emotion on memory encoding (reviewed in Dolcos et al., 2012; Dolcos et al., 2017; LaBar and Cabeza, 2006; Murty et al., 2011). On the one hand, it has been shown that successful encoding of emotional items involves the structures within the medial temporal lobe (MTL), with the AMY directly exerting modulatory influences over the memory-related regions such as the hippocampus (HC) (Dolcos et al., 2004b). On the other hand, successful emotional encoding also appears to be mediated by regions within the PFC and parietal cortex, possibly by virtue of processes such as semantic elaboration, executive control, and attention (Dolcos et al.,

¹ It is important to note that the inconsistent findings reported here may be at least in part driven by the heterogeneity of the task instructions across studies (see also Webb et al., 2012). For instance, whereas the studies by Gross and colleagues have typically emphasized in their instructions only the inhibition of outward emotional expression (Gross, 1998; Gross and Levenson, 1997; Richards and Gross, 1999, 2000), more recent studies have defined emotional suppression at a more general level, and instructed participants to suppress both the *external expression* and *internal experience* of emotions (Binder et al., 2012; Dunn et al., 2009). However, this distinction between “purely expressive” vs. “mixed expressive/experiential” forms of suppression does not appear to be the sole factor explaining the aforementioned inconsistencies in behavioral outcomes, given that some studies using purely expressive suppression still observed reduction in emotional experience relative to passive viewing (Bebko et al., 2011; Dorfel et al., 2014; Hayes et al., 2010).

2004a; Kaneda et al., 2017; Ritchey et al., 2011).

The few fMRI studies examining the effect of emotional suppression on episodic memory suggest that the explicit engagement of this ER strategy influences both the MTL-based and PFC-based mechanisms involved in memory encoding (Binder et al., 2012; Hayes et al., 2010). In particular, significant co-activation of the AMY and HC linked to successful memory encoding was observed during passive viewing, which was attenuated during the engagement of emotional (expressive) suppression (Hayes et al., 2010). Furthermore, decreased activity related to successful encoding was observed in the HC during the engagement of emotional suppression compared to passive viewing (Binder et al., 2012). Interestingly, Binder et al. (2012) also showed that the strength of encoding-related functional connectivity between the HC and dorsolateral PFC (dlPFC) was significantly diminished by the engagement of emotional suppression, and no longer predicted subsequent memory for the suppressed stimuli. Taken together, these findings show that the engagement of emotional suppression reduces subsequent memory by modulating both the MTL-based and PFC-based mechanisms implicated in emotional memory encoding.

1.2. Explicit vs. implicit emotion regulation

Another area of research that has received relatively less attention in investigating the impact of ER on episodic memory concerns the role of implicit ER. Numerous studies from the self-regulation literature using priming techniques have demonstrated that implicitly operating goals typically produce similar outcomes as when the same goals are pursued explicitly (reviewed in Bargh et al., 2010; Sheeran et al., 2013). Extending this evidence to the literature on ER, a few studies have shown that ER goals implicitly activated via priming can achieve similar behavioral or physiological responses (e.g., reduced emotional reaction) as their explicit counterparts in some negative emotional situations (Mauss et al., 2007; Williams et al., 2009; Yuan et al., 2015). These findings are important given that explicit emotional suppression may come with cognitive, physiological, and/or social costs (Butler et al., 2007; Gross and Levenson, 1993; Richards et al., 2003), and therefore may not be successfully or efficiently engaged by individuals whose cognitive resources are already limited (e.g., by chronic rumination; Nolen-Hoeksema et al., 2008). For instance, among individuals with higher levels of anxiety and depression symptoms, effortful attempts to suppress negative emotions upon recollection of distressing personal memories actually increased negative emotional responses (Dalgleish et al., 2009). Therefore, it is possible that implicit emotional suppression may be useful in reducing unwanted memories for negative events, particularly among those who are unable to engage explicit emotional suppression effectively. However, to our knowledge, no prior published studies have examined the effect of implicit emotional suppression on episodic memory, and the associated neural correlates.

1.3. The present study

As summarized above, the available evidence suggests that, although the effect of instructed emotional suppression on immediate emotional experience remains inconclusive, the engagement of this ER strategy appears to consistently reduce subsequent memory for the previously encoded stimuli. At the neural level, the memory-reducing effect of emotional suppression seems to be associated with decreased interactions between the AMY and HC, and between the lateral PFC and HC, both of which have been previously implicated in emotional memory encoding. In addition, the current evidence also suggests that implicit emotional suppression can modulate immediate emotional experience similar to its explicit counterpart. However, the long-term impact of implicit emotional suppression on episodic memory and its associated neural correlates remain unclear. To fill in this important gap in the literature, the present study used an experimental design that assessed both the immediate (emotional ratings) and long-term

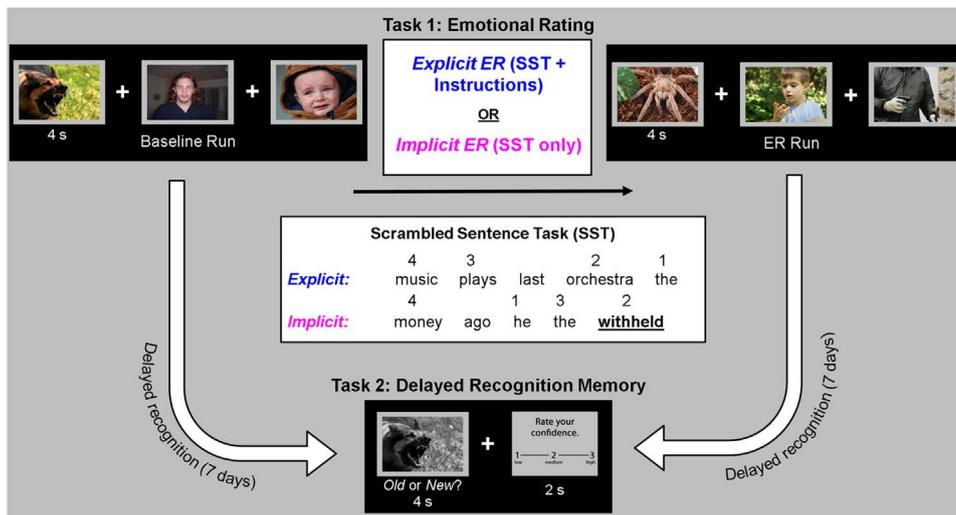


Fig. 1. Diagram of the protocol. The emotional suppression goal was induced in each participant both explicitly and implicitly, but the order of induction was counterbalanced across participants – i.e., those assigned to the explicit condition in the first part completed the implicit manipulation in the second part, and vice versa; each manipulation was preceded by its own baseline run. Negative and neutral images part of this figure are used only for illustration purposes, and do not represent the actual stimuli with which participants were presented in the tasks.

(episodic memory) effects of ER, with a focus on the explicit and implicit forms of emotional suppression. Participants in the experimental group underwent fMRI recording while they performed an emotional rating task involving the evaluation of negative and neutral images. One week later, the participants performed a surprise memory test for the images encoded in the MRI scanner. Emotional suppression goals were induced before the emotional rating task through verbal instructions (*explicit* emotional suppression) and a priming task in which participants were exposed to words conveying the idea of emotion control (*implicit* emotional suppression). An independent group of participants who performed both tasks outside the MRI scanner without the induction of emotional suppression goals served as a control group. Following previous brain imaging studies of ER focusing on emotional stimuli (e.g., Dorfel et al., 2014; Hayes et al., 2010; Jackson et al., 2000; Kim and Hamann, 2007b; McRae et al., 2008; Ochsner et al., 2002; Ochsner et al., 2004; Silvers et al., 2015; Urry et al., 2006; van Reekum et al., 2007; Wager et al., 2008), the present study focused on elucidating the neural mechanisms underlying the effects of explicit and implicit emotional suppression on emotional ratings and memory for emotional (negative) stimuli. This was also justified by previous research showing that participants found it confusing to try to regulate emotional reactions for stimuli that have little intrinsic emotional content (Jackson et al., 2000; Kim and Hamann, 2007a, 2007b), which may result in ambiguous emotional responses (e.g., Ahn et al., 2015).

Based on the extant evidence reviewed above, we tested the following hypotheses. Across different levels of analysis, we expected that the effects of explicit and implicit emotional suppression would be similar (Bargh et al., 2010; Gyurak et al., 2011). Regarding the behavioral effects, (1) we expected to observe reduction in emotional ratings following the induction of emotional suppression goals compared to the preceding baseline runs (*immediate* effects). Second, (2) we also expected to observe reduced memory for stimuli encoded following the induction of emotional suppression goals compared to the preceding baseline runs (*long-term* effects). Regarding the neural correlates, (3) we expected to observe increased activity in regions including the lateral PFC and parietal cortex, and decreased activity in the AMY, following the induction of emotional suppression goals. Finally, (4) we expected to observe decreased activity in and/or connectivity among the AMY, HC, and lateral PFC related to successful emotional memory encoding following the induction of emotional suppression goals. We also expected that the association between functional connectivity among these regions and memory performance would be diminished following the induction of emotional suppression goals.

2. Method

2.1. Participants

A total of 41 young adults (24 females, $M_{age} = 21.36$, $SD_{age} = 3.76$) participated in this study. Twenty three young adults (15 females, $M_{age} = 23.38$, $SD_{age} = 3.70$) participated as the experimental group, who performed an emotional rating task while fMRI data were recorded. Eighteen additional participants (9 females, $M_{age} = 19.11$, $SD_{age} = .90$) were also recruited as a control group, who performed the same tasks outside the MRI scanner following similar delays, but without the induction of emotional suppression goals during the emotional rating task. The control group was tested in order to make sure that the results observed in the experimental group were not driven by possible effects due to habituation to emotional stimuli. All participants were healthy, right-handed, native English speakers, with no history of psychiatric or neurological conditions. Data from five participants from the experimental group were excluded from the analyses due to typical reasons contributing to data attrition (e.g., ratings or memory data not being recorded, other technical issues such as response box problems, participants feeling uncomfortable in the scanner). In addition, data from two participants (one from each participant group) were excluded from the analyses due to low memory performance for negative relative to neutral images during the “baseline” runs ($Z < -2.5$). This ensured that our behavioral analyses focused on those participants showing the expected effect of emotion on memory at the basic level (Bradley et al., 1992). All participants provided written informed consent under a protocol approved by the Institutional Review Board, and received payment for their participation.

2.2. Experimental procedures

Participants in the experimental group completed two tasks: an emotional rating task, completed in the MRI scanner, and a recognition memory task, completed outside the MRI scanner one week later (see task diagram illustrated in Fig. 1, and also Dolcos et al., 2011). The control group completed both tasks outside the MRI scanner.

2.2.1. Emotional rating task

fMRI data were recorded while participants in the experimental group viewed and rated a total of 180 negative and neutral images (90 in each emotional category), selected from the International Affective Picture System (IAPS; Lang et al., 2008). Additional neutral images were selected from other sources (Dolcos et al., 2004a; Dolcos and McCarthy, 2006), to equate the images for visual complexity and

human content across the emotional categories. The average IAPS valence ratings for negative and neutral images were 2.47 ($SD = .57$) and 4.98 ($SD = .28$), respectively. The pool of 180 images was divided into sets of 30 images, which were randomly assigned to six study runs, between which the average IAPS valence ratings were equated. The run orders were randomly assigned to the participants. To avoid mood induction, images were pseudo-randomized within each run so that no more than three images of the same valence were presented consecutively. Each image was presented on the screen for 4 s, and then was removed to minimize the confounding effects of eye movements associated with prolonged scanning of images. Participants were asked to view the images and rate their subjective emotional experience triggered by the images on an 8-point scale (1 = *Neutral*, 8 = *Extremely negative*). All responses were made on a response pad attached to the participant's right hand. Specifically, ratings ranging from 1 to 4 were made by single clicks, whereas those ranging from 5 to 8 were made by double clicks on the buttons. The rating scale was presented at the bottom of each image. The screen containing the image and rating scale was followed by a fixation cross, presented on the screen for 12 s. Participants were instructed to rate the images while they were on the screen, and to do so only after being aware of the content of the image and of their emotional response to it.

Participants completed the first and fourth runs of the emotional rating task with no induction of emotional suppression goals; these runs were defined as the baseline runs, and tested participants' spontaneous processing and evaluation of images (Dolcos et al., 2014). Each baseline run was immediately followed by either the explicit or implicit induction of emotional suppression goals (i.e., $BASE_{EXP}$ followed by EXP and $BASE_{IMP}$ followed by IMP, respectively), with the order of induction counterbalanced across participants. In the EXP condition, participants were instructed to view and rate the next two runs of images (EXP runs), while trying to suppress the experience and expression of emotional responses triggered by the images. The instructions emphasized both the inhibition of experience and expression of emotional responses, and thus are more consistent with those of previous studies using a broader definition of emotional suppression (Binder et al., 2012; Dunn et al., 2009; see also Webb et al., 2012), than with those used by others focusing on the inhibition of emotional expression (e.g., Gross and Levenson, 1993; Richards and Gross, 1999, 2000, 2006). In the IMP condition, participants performed an adaptation of the Scrambled Sentence Task (SST) (Srull and Wyer, 1979) in which they were asked to construct 20 four-word grammatically correct sentences from five-word jumbles that had embedded words conveying the idea of emotion control (e.g., "restrain", "stable", "covered"), thus priming participants to suppress their emotional responses (Mauss et al., 2007). The target words related to emotion control were taken from previous studies (Mauss et al., 2007). The two runs of images following the IMP goal induction were defined as IMP runs. Importantly, to maintain the same structure of the task in both emotional suppression conditions, a SST was also performed as part of the EXP goal induction, but in this case participants were presented with 20 sentences containing only neutral words (Fig. 1).

2.2.2. Recognition memory task

One week following the emotional rating task, participants performed a surprise memory task that tested recognition memory for the negative and neutral images presented as part of the emotional rating task. The task included a total of 360 images (180 in each emotional category) consisting of equal numbers of old (previously seen) and new (never seen before) images. Old and new images were equated with respect to their normative valence scores. All images were displayed in grayscale for increased task difficulty (Dolcos et al., 2013). Each image was displayed on the screen for 4 s, and participants were asked to indicate by a button press, while the image was on the screen, whether the image had been previously seen during the emotional rating task (*Old*) or not (*New*). Following the Old/New decision, participants also

rated the level of confidence (LOC) of their responses on a 3-point scale (1 = *Low*, 2 = *Medium*, 3 = *High confidence*) during the presentation of a prompt, which was displayed on the screen for 2 s. The LOC rating was followed by a fixation cross, presented on the screen for 2 s (Fig. 1).

2.3. Behavioral data analysis

In the present study, our main goal was to clarify the effects of explicit and implicit emotional suppression on the immediate evaluation of and long-term memory for emotional (negative) stimuli, given the implications of this ER strategy for alleviating the impact of negative events (Dunn et al., 2009; Nørby, 2015). Our stimuli consisted of both negative and neutral images, although the latter were included primarily to avoid overall negative mood induction during the tasks (Ochsner et al., 2004). The immediate impact of emotional suppression on emotional ratings was measured by comparing the ratings between the two runs within each emotional suppression condition and its own baseline run (i.e., $BASE_{EXP}$ vs. EXP and $BASE_{IMP}$ vs. IMP), as well as by comparing the ratings between the two emotional suppression conditions (i.e., EXP vs. IMP). Responses in the memory task were classified into one of the four categories: (1) *Hits* (old images correctly identified as old), (2) *Misses* (old images incorrectly classified as new), (3) *Correct Rejections* (new images correctly classified as new), and (4) *False Alarms* (FAs, new images incorrectly classified as old). The long-term impact of emotional suppression on episodic memory was measured by comparing across the experimental conditions raw proportions of Hits (hit rate) as well as d' , a measure of memory performance controlling for individual response bias ($d' = z[\text{Hits}] - z[\text{FAs}]$).

Unless otherwise noted, the behavioral effects of emotional suppression on emotional ratings and recognition memory were investigated using one-tailed hypothesis testing in the present study. This procedure was justified by our directional hypotheses, which were informed by previous studies consistently showing that the engagement of emotional suppression is associated with decreased, but not increased, ratings and/or memory for (emotional) stimuli (Binder et al., 2012; Dillon et al., 2007; Dunn et al., 2009; Goldin et al., 2008; Hayes et al., 2010; Richards and Gross, 1999, 2000, 2006).

2.4. fMRI data acquisition, preprocessing, and analyses

2.4.1. fMRI data acquisition and preprocessing

fMRI data were recorded using a 1.5 T Siemens Sonata scanner, and consisted of a series of T2*-weighted images acquired axially, using an echoplanar sequence (repetition time [TR] = 2000 ms, echo time [TE] = 40 ms, field of view = $256 \times 256 \text{ mm}^2$, number of slices = 28, voxel size = $4 \times 4 \times 4 \text{ mm}^3$, flip angle = 90°). All preprocessing and statistical analyses of fMRI data were performed using SPM12 (Wellcome Department of Cognitive Neurology, London, UK), along with in-house custom scripts written in MATLAB. During preprocessing, fMRI data were first corrected for differences in acquisition time between slices for each image. Second, each functional image was spatially realigned to the first image of each run to correct for head movement. Third, these images were transformed into the standard anatomical space defined by the Montreal Neurological Institute (MNI) template implemented in SPM12; no voxel resampling was performed at the spatial normalization step. Finally, the normalized functional images were spatially smoothed using an 8 mm Gaussian kernel, full-width-at-half-maximum (FWHM), to increase the signal-to-noise ratio. Statistical analyses of fMRI data were separately conducted to assess both the immediate (emotional ratings) and long-term (episodic memory) impact of emotional suppression (Dolcos et al., 2004a), as described below.

2.4.2. Immediate impact of emotional suppression

At the first level, each participant's preprocessed functional data were analyzed using an event-related design in the general linear model (GLM) framework. Evoked hemodynamic responses during the image

presentation period in each trial were modeled by convolution with a canonical hemodynamic response function. The GLM included regressors for trials with negative images as the events of interest, separately for each run. In addition, trials with neutral images as well as six motion parameters calculated during spatial realignment for each run were also modeled as the events of no interest. These analyses generated contrast images identifying differential BOLD activation associated with the events of interest relative to baseline (fixation screens) for different runs within each participant. At the second level, paralleling the behavioral data analyses, the contrast images generated for each participant were analyzed by random-effects *t*-tests to identify brain regions showing differential BOLD activation between emotional suppression and baseline runs.

2.4.3. Long-term impact of emotional suppression

Analyses of the long-term impact of emotional suppression were performed in the GLM framework similarly to those of the immediate impact, except that we calculated the *difference due to memory* (Dm) effect for each condition based on each participant's memory performance (Paller and Wagner, 2002; Shafer et al., 2011). At the first level, trials with negative images were divided into subsequently remembered (Hits) and forgotten (Misses) trials and were modeled separately for each run. Also included for each run in the GLM were regressors for trials with neutral images, trials with no responses, and six motion parameters calculated during spatial realignment as events of no interest. These analyses generated contrast images identifying differential BOLD activation associated with the events of interest relative to baseline (fixation screens) for each run. The Dm effect was then calculated for each experimental condition (e.g., $\text{BASE}_{\text{EXP}} \text{Dm} = \text{BASE}_{\text{EXP}} \text{Hits} - \text{BASE}_{\text{EXP}} \text{Misses}$) for each participant. At the second level, the contrast images identifying the Dm effect for different runs within each participant were analyzed by random-effects *t*-tests to identify brain regions showing differential BOLD activation linked to successful encoding between emotional suppression and baseline runs [e.g., $(\text{BASE}_{\text{EXP}} \text{Hits} - \text{Misses})$ vs. $(\text{EXP Hits} - \text{Misses})$].

To further investigate modulation of functional interaction between brain regions identified by the above analyses of activation as showing significant differences in Dm effects across the experimental conditions, functional connectivity analyses were performed using the beta-series correlation method (Rissman et al., 2004), as implemented in the BASCO toolbox (Version 2.1; Gottlich et al., 2015). The seeds for connectivity analyses were defined as spheres with a 4 mm radius centering around the peak voxels in the left AMY (Talairach coordinates: $x = -23$, $y = -3$, $z = -18$) and the right inferior frontal gyrus (IFG) ($x = 47$, $y = 11$, $z = 24$, BA 44) showing decreased Dm activity for explicit emotional suppression compared to the preceding baseline run. The inclusion of these regions as seeds was justified also based on independent studies identifying the involvement of these and similar regions in emotional episodic memory encoding (Dolcos et al., 2013; Murty et al., 2011; Ritchey et al., 2011) and in the engagement of emotional suppression (Goldin et al., 2008).

At the first level, a GLM was created in which the BOLD response during the image presentation period was modeled by convolution with a canonical hemodynamic response function individually by a separate covariate, producing different parameter estimates for each trial with a negative image for each participant. Trials with neutral images and six motion parameters calculated from spatial realignment for each run were also included in this GLM. Next, seed-based correlations were calculated voxel-wise for Hits and Misses for each participant. This procedure yielded an individual correlation map between each of the seed regions and all other voxels in the brain separately for each condition for each run, which was normalized using Fisher's *z* transformation.² The Dm effect was then calculated for each experimental

condition for each participant. At the second level, these individual correlation maps were entered into random-effects *t*-tests to identify voxels that showed changes in functional connectivity (measured by trial-by-trial variability in parameter estimates) with the seeds linked to successful emotional encoding between emotional suppression and baseline runs. In the present report, unless otherwise noted, we define 'decreased connectivity' as reduced functional connectivity in the explicit/implicit emotional suppression conditions relative to the preceding baseline runs.

Finally, to identify brain regions whose functional connectivity with the seed regions was related to individual variation in memory performance across conditions, brain-behavior covariations were investigated by calculating between-subjects covariations between the BOLD response (parameter estimates) and memory performance for the relevant conditions. These analyses were restricted to brain regions identified as showing significant differences in functional connectivity from the analyses discussed above. For each significant cluster, mean parameter estimates were extracted and were submitted to bivariate correlation analyses to examine the relations between functional connectivity and memory performance in different conditions.

In the present study, brain activity and connectivity were investigated in two ways – one at the level of the whole brain (using the group-level mask image generated in SPM, containing 19,938 voxels) and another at the level of our regions of interest (ROIs) within the MTL (610 voxels). The MTL ROI mask was created based primarily on the structural images for bilateral AMY, HC, and PHC from the Automated Anatomical Labeling Atlas (AAL, Tzourio-Mazoyer et al., 2002) in SPM, given our a priori hypotheses regarding the involvement of these regions in emotional memory encoding (Dolcos et al., 2017; Murty et al., 2011). A combination of whole-brain and ROI-based analyses has similarly been employed in recent studies of emotional memory from our group and from others (Dew et al., 2014; Dolcos et al., 2013; Kaneda et al., 2017; Shafer and Dolcos, 2012, 2014). Also following previous studies from our group (Dolcos et al., 2013; Shafer and Dolcos, 2014), these ROI images were used in conjunction with an in-house AMY mask³ to correct for inaccurate spatial coverage provided by the AAL mask. Specifically, the in-house AMY mask is based on a synthesis of tracing criteria employed in previous publications (Dolcos et al., 2004b, 2005). These criteria were also the basis of a recent comprehensive protocol for manual segmentation of the MTL structures, which provides clear guidelines to identify their borders based on anatomical landmarks (Moore et al., 2014). This approach improves the ability to capture amygdala activity with increased anatomical specificity.

Correction for multiple comparisons was conducted using the updated version (June 2017) of the 3dFWMx and 3dClustSim programs available as part of the AFNI software suite (Cox, 1996). First, we executed AFNI's 3dFWMx using the “-acf” option on the residual time series resulting from each participant's GLM constructed in SPM (obtained from the model estimation step). This procedure yielded two sets of three estimated smoothness parameters per participant, one for the whole brain and the other within the MTL ROI mask only. Second, group-level mixed ACF model parameters were calculated by taking the average of these parameters across all participants included in the analyses. Finally, we executed 3dClustSim using these group-level smoothness parameters using the “-acf” option with 10,000 independent iterations (one-sided thresholding, $NN = 2$). Results indicated that, for an uncorrected voxel-wise threshold of $p < .005$, 27 contiguous voxels (1728 mm^3) for the whole brain and 5 contiguous

(footnote continued)

the *Z*-transformed correlation coefficients were divided by their known standard deviation, $1/\sqrt{N-3}$, where *N* is the number of trials in a given condition. However, because our analyses of functional connectivity involved comparisons of conditions with unequal number of trials, this scaling procedure was not performed in the present study (see also Gottlich et al., 2015).

³ The in-house AMY ROI mask is available to interested readers upon request.

² In the beta series correlation method originally described by Rissman et al. (2004),

Table 1

Descriptive statistics of emotional ratings and recognition memory for negative and neutral images in the experimental group.

| | BASE _{EXP} | EXP | BASE _{IMP} | IMP |
|--------------------------|---------------------|-------------|---------------------|-------------|
| Ratings | | | | |
| Negative | 5.36 (1.18) | 4.83 (1.37) | 5.21 (1.27) | 5.22 (1.21) |
| Neutral | 1.59 (.55) | 1.49 (.39) | 1.71 (.46) | 1.66 (.38) |
| Memory (hit rate) | | | | |
| Negative | .78 (.49) | .71 (.18) | .79 (.15) | .72 (.14) |
| Neutral | .70 (.16) | .58 (.12) | .62 (.13) | .62 (.14) |

Values preceding and within parentheses denote the means and standard deviations, respectively. BASE_{EXP}, baseline run preceding the explicit induction of emotional suppression goal; EXP, runs following the explicit induction of emotional suppression goal; BASE_{IMP}, baseline run preceding the implicit induction of emotional suppression goal; IMP, runs following the implicit induction of emotional suppression goal.

voxels (320 mm³) within the MTL ROI mask would be needed to achieve a cluster-wise threshold of $p < .05$, corrected for family-wise error rate.

3. Results

3.1. Behavioral results

Descriptive statistics of the ratings and memory performance for both negative and neutral images in the experimental group are summarized in Table 1.

3.1.1. Effect of emotional suppression on emotional ratings

As expected, emotional ratings for negative images were significantly reduced following the explicit induction of emotional suppression goal ($M = 4.83$, $SD = 1.37$) compared to the preceding baseline run ($M = 5.36$, $SD = 1.18$): $t(16) = 2.02$, $p = .030$. However, no significant difference was observed in the ratings following the implicit induction of emotional suppression goal ($M = 5.22$, $SD = 1.21$), compared to its preceding baseline run ($M = 5.21$, $SD = 1.27$): $t(16) = -.01$, $p = .457$. A direct comparison of the ratings between the two emotional suppression conditions identified a significant decrease for explicit compared to implicit emotional suppression: $t(16) = -2.85$, $p = .006$ (two-tailed) (Fig. 2A). Regarding the ratings for neutral images during the baseline runs, they were significantly lower than those for negative images viewed in any condition ($M = 1.67$, $SD = .42$; $t[16] > 10.15$, $p < .001$, for all comparisons). In addition, analyses comparing the ratings between the experimental and control

groups showed that the reduction in ratings was significantly larger in the former than in the latter group (Supplementary Material, S1). This suggests that the reduced emotional ratings observed in the experimental group were due to the explicit induction of emotional suppression goal to regulate emotional responses, and was not due to habituation following repeated exposure to emotional stimuli. Overall, these results partially confirm our first hypothesis and show that the explicit, but not implicit, induction of the suppression goal reduces emotional ratings of negative images.

3.1.2. Effect of emotional suppression on recognition memory

Recognition memory (hit rate) was significantly reduced for negative images encoded following the explicit induction of emotional suppression goal ($M = .71$, $SD = .18$), compared to those encoded during its preceding baseline run ($M = .78$, $SD = .49$): $t(16) = 1.84$, $p = .042$. Similarly, memory reduction was also identified for images encoded following the implicit induction of emotional suppression goal ($M = .72$, $SD = .14$), compared to those encoded during its preceding baseline run ($M = .79$, $SD = .15$): $t(16) = 2.03$, $p = .029$. A direct comparison of hit rate between the two emotional suppression conditions did not identify a significant difference: $t(16) = -.24$, $p = .816$ (two-tailed) (Fig. 2B). Analyses of d' yielded overall similar results, identifying memory reduction for images encoded following the explicit (BASE_{EXP}: $M = 1.63$, $SD = .77$ vs. EXP: $M = 1.39$, $SD = .68$; $t[16] = 1.70$, $p = .054$) and implicit (BASE_{IMP}: $M = 1.61$, $SD = .55$ vs. IMP: $M = 1.40$, $SD = .60$; $t[16] = 1.83$, $p = .043$) induction of emotional suppression goals, but no difference between the two emotional suppression conditions ($t[16] = -.08$, $p = .935$ [two-tailed]).

Regarding the memory performance for neutral images during the baseline runs, both hit rate ($M = .66$, $SD = .11$) and d' ($M = 1.34$, $SD = .63$) were significantly lower than those for negative images viewed during the baseline runs: $t(16) > 2.50$, $p < .012$. Hit rate was also lower for these neutral images compared to negative images viewed following the induction of emotional suppression goals: $t(16) = 2.20$, $p = .022$. In addition, analyses comparing memory performance between the experimental and control groups showed that the reduction in memory was marginally larger in the former than in the latter group (Supplementary Material, S1). This suggests that the reduced memory performance observed in the experimental group was at least in part due to the induction of emotional suppression goals to regulate emotional responses, and was not merely due to habituation following repeated exposure to emotional stimuli. These findings confirm our second hypothesis and show that both explicit and implicit emotional suppression reduced subsequent recognition memory one week later.

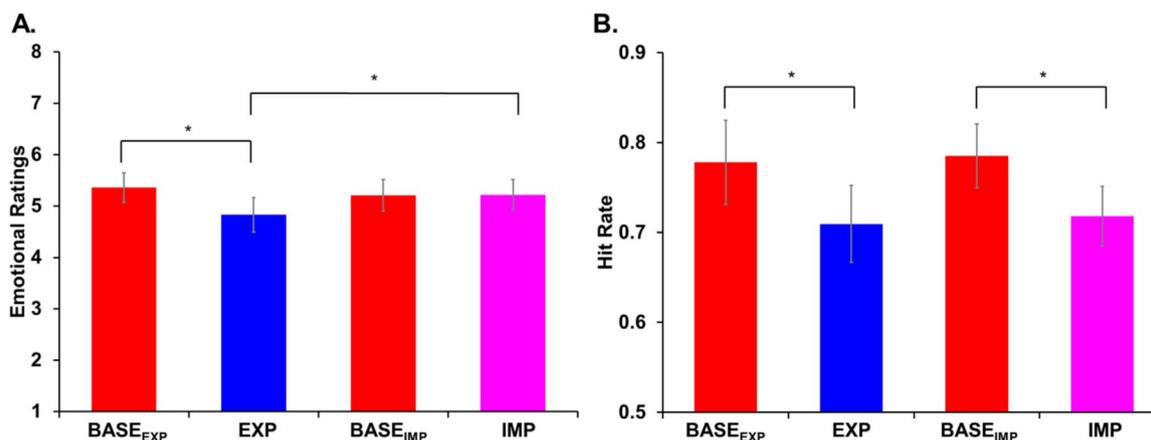


Fig. 2. The immediate and long-term impact of emotional suppression. (A) Emotional ratings for negative images were significantly reduced following the explicit, but not implicit, induction of emotional suppression goal. (B) Delayed recognition memory was reduced for the images encoded following the explicit and implicit induction of emotional suppression goal relative to those encoded during the preceding baseline runs. Error bars indicate the standard error of the mean for each condition. BASE_{EXP} = baseline run preceding the explicit induction of emotional suppression goal; EXP = runs following the explicit induction of emotional suppression goal; BASE_{IMP} = baseline run preceding the implicit induction of emotional suppression goal; IMP = runs following the implicit induction of emotional suppression goal. * $p < .05$.

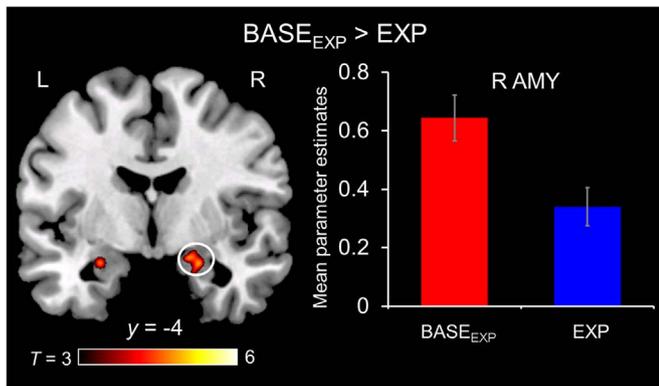


Fig. 3. Decreased amygdala activity associated with the explicit induction of emotional suppression goal. The evaluation of negative images following the explicit induction of emotional suppression goal was associated with decreased activity in bilateral amygdala compared to the preceding baseline run. The bar graph on the right panel illustrates mean parameter estimates extracted from the right amygdala cluster. Error bars indicate the standard error of the mean for each condition. $BASE_{EXP}$ = baseline run preceding the explicit induction of emotional suppression goal; EXP = runs following the explicit induction of emotional suppression goal.

3.2. fMRI results

3.2.1. Immediate impact of emotional suppression

The explicit induction of the emotional suppression goal was associated with decreased activity in bilateral AMY during the evaluation of negative images, compared to its preceding baseline run (Fig. 3 and Table 2); no brain regions were identified as showing significant activation differences in the reverse contrast. Moreover, no brain regions were identified as showing significant activation differences between the implicit induction of emotional suppression goal and its preceding baseline in either direction. Direct comparisons of brain activity associated with the explicit and implicit induction of emotional suppression goals identified regions including the right AMY and HC showing decreased activity for explicit compared to implicit emotional suppression (Table 2). Overall, these results partially confirm our third hypothesis and show that the explicit but not implicit induction of emotional suppression goal was associated with decreased AMY activity during the evaluation of negative images, paralleling the behavioral effects.

3.2.2. Long-term impact of emotional suppression

The explicit induction of the emotional suppression goal was

Table 2

Brain regions showing the immediate impact of the induction of emotional suppression goals during emotional ratings.

This table identifies brain regions showing differential activity between the experimental conditions during emotional ratings. All clusters reported in this table meet the significance threshold determined based on a Monte Carlo simulation, corrected for multiple comparisons at $p < .05$ (see Methods). BA, Brodmann's area; L, left; R, right; $BASE_{EXP}$, baseline run preceding the explicit induction of emotional suppression goal; EXP , runs following the explicit induction of emotional suppression goal; $BASE_{IMP}$, baseline run preceding the implicit induction of emotional suppression goal; IMP , runs following the implicit induction of emotional suppression goal.

| Brain Region | Side | BA | Talairach peak coordinates | | | t | Voxels | Volume (mm ³) |
|---|------|----|----------------------------|-----|-----|------|--------|---------------------------|
| | | | x | y | z | | | |
| <i>BASE_{EXP} > EXP</i> | | | | | | | | |
| Amygdala | L | | -23 | -4 | -11 | 3.05 | 6 | 384 |
| Amygdala | R | | 18 | -8 | -11 | 5.95 | 66 | 4224 |
| Parahippocampal gyrus | R | 35 | 14 | -26 | -12 | 4.05 | | |
| <i>EXP > BASE_{EXP}</i> | | | | | | | | |
| No suprathreshold voxels. | | | | | | | | |
| <i>BASE_{IMP} > IMP, IMP > BASE_{IMP}</i> | | | | | | | | |
| No suprathreshold voxels. | | | | | | | | |
| <i>EXP > IMP</i> | | | | | | | | |
| No suprathreshold voxels. | | | | | | | | |
| <i>IMP > EXP</i> | | | | | | | | |
| Amygdala | R | | 25 | -4 | -14 | 3.19 | 49 | 3136 |
| Hippocampus | R | | 33 | -11 | -14 | 4.33 | | |
| Putamen | R | | 29 | -9 | -3 | 4.34 | | |

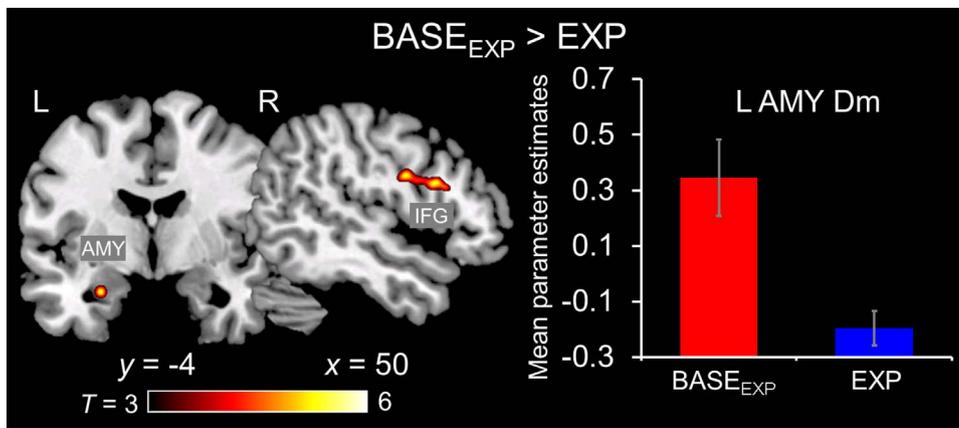


Fig. 4. Decreased encoding-related activity in the amygdala and IFG following the explicit induction of emotional suppression. Successful memory encoding following the explicit induction of emotional suppression goal was associated with decreased activity in a host of brain regions, including the left amygdala and the right inferior frontal gyrus (BA 44), compared to the preceding baseline run. The bar graph on the right panel illustrates mean differences in brain activity (parameter estimates) for Hits vs. Misses each condition – i.e., “Dm” effect, extracted from the left amygdala cluster. Error bars indicate the standard error of the mean for each condition. AMY = amygdala; IFG = inferior frontal gyrus; BASE_{EXP} = baseline run preceding the explicit induction of emotional suppression goal; EXP = runs following the explicit induction of emotional suppression goal.

Table 3

Brain regions showing the long-term impact of the induction of emotional suppression goals.

This table identifies brain regions showing significant differences in Dm activity (i.e., differential activity for remembered vs. forgotten trials) between the experimental conditions. All clusters reported in this table meet the significance threshold determined based on a Monte Carlo simulation, corrected for multiple comparisons at $p < .05$ (see Methods). BA, Brodmann’s area; L, left; R, right; BASE_{EXP}, baseline run preceding the explicit induction of emotional suppression goal; EXP, runs following the explicit induction of emotional suppression goal; BASE_{IMP}, baseline run preceding the implicit induction of emotional suppression goal; IMP, runs following the implicit induction of emotional suppression goal.

| Brain Region | Side | BA | Talairach peak coordinates | | | t | Voxels | Volume (mm ³) |
|---|------|----|----------------------------|-----|-----|------|--------|---------------------------|
| | | | x | y | z | | | |
| <i>BASE_{EXP} > EXP</i> | | | | | | | | |
| Frontal cortex | | | | | | | | |
| Inferior frontal gyrus | R | 44 | 47 | 11 | 24 | 4.09 | 33 | 2112 |
| Inferior frontal gyrus | R | 6 | 47 | -4 | 26 | 4.76 | | |
| Medial temporal cortex | | | | | | | | |
| Amygdala | L | | -23 | -3 | -18 | 3.79 | 8 | 512 |
| Lateral temporo-occipital cortex | | | | | | | | |
| Middle temporal gyrus | L | 21 | -46 | -43 | 3 | 4.37 | 33 | 2112 |
| Middle temporal gyrus | L | 39 | -53 | -58 | 5 | 3.39 | | |
| Superior temporal gyrus | L | 22 | -57 | -39 | 3 | 3.45 | | |
| Fusiform gyrus | L | 37 | -45 | -37 | -14 | 3.98 | 27 | 1728 |
| Declive | L | | -31 | -56 | -20 | 4.07 | | |
| <i>EXP > BASE_{EXP}</i> | | | | | | | | |
| No suprathreshold voxels. | | | | | | | | |
| <i>BASE_{IMP} > IMP</i> | | | | | | | | |
| No suprathreshold voxels. | | | | | | | | |
| <i>IMP > BASE_{IMP}</i> | | | | | | | | |
| Lateral parieto-temporal cortex | | | | | | | | |
| Insula | L | 13 | -31 | -25 | 16 | 6.36 | 51 | 3264 |
| Postcentral gyrus | L | 1 | -57 | -18 | 20 | 4.66 | | |
| Precentral gyrus | L | 4 | -53 | -15 | 27 | 4.03 | | |
| Inferior parietal lobule | L | 40 | -61 | -26 | 26 | 4.43 | | |
| <i>EXP > IMP</i> | | | | | | | | |
| No suprathreshold voxels. | | | | | | | | |
| <i>IMP > EXP</i> | | | | | | | | |
| Frontal cortex | | | | | | | | |
| Inferior frontal gyrus | L | 9 | -42 | -3 | 21 | 4.78 | 35 | 2240 |
| Inferior frontal gyrus | L | 44 | -53 | 12 | 15 | 3.77 | | |
| Subcortical | | | | | | | | |
| Thalamus | L | | -12 | -11 | 17 | 4.33 | 27 | 1728 |

Taken together, these findings partially confirm our fourth hypothesis and show that the explicit induction of emotional suppression goal was associated with decreased memory-related activity in regions typically involved in emotional memory encoding, including the AMY, HC, and IFG, whereas the implicit induction of emotional suppression goal was not associated with significant reduction in Dm activity in these regions. However, both the explicit and implicit induction of emotional suppression goals was associated with decreased functional connectivity linked to successful encoding, and the strength of AMY-HC connectivity no longer predicted subsequent memory for stimuli encoded following the explicit (but not implicit) induction of emotional suppression goal.

4. Discussion

The present study provides evidence regarding the neural mechanisms underlying the effects of explicit and implicit suppression on emotional experience and episodic memory. To our knowledge, this is the first empirical study investigating the neural correlates of both immediate and long-term effects of the explicit and implicit forms of this ER strategy within the same sample. The main findings are discussed in turn below.

4.1. Behavioral results: effect of emotional suppression on emotional ratings

First, our results identified reduced subjective ratings of negative

Table 4

Medial temporal lobe regions showing the long-term impact of emotional suppression on functional connectivity with the amygdala and inferior frontal gyrus.

This table identifies brain regions within the medial temporal lobe showing significant differences in Dm functional connectivity (i.e., differential connectivity for remembered vs. forgotten trials) with the left amygdala seed ($x = -23, y = -3, z = -18$) and the right inferior frontal gyrus seed ($x = 47, y = 11, z = 24, BA 44$), both of which were identified as showing significantly reduced Dm activity following the explicit induction of emotional suppression goal compared to the preceding baseline run. All clusters reported in this table meet the significance threshold determined based on a Monte Carlo simulation, corrected for multiple comparisons at $p < .05$ (see Methods). BA, Brodmann's area; L, left; R, right; AMY, amygdala; IFG, inferior frontal gyrus; BASE_{EXP}, baseline run preceding the explicit induction of emotional suppression goal; EXP, runs following the explicit induction of emotional suppression goal; BASE_{IMP}, baseline run preceding the implicit induction of emotional suppression goal; IMP, runs following the implicit induction of emotional suppression goal.

| Brain Region | Side | BA | Talairach peak coordinates | | | <i>t</i> | Voxels | Volume (mm ³) |
|------------------------------------|------|----|----------------------------|----------|----------|----------|--------|---------------------------|
| | | | <i>x</i> | <i>y</i> | <i>z</i> | | | |
| BASE_{EXP} > EXP | | | | | | | | |
| L AMY seed | | | | | | | | |
| Hippocampus | R | | 18 | -12 | -11 | 5.51 | 35 | 2240 |
| Parahippocampal gyrus | R | 27 | 17 | -31 | -2 | 5.78 | 14 | 896 |
| | R | 19 | 17 | -43 | -3 | 3.80 | | |
| Amygdala | L | | -23 | -8 | -8 | 4.96 | 30 | 1920 |
| Parahippocampal gyrus | L | 35 | -19 | -34 | -10 | 3.90 | | |
| Hippocampus | L | | -27 | -23 | -9 | 3.44 | | |
| R IFG seed | | | | | | | | |
| Hippocampus | L | | -31 | -15 | -9 | 5.47 | 10 | 640 |
| Hippocampus | R | | 14 | -8 | -11 | 3.72 | 5 | 320 |
| BASE_{IMP} > IMP | | | | | | | | |
| L AMY seed | | | | | | | | |
| Hippocampus | L | | -19 | -11 | -12 | 6.84 | 16 | 768 |
| Parahippocampal gyrus | R | 34 | 18 | -11 | -18 | 4.85 | 5 | 320 |
| R IFG seed | | | | | | | | |
| Amygdala | L | | -23 | -4 | -14 | 4.82 | 14 | 896 |
| Hippocampus | R | | 25 | -39 | -3 | 4.18 | 8 | 512 |

images following the explicit induction of emotional suppression goal relative to the preceding baseline run. This is consistent with previous evidence from the studies using similar task instructions, and thus confirms the effect of emotional suppression on down-regulating negative emotional experience when explicitly instructed to do so (Binder et al., 2012; Dunn et al., 2009; Goldin et al., 2008; Hayes et al., 2010). However, the implicit induction of emotional suppression goal did not result in the reduction of emotional ratings compared to the preceding baseline run as previously reported by others (e.g., Mauss et al., 2007). One possible explanation for this inconsistency is related to differences in the experimental conditions included in the analyses. More specifically, the results reported by Mauss and colleagues (2007) regarding the differences in emotional experience were based on comparing subjective emotional ratings following the emotional control priming vs. the emotional expression priming, the latter of which required

participants to unscramble sentences with words conveying the idea of emotional expression (e.g., “volatile”, “feel”, and “boiled”). Therefore, it is possible that Mauss et al.'s (2007) emotion expression priming resulted in significant up-regulation of immediate emotional experience, which overall contributed to the differences in ratings between this condition and the emotional control priming condition. Consistent with this idea, a study examining the effects of explicit and implicit cognitive reappraisal (an ER strategy involving attempts to change the meaning of stimuli/situations; Gross, 2008) showed that only explicit but not implicit reappraisal reduced the negative emotional experience relative to the condition with neutral priming (Yuan et al., 2015). However, implicit reappraisal showed the same decrease in heart-rate reactivity as explicit reappraisal (Yuan et al., 2015). This suggests that, for subjective emotional ratings, the effect of implicit emotional suppression (induced via priming) may not emerge when compared to

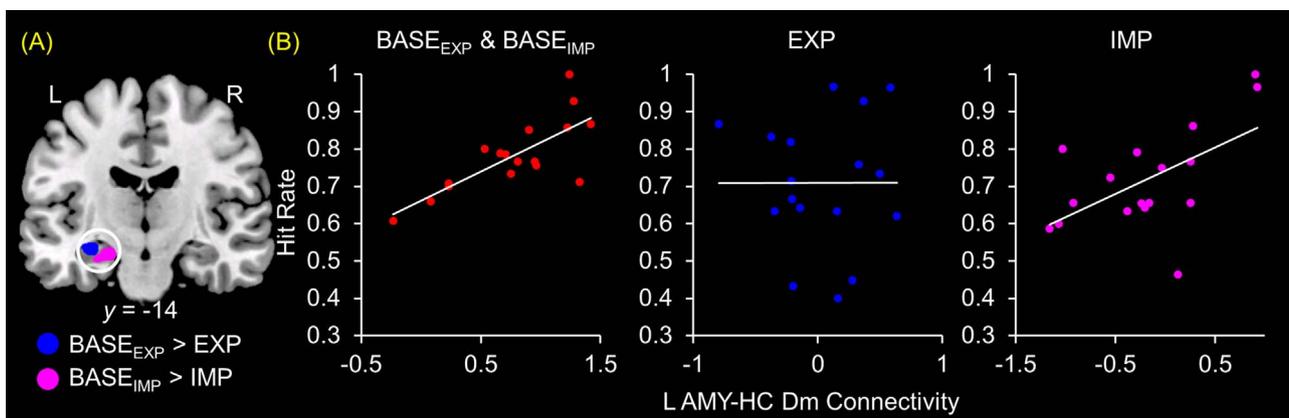


Fig. 5. Decreased encoding-related functional connectivity between the amygdala and hippocampus linked to emotional suppression. (A) Both the explicit and implicit induction of emotional suppression goals was associated with decreased functional connectivity between the left amygdala (AMY) and hippocampus (HC) related to successful encoding. (B) The scatter plots represent between-subjects covariation of the strength of successful encoding-related (Dm) functional connectivity between the left AMY and HC (*x*-axis) and subsequent memory performance (*y*-axis). AMY-HC Dm functional connectivity predicted subsequent memory for images encoded during the baseline runs as well as following the implicit induction of emotional suppression goal, but not the explicit induction of emotional suppression goal. For visualization purposes, the AMY-HC functional connectivity and memory performance were averaged across the two baseline runs. BASE_{EXP} = baseline run preceding the explicit induction of emotional suppression goal; EXP = runs following the explicit induction of emotional suppression goal; BASE_{IMP} = baseline run preceding the implicit induction of emotional suppression goal; IMP = runs following the implicit induction of emotional suppression goal.

passive viewing.

4.2. Behavioral results: effect of emotional suppression on episodic memory

Our findings show that recognition memory performance was significantly reduced for stimuli encoded following both the explicit and implicit induction of emotional suppression goals compared to those encoded during the preceding baseline runs. These results are overall consistent with previous evidence identifying the memory-reducing effect of deliberate emotional suppression (Binder et al., 2012; Dillon et al., 2007; Dunn et al., 2009; Hayes et al., 2010; Richards and Gross, 1999, 2000), and further demonstrate comparable efficacy of implicit emotional suppression in reducing subsequent memory. Importantly, these findings advance our understanding of the effects of implicit or spontaneous ER on episodic memory, for which available evidence is still scarce (e.g., Egloff et al., 2006). It has been suggested that, because of its emphasis on inhibiting the external expression (and/or internal experience) of emotion, engaging emotional suppression diverts attention away from the to-be-encoded material, thus resulting in reduced stimulus elaboration that would otherwise help facilitate the encoding process (Dillon et al., 2007; Hayes et al., 2010). This interpretation is also consistent with prior evidence based on eye tracking data showing that emotional suppression was associated with decreased proportions of fixations on emotional aspects of the stimuli than cognitive reappraisal (Bebko et al., 2011). More research is necessary to further examine the link between explicit/implicit emotional suppression and attentional deployment using eye tracking, and clarify how modulation of attention by suppression relates to subsequent memory.

One potentially interesting aspect related to the present memory findings concerns the role of the SST. In the present study, participants always performed the SST following a baseline run, once with the words conveying the idea of ER (in the IMP condition) and another with neutral words only (i.e., SST_{Neu}, in the EXP condition). Because the SST_{Neu} was not performed before the baseline runs, it remains unclear to what extent the observed reduction in memory between the baseline vs. emotional suppression runs can be accounted for by the SST_{Neu} alone. However, previous studies have identified no difference in memory performance between groups of young adults regardless of whether they had performed SST_{Neu} prior to a memory test or not (Geraci and Miller, 2013). Therefore, it is unlikely that the observed difference in memory between the baseline and emotional suppression runs was merely due to performing the SST between the two runs.

4.3. fMRI results: immediate impact of emotional suppression

Paralleling the behavioral results regarding the emotional ratings, our fMRI results identified decreased activity in bilateral AMY during the evaluation of negative images following the explicit, but not implicit induction of emotional suppression goal compared to the baseline run. These findings are consistent with previous studies identifying decreased AMY activity associated with the engagement of emotional suppression during the evaluation of visual emotional stimuli (Dorfel et al., 2014; Hayes et al., 2010; Ohira et al., 2006; but see Goldin et al., 2008). Also mirroring the behavioral results, the implicit induction of emotional suppression goal was not associated with significant differences in brain activity during the evaluation of negative images compared to the preceding baseline run. One possible explanation for this result concerns potential differences in timing at which explicit and implicit ER may take effect. Because implicit ER is by definition relatively more automatic than its explicit counterpart (Gyurak et al., 2011; Koole et al., 2015), it is possible that the former modulates the mechanisms of emotion processing faster than the latter. In support of this idea, a recent study using event-related potentials (ERPs) has shown that implicit ER (via priming by control-related words) was associated with modulation of ERPs during early perceptual processing (N170, peaking at around 170 ms post-stimulus), but not during the later

evaluation of negative emotional stimuli (late positive potential [LPP], peaking at around 600 ms post-stimulus), compared to the condition with neutral priming (Wang and Li, 2017). This finding, along with evidence identifying modulation of the LPP by explicit ER (Hajcak and Nieuwenhuis, 2006; Paul et al., 2013), highlight the importance of using tools with high temporal resolution in future studies examining the effects of explicit and implicit emotional suppression. Related to this point, a recent fMRI study using implicit priming via the SST failed to observe significant differences in neural activity associated with the processing of social vs. non-social stimuli (Powers and Heatherton, 2013). The authors suggest that some effects of implicit priming might be too subtle to detect in the MRI environment. This evidence, again, emphasizes the need to examine the mechanisms of explicit and implicit ER using a multitude of behavioral and neural/physiological assessment tools in future research.

4.4. fMRI results: long-term impact of emotional suppression

Finally, our results identified decreased activity linked to successful encoding in brain regions including the left AMY and right IFG, along with temporal and occipital cortical regions following the explicit induction of emotional suppression goal relative to the preceding baseline run. These findings are overall consistent with previous evidence identifying the involvement of these regions in emotional memory encoding (Dolcos et al., 2012, 2017; LaBar and Cabeza, 2006; Murty et al., 2011). Of note, given that both the left AMY and right IFG showed suppression-related reduction in Dm activity, our results suggest that the engagement of explicit emotional suppression diminishes both the MTL-based and PFC-based mechanisms that have been previously implicated in emotional memory encoding (Dolcos et al., 2004a, 2004b; Kaneda et al., 2017; Ritchey et al., 2011). One possibility is that the engagement of explicit emotional suppression requires resources to inhibit the external expression and internal experience of emotional responses, which might have led to overall decreased availability of resources for memory encoding (Binder et al., 2012). In contrast, despite the fact that the implicit induction of emotional suppression goal was associated with reduced subsequent memory, no regions were identified as showing significantly decreased Dm activity compared to the preceding baseline run. However, our analyses of functional connectivity showed that both the explicit and implicit induction of emotional suppression goals was associated with decreased memory-related functional connectivity involving the left AMY and right IFG, compared to the preceding baseline runs.

The few fMRI studies examining the impact of emotional suppression on episodic memory have demonstrated that this ER strategy modulates the interaction of brain regions typically involved in episodic encoding (Binder et al., 2012; Hayes et al., 2010). Regarding the MTL-based mechanisms, the engagement of emotional suppression decreased co-activation of the AMY and HC linked to successful encoding relative to passive viewing (Hayes et al., 2010). Similarly, regarding the PFC-based mechanisms, emotional suppression was associated with decreased functional connectivity between the HC and dlPFC linked to successful encoding compared to passive viewing (Binder et al., 2012). Our connectivity results are consistent with evidence identified in both of these studies, and lend support to the idea that the explicit and implicit induction of emotional suppression goals reduces subsequent memory, at least in part, by interfering with the interaction of brain regions part of MTL-based and PFC-based mechanisms involved in episodic memory encoding.

Furthermore, in the context of similar effects on encoding-related functional connectivity by explicit and implicit emotional suppression, our results also identified dissociable effects concerning brain-behavior covariation. In particular, although encoding-related connectivity between the left AMY and HC predicted subsequent memory during the baseline runs and following the implicit induction of emotional suppression goal, the explicit induction of emotional suppression goal

diminished this effect. This suggests that explicit emotional suppression reduces not only the overall quantity (magnitude) but also the quality of AMY-HC interactions important for emotional memory formation (Dolcos et al., 2017; LaBar and Cabeza, 2006), to the extent that greater interactions of these regions during the engagement of explicit emotional suppression are not related to enhanced subsequent memory. This finding is consistent with previous evidence showing that, although HC-dlPFC functional connectivity predicted subsequent memory for image stimuli encoded during passive viewing, the engagement of explicit emotional suppression diminished this effect (Binder et al., 2012). Taken together, our results extend current evidence and suggest that, whereas both explicit and implicit emotional suppression similarly reduce subsequent memory, explicit emotional suppression may uniquely exert interference over neural interactions critical for memory encoding.

4.5. Limitations and future directions

The following limitations of the present study should be acknowledged. First, one major limitation is that it identified evidence for the neural mechanisms underlying explicit and implicit emotional suppression based only on negative stimuli. Although this approach to examine within-valence effects of ER (as opposed to examining valence-based interaction effects by factoring in neutral stimuli) appears to be the norm in the larger functional neuroimaging literature on this topic to date, it remains largely an open question the extent to which emotional suppression exerts its effects specifically by influencing emotion-related processes or by way of other mechanisms involved in visual information processing in general. On the one hand, given that similar regions (left AMY and right IFG) have been previously identified as showing increased memory-related activity by valence (i.e., emotional vs. neutral remembered items; Dolcos et al., 2013), it is possible that the present findings identifying modulation of activity in these regions by suppression are linked at least in part to processes related to “emotional” memory encoding. On the other hand, it is also possible that differential activity in these areas is not specific to encoding of emotional stimuli per se. Instead, this might be more generally related to other mechanisms such as the engagement of attentional processes, the degree of which might influence episodic encoding regardless of stimulus valence (e.g., reduced stimulus encoding by divided attention; Buckner et al., 1999). In light of this limitation, future research should employ task paradigms that would allow further examination of the role of stimulus valence, and clarify what mechanisms are commonly and differentially engaged by emotional vs. neutral stimuli.

Second, the present study manipulated the emotional suppression goals using a within-subject design, in which each participant was exposed to both the explicit and implicit emotional suppression condition. Although this design allowed us to incorporate the implicit induction of emotional suppression goal, and also to overcome possible limitations previously identified in between-subjects designs (Binder et al., 2012), it is possible that the induction of the first emotional suppression goal had carried over to the subsequent runs (e.g., the second baseline run). A similar issue has been identified in previous neuroimaging studies of “uninstructed” ER, in the context of trial-by-trial manipulations of ER conditions (Silvers et al., 2015). In the present study, analyses of fMRI and behavioral data related to negative images comparing the two baseline runs did not yield similar results as those of the main analyses. This suggests that the impact of the possible carry-over effect was minimal on processing of these stimuli (probably due to cautions taken by counterbalancing the order of ER goal induction across participants). However, it is also possible that this effect may be modulated by the stimulus valence, as suggested by our behavioral results regarding neutral stimuli (see Table 1), and future research should further clarify this issue in light of the caveat discussed above. One possibility is to use mixed designs assessing brain activity both within (comparing pre- and post-ER goal induction) and between (comparing explicit vs. implicit

inductions) groups.

Finally, it is important for future studies to explore further the immediate and long-term impact of emotional suppression using larger and more diverse subject samples. Such investigations might allow clarification of the role of individual differences in modulating the effect of emotional suppression (e.g., Butler et al., 2007; Denkova et al., 2012; Emery and Hess, 2011; Schmeichel et al., 2008), and how it might relate to long(er)-term consequences on psychological well-being. It has been suggested that emotional suppression (particularly expressive suppression) is a relatively maladaptive form of ER, as its habitual use has been linked to increased vulnerability to symptoms of emotional dysregulation (Aldao and Nolen-Hoeksema, 2012; Lewellyn et al., 2013). However, these findings seem counterintuitive when compared to the memory-reducing effects of emotional suppression as identified in the present study and by others, because this ER strategy may actually help alleviate the impact of unwanted memories for distressing events both in healthy functioning and in affective disturbances, such as depression and post-traumatic stress disorder (Dolcos, 2013; Hayes et al., 2011). In fact, some researchers have posited that emotional suppression, involving both the inhibition of external expression and internal experience of emotions, may be an adaptive ER strategy, at least in healthy individuals (Dunn et al., 2009). Future research should clarify how measures of explicit and implicit emotional suppression, broadly defined, relate to individual differences in emotional experiences in everyday life, and how such relationships may in turn predict symptoms of affective disturbances in healthy and clinical populations (see also Kupper et al., 2014).

4.6. Conclusions

Despite the limitations mentioned above, the present study makes novel contributions to the literature on the neural correlates of explicit and implicit ER. By using an experimental paradigm assessing both immediate and long-term consequences of emotional suppression, the present study sheds light on how the two forms of emotional suppression similarly or differentially modulate emotional ratings and episodic memory, at the level of behavioral and neural responses. Evidence provided by behavioral assessments shows that explicit emotional suppression reduced the subjective emotional ratings of negative images, whereas both forms of emotional suppression reduced subsequent memory. Mirroring these behavioral findings, fMRI results demonstrated that only explicit emotional suppression was associated with decreased activity in the AMY during the evaluation of negative images, but both forms of emotional suppression were associated with overall reduced functional connectivity involving brain regions implicated in emotional memory encoding (AMY and IFG). In the context of overall similar effects on memory-related changes in functional connectivity, explicit emotional suppression was uniquely associated with altered AMY-HC interactions, to the extent that greater AMY-HC interactions during the explicit engagement of emotional suppression were not related to enhanced subsequent memory. Taken together, these findings advance our understanding of the mechanisms underlying the effects of explicit vs. implicit emotional suppression, and provide insights into possible ways of modulating the immediate and long-term impact of emotional stimuli.

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Disclosure of interest

The authors report no conflicts of interest.

Ethical approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent

Informed consent was obtained from all individual participants included in the study.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2018.02.010>.

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