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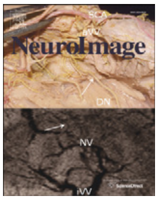

Emotion suppression reduces hippocampal activity during successful memory encoding

Julia Binder [a,b,c,*], Dominique J.-F. de Quervain [d], Malte Friese [e], Roger Luechinger [f], Peter Boesiger [f], Björn Rasch [a,g,h,**]

[a] Division of Biopsychology, University of Zurich, Switzerland
[b] Division of Gerontopsychology, University of Zurich, Switzerland
[c] International Normal Aging and Plasticity Imaging Center (INAPIC), Zurich, Switzerland
[d] Division of Cognitive Neuroscience, University of Basel, Switzerland
[e] Division of Social Psychology, University of Basel, Switzerland
[f] Institute for Biomedical Engineering, ETH Zurich, Switzerland
[g] Neuroscience Center Zurich (ZNZ), University and ETH Zurich, Switzerland
[h] Zurich Center for Integrative Human Physiology (ZIHP), University of Zurich, Switzerland

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ABSTRACT

People suppressing their emotions while facing an emotional event typically remember it less well. However, the neural mechanisms underlying the impairing effect of emotion suppression on successful memory encoding are not well understood. Because successful memory encoding relies on the hippocampus and the amygdala, we hypothesized that memory impairments due to emotion suppression are associated with down-regulated activity in these brain areas. 59 healthy females were instructed either to simply watch the pictures or to down-regulate their emotions by using a response-focused emotion suppression strategy. Brain activity was recorded using functional magnetic resonance imaging (fMRI), and free recall of pictures was tested afterwards. As expected, suppressing one's emotions resulted in impaired recall of the pictures. On the neural level, the memory impairments were associated with reduced activity in the right hippocampus during successful encoding. No significant effects were observed in the amygdala. In addition, functional connectivity between the hippocampus and the right dorsolateral prefrontal cortex was strongly reduced during emotion suppression, and these reductions predicted free-recall performance. Our results indicate that emotion suppression interferes with memory encoding on the hippocampal level, possibly by decoupling hippocampal and prefrontal encoding processes, suggesting that response-focused emotion suppression might be an adaptive strategy for impairing hippocampal memory formation in highly arousing situations.

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Introduction

Emotional arousal facilitates memory formation, which can be seen as an adaptive phenomenon (see LaBar and Cabeza, 2006, for a systematic overview), while highly dangerous and painful situations can lead to the induction of long-lasting and intrusive traumatic memories (McNally, 2003). During emotionally arousing situations, some people express or even act according to their emotions. Others try to cope with the situation by down-regulating their emotions and stay calm at least from the exterior, possibly in order to conform with personal and social norms (Snyder, 1974). It is still an open question which of these strategies is more advantageous during highly arousing situations, which is a particularly important question with regard to the prevention of the development of traumatic memories.

Emotion suppression is a response-focused emotion regulation strategy and refers to the conscious inhibition of an emotional reaction once an emotion is being experienced, mostly with regard to the suppression of facial reactions (expressive suppression; Gross, 1998). While emotion suppression is efficient in reducing emotion expression as shown by video analysis (Gross and Levenson, 1993, 1997), studies using physiological or neural correlates of emotional reactions revealed mixed results with regard to the success of down-regulating the inner emotional experience (Demaree et al., 2006b; Gross, 1998, 2002; Gross and Levenson, 1993, 1997). In spite of these mixed results, emotion suppression consistently leads to an impairment of memory encoding and subsequent worse recall of the emotion-eliciting event: When participants view high and low arousing slides of injured people paired with biographical information, later memory for the biographical information is impaired for

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* Correspondence to: J. Binder, University of Zurich, Department of Gerontopsychology, Binzmühlestrasse 14/24, 8050 Zürich, Switzerland. Fax: +41 44 635 74 19.
** Correspondence to: B. Rasch, University of Zurich, Department of Biopsychology, Binzmühlestrasse 14/5, 8050 Zürich, Switzerland. Fax: +41 44 635 72 36.
E-mail addresses: julia.binder@psychologie.uzh.ch (J. Binder), Bjoern.Rasch@psychologie.uzh.ch (B. Rasch).

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those participants that are instructed to suppress their emotions during slide viewing (Richards and Gross, 1999). Similarly, instructed emotion suppression during film or slide viewing leads to poorer memory for details (Bonanno et al., 2004; Dillon et al., 2007; Dunn et al., 2009; Richards, 2004; Richards and Gross, 1999, 2000, 2006). Furthermore, self-implemented, spontaneous use of emotion suppression reduces memory for details of a film, content of a stressful speech and everyday situations (Egloff et al., 2006; Gross et al., 2006; Richards and Gross, 2000). Typically, emotion suppression impaired memory for both high and low arousing events in these studies. While these memory-impairing effects of instructed and spontaneous emotion suppression are well known on the behavioral level, the underlying neural mechanisms of emotion suppression on memory encoding are still unknown.

Generally, the encoding of declarative memories of events and facts critically depends on the integrity of the medial temporal lobe, especially the hippocampus, and lesions in these areas hinder declarative memory formation (Squire, 1992). Brain activation in hippocampal areas is consistently increased during encoding of later remembered as compared to later forgotten events (difference due to memory, DM-effect), thereby accurately predicting successful memory encoding (Spaniol et al., 2009). In addition to hippocampal activity, successful memory encoding is also associated with increased hippocampal connectivity with neocortical regions, e.g., the cingulate cortex, the medial parietal cortex and dorsolateral prefrontal cortex (Ranganath et al., 2005; Schott et al., 2011). With regard to the memory enhancing effect of emotional information, concurrent activation of the amygdala exhibits a modulatory influence on the encoding processes in hippocampal areas, which is seen as increased BOLD activation in amygdala and hippocampal activation during successful encoding of emotional information (Dolcos et al., 2004; Murty et al., 2011). Drawing on these findings, we expected emotion suppression to affect brain activity in these memory-related brain regions, particularly in the hippocampus and the amygdala, resulting in subsequent impairments of memory recall. Furthermore, we expect emotion suppression to interfere with the hippocampo–neocortical connectivity during successful memory encoding.

In brain imaging studies of emotion suppression independent of possible effects on subsequent memory performance, the down-regulation of amygdala activity was not always successful (Goldin et al., 2008; Hayes et al., 2010; Ohira et al., 2006). However, emotion suppression is consistently associated with increases in brain activity in prefrontal control regions such as the dorsolateral prefrontal cortex, orbitofrontal cortex and anterior cingulate cortex (Goldin et al., 2008; Hayes et al., 2010; Ohira et al., 2006). We expect that activity differences in these prefrontal regions associated with emotion suppression might affect encoding processes in memory-related activity in the hippocampus and amygdala. In addition, down-regulation of emotions has been shown to be accompanied by an inverse coupling of prefrontal control regions and subcortical emotion generating regions such as the amygdala or the striatum, at least when a reappraisal strategy was used (Ochsner and Gross, 2005, 2008; Phan et al., 2005; Urry et al., 2006), and this inverse coupling might interfere with the hippocampo–neocortical connectivity necessary for successful memory encoding.

In the present study we aimed at investigating the neural processes underlying the interference of emotion suppression with successful memory encoding. One group of participants was instructed to down-regulate their emotions during viewing of emotional pictures by suppressing their facial expression as well as their inner feelings. The other group of participants was told to simply watch the pictures without any emotion regulation. Thirty minutes later, they were asked to freely recall the pictures. Brain activity during picture viewing was recorded using functional magnetic resonance imaging (fMRI), and regions in the bilateral hippocampi and amygdalae – derived from a recent meta-analysis on successful memory encoding (Kim, 2011) – served as regions of special interest. We show that emotion suppression impairs free recall of pictures, accompanied by decreased activation in the right hippocampus, which is related to successful memory encoding. Furthermore, emotion suppression decreased the connectivity between the hippocampus and the right dorsolateral prefrontal cortex, a brain area involved in controlling emotional reactions.

Methods

Participants

Sixty-five females participated in the present study. They were recruited in an online platform of the University of Zurich. We included only females because of the known gender-effects in emotional processing and related brain activity (Cahill, 2006). We excluded four participants due to head movements greater than 1 mm during the fMRI measurement (two participants in the watch group, two participants in the emotion suppression group) and two because they were outliers in hippocampal brain activity (both $Zs > 3.5$, both in the watch group). In the final sample of 59 participants, the emotion suppression group contained 31 participants, the watch group 28. Mean age was 23.54 years ($SD = 2.99$, range 19–33 years; emotion suppression group: $M = 23.29$, $SD = 2.99$; watch group: $M = 23.89$, $SD = 3.01$). Participants were free of any psychiatric illness and did not take any medication at the time of the experiment. They received CHF 25/hour as remuneration (approximately US $23 at the time of the study). Written informed consent was obtained by all participants before the study. The Ethical Committee of the University of Zurich had approved the study.

Study design and procedure

All participants viewed emotionally negative and neutral pictures and were asked to rate the pictures according to their subjectively experienced arousal. Following previous behavioral studies that reported an impairing effect of emotion suppression on subsequent memory performance (e.g. Bonanno et al., 2004; Dunn et al., 2009; Hayes et al., 2010; Richards and Gross, 1999, 2000), we used a between-subjects design, in which participants in the emotion suppression group were instructed to suppress their emotions elicited by the pictures, whereas the others simply watched the pictures (see Fig. 1.A). Participants were randomly assigned to the experimental conditions, rendering confounding group-differences (e.g. in memory capacity) rather unlikely. First, participants shortly practiced the picture-viewing task outside the fMRI scanner. After practicing, participants were positioned in the fMRI scanner. They received earplugs and headphones to reduce scanner noise. Their head was fixated in the coil using small cushions, and they were told not to move their head. Next, they performed the picture-viewing task, while functional MR-images were acquired. Then, participants completed a Stroop task followed by an anatomical scan. Results of the Stroop task will be reported elsewhere. The Software Presentation (Neurobehavioral Systems, Inc., San Francisco) controlled stimulus presentation and data acquisition. A projector in the scanner room displayed stimuli on a screen. Participants saw the pictures over mirrors on a screen in the MRI-scanner. They wore contact lenses if eye correction was needed. Participants did not know that the pictures had to be recalled afterwards and were not instructed to remember the pictures for later free recall. Outside the fMRI scanner, participants filled in a questionnaire including several control questions, the manipulation check, and demographic data, and were finally debriefed (see Fig. 1.A).

Materials and measures

Picture-viewing task

Twenty-four normatively neutral and twenty-four normatively negative pictures were taken from the International Affective Picture

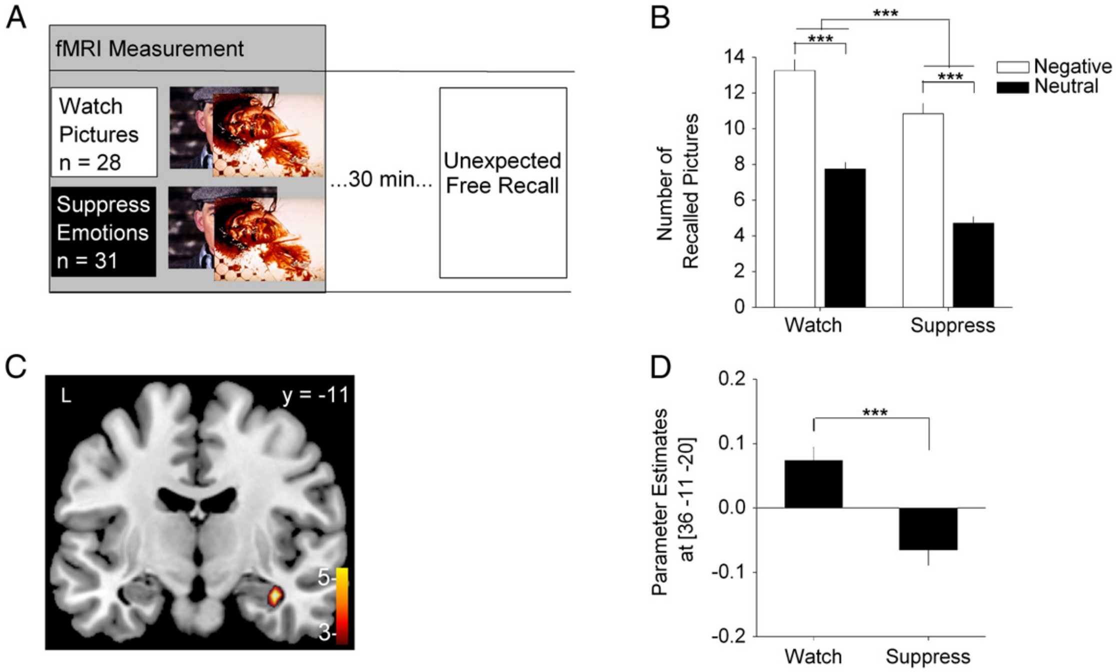

Fig. 1. (A) Experimental design and procedure. (B) Number of recalled pictures (mean ± *SEM*). Subjects in the emotion suppression group remembered fewer negative and neutral pictures (***$P<.001$) independent of valence (interaction of the experimental condition and picture valence $P>.50$). (C) Brain activity in the right hippocampus for group comparison of subsequently recalled as compared to forgotten pictures. Participants in the watch group showed more activity in the right hippocampus compared to subjects in the emotion suppression group during encoding of subsequently recalled pictures independent of picture valence ($P(\text{SVC})<.05$, displayed at an uncorrected threshold of $P=.005$). (D) The corresponding parameter estimates at the peak voxel in the right hippocampus (***$P<.001$). For exploratory purposes we show the parameter estimates at the peak voxel in the right hippocampus for negative and neutral pictures separately as Supplementary Fig. 1.

System (range from 1 to 9, with the ratings 1 = most negative, 5 = neutral, 9 = positive; Lang et al., 2008). The sets differed significantly in valence (negative pictures: $M=1.97$, SD = 0.33, neutral pictures $M=5.07$, $SD=0.23$, $F(1, 46)=1409.25$, $P<.001$). In addition, negative pictures were significantly more arousing than neutral pictures (negative pictures $M=5.85$, $SD=0.76$, neutral pictures $M=3.08$, $SD=0.62$, $F(1, 46)=190.99$, $P<.001$). Using similar picture sets, previous studies found that these pictures elicit strong amygdala activity (e.g. Rasch et al., 2009). Pictures of the same valence were randomized within blocks of 4 pictures (6 neutral blocks, 6 negative blocks, 48 pictures in total). The order of the blocks was also randomized, except that two blocks of negatively valenced pictures were always presented at the end of the task. Prior to every picture block, a fixation-cross appeared on the screen for 500 ms followed by the instruction, which was repeated with the single word "suppress" or "attend" for 1.5 s (depending on the experimental group assigned). Each picture was presented for 7 s. The interblock-interval was 5 s. The whole picture-viewing task lasted 8 min. In the control group, participants were told that it was okay to allow emotions in response to the pictures. Whenever the pictures elicited an emotional reaction, they were instructed to experience their emotional reactions naturally. In addition, they were allowed to show facial reactions naturally. The instructions were as follows (translated from German):

> *"…You are allowed to feel your inner emotions. Some pictures can be very touching. You can also show your feelings to the exterior when you see an emotional picture (*e.g. *as a facial expression). Do not try to alter your natural emotional reaction..."*

Participants in the emotion suppression group were instructed to use a response-focused emotion suppression strategy by suppressing their inner and outer emotional responses elicited by the pictures. More specifically, the participants were asked to make an effort to keep as cool as possible as well as not to show any facial reaction either. This instruction was independent of picture valence, however they were told that it might be harder to suppress their emotions for some pictures.

> *"…Please try to suppress your inner emotions as good as possible and stay as calm as possible. Imagine you have an inner shield, which easily reflects your emotions. In addition, you should try not to show any emotions at the exterior. Your facial expression should be absolutely calm during picture viewing (pokerface). For the success of this study, it is extremely important that you really follow the instructions by trying to suppress your emotions during picture viewing as good as possible. Please do not be surprised that it will be more difficult to suppress your emotions for some of the pictures…"*

Similar instructions have been used in previous research of response-focused emotion suppression (e.g. Campbell-Sills et al., 2006; Dunn et al., 2009; Ohira et al., 2006) and were intended to induce a suppression of inner feelings and facial expression without cognitive reappraisal. In a post-experimental questionnaire asking about the subjects' emotion regulation strategies, indeed none of our subjects indicated that they cognitively reappraised the content of the pictures. However, we cannot completely exclude that some reappraisal processes were used during the study. But even when instructed with a pure expressive suppression instruction, some people additionally use reappraisal to regulate their emotions (Demaree et al., 2006a).

Arousal ratings

After each picture block, participants indicated their subjective arousal (large, medium, small) on a three-point scale (Self Assessment Manikin, SAM) by pressing a button on a bottom box with their dominant hand. The arousal ratings of one participant were not available due to technical problems.

Free recall of pictures

Thirty minutes after the picture presentation, memory was assessed using a free-recall memory test. Participants were instructed to recall as many pictures as possible of those they had seen earlier in the picture-viewing task by writing short descriptions of the pictures' content (few words). Erroneously reported pictures from the training phase were excluded from the analysis. No time limit was set. Picture descriptions were rated for recall success by a trained investigator who was blind to the experimental conditions.

fMRI methods and procedures

Measurements were performed on a Philips Achieva 1.5 T whole body MR unit equipped with an eight-channel Philips SENSE head coil. Functional time series were acquired with a sensitivity encoded (Pruessmann et al., 1999) single-shot echo-planar sequence (SENSE-sshEPI). We used the following acquisition parameters: TE (echo time) = 45 ms, FOV (field of view) = 22 cm, acquisition matrix = 80 × 80, interpolated to 128 × 128, voxel size: 2.75 × 2.75 × 4 mm^3, SENSE acceleration factor R = 2.0. Using a midsaggital scout image, 32 contiguous axial slices were placed tilted by 20° to the anterior-posterior commissure (AC–PC) plane covering the entire brain with a TR = 3000 ms ($\theta = 82°$). The first two acquisitions were discarded due to T1 saturation effects. The picture-viewing task consisted of 155 functional runs. For each subject, we also acquired high-resolution T1-weighted anatomical images (0.86 × 1 × 2 mm^3, 55 slices, TE = 15 ms, 3 averages).

Preprocessing was performed using SPM5, data analyses were performed using SPM8 (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab 2009a (The Mathworks Inc., Natick, MA, USA). Volumes were slice-time corrected to the first slice, realigned to the first acquired volume, normalized to each individual T1-image, and smoothed using an 8 mm full-width-at-half-maximum Gaussian kernel. A 128 s cut-off high pass filter was added to the confound partition of the design matrix to account for low-frequency drifts, and a correction for intrinsic autocorrelations was included in the analysis.

Statistical analyses of the fMRI data

First level analysis

Our main effect of interest was brain activation related to successful memory encoding, more specifically higher brain activation for subsequently remembered as compared to subsequently forgotten pictures. Thus, we included the following regressors in the model: negative remembered, negative forgotten, neutral remembered and neutral forgotten pictures (single picture wise). In addition, button presses during arousal ratings as well as six movement parameters from spatial realigning were included as regressors of no interest. Based on our behavioral analyses, which did not reveal a valence-dependent memory impairment (see behavioral results), we collapsed negative and neutral pictures resulting in the main contrast of remembered (negative and neutral) minus forgotten (negative and neutral) pictures. In a post-hoc analysis, we also analyzed the remembered minus forgotten contrast for negative and neutral pictures separately (see Supplementary Material). Although we are aware that the presentation of pictures was blocked, our main effect of remembered minus forgotten pictures revealed activity in a network consistently implicated in successful memory encoding in studies using a true event-related design (Kim, 2011), namely primary and secondary visual areas (bilateral occipital and parietal areas) as well as bilateral activity in the inferior and middle temporal gyrus, the right medial temporal lobe and the right inferior frontal gyrus (see Table S1). Hence, despite the blocked presentation of pictures, our statistical model was able to reliably capture well-known effects related to successful memory encoding.

Second level analysis

On the group level, we compared the contrast of remembered minus forgotten pictures between the group who suppressed its emotions during picture viewing and the watch group using a two-sample *t*-test. For explorative purposes, we analyzed post-hoc group differences for negative and neutral pictures separately. In addition, we controlled for differences in memory performance by including the absolute number of recalled pictures as a covariate in a separate analysis. Based on our theoretical prediction, we focused on effects of emotion suppression on encoding-related activation in the hippocampus and the amygdala in our analysis. We report coordinates according to the conventions defined by the Montreal Neurological Institute (MNI) and labels for cluster activations according to the Anatomical Automatic Labeling toolbox (Tzourio-Mazoyer et al., 2002) implemented in SPM8. We defined three regions of interest based on peak activations identified in a recent meta-analysis of subsequent memory studies (Kim, 2011): left hippocampus/amygdala [−22 −16 −13], right hippocampus [32 −18 −25] and right amygdala [16 −7 −20] (MNI coordinates, converted via tal2mni.m). We defined our regions of special interests (ROIs) as 10 mm spheres centered on these peaks. To further analyze the impact of emotion regulation on amygdala activation, we additionally used the bilateral amygdala (defined by the WFU_PickAtlas of Maldjian et al., 2003, 2004) as ROI for the contrast negative vs. neutral pictures. Within the ROIs, a significance threshold of $P < .05$ corrected for multiple comparisons (family-wise error correction) was used. In addition, we performed an exploratory whole brain analysis using a threshold of $P < .001$, uncorrected, in a minimum of 5 adjacent voxels (kE = 5).

Functional connectivity analyses

To further investigate the neural processes underlying the memory-impairing effect of emotion suppression, we performed a psychophysiological interaction (PPI) analysis as a measure of task-related functional connectivity as implemented in SPM8 (Friston et al., 1997). We used as seed the cluster of activation in the right hippocampus identified in the comparison between the emotion suppression and watch group (Montreal Neurological Institute coordinates: [36 −11 −20] thresholded at $P < .01$, uncorrected). The time course of the hippocampal seed was extracted for each subject, mean-centered, high-pass filtered, and deconvolved. A general linear model was then computed by using three regressors: a physiological regressor (the time course response in the seed region), a psychological regressor (subsequently remembered as compared to forgotten pictures; in a post-hoc analysis also negative remembered, negative forgotten, neutral remembered and neutral forgotten pictures separately), and a PPI term, calculated as the cross-product of the previous two terms. The individual PPI contrasts were entered in a second-level random-effects analysis to investigate differences in connectivity between the emotion suppression and watch group ($P < .001$ uncorrected; kE = 5).

Results

Behavioral results

As expected, down-regulating one's emotions during picture-viewing strongly impaired subsequent free recall of these pictures (for means see Table 1). Participants in the emotion suppression group remembered on average 15.55 ± 0.64 (*M* ± *SEM*) pictures, whereas participants in the watch group recalled 21.00 ± 0.87 (*M* ± *SEM*) of the 48 pictures. The impairing effect of emotion suppression on memory recall was highly significant (main effect of group: $F(1, 57) = 26.13$, $P < .001$). The effect of emotion suppression on memory recall was equally strong for negative and neutral pictures (Fig. 1.B) as indicated by a non-significant interaction between the experimental group (suppress vs. watch) and picture valence (negative vs. neutral; $F(1, 57) < 1$, $P > .50$). This unspecific effect of emotion suppression on recall of negative as well as neutral information has been consistently reported previously (Richards, 2004; Richards and Gross, 1999, 2000, 2006). In addition, it might be possible that the participants were also engaged in some regulatory processes during viewing of neutral pictures, although one would expect that efforts to suppress emotions are smaller during viewing of neutral as compared to emotional pictures. While recall time was not precisely measured, session protocols did not indicate any large difference in recall time between the groups. Independent of the experimental groups, participants recalled twice as many negative as compared to neutral pictures (main effect of picture valence: $F(1, 57)=156.53$, $P<.001$), replicating the well-known memory enhancing effect of emotional arousal (LaBar and Cabeza, 2006). The subjectively rated arousal (for means see Table 1) was significantly higher in the watch group as compared to the emotion suppression group ($F(1, 56)=54.65$, $P<.001$) with greater group differences for negative as compared to neutral pictures (interaction of experimental group and picture valence: $F(1, 56)=16.56$, $P<.001$). The negative pictures were rated as significantly more arousing compared to the neutral pictures (main effect of valence: $F(1, 56)=376.04$, $P<.001$).

Imaging results

Based on our hypothesis, we then tested whether suppressing one's emotions affected brain activity in the hippocampi or amygdalae during memory encoding. As predicted, we observed strongly reduced activity related to successful memory encoding in the right hippocampus when participants suppressed their emotions as compared to the control group (peak difference at [36 −11 −20], $t(57)=4.30$, $Z=3.98$, $P(\mathrm{SVC})=.003$, Figs. 1.C–D). We observed no significant activity differences in the amygdalae in this contrast (all $P\mathrm{s}>.01$, uncorrected). Post-hoc analyses revealed that emotion suppression equally reduced hippocampal activity for both emotional and neutral pictures (see Fig. S1). The exploratory whole brain analysis additionally revealed that the emotion suppression group exhibited reduced activity in the occipital lobe and the left cerebellum. For the reverse contrast, the emotion suppression group showed more activity in the right striatum (caudate nucleus) and the right cerebellum (see Table 2). However, these additional clusters did not survive multiple-comparison correction for the whole brain.

Since groups highly differed in memory performance, we conducted an additional analysis in which we controlled for confounding differences of performance by including recall performance as a covariate in the design matrix. The results remained almost unchanged except that the statistical power slightly increased in the hippocampus (peak difference at [30 −11 −24], $t(57)=4.38$, $Z=4.04$, $P(\mathrm{SVC})=.003$), in bilateral visual areas as well as in the right cerebellum (see Table S2). Consequently, our brain activity results are not confounded by the systematic memory recall performance difference between our two experimental groups. Independent of experimental group, successful picture encoding of subsequently remembered as compared to forgotten pictures was associated with a network consisting of primary and secondary visual areas (bilateral occipital and parietal areas) as well as bilateral activity in the medial temporal lobe and the right inferior frontal gyrus (for coordinates see Table S1). This brain activity pattern is highly similar to peak activations reported in a recent meta-analysis of several subsequent memory studies (Kim, 2011), indicating that our main parameter successfully captured activation related to successful memory encoding.

Table 1
Descriptive means for free recall of the pictures and the arousal ratings as a function of valence and experimental condition.

Measure	Suppress emotions (n = 31)		Watch pictures (n = 28)	
	M	*SEM*	*M*	*SEM*
Number of recalled pictures				
Negative pictures	10.84	.59	13.25	.62
Neutral pictures	4.71	.36	7.75	.38
Arousal ratings				
Negative pictures	2.11	.08	2.90	.08
Neutral pictures	1.15	.05	1.47	.05

Table 2
Result summary of brain activation for group comparison in the picture-viewing task for subsequently remembered versus forgotten negative and neutral pictures.

				MNI coordinates (mm)					
Watch > Suppress		BA	k_E	*x*	*y*	*z*	t_{max}	*Z*	*P*
Middle and superior occipital gyrus	R	19	40	*36*	*−72*	*8*	4.34	4.02	.000
Hippocampus	R		6	*36*	*−11*	*−20*	4.30	3.98	.000**
Cerebellum	L		7	*−8*	*−77*	*−20*	4.04	3.77	.000
Watch < Suppress									
Striatum (caudate nucleus)	R		15	*25*	*0*	*16*	4.14	3.85	.000
Cerebellum	R		8	*11*	*−55*	*−16*	4.13	3.84	.000

BA: Brodmann area; R: right hemisphere; L: left hemisphere; k_E : number of voxels. Analysis thresholded at $P<.001$ uncorrected for multiple comparisons in a minimum of $k_E=5$ adjacent voxels , $^{**}P<0.01$, small volume corrected (SVC).

Independent of memory, emotional processing of negative as compared to neutral pictures was generally associated with increased activity in the bilateral visual cortex, bilateral prefrontal regions, the left hippocampus as well as additional temporal areas and the bilateral insula in both groups (see Table S3; for meta-analyses see Phan et al., 2002, 2004). In addition, the left amygdala was highly activated in this contrast (at [−19 −6 −12], $t(58)=7.77$, $Z=6.41$, P(FWE corrected for whole brain)$<.001$), indicating that the emotional pictures reliably induced emotional reactions similar to previous results of our group (e.g. Rasch et al., 2009). Also in the watch group alone, the left and right amygdalae exhibited higher activity for emotional vs. neutral pictures (at [−22 −8 −12], $t(27)=6.38$, $Z=4.94$, $P(\mathrm{SVC})<.001$) and at [22 −3 −16], $t(27)=4.93$, $Z=4.12$, $P(\mathrm{SVC})=.002$). In the emotion suppression group, only left amygdala activation remained significant (at [−19 −3 −12], $t(30)=5.72$, $Z=4.67$, $P(\mathrm{SVC})<.001$). However, we did not observe any suprathreshold activation in the amygdalae for the interaction effect of picture valence (negative vs. neutral) and experimental group (watch vs. suppress; see Supplementary Table S4), suggesting that emotion suppression did not reliably reduce amygdala activity in our study. However, suppression of emotion as compared to watching the pictures was significantly associated with increased activation in the right middle frontal gyrus (BA 6 at [28 0 56], $t(58)=4.75$, $Z=3.34$, $P<.001$) and superior lateral prefrontal areas (BA 9 at [44 19 40], $t(58)=3.37$, $Z=3.52$, $P<.001$), probably reflecting effortful engagement of prefrontal brain areas during emotion suppression Table S4 for a complete list of results; Phillips et al., 2008). However, these results did not survive whole brain correction for multiple comparison.

Since successful memory encoding is associated with increased hippocampal connectivity with neocortical brain regions, e.g., the cingulate cortex, medial parietal cortex and the dorsolateral prefrontal cortex (Ranganath et al., 2005; Schott et al., 2011) and emotion suppression possibly interferes with this connectivity, we calculated the functional connectivity (psychophysiological interaction (PPI)) between the right hippocampus cluster at [36 −11 −20] and all other brain areas during encoding of subsequently remembered versus forgotten pictures. We observed that coupling between the right hippocampus and a region in the right dorsolateral prefrontal cortex (DLPFC, BA 9) was significantly higher in the watch group as compared to the emotion suppression group (at [36 41 32], $t(57)=3.73$; $Z=3.52$; $P<.001$, cluster size (kE) = 7 voxels, Fig. 2A–B, see Fig. S2 for parameter estimates separately for negative and neutral pictures).

Connectivity with the right hippocampus in the watch group was also increased in the right fusiform gyrus (at [30 –69 −4], $t(57)=3.69$; $Z=3.52$, $P<.001$). Note, however, these results did not survive whole brain correction for multiple comparison. No brain regions exhibited significantly decreased connectivity with the right hippocampus for the watch group as compared to the emotion suppression group.

To examine the behavioral relevance of the observed differences in connectivity between the right hippocampus and the right DLPFC, we extracted the connectivity parameters in the right DLPFC cluster for each subject and calculated a correlation between the connectivity measures and the total number of recalled pictures. Overall, the strength in coupling between the right hippocampus and the right DLPFC positively predicted the amount of freely recalled pictures ($r(59)=.32$, $P=.01$, see Fig. 2.C). The same strength of association was observed when analyzing the watch group only ($r(28)=.36$, $P=.06$, whereas the strength of hippocampal–DLPFC connectivity no longer predicted later memory recall when participants suppressed their emotions during picture viewing ($r(31)=-.20$, $P>.20$). The two correlation coefficients significantly differed between the two groups ($Z=-2.12$, $P=.03$).

Discussion

Our results indicate that the memory-impairing effect of suppressing one's emotions is accompanied by a decrease in right hippocampal activation during successful memory encoding. The hippocampus is critically involved in declarative memory formation (McGaugh, 2000; Wang and Morris, 2010), and differences in hippocampal activation during memory encoding are typically highly predictive for successful memory formation and subsequent recall success (Spaniol et al., 2009). The observed activation decrease indicates that hippocampal activation is less predictive for subsequent recall success when participants are engaged in suppressing their emotions, and this relative disengagement of the hippocampus might well explain the impairing consequences of emotion suppression on memory formation. Simultaneously, activation in striatal regions increased their predictive value for later recall performance in the emotion suppression group relative to the watch group. Striatal brain regions are typically involved in more procedural and implicit learning processes (e.g. sequential or category learning), but might also interact with declarative learning processes in the medial temporal lobe (Seger, 2006). Thus, in addition to the reduced involvement of the hippocampus in successful memory encoding, emotion suppression might possibly enhance the involvement of striatal learning processes. However, as we did not a priori define the striatum as region of interest and activity in this region did not survive whole brain correction for multiple comparisons, further studies are required to systematically test this observation. It is important to note that during the encoding phase, all participants were instructed to rate the pictures according to their subjectively experienced arousal (arousal indicated after each picture block), and they were completely unaware that memory would be tested afterwards (incidental encoding). Interestingly, no group differences with regard to subsequent memory performance were observed in the amygdalae, giving a hint that emotion suppression did not selectively reduce the enhancing effect of emotions on memory formation.

One explanation for the reduced involvement of hippocampus-based memory encoding might be that suppressing one's emotions during picture viewing increases self-regulatory demands, which leads to a decrease in the availability of cognitive resources for successful memory encoding. These effortful self-regulatory processes are

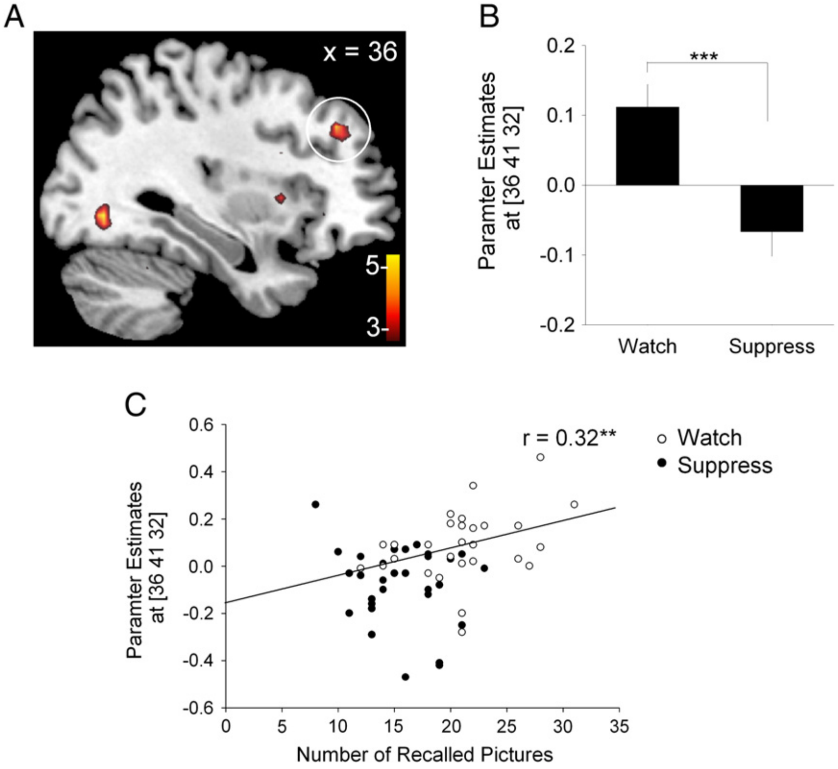

Fig. 2. Differences in connectivity for the comparison of the suppression and the watch group between the right hippocampus and all other brain regions during picture encoding of subsequently remembered as compared to forgotten pictures. (A) Participants in the watch group showed increased connectivity between the right hippocampus and the right dorsolateral prefrontal cortex (DLPFC) at [36 41 32] (white circle) and the right fusiform gyrus at [30 −69 −4] compared to subjects in the suppression group during encoding of subsequently recalled pictures (***$Ps<.001$, displayed at an uncorrected threshold of $P=.005$). (B) The corresponding parameter estimates at the peak voxel of the right DLPFC-cluster. For exploratory purposes, we also show the corresponding parameter estimates of our post-hoc analysis at the peak voxel of the right DLPFC-cluster for negative and neutral pictures separately as Supplementary Fig. 2. (C) Independent of experimental group, the strength in coupling of the right hippocampus and the right DLPFC correlated positively with the total number of remembered pictures ($r(59)=.32$, **$P=0.01$).

usually associated with increased activation in prefrontal regions like the inferior or dorsolateral prefrontal cortex (Heatherton and Wagner, 2011). This is supported by our finding of a reduced functional coupling during successful memory encoding between the hippocampus and the right DLPFC (BA 9) in the emotion suppression group relative to the watch group. The right DLPFC has been repeatedly implicated in processes of down-regulating emotions (Diekhof et al., 2011; Kalisch, 2009; Ochsner and Gross, 2005; Phillips et al., 2008). In addition, hippocampal connectivity with the DLPFC during memory encoding is increased for later remembered as compared to forgotten items (Ranganath et al., 2005; Schott et al., 2011), suggesting that hippocampo–prefrontal coupling is critical for successful encoding of memories. Interestingly, emotion regulation is assumed to be implemented by an *inverse* coupling of prefrontal control-regions and emotion-generating subcortical regions such as the amygdala (Ochsner and Gross, 2005, 2008; Phan et al., 2005; Urry et al., 2006). Thus, involvement of the DLPFC in the suppression of activation in subcortical areas might interfere with an appropriate coupling with hippocampal regions, leading to impaired memory encoding during emotion suppression. Interestingly, we in fact observed a general increase of activity in the same right prefrontal area (BA 9) in the emotion-suppression group as compared to the watch group independent of successful memory encoding, although this activity did not directly overlap with the reduced functional coupling but was located 22 mm more posterior. It is important to note that our result of a reduced hippocampo-prefrontal connectivity during emotion suppression did not survive a more conservative correction for multiple comparison and awaits further verification. In addition, please note that our measure of connectivity particularly captures the memory-related connectivity, as it is based on the difference in connectivity measures between remembered and forgotten pictures. The behavioral relevance of this interaction for memory processes is further supported by the positive correlation between the degree of prefrontal–hippocampal coupling and later free-recall performance, while this prediction breaks down when participants attempt to suppress their emotions. Taken together, these findings suggest that self-regulatory processes operating during emotion suppression in prefrontal brain regions might interfere with proper engagement of the hippocampus during memory encoding, ultimately leading to impairments in later memory recall. Of note, such an interference effect could possibly be caused by any “second task” involving self-regulatory processes in prefrontal regions, even independent of attempts to regulate emotions. Interestingly, reductions in hippocampal activity associated with successful memory encoding during dual-task paradigms have been reported by some authors (e.g. Kensinger et al., 2003), but not by others (e.g. Uncapher and Rugg, 2005). Future studies need to extend to and compare our findings with general divided attention effects to examine the specificity of our results of reduced hippocampal activation during down-regulation of emotions.

In contrast to emotion suppression, cognitive reappraisal is assumed to be a less resource-demanding emotion regulation strategy (Gross, 2002). Consistent with this view, no impairments in memory performance have been observed after cognitive reappraisal of emotional stimuli (Richards and Gross, 2000). Actually, there have been reported even memory enhancements after cognitive re-appraisal, and these enhancements were accompanied by increased functional coupling between activation in the amygdala and hippocampus during successful memory encoding of emotional pictures (Hayes et al., 2010). This finding is astonishing, because cognitive re-appraisal is regarded as quite efficient in down-regulating one's emotional reaction to emotional stimuli, which should lead to a decrease in emotional memory. However, these results may be confounded by a deeper level of processing during cognitive reappraisal (Dillon et al., 2007): during cognitive re-appraisal, participants are asked to invent an alternative and less emotional meaning for an emotional scene (e.g., the dead person is an actor, no real blood is shown; see Ochsner and Gross, 2008). The invention of such a new “story” might be regarded as a mnemonic strategy, which might ultimately lead to a better memory in spite of down-regulated emotional reactions. Interestingly, when examining the long-term effects after one year, cognitive reappraisal of emotional pictures resulted in reduced activation of the right hippocampus as compared to the passive viewing control group, while recognition performance remained unaffected (Erk et al., 2010). Further studies are required to disentangle the short- and long-term effects of different emotion regulation strategies on memory and their underlying memory-related brain activation.

Memory impairments during emotion suppression might also be explained by shifts in attentional deployment and a less elaborated visual processing of the stimuli. In other words, participants might simply change their viewing patterns during emotion suppression, intentionally avoiding emotional aspects of the pictures. Generally, it is well known that emotion regulation strategies like emotion suppression or cognitive reappraisal can implicate attentional shifts and reduce stimulus elaboration (Dillon et al., 2007; Gross, 1998, 2008). In an fMRI-study combined with eye-tracking measurement, participants spent less time fixating the relevant emotion-eliciting portions of the pictures as compared to the control group when down-regulating their emotions with cognitive reappraisal. Moreover, brain activity accounted to gaze patterns explained a significant portion of the variance in the left amygdala and prefrontal regions activated during cognitive reappraisal (van Reekum et al., 2007). Different gaze patterns due to emotion regulation strategies could well influence stimulus encoding and hence explain memory differences between the emotion suppression and watch group in our study. However, the contribution of gaze patterns to memory impairments during emotion suppression and its associated neural activity are still unknown, and future studies need to control for viewing patterns using eye tracker equipment. In a pilot study of our lab, we still observed memory impairments for encoded pictures during emotion suppression when reducing the picture presentation duration to 250 ms to avoid explorative saccades (unpublished data), providing a first hint that differences in gaze patterns cannot fully account for emotion suppression induced memory impairments.

Independent of memory, emotional as compared to neutral pictures reliably activated the amygdala in both groups, but we observed no significant reduction in amygdala activation in the emotion suppression group. It is possible that our between-subject design was not sensitive enough to capture effects of emotion suppression on amygdala activity. However, using response-focused emotion suppression of facial expressions in a within-subject design, other researchers did not consistently observe reductions in amygdala activity (see e.g. Goldin et al., 2008) whereas emotional down-regulation by reappraisal appears to result more reliably in attenuated amygdala activity (see Diekhof et al., 2011, for a meta-analysis of reappraisal studies). Thus, it might be possible that response-focused emotion suppression by suppressing inner and outer feelings is effortful and impairs memory encoding even without strongly affecting emotional engagement, e.g. in the amygdala. Future studies should include additional psychophysiological measures of emotional reactivity (e.g. heart rate, skin conductance response, electromyogram (EMG)), which was not done in the current study and is an important limitation.

In sum, our results indicate that memory impairments induced by emotion suppression are accompanied by a relative hippocampal disengagement and a reduction of prefrontal–hippocampal coupling during successful memory encoding. In addition to the theoretical relevance, our findings have important implications for clinical contexts: while a good memory is usually desired, extreme situations are capable of inducing very strong emotions, which in some cases leads to the development of highly intrusive traumatic memories and posttraumatic stress disorders. While suppressing one's emotions during such situations is probably not effective in reducing the physiological reactions, our results suggest that response-focused emotion suppression might interfere with hippocampal encoding of these memories, possibly reducing the probability of traumatic memory formation.

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