Neural Correlates of Positive and Negative Emotion Regulation

Sang Hee Kim and Stephan Hamann

Abstract

■ The ability to cope adaptively with emotional events by volitionally altering one's emotional reactions is important for psychological and physical health as well as social interaction. Cognitive regulation of emotional responses to aversive events engages prefrontal regions that modulate activity in emotion-processing regions such as the amygdala. However, the neural correlates of the regulation of positive emotions remain largely unexplored. We used event-related functional magnetic resonance imaging to examine the neural correlates of cognitively increasing and decreasing emotional reactions to positive and negative stimuli. Participants viewed negative, positive, and neutral pictures while attempting to increase, decrease, or not alter their emotional reactions. Subjective reactions were assessed via on-line ratings. Consistent with previous studies, increasing negative and positive emotion engaged primarily left-lateralized prefrontal regions, whereas decreasing emotion activated bilateral prefrontal regions. Different activations unique to increasing versus decreasing emotion were observed for positive and negative stimuli: Unique increase-related activations were observed only for positive stimuli, whereas unique decrease-related activations were observed only for negative stimuli. Regulation also modulated activity in the amygdala, a key emotion-processing region. Regulation effects on amygdala activity were larger for positive than for negative stimuli, potentially reflecting a greater malleability of positive emotional reactions. Increasing and decreasing positive and negative emotion can thus increase and decrease subjective reactions and associated amygdala activity in line with regulatory goals, and is associated with different patterns of prefrontal activation as a function of emotional valence and regulatory goal. ■

INTRODUCTION

Individuals can cognitively regulate their emotional responses to events, increasing or decreasing their emotional reactions in line with their behavioral goals. This process of regulating emotional responses by changing the cognitive representation of events, often referred to as reappraisal, is important for mental and physical health as well as social interaction. When successful, emotion regulation allows us to adaptively cope with aversive situations by minimizing negative, distressing emotions, or alternatively, by maximizing the positive aspects of situations (Gross, 1998). Emotion regulation can alter both psychological and physiological reactions to emotional stimuli (Jackson, Malmstadt, Larson, & Davidson, 2000). Impaired emotion regulation is associated with affective disorders and a variety of other maladaptive psychological conditions. Compared to other types of emotion regulation strategies such as suppression of behavioral expressions, reappraisal has been proposed to be more effective because its influence begins at an early stage of emotion generation, before emotional reactions have fully unfolded (Richards & Gross, 2000). In support of this notion, recent studies of the neural correlates of reappraisal have found that voluntary reappraisal can modulate the activity in the amygdala, a subcortical structure which plays a critical role in detecting and evaluating emotional significance of stimuli (Ochsner et al., 2004; Ochsner, Bunge, Gross, & Gabrieli, 2002; Schaefer et al., 2002; Beauregard, Levesque, & Bourgouin, 2001).

Although only a few studies have examined the neural bases of emotion regulation to date, a general pattern has emerged in which prefrontal and anterior cingulate regions involved in cognitive control show increased activity during active attempts to regulate emotion, together with modulation of activity in regions involved in emotion processing such as the amygdala (Ochsner & Gross, 2005). For example, in a functional magnetic resonance imaging (fMRI) study, Ochsner et al. (2004) examined regions associated with reappraisal of negative scenes to decrease or increase their emotional significance. Both up-regulation and down-regulation of emotion was associated with increased activity in the prefrontal cortex (PFC) and the anterior cingulate, and emotion-related activity in the amygdala increased or decreased in accordance with the regulatory goal.

Emory University

These neuroimaging studies of emotion regulation have focused on negative emotion. The neural correlates of regulating positive emotion remain largely unknown, however, with the exception of one study that examined down-regulation of sexual arousal to erotic stimuli in men (Beauregard et al., 2001). Although regulation of emotion likely recruits common regions regardless of the specific emotion involved, the neural correlates of regulation for positive and negative emotional stimuli may also differ in important respects. To explore this issue, in the current study, we investigated the neural correlates of regulating positive and negative emotional reactions. Given the involvement of the amygdala in responses to both positive and negative emotionally arousing stimuli (Anderson et al., 2003; Hamann, Ely, Hoffman, & Kilts, 2002; Dolan, Lane, Chua, & Fletcher, 2000; Hamann, Ely, Grafton, & Kilts, 1999), we predicted that both positive and negative stimuli would elicit amygdala activity relative to neutral stimuli, and that regulation-related changes in emotional arousal would be reflected in increased activity during successful attempts to increase emotion and decreased activity when decreasing emotion. In addition, because activity in the ventral striatum has been linked specifically to reward and appetitive processing (Hamann & Mao, 2002; Montague & Berns, 2002), we also examined whether attempts to increase and decrease responses to positive emotional pictures would result in corresponding increases and decreases in ventral striatal activity.

In the current study, we used event-related fMRI to examine the neural correlates of cognitively increasing and decreasing emotional reactions to affectively positive and negative stimuli. Participants viewed pleasant, unpleasant, and neutral pictures while attempting to increase, decrease, or not alter their emotional reactions. Subjective reactions were assessed on-line. We predicted that reappraisal processes involved in increasing and decreasing emotion would recruit prefrontal regions generally implicated in cognitive control, as well as regions involved specifically in increasing or decreasing emotional responses. We hypothesized that emotion regulation would alter activity in emotion-processing regions such as the amygdala, in line with the regulatory goal, with increased activity associated with successful efforts to increase emotion and decreased activity associated with decreasing emotion.

METHODS

Participants

Ten healthy right-handed female volunteers (ages 18–29, $M = 20.7$) were recruited from the Emory University community and monetarily compensated for their participation. Written informed consent was obtained from all participants prior to the study, and the study was approved by the local human participants protection committee.

Stimuli and Task

Three sets of 16 negative and 16 positive color pictures and one set of 16 neutral color pictures were selected from the International Affective Picture System (Lang, Bradley, & Cuthbert, 1995) for the regulation task. Negative pictures depicted a variety of aversive stimuli (e.g., traffic accidents, vermin, domestic violence, and bodily injury). Positive pictures depicted a variety of pleasant stimuli (e.g., celebrations, domestic pets, sporting events, and romantic couples). Each set of negative and positive pictures was matched on normative ratings of arousal and valence (because valence is assessed with a bipolar scale, the absolute value of the mean difference from neutral valence was used for matching positive and negative stimulus sets) (Lang et al., 1995), and was assigned to either the increase, decrease, or watch condition, with the assignment counterbalanced across participants. Neutral pictures were always assigned to the watch condition, as our primary interest was in characterizing the effects of emotion regulation on emotional stimuli, and preliminary work indicated that participants found it confusing to attempt to increase or decrease emotional reactions for stimuli that had little intrinsic emotional content. An additional 18 pictures were selected for use in a practice task to familiarize participants with the experimental procedure prior to scanning.

In the regulation task, participants were instructed to either increase or decrease their emotional reactions to each picture. In the increase condition, participants were instructed to think about the negative or positive pictures in such a way that they felt the emotion elicited by the presented picture more intensely. In the decrease condition, participants were instructed to think about the negative or positive picture in such a way that they felt the emotion elicited by the presented picture less intensely. For the increase and decrease conditions, participants were specifically instructed not to regulate their emotions by attempting to generate an emotion opposite in valence to the one they would normally experience (i.e., substituting a positive emotion for a negative emotion). In the watch condition, participants were instructed to view the picture in a natural way and not to try to change the emotion elicited by the picture. To assist participants in regulating their emotions, example strategies identified by participants from an earlier study (Jackson et al., 2000) and from a behavioral pilot study were suggested. These strategies included imagining the scenes as more personally relevant (e.g., associating the main figure of the scene to themselves or their close family members/friends) or less personally relevant (e.g., dissociating themselves from the main figures), imagining the scenes

as unreal, and imagining the scenes as physically closer or farther away from themselves. Participants were encouraged to use the strategies they found most effective, although most participants used the suggested strategies, as indicated by postscan interviews (see Results).

Procedure

Prior to scanning, participants received instructions on the regulation task and performed a practice task with 18 pictures depicting similar contents to those presented during scanning. In the practice trials, a regulation instruction (watch, decrease, increase) was presented on a blank screen for 2 sec, followed by a picture for 8 sec. Next, a Likert-type rating scale ranging from 1 (*weak*) to 4 (*strong*) was presented, and participants were asked to rate the strength of the emotion they were currently feeling. Participants were asked to verbally report the strategies they used while performing the regulation task. To help insure that only participants who could successfully regulate their emotions were scanned, participants were required to pass a criterion such that their mean subjective emotion ratings for the decrease condition were less than 3 and their mean ratings for the increase condition were greater than 2. All participants met these inclusion criteria and could perform the regulation task as instructed.

In the scanner, participants again completed six practice trials with a subset of the same pictures that they had practiced outside of the scanner to ensure that they were comfortable with performing the task inside the scanner. Each instruction appeared on the screen for 2 sec (Figure 1), followed by a picture for 8 sec. Following the picture, the 1–4 rating scale was presented for 4 sec and participants were asked to rate the strength of the emotion they were currently feeling by pressing a button on an MRI-compatible four-button fiber-optic response box. Next, a fixation cross in a blank screen was presented for 2 sec while participants were instructed to rest. Images were rear-projected onto a projection screen positioned at the head end of the MRI scanner bore, controlled by a PC laptop computer using the Presentation software program (version 0.50, Neurobehavioral Systems, 2002; http://nbs.neuro-bs.com/). Participants viewed the screen through a mirror mounted on the head coil. Once the practice trials were complete, the experimental task began.

A total of 112 trials were completed over four separate runs. Each run consisted of four repetitions of seven conditions (i.e., decrease negative, watch negative, increase negative, decrease positive, watch positive, increase positive, and watch neutral). The conditions were presented in pseudorandom order in each run such that no more than two identical regulation conditions nor conditions with the same emotional valence (positive, negative, or neutral) were presented consecutively. No picture stimuli were repeated during scanning. The order of conditions was counterbalanced across runs. After scanning had completed, participants exited the scanner and were asked to write down brief descriptions of the typical strategies they used in each regulation condition and to provide a brief example of how each strategy was used. Participants also indicated how successful they believed they were in accomplishing each regulation task, separately for negative and positive pictures. They were given a 5-point Likert-type scale and were asked to indicate their degree of success at carrying out each regulation task from 1 to 5 (1 = *not successful at all*; 3 = *moderately successful*; 5 = *very successful*).

Participants returned after 1 week and viewed all pictures they had seen previously in the scanner and rated them on a 7-point Likert-type scale (1 = *not arousing*; 4 = *moderately arousing*; 7 = *highly arousing*) to indicate the level of arousal elicited by each picture in the absence of active regulation attempts. For this rating task, two pseudorandomly ordered picture lists were created and administered in a counterbalanced manner across participants. Next, participants were debriefed and encouraged to ask any questions they had about the study. Finally, participants were thanked for their participation and excused.

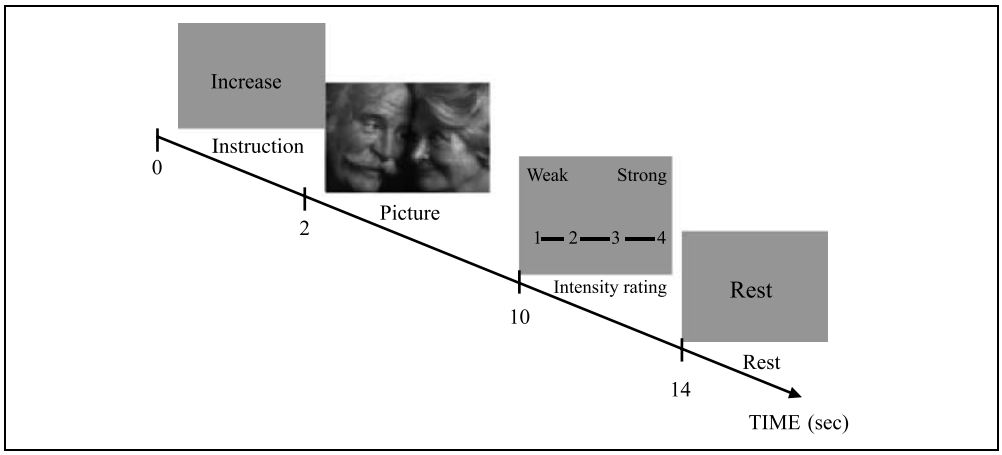

Figure 1. Design of experimental trials.

Data Acquisition

All imaging data were acquired using a Siemens 3.0-Tesla MRI scanner. Brain imaging involved acquisition of 30 axial slices of 3 mm thickness acquired parallel to the AC–PC line. Functional scans were acquired using T2*-weighted gradient-echo, echo-planar pulse sequences (TR = 2516 msec, TE = 30 msec, 64 × 64 matrix, 3 × 3 × 3 mm voxel size). A total of 185 scans were acquired in each of four runs. Structural images were acquired using a gradient-echo, T1-weighted pulse sequence (TR = 500 msec, TE = 20 msec, 256 × 256 matrix, 1 × 1 × 1 mm voxel size).

Data Analysis

Data were analyzed using Statistical Parametric Mapping software (SPM99, Wellcome Department of Cognitive Neurology; www.fil.ion.ucl.ac.uk; Friston et al., 1995). Functional images were realigned and spatially normalized (voxel size 3 × 3 × 3 mm) to the Montreal Neurological Institute (MNI) template (Ashburner & Friston, 1999). Normalization parameters were generated from the mean realigned EPI image. Images were smoothed using a 6-mm Gaussian kernel. Low-frequency noise was removed using a high-pass filter (Holmes, Josephs, Buchel, & Friston, 1997). Individual participants' data were analyzed using a fixed-effects model (Friston, Jezzard, & Turner, 2004). Group data were analyzed using a random-effects model (Holmes & Friston, 1998).

Condition effects were modeled using a box-car regressor convolved with a canonical hemodynamic response function corresponding to the picture presentation interval (8 sec). To ensure that regions of lower signal were not excluded from statistical analysis, the more inclusive threshold for including gray matter used in SPM2 was used rather than the stricter SPM99 criterion. Inspection of regions of signal dropout in individual subjects confirmed that signal dropout was minimal near the amygdala, although signal attenuation was present in some parts of the orbito-frontal cortex (OFC), a common occurrence particularly at high field strengths. Voxel values for each contrast yielded a statistical parametric map of the t statistic, subsequently transformed to the unit normal distribution. For the group analysis, one-sample t tests were conducted on participants' contrast images to create statistical maps depicting differences in brain activation between conditions across participants.

The amygdala regions of interest (ROIs) were spherically defined using an automated algorithm (SPM ROI Toolbox; http://spm-toolbox.sourceforge.net) with central coordinates at $x = \pm 18$, $y = -3$, $z = -18$ in Montreal Neurological Institute (MNI) space, an approximation of Talairach space (Talairach & Tournoux, 1988), and with a radius of 8 mm. For each participant, the average percent signal change across the peristimulus time interval for each trial type was estimated. The peak responses for each condition, defined as the peristimulus latency between 5.03 and 12.58 sec (corresponding to TRs 3–5 of the peristimulus interval), where the group average was maximal, were selected for statistical analysis. Planned t tests (one-tailed, given the directional nature of the hypothesized effects) were subsequently performed for statistical inference. Because this ROI analysis averaged over all voxels in the amygdala ROIs, it was possible that this analysis might fail to detect portions of the amygdala exhibiting opposite responses (e.g., increasing and decreasing activity in separate subregions). To address this possibility, we conducted a follow-up small-volume-corrected voxel-wise analysis (SVC, $p < .05$, corrected) using the center coordinates and radius used in defining the amygdala ROIs, to probe the amygdala for activated voxels clusters that varied as a function of emotion regulation.

To investigate modulation of activity in the ventral striatum during regulation of positive emotion, left and right ventral striatum ROIs were spherically defined using the same methods used for the amygdala ROIs, with central coordinates located at $x = \pm 15$, $y = 12$, $z = -6$. ROI analyses were conducted using the same methods used for the amygdala ROIs.

A priori regions were defined on the basis of previous neuroimaging studies on emotion regulation (Ochsner et al., 2002, 2004; Beauregard et al., 2001). These a priori regions included the PFC, the anterior cingulate, and the amygdala. For group contrasts and regression analysis, a threshold of $p < .005$ was applied for a priori regions, $p < .001$ for all other regions, with an extent threshold of 5 contiguous voxels. Coordinates of activated regions are reported in MNI space, an approximation of Talairach space (Talairach & Tournoux, 1988).

RESULTS

Behavioral Results

Self-ratings of Emotional Arousal

A 2 (emotion: positive, negative) × 3 (regulation: decrease, watch, increase) repeated-measures analysis of variance (ANOVA) on on-line ratings for emotional arousal was conducted. Significant main effects of emotion [$F(1, 9) = 27.10$, $p < .001$] and regulation [$F(2, 18) = 65.07$, $p < .000$] were found. No significant interaction was found. Consistent with the predicted effect of regulation, participants reported experiencing greater arousal during the increase condition than the watch condition [$t(9) = 6.45$, $p < .000$], and lower arousal during the decrease condition than the watch condition [$t(9) = 5.78$, $p < .001$]. Although negative and positive pictures had been matched on normative ratings of arousal and valence, participants reported greater arousal while viewing negative pictures than positive pictures (Figure 2).

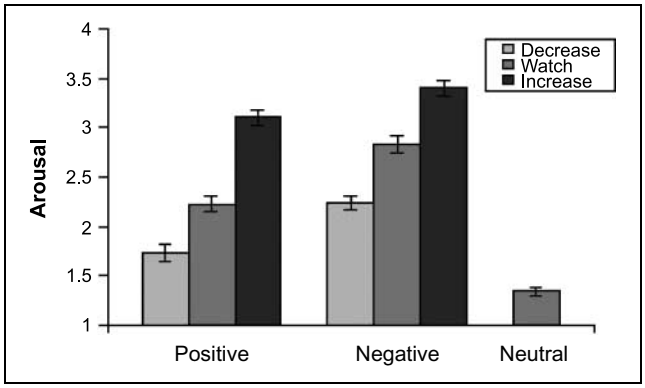

Figure 2. Mean on-line ratings of emotional arousal during each regulation task for positive, negative, and neutral pictures.

To confirm that subjective arousal differed across stimulus types when participants were not actively attempting to regulate their emotional responses, an ANOVA was conducted on on-line arousal ratings for positive, negative, and neutral pictures that had been presented during the watch condition. A main effect of emotion was observed [$F(2, 18) = 59.36$, $p < .000$]. Follow-up comparisons confirmed that positive pictures [$t(9) = 5.83$, $p < .000$] and negative pictures [$t(9) = 13.32$, $p < .000$] were rated higher than neutral pictures on arousal. Moreover, negative pictures were rated higher than positive pictures on arousal [$t(1,9) = 4.15$, $p < .002$], although they had been matched pre-experimentally on normative arousal (Lang et al., 1995).

An ANOVA conducted on arousal ratings assessed 1 week later for all of the pictures used during the scanning verified that positive and negative pictures were more arousing than neutral pictures (Table 1). A main effect of emotion was found [$F(2, 18) = 57.48$, $p < .000$]. Further comparisons confirmed that positive pictures [$t(9) = 6.22$, $p < .000$] and negative pictures [$t(9) = 10.36$, $p < .000$] were rated higher in arousal than in neutral pictures. Consistent with on-line ratings assessed during scanning, negative pictures were rated higher in arousal than positive pictures [$t(9) = 3.91$, $p < .003$].

Table 1. Postscanning Arousal Ratings for Positive, Negative, and Neutral Stimuli

	Decrease		*Watch*		*Increase*	
	Mean	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*
Positive	4.10	0.40	4.07	0.32	4.20	0.37
Negative	5.06	0.21	4.88	0.27	5.03	0.27
Neutral			2.03	0.16		

Arousal ratings were made on a scale that ranged from 1 (*not arousing*) to 7 (*highly arousing*). *SEM* = standard error of the mean. For positive and negative stimuli, assignment of stimulus sets was counterbalanced across conditions across participants.

Strategy Use and Self-ratings of Regulation Success

Postscan ratings of how successful the participants believed they were in carrying out the instructions associated with each regulation condition were compared in a 2 (emotion: positive, negative) × 3 (regulation: decrease, watch, increase) repeated-measures ANOVA (Table 2). There was a significant main effect of regulation [$F(2,18) = 6.11$, $p < .01$]. Overall, participants rated their performance in the decrease condition as less successful than in the control (watch) condition [$t(9) = 2.37$, $p < .05$], and rated their performance in the increase condition as more successful than in the decrease condition [$t(9) = 3.35$, $p < .01$]. Success ratings for the watch condition reflected success in refraining from active regulation and experiencing natural emotional reactions to the stimuli. The effect of emotion on regulation success was marginally significant, with participants rating regulating positive emotion as being easier than regulating negative emotion [$F(1, 9) = 1.10$, $p < .09$]. No interaction was found between emotion and regulation type.

To determine whether participants' success ratings correlated with their on-line arousal ratings, we conducted correlation analyses between post hoc regulation success ratings and mean on-line arousal ratings in each condition. Participants who reported being more successful in decreasing negative emotion rated stimulus-elicited arousal lower during the decrease-negative condition ($r = -.552$, two-tailed, $p = .098$), and participants who reported being more successful in increasing negative emotion reported higher arousal during the increase-negative condition ($r = .695$, $p = .026$). Correlations in other conditions were not significant (all p values >.3). We also assessed whether regulation success as indexed by differences in on-line arousal ratings between each regulation condition and the watch condition (i.e., increase positive − watch positive) correlated with corresponding self-reported success ratings (i.e., self-reported success in increasing positive emotion). No significant correlations were found (all p values >.3).

Next, we examined the possible role of differences in the specific regulation strategies used for regulating positive and negative emotion. For increasing emotional

Table 2. Self-ratings of Regulation Success across Regulation Conditions

	Decrease		*Watch*		*Increase*	
	Mean	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*
Positive	3.7	0.21	4.2	0.25	4.3	0.30
Negative	3.2	0.13	3.7	0.37	4.5	0.30

Ratings were made on a scale that ranged from 1 (*not successful at all*) to 5 (*very successful*). Success ratings for the watch condition reflected success in refraining from active regulation and experiencing natural emotional reactions to stimuli. *SEM* = standard error of the mean.

reactions, all participants used the suggested strategy of increasing personal relevance to increase both positive and negative emotional reactions. For decreasing emotional reactions to negative pictures, all but one participant reported pretending that the scene was unreal. For decreasing emotional reactions to positive pictures, four participants reported that they used the ''pretend unreal'' strategy and four participants attempted to focus on less positive elements of the scene. Two participants did not specify their strategies in this condition. To further investigate whether these two different types of strategy employed for decreasing positive emotion resulted in different outcomes in on-line arousal ratings and post hoc success ratings, we compared the two strategy groups on on-line arousal ratings and post hoc success ratings. There were no differences in on-line arousal ratings [''pretend unreal'' $M = 1.98$; ''less positive elements'' $M = 1.70$, $t(6) = 0.60$, $p > .5$] and post hoc success ratings [''pretend unreal'' $M = 3.50$; ''less positive elements'' $M = 3.50$, $t(6) = 0$] between these two strategies, suggesting that both resulted in similar levels of regulation efficacy as indexed by these measures.

Brain Imaging Results

Brain Regions Activated by Voluntarily Increasing and Decreasing Emotion

Activation by decreasing emotion. Brain regions associated with decreasing negative and positive emotion were identified by comparing activations in the decrease condition and the watch condition (i.e., the decrease − watch contrast), separately for positive and negative pictures. Based on previous neuroimaging studies on emotion regulation (Ochsner et al., 2002, 2004; Beauregard et al., 2001), a priori regions were defined, including the PFC, the anterior cingulate cortex, and the amygdala. A threshold of $p < .005$ was applied for a priori regions, $p < .001$ for all other regions. For correlations between brain activations and behavioral variables, a threshold of $p < .05$ was used. In addition, an extent threshold of five contiguous voxels was used for all whole-brain analyses. All activation images are displayed in neurological format overlaid on a structural image normalized to MNI space from a single subject from the SPM99 standard image library (www.fil.ion.ucl.ac.uk/spm), with the left hemisphere on the left side of the image.

Negative pictures. Brain regions showing greater activation in the decrease condition than in the watch condition included the bilateral lateral PFC (LPFC, BA 9, 10, 45), dorsomedial PFC (DMPFC, BA 6/32), medial PFC (MPFC, BA 9/10), bilateral lateral OFC (LOFC, BA 47), and anterior cingulate (BA 24/32) (Table 3, Figure 3). In addition, the middle temporal gyrus and the pallidum were also activated.

Positive pictures. Brain regions showing greater activation in the decrease condition than in the watch condition included the right LPFC (BA 9, 46), DMPFC (BA 6), MPFC (BA 10), and bilateral LOFC (BA 47) (Table 4, Figure 4).

Differences between decreasing negative and decreasing positive emotion. We directly compared brain activity associated with decreasing emotional reactions to negative and positive pictures. Because participants rated the negative pictures higher in mean arousal than the positive pictures, we controlled for this factor by including mean arousal ratings as a covariate in the random effects analyses. To identify brain regions more responsible for decreasing negative emotion than for decreasing positive emotion, brain activity associated with decreasing negative emotion (vs. the watch negative condition) was contrasted with brain activity associated with decreasing positive emotion (vs. the watch positive condition) [i.e., (decrease negative − watch negative) − (decrease positive − watch positive)]. The bilateral LPFC (BA 46, 10), DMPFC (BA 8/32), bilateral MOFC (BA 11), right LOFC (BA 47), and bilateral anterior cingulate were activated in this contrast (Table 5). When post hoc success ratings were entered as a covariate instead of arousal ratings, the activation was the same as for the analysis with arousal ratings as a covariate. When no covariates were entered, the pattern was highly similar, with the exception of the activation in the left OFC (BA 11), which was eliminated.

The reverse contrast [i.e., (decrease positive − watch positive) − (decrease negative − watch negative)] was also conducted to identify brain regions more responsible for decreasing positive emotion than negative emotion, with arousal ratings entered as a covariate. No areas were identified that showed greater activation for decreasing positive emotion than decreasing negative emotion; the same result was found when post hoc success ratings were entered and when no covariates were entered.

Activation by increasing emotion. Brain regions associated with increasing negative and positive emotion were identified by greater activation during the increase condition than the watch condition (i.e., the increase − watch contrast), separately for positive and negative pictures.

Negative pictures. Brain regions showing greater activation in the increase condition than in the watch condition included the left LPFC (BA 46/10), DMPFC (BA 8), left LOFC (BA 47), left MOFC (BA 11), and the anterior cingulate (BA 24/32) (Table 6, Figure 3). Additional activations were observed in the lingual gyrus and caudate.

Table 3. Brain Areas Activated for the Decrease > Watch Contrast for Negative Pictures

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Inf. Orbito-frontal G.	L	47	−42	36	−12	290	5.23
Inf. Orbito-frontal G.	L	47	−48	30	−9	(LM)	4.17
Sup. Temporal pole	L	38	−42	21	−15	(LM)	3.63
Mid. Frontal G.	L	9	−45	15	39	161	4.72
Mid. Frontal G.	L	46	−39	21	42	(LM)	3.94
Mid. Frontal G.	L	46	−27	21	33	(LM)	3.41
Mid. Frontal G.	L	10	−27	54	12	108	4.69
Mid. Frontal G.	L	46	−36	48	15	(LM)	3.84
Mid. Frontal G.	L	45	−42	39	18	(LM)	2.81
Mid. Frontal G.	R	44	36	9	39	169	4.35
Mid. Frontal G.	R	46	39	21	45	(LM)	4.09
Mid. Frontal G.	R	9	42	12	48	(LM)	4.04
Mid. Frontal G.	R	10	36	60	9	5	3.12
Inf. Frontal G.	R	45	57	27	9	364	4.42
Inf. Orbito-frontal G.	R	47	48	30	−12	(LM)	4.25
Inf. Orbito-frontal G.	R	47	60	27	0	(LM)	4.12
Inf. Frontal G.	L	44	−54	21	30	20	3.02
Inf. Frontal G.	L	44	−54	18	21	(LM)	3.00
Inf. Frontal G.	L	45	−51	39	12	5	2.67
Sup. Med. Frontal G.		32	0	30	39	570	4.39
pre-SMA		6	0	12	63	(LM)	4.24
Sup. Med. Frontal G.	L	8	−3	30	51	(LM)	3.97
Sup. Med. Frontal G.	R	9	12	60	30	6	3.32
Sup. Frontal G.	R	10	18	63	21	18	3.51
Sup. Frontal G.	L	10	−18	57	27	12	3.26
Sup. Frontal G.	L	9	−24	51	36	9	3.07
Sup. Frontal G.	L	9	−15	48	33	(LM)	2.87
Sup. Frontal G.	L	10	−27	54	3	5	2.84
Sup. Frontal G.	R	10	18	63	21	18	3.51
Sup. Frontal G.	L	10	−18	57	27	12	3.26
Sup. Frontal G.	L	9	−24	51	36	9	3.07
Sup. Frontal G.	L	9	−15	48	33	(LM)	2.87
Sup. Frontal G.	L	10	−27	54	3	5	2.84
Ant. Cingulate	R	24	9	21	21	39	4.50
Ant. Cingulate	L	32	−6	18	27	11	2.94
Ant. Cingulate	L	32	−12	27	24	10	2.82
Mid. Temporal G.	L	22	−57	−45	3	143	4.98
Mid. Temporal G.	L	21	−57	−30	−3	(LM)	4.05
Mid. Temporal G.	R	21	60	−39	−3	104	3.70
Pallidum	L		−15	0	0	24	3.69

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; G. = gyrus; SMA = supplementary motor area.

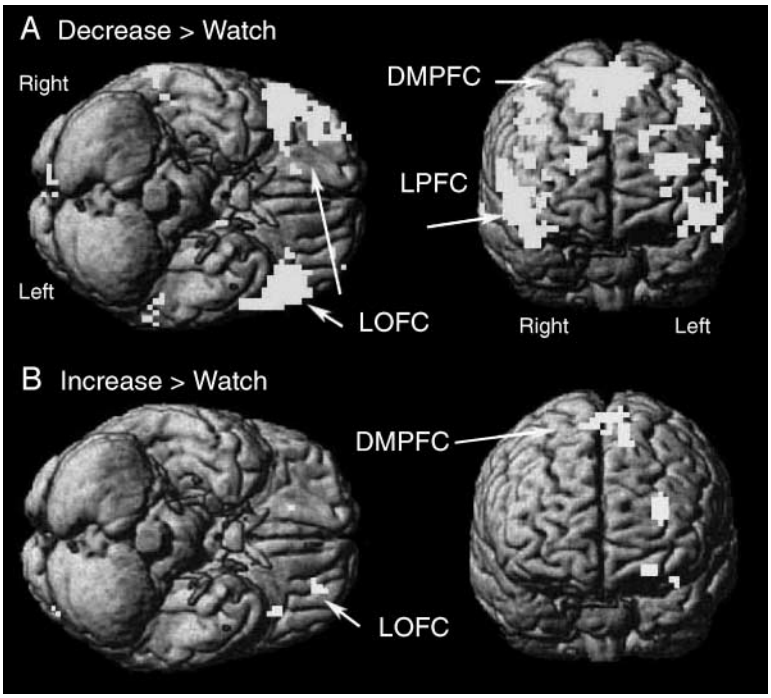

Figure 3. Activated brain regions for the contrasts of (A) decrease > watch and (B) increase > watch for negative pictures.

Table 4. Brain Areas Activated for the Decrease > Watch Contrast for Positive Pictures

			Coordinates				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Inf. Orbito-frontal G.	L	47	−57	21	−3	97	4.00
Sup. Temporal Pole	L	47	−51	21	−12	(LM)	3.45
Inf. Orbito-frontal G.	L	47	−45	39	−12	(LM)	3.44
Inf. Orbito-frontal G.	R	47	39	36	−9	50	3.55
Inf. Orbito-frontal G.	R	47	48	21	−9	(LM)	3.41
Inf. Orbito-frontal G.	R	47	33	27	−12	(LM)	3.38
Inf. Orbito-frontal G.	R	47	54	42	−9	6	3.28
Inf. Orbito-frontal G.	R	47	42	24	−21	5	3.20
Sup. Frontal G./Pre-SMA	R	6	9	15	63	149	3.74
Sup. Frontal G.	R	8	15	12	69	(LM)	3.50
Sup. Frontal G.	R	8	21	15	54	(LM)	3.32
Sup. Frontal G.	R	10	15	66	21	29	3.31
Sup. Frontal G.	R	10	21	63	30	(LM)	2.74
Mid. Frontal G.	R	9	51	12	45	22	3.74
Mid. Frontal G.	L	9	−18	30	30	7	3.05
Mid. Frontal G.	L	9	−24	33	36	(LM)	2.59
Mid. Frontal G.	R	46	45	42	−21	7	3.02
Inf. Frontal G.	R	47	60	24	0	7	3.62

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; G. = gyrus; SMA = supplementary motor area.

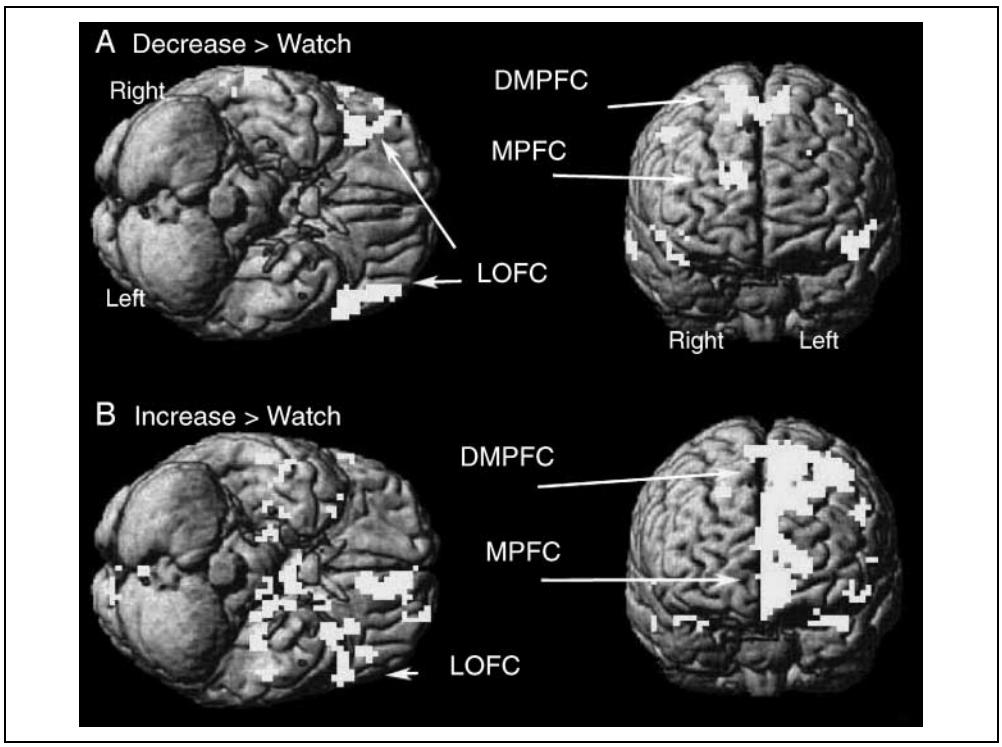

Figure 4. Activated brain regions for the contrast of (A) decrease > watch and (B) increase > watch for positive pictures.

Table 5. Brain Areas More Active for Decreasing Negative Emotion than for Decreasing Positive Emotion, Controlling for On-line Arousal Ratings

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Mid. Frontal G.	R	47	36	45	6	49	4.46
Mid. Frontal G.	R	46	42	57	9	(LM)	3.63
Mid. Frontal G.	L	46	−36	57	15	8	3.05
Sup. Frontal G.	R	10	30	63	12	13	2.97
Sup. Med. Frontal G.	R	8/32	6	27	45	14	2.89
Sup. Med. Frontal G.	L	32	−3	21	39	(LM)	2.8
Mid. Orbito-frontal G.	L	11	−3	36	−12	14	3.62
Sup. Orbito-frontal G.	L	11	−21	39	−18	5	3.53
Mid. Orbito-frontal G.	R	11	3	48	−6	7	3.52
Inf. Orbito-frontal G.	R	47	48	30	−9	12	3.48
Ant. Cingulate	R	24	9	24	24	41	4.11
Ant. Cingulate	L	24	−3	21	24	(LM)	3.48
Ant. Cingulate	R	24	6	33	18	(LM)	2.88
Ant. Cingulate	L	24	−6	30	18	5	3.05

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; G. = gyrus.

Table 6. Brain Areas Activated for the Increase > Watch Contrast for Negative Pictures

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Sup. Frontal G./Pre-SMA	R	8	3	24	66	93	4.49
Sup. Med. Frontal G.	L	8	−9	27	57	(LM)	3.69
Sup. Frontal G./Pre-SMA	L	6/8	−3	18	69	(LM)	3.69
Inf. Frontal G.	L	13	−39	15	12	5	3.37
Mid. Frontal G.	L	46/10	−30	51	18	27	3.28
Inf. Orbito-frontal G.	L	47	−36	27	−18	15	3.14
Sup. Orbito-frontal G.	L	11	−21	48	−15	8	3.09
Ant. Cingulate	L	32	−15	24	36	47	3.84
Ant. Cingulate	L	24	−3	33	21	(LM)	3.27
Mid. Cingulate		24	0	18	39	(LM)	2.91
Ant. Cingulate	R	32	15	33	−6	6	3.08
Lingual G.	R	19	30	−54	0	10	4.30
Caudate	R		21	9	18	6	4.12
Caudate	L		−18	9	21	20	3.82
Caudate	L		−9	0	24	(LM)	3.72

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; G. = gyrus; SMA = supplementary motor area.

Positive pictures. Brain regions showing greater activation in the increase condition than in the watch condition included the left LPFC (BA 8), DMPFC (BA 6), MPFC (BA 10), MOFC (BA 11), and left LOFC (BA 47) (Table 7, Figure 4). Additional activations were observed in the middle temporal gyrus, primary visual areas, the caudate, the putamen, and the pallidum.

Differences between increasing negative and increasing positive emotion. Next, we compared brain activity associated with increasing emotional reactions to negative and positive pictures. Specifically, brain activity associated with increasing negative emotion was contrasted with brain activity associated with increasing positive emotion [i.e., (increase negative − watch negative) − (increase positive − watch positive)], controlling for differences in on-line arousal ratings. Only one small cluster in the superior frontal gyrus (DMPFC, BA 8) (size = 5 voxels, $z = 3.32$) showed greater activation for increasing negative emotion than increasing positive emotion. When post hoc success ratings were controlled for instead of on-line arousal ratings, the results showed the same areas of activation. When no covariates were entered, the LPFC (BA 46) was activated in addition to the DMPFC activation identified in the analysis controlling for on-line arousal ratings.

To identify brain regions more responsible for increasing positive emotion than for increasing negative emotion, brain activity associated with increasing positive emotion was contrasted with brain activity associated with increasing negative emotion [i.e., (increase positive − watch positive) − (increase negative − watch negative)], controlling for differences in on-line arousal ratings. The left rostromedial PFC (BA 10), left LPFC (BA 9), right LPFC (BA 45, 48), and the left amygdala were activated (Table 8). When success ratings were controlled instead of on-line arousal ratings, the anterior cingulate (BA 32) and the precuneus (BA 30) were activated in addition to the regions noted above for the analysis with on-line arousal as a covariate. When no covariates were entered, the DMPFC (BA 6), the right OFC (BA 11/47), the precuneus (BA 23, 30), the hippocampus, as well as left occipital and temporal regions, were activated in addition to the regions noted above for the analysis with on-line arousal as a covariate.

Similarities between regions involved in increasing and decreasing emotion. Brain areas involved in both increasing and decreasing emotion were characterized by identifying regions that commonly activated for the increase − watch contrast and the decrease − watch

Table 7. Brain Areas Activated for the Increase > Watch Contrast for Positive Pictures

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Mid. Frontal G.	L	8	−27	24	48	512	4.75
SMA	L	6	−9	9	60	(LM)	3.91
Sup. Frontal G.	L	32	−15	27	39	(LM)	3.74
Mid. Orbito-frontal G.	L	10	−3	48	−6	401	4.38
Ant. Cingulate		32	0	51	15	(LM)	3.76
Sup. Med. Frontal G.	L	9	−3	57	39	(LM)	3.76
Inf. Orbito-frontal G.	L	47	−30	15	−21	84	4.00
Inf. Orbito-frontal G.	L	47	−42	24	−9	(LM)	3.42
Sup. Temporal Pole	L	38	−39	21	−24	(LM)	3.34
Inf. Frontal G.	R	47	60	24	−3	7	3.28
Inf. Frontal G.	L	9	−51	18	33	24	3.07
Mid. Frontal G.	L	44/45	−45	24	33	(LM)	2.67
Inf. Frontal G.	L	45	−54	21	9	5	3.06
Inf. Frontal G.	L	47	−39	30	−3	15	3.02
Inf. Orbito-frontal G.	L	47	−42	36	−9	(LM)	2.94
Mid. Temporal G.	R	21	48	−45	3	40	4.23
Mid. Temporal G.	R	21	45	−36	6	(LM)	3.42
Mid. Temporal G.	R	21	54	−6	−18	43	3.88
Calcarine Sulcus	R	18	6	−87	9	32	4.04
Amygdala	R		18	3	−18	9	3.44
Hippocampus	L		−30	−18	−18	946	4.39
Thalamus	L		−6	−6	0	(LM)	4.10
Post. Cingulate	L		−6	−48	30	(LM)	4.09
Post. Cingulate	L		−6	−48	30	69	4.09
Precuneus	L		−9	−57	24	(LM)	3.77
Precuneus	L		−6	−60	51	(LM)	3.51
Putamen	L		−21	15	3	24	3.91
Putamen	L		−18	6	−9	(LM)	3.32
Caudate	L		−6	12	15	11	3.80
Caudate	L		−15	−12	−18	6	3.48
Caudate	L		−12	9	24	6	3.30
Caudate	L		−15	0	18	(LM)	3.26
Caudate	L		−15	9	12	5	3.20
Putamen	L		−24	9	12	(LM)	3.15
Pallidum	R		18	12	6	12	3.51
Pallidum	R		18	12	15	(LM)	3.38
Thalamus	L		−6	−6	0	15	4.10
Thalamus	L		−9	−27	18	6	3.50

Table 7. (*continued*)

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Cerebellum	R		6	−81	−18	12	4.34
Cerebellum			0	−78	−12	(LM)	3.29
Cerebellum	R		27	−84	−24	6	3.49
Cerebellum	R		18	−84	−21	(LM)	3.25
Cerebellum	L		−6	−36	−6	16	3.77
Cerebellum	L		−3	−36	−6	(LM)	3.75

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; Post. = posterior; G. = gyrus; SMA = supplementary motor area.

contrast, using inclusive masking procedures at the group level (with a threshold level of .005, uncorrected).

Negative pictures. The DMPFC (BA 6, 8), the LPFC, the anterior cingulate (BA 24/32), and the left OFC (BA 47) were commonly activated for regulating negative emotion (Table 9).

Positive pictures. The DMPFC (BA 6, 8) and the left OFC (BA 47) were commonly activated for regulating positive emotion (Table 9).

Differences between regions involved in increasing and decreasing emotion. Brain areas more involved in increasing emotion than in decreasing emotion were characterized by identifying regions that showed greater activation during the increase condition than the decrease condition (i.e., the increase − decrease contrast), within the regions that showed greater activation in the increase − watch contrast. That is, the increase − decrease contrast was inclusively masked by the increase − watch contrast at the threshold level of $p < .005$, uncorrected. Conversely, brain areas more involved in decreasing emotion than increasing emotion were identified by greater activation during the decrease condition than the increase condition, within the regions that showed greater activation in the decrease − watch contrast. That is, the decrease − increase contrast was inclusively masked by the decrease − watch contrast at the threshold level of $p < .005$, uncorrected.

Negative pictures. No areas were identified that exhibited significantly greater activation during the increase condition than the decrease condition for negative pictures. Areas more activated for decreasing than for increasing negative emotion included the right

Table 8. Brain Areas More Active for Increasing Positive Emotion than for Increasing Negative Emotion, Controlling for On-line Arousal Ratings

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Sup. Frontal G.	L	10	−24	63	6	41	3.75
Sup. Frontal G.	L	10	−12	60	12	(LM)	3.58
Mid. Frontal G.	L	9	−33	15	54	5	3.24
Inf. Frontal G.	R	45	54	33	24	22	3.57
Inf. Frontal G.	R	45	54	39	18	(LM)	3.02
Inf. Frontal G.	R	48	39	15	21	5	3.01
Sup. Med. Frontal G.	L	9	−6	54	39	8	3.17
Amygdala	L		−27	0	−21	5	2.72

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; G. = gyrus.

Table 9. Brain Areas Commonly Recruited for Both Increasing and Decreasing Emotion

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Negative pictures							
Sup. Frontal G./Pre-SMA	R	8	3	24	66	40	4.49
Sup. Frontal G./Pre-SMA	R	6	−3	6	69	(LM)	3.08
Frontal Sup. Med. G.	L	8	−9	27	57	16	3.69
Frontal Sup. Med. G.	L	8	−9	21	66	(LM)	2.93
Mid. Frontal G.	L	46	−30	51	18	18	3.28
Ant. Cingulate	L	24/32	−9	24	36	10	3.19
Ant. Cingulate			0	21	39	(LM)	2.71
Inf. Orbito-frontal G.	L	47	−36	27	−18	8	3.14
Positive pictures							
Sup. Frontal G./Pre-SMA	L	6	−9	12	57	29	3.85
Sup. Med. Frontal G.	L	8	−9	24	63	(LM)	3.34
Sup. Frontal G./Pre-SMA	L	6	−9	15	66	(LM)	3.18
Inf. Orbito-frontal G.	L	47	−42	24	−9	23	3.42
Inf. Orbito-frontal G.	L	47	−51	24	−3	(LM)	2.65

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; G. = gyrus; SMA = supplementary motor area.

LPFC, the MPFC, the bilateral LOFC, and the supramarginal gyrus (Table 10).

Positive pictures. Areas more activated for increasing than for decreasing emotion included the anterior region of the MPFC, the MOFC, the anterior cingulate, the precuneus, the caudate, and the thalamus. No areas were more activated for decreasing than for increasing positive emotion (Table 11).

These findings are broadly consistent with those of the analyses described above that directly contrasted regulation-related activations for positive versus negative stimuli (Tables 5 and 8), particularly with respect to the substantially greater number of brain regions involved in down-regulation of negative emotion relative to positive emotion, and the greater number of brain regions involved in up-regulation of positive emotion relative to negative emotion.

Effects of Emotion Regulation on Activity in Emotion Processing

Amygdala ROI analysis. To determine whether emotion regulation modulated activity in the amygdala elicited by emotional pictures, fMRI signal change within the left and right amygdala ROIs was analyzed. A representative peristimulus timecourse of amygdala activity is shown in Figure 5C. For comparisons between ROI activity, planned one-tailed t tests were used in line with the directional nature of the predicted effects. Consistent with previous findings of greater amygdala activity for emotionally arousing stimuli (Hamann et al., 1999, 2002; Dolan et al., 2000), we found greater activity in both the left [$t(9) = 2.25, p < .03$] and the right [$t(9) = 2.46, p < .02$] amygdala in response to the negative pictures, and in the right [$t(9) = 2.5, p < .02$] amygdala in response to the positive pictures, compared to the neutral pictures.

Negative pictures. A t test on the means of the increase and decrease conditions showed that the difference between the two conditions was marginally significant [$t(9) = 1.6, p < .07$; Figure 5A]. Differences between each of these two conditions and the watch condition were not statistically significant, however.

Positive pictures. Activity in the left [$t(9) = 4{,}2, p < .001$] and right [$t(9) = 4.42, p < .001$] amygdala ROIs during the increase condition was greater than during the watch condition, $p < .001$ for both comparisons. Activity in the right amygdala ROI was also lower during the decrease condition than during the watch condition [$t(9) = 3.9, p < .002$; Figure 5B].

Table 10. Brain Areas Differentially Recruited by Increasing or Decreasing Negative Emotion

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Increase > Decrease							
No activations							
Decrease > Increase							
Inf. Orbito-frontal G.	R	47	39	45	−18	36	4.52
Mid. Orbito-frontal G.	R	47	42	51	−12	(LM)	4.40
Mid. Orbito-frontal G.	R	47	39	60	−6	(LM)	3.88
Inf. Orbito-frontal G.	L	47	−51	36	−9	47	3.79
Inf. Orbito-frontal G.	L	47	−39	39	−9	(LM)	3.17
Frontal. Sup. Med. G.	R	32/8	3	36	36	37	4.5
Frontal. Sup. Med. G.	L	32	−9	27	42	(LM)	3.09
Frontal. Sup. Med. G.	R	8	6	42	45	16	4.31
Mid. Frontal G.	R	9	42	18	48	55	4.08
Mid. Frontal G.	R	45	54	39	21	55	3.85
Mid. Frontal G.	R	45	45	36	21	(LM)	3.73
Mid. Frontal G.	R	45	42	33	36	(LM)	3.70
Sup. Frontal G.	R	8	15	27	57	32	3.96
Frontal. Sup. Med. G.	R	8	6	30	63	(LM)	3.20
Sup. Frontal G.	R	10	21	63	18	9	3.24
Inf. Frontal G.	R	45/47	51	36	−3	26	3.56
Inf. Frontal G.	R	45	57	33	9	5	2.92
Supramarginal G.	R	40	57	−42	39	17	4.04
Angular G.	R	40	57	−51	36	(LM)	3.89
Inf. Parietal G.	R	40	42	−51	54	(LM)	3.56
Mid. Temporal G.	R	21	60	−39	−6	8	3.71

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; G. = gyrus.

Voxelwise small-volume-corrected amygdala analysis. To examine whether subregions within the left and right amygdala ROIs exhibited different responses not detected in the primary ROI analysis that averaged signal change across all voxels in each ROI, we used an SVC voxelwise analysis ($p < .05$, corrected for multiple comparisons) using the center coordinates and radius used in defining the amygdala ROIs. The results of this analysis matched the results of the primary ROI analysis. No additional activation clusters with responses differing from the primary ROI analysis were observed.

Correlations between arousal and amygdala activity. To investigate whether changes in on-line arousal ratings correlated with changes in amygdala activity, correlation analyses were conducted between changes in arousal for each regulation condition relative to the watch condition (e.g., increase − watch) and changes in amygdala activity for the corresponding conditions. On-line arousal ratings associated with increasing positive emotion showed a marginal correlation with corresponding increases in activity in the left amygdala ROI, $r = .57$, $p < .086$. All other correlations were not statistically significant ($ps > .15$).

Ventral striatum ROI analysis. To investigate the effect of emotion regulation on the activity in the ventral striatum during viewing of positive emotional pictures,

Table 11. Brain Areas Differentially Recruited by Increasing versus Decreasing Positive Emotion

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Increase > Decrease							
Frontal Sup. Med. G.	L	10	−3	54	15	189	4.11
Frontal Sup. Med. G.	L	10	−9	57	0	(LM)	4
Frontal Sup. Med. G.	L	10	−9	60	9	(LM)	3.94
Frontal Sup. Med G.		9	0	54	39	10	3.27
Mid. Frontal G.	L	9	−33	9	48	5	3.14
Mid. Orbito-frontal G.	L	11	−3	57	−15	5	3.45
Sup. Frontal G.	L	9	−21	27	42	33	3.32
Ant. Cingulate	L	25	−3	30	12	6	3.62
Precuneus	L	23	−6	−51	33	17	4.08
Thalamus	L		−3	−9	0	11	4.26
Caudate	R		21	−27	21	6	3.60
Vermis	L		−3	−45	3	21	3.53
	L		−6	−54	15	(LM)	3.28
Decrease > Increase							
No activations							

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Sup. = superior; Mid. = middle; Med. = medial; Ant. = anterior; G. = Gyrus.

signal change within the left and right ventral striatum ROIs was analyzed as a function of regulation condition. The mean peak responses for each condition are summarized in Table 12. Two-tailed t tests were conducted to examine increase and decrease in activity of ventral striatum due to up- and down-regulation of emotion.

Consistent with the role of the ventral striatum in positive emotion, activity in the left [$t(9) = 3.86$, $p < .004$] and right [$t(9) = 3.00$, $p < .015$] ventral striatum ROI was greater when subjects attempted to up-regulate positive emotion, relative to the watch condition. Activity in the left [$t(9) = 3.09$, $p < .013$] and right [$t(9) = 2.52$, $p < .033$] ventral striatum ROI was also greater during the increase condition than the decrease condition. However, activity in the left and right ventral striatum ROIs did not differ significantly between the decrease and the watch conditions, $ps > .3$.

Correlation between arousal and whole-brain activity. To investigate brain areas associated with changes in emotional arousal during up- and down-regulation of emotion, whole-brain correlation analyses were conducted for each regulation contrast (e.g., increase negative − watch negative) with corresponding on-line arousal changes.

Negative pictures. Brain areas whose activity was positively correlated with changes in on-line arousal ratings due to decreasing negative emotion included the bilateral DMPFC (BA 6, 8, 32), the MPFC (BA 10), the left LPFC (BA 44, 45), the right LOFC (BA 47), the bilateral amygdala, the right SMG (BA 40/48), and the right angular gyrus (Table 13). However, no areas were correlated with changes in on-line arousal ratings due to increasing negative emotion.

Positive pictures. Activity in the right LOFC (BA 47) (MNI coordinates at 51 30 −9, $z = 3.18$, $k = 5$) was positively correlated with changes in on-line arousal ratings due to decreasing positive emotion. Brain activity in the areas including the left DMPFC (BA 6), the bilateral LPFC (BA 44), and the right LOFC (BA47) (Table 14) showed positive correlation with changes in on-line arousal ratings due to increasing positive emotion.

DISCUSSION

In the current study, we investigated the neural correlates of emotion regulation for negative and positive emotional stimuli. Consistent with prior findings from studies ex-

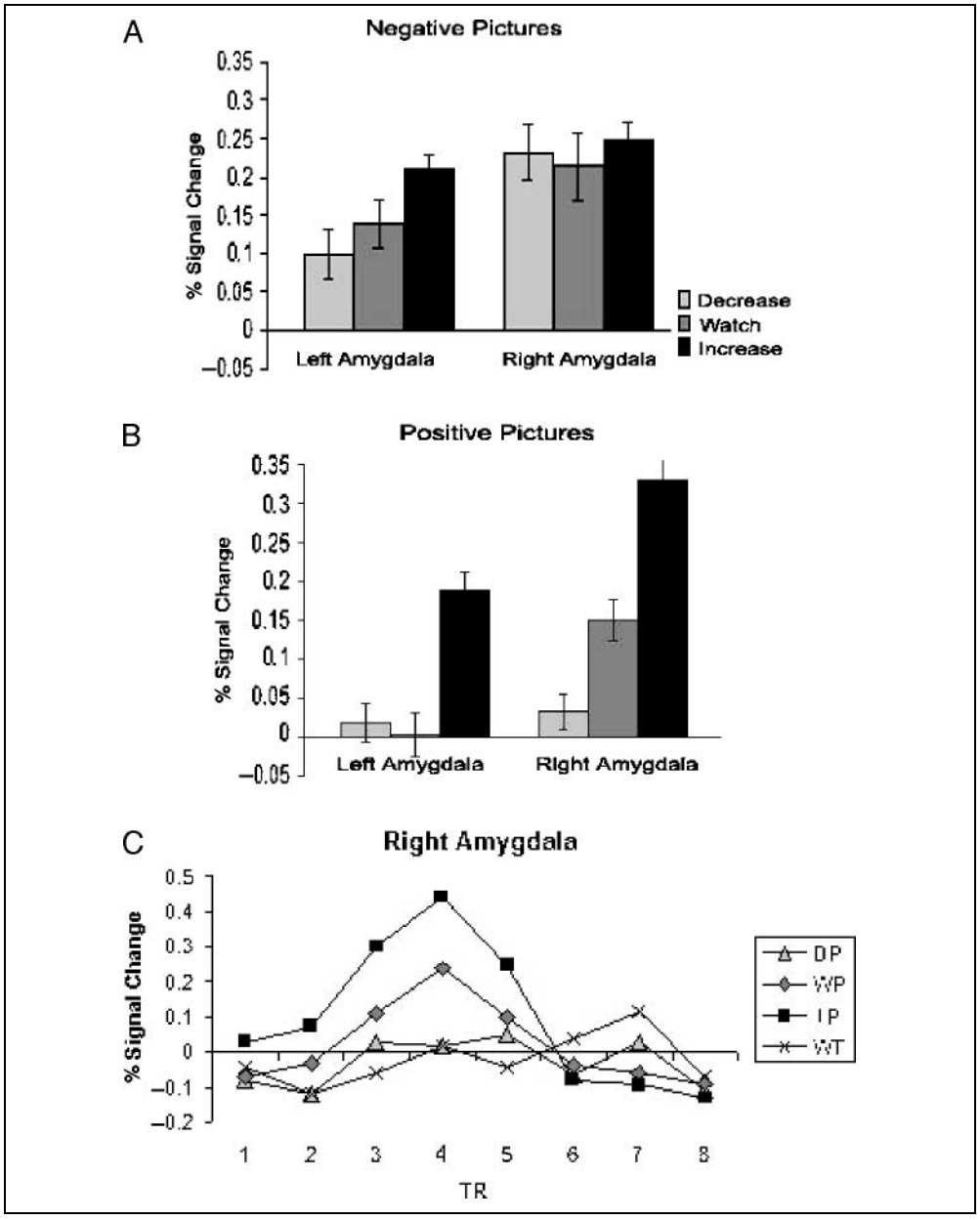

Figure 5. Activity in the left and right amygdala ROIs averaged across participants during each regulation condition for (A) negative pictures and (B) positive pictures. Mean percent signal change relative to the global baseline mean for neutral pictures was −0.09 (*SEM* = 0.07) for the left amygdala and −0.03 (*SEM* = 0.04) for the right amygdala. (C) Representative peristimulus time-series representing percent signal change in the right amygdala ROI averaged across participants (DP = decrease positive, WP = watch positive, IP = increase positive, WT = watch neutral).

amining the regulation of negative emotion, activity in the amygdala was modulated for emotional stimuli in line with participants' regulatory goals. Regulation-related activity was also observed in several prefrontal and cingulate regions previously implicated in emotion regulation and cognitive control (Ochsner et al., 2002, 2004). The current results are consistent with appraisal theories of emotion (Ochsner & Gross, 2005; Lazarus, 1991; Frijda, 1986), with reappraisal processes mediated primarily by prefrontal and cingulate regions which, in turn, modulate regions involved in the representation of emotional states, including the amygdala. The inclusion of both increase and decrease regulation instructions, together with positive and negative emotional stimuli, allowed us to compare the neural correlates of up-regulation and down-regulation, and to assess whether these correlates were similar for regulation of positive and negative affective responses.

Table 12. Mean and Standard Deviation of Activity in the Left and Right Ventral Striatum ROIs as a Function of Regulation Condition for Positive Emotion

	Decrease		*Watch*		*Increase*	
	Mean	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*
Left	0.02	0.05	0.05	0.04	0.17	0.03
Right	0.05	0.03	0.05	0.03	0.14	0.03

On-line behavioral ratings of emotional arousal confirmed that participants were successful in using regulation to alter their subjective emotional reactions, for

Table 13. Regional Activity Correlated with Changes in Emotional Arousal during Decreasing Negative Emotion, Relative to the Watch Negative Condition

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Sup. Frontal G./SMA	R	32	9	21	45	41	3.36
Sup. Frontal G.	R	32	18	12	45	(LM)	3.1
Sup. Med. Frontal G.	L	8	−3	30	51	(LM)	3.01
Sup. Frontal G./SMA	L	6	−6	3	66	8	3.31
Sup. Frontal G./SMA	L	6	−9	15	57	15	2.91
Sup. Med. Frontal G.	L	10	−6	66	15	23	3.67
Sup. Med. Frontal G.		10	0	63	21	(LM)	3.42
Mid. Frontal G.	R	6	36	6	54	28	3.94
Mid. Frontal G.	R	6	36	9	42	(LM)	2.6
Mid. Frontal G.	L	8	−27	24	51	21	3.78
Mid. Frontal G.	L	8	−27	18	42	(LM)	3.15
Mid. Frontal G.	L	8	−27	9	63	5	2.86
Inf. Frontal G.	R	47	48	33	−9	33	3.77
Inf. Frontal G.	R	44	57	18	15	9	3.59
Inf. Frontal G.	R	48	39	27	15	14	3.59
Inf. Frontal G.	L	45	−51	33	12	37	3.46
Inf. Frontal G.	L	15	−48	42	12	(LM)	3.36
Inf. Frontal G.	L	45	−42	33	6	(LM)	3.26
Inf. Frontal G.	R	45	51	36	18	18	3.44
Inf. Frontal G.	R	45	60	24	21	13	3.13
Inf. Frontal G.	R	45	54	27	12	(LM)	2.79
Inf. Frontal G.	L	48	−33	30	12	16	3.12
Inf. Frontal G.	R	48	39	12	18	19	3.03
Inf. Frontal G.	R	44/45	45	12	24	(LM)	2.91
Inf. Orbito-frontal G.	R	47	33	30	−21	53	3.95
Inf. Orbito-frontal G.	R	47	30	27	−9	(LM)	3.5
Mid. Orbito-frontal G.	R	11	33	45	−15	(LM)	3.31
Precentral G.	L	6	−33	−3	36	29	4.08
Precentral G.	L	6	−42	−3	39	(LM)	3.47
Precentral G.	L	6	−42	−3	48	(LM)	3.28
Sup. Temporal Pole	R	38	42	15	−24	9	4.38
Sup. Temporal Pole	R	38	36	9	−24	(LM)	3.65
Sup. Temporal Pole	L	38	−27	6	−24	11	4.03
Mid. Temporal G.	L	48	−45	−12	−21	5	3.4
Inf. Temporal G.	R	37	39	−51	−12	5	4.18
Parahippocampal G.	R	30	27	−33	−15	14	4.12
Sup. Parietal G.	R	7	24	−63	60	8	3.67

Table 13. (*continued*)

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Supramarginal G.	R	48/40	45	−33	33	94	4.46
Lingual G.	R	37	33	−57	3	14	4.32
Angular G.	R	7	30	−60	42	22	4.23
Cuneus	R	7	21	−57	33	8	4.06
Calcarine	R	17	24	−66	12	31	4.06
Sup. Occipital G.	R		21	−72	18	(LM)	3.47
Sup. Occipital G.	L	19	−24	−84	30	7	3.28
Hippocampus	R		36	−3	−18	12	3.67
Hippocampus	L		−36	−18	−18	12	3.58
Fusiform G.	L	48/20	−36	−15	−27	(LM)	3.53
Insula	L		−30	24	−6	5	3.53
Insula	R		33	−12	24	7	3.47
Insula	R		39	6	−9	14	3.42
Caudate	L		−12	12	18	6	3.37

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; Med. = medial; G. = gyrus; SMA = supplementary motor area.

both positive and negative stimuli. Regulation success ratings indicated that participants reported down-regulation as more difficult than up-regulation, in line with similar results from a previous regulation study (Ochsner et al., 2004), in which it was noted that reversing an emotional reaction is typically more difficult than amplifying an emotional reaction. A trend ($p < .09$) was found suggesting that regulation was

Table 14. Regional Activity Correlated with Changes in Emotional Arousal during Increasing Positive Emotion, Relative to the Watch Positive Condition

			Coordinates (MNI)				
	HEM	*BA*	*x*	*y*	*z*	*k (volume)*	*Z*
Sup. Frontal G./SMA	L	6	−9	3	51	8	3.51
SMA	L	6	−15	−3	48	(LM)	3.46
Sup. Frontal G./SMA	L	6	−12	−6	75	6	3.24
Mid. Frontal G.	R	44/6	42	9	39	25	4.27
Mid. Frontal G.	L	44/6	−27	6	36	8	3.21
Inf. Orbito-frontal G.	R	47	39	33	−15	14	3.39
Inf. Orbito-frontal G.	R	47	36	39	−9	(LM)	2.80
Mid. Temporal G.	R	21	69	−27	−6	5	3.34
Mid. Temporal G.	R	21	63	−27	0	(LM)	3.23

Clusters of 5 contiguous voxels whose global maxima meet a p threshold of .005, for a priori regions, and p threshold of .001, for any other regions, uncorrected, are reported. Local maxima for these clusters are denoted with (LM). BA = Brodmann's area; HEM = hemisphere; L = left; R = right; k = volume in voxel units; Z = maximal Z score for contrast; Inf. = inferior; Sup. = superior; Mid. = middle; G. = gyrus; SMA = supplementary motor area.

subjectively easier for positive emotion than for negative emotion. Although positive and negative pictures had been matched on normative arousal ratings, negative pictures were, nevertheless, rated by participants as being more arousing than positive pictures, possibly contributing to greater difficulty in regulating reactions to negative pictures. Alternately, reactions to positive emotion stimuli may be intrinsically more malleable than reactions to negative emotion stimuli, independent of differences in arousal. The finding of greater regulation-related modulation in amygdala activity for positive stimuli relative to negative stimuli is also consistent with a greater malleability of positive emotional reactions.

Similarities between Up-regulation and Down-regulation

Increasing and decreasing negative emotion recruited similar activations in the DMPFC, left LPFC, anterior cingulate, and left OFC, consistent with previous results (Ochsner et al., 2004). Both increasing and decreasing negative emotion recruited regions in the anterior cingulate and the PFC that have been linked to emotion regulation, working memory, and cognitive control. As with negative emotion, regulating positive emotion also recruited prefrontal regions that have been previously implicated in cognitive regulation of emotional responses, including the DMPFC and the left OFC. This overlap in activations is consistent with previous proposals that emotion regulation recruits certain core processes involved in cognitively reinterpreting an event, regardless of the reappraisal goal (Ochsner et al., 2004). The dorsal sector of the MPFC, the superior prefrontal gyrus (Ochsner et al., 2004) or pre-SMA (Picard & Strick, 1996), has been implicated in maintaining spatial (D'Esposito et al., 1998; Petit, Courtney, Ungerleider, & Haxby, 1998; Goldberg, Berman, Randolph, Gold, & Weinberg, 1996) and nonspatial information during the delay for a response (D'Esposito et al., 1998; Petit et al., 1998; Braver et al., 1997; Jonides et al., 1997; Goldberg et al., 1996; Smith, Jonides, & Koeppe, 1996). Accordingly, activation in this region during active regulation may reflect the maintenance of regulation strategies throughout each trial. The cognitive division of the anterior cingulate (Bush, Luu, & Posner, 2000) was activated for both increasing and decreasing negative emotion. This region has been implicated in the monitoring of ongoing responses (Botvinick, Braver, Barch, Carter, & Cohen, 2001), suggesting that activity in this region may reflect monitoring internal and external emotional responses required for accurate feedback relevant to current regulatory goals.

The left orbito-frontal region was also commonly activated for both increasing and decreasing emotion. The OFC has been implicated in the down-regulation of negative emotion such as aggression and violence (Davidson et al., 2002; Gur, Gunning-Dixon, Biker, & Gur, 2002; Davidson, Putnam, & Larson, 2000), and increased right lateral OFC activity has been associated with down-regulating rather than up-regulating negative affect (Ochsner et al., 2004). The left lateral prefrontal area (BA 46) was also commonly activated for both decreasing and increasing negative emotion. Activity in this region has been reported to be inversely correlated with the activity in the emotion-processing regions such as the amygdala and the MOFC (Ochsner et al., 2002), suggesting that this region has a modulatory role in down-regulating emotion.

Differences between Up-regulation and Down-regulation

Ochsner et al. (2004) found that up-regulation of negative emotion engaged primarily left-lateralized prefrontal regions, whereas down-regulation engaged primarily bilateral prefrontal regions. This was interpreted as most likely reflecting greater self-generation of affective descriptors to increase emotion and greater recruitment during down-regulation of right prefrontal regions involved in mediating interference between prepotent responses and cognitive reappraisals. The current results for regulation of negative and positive emotion are generally consistent with these prior findings. Relative to the watch condition, up-regulation for both negative and positive stimuli was associated with primarily left prefrontal activation, whereas down-regulation was associated with a bilateral pattern of activation. This consistent pattern suggests that up-regulation and down-regulation recruit specific common cognitive processes independent from the type of emotion that is regulated.

A consistent pattern was observed when activations unique to up-regulation versus activations unique to down-regulation were compared. For negative emotion, although up-regulation activated several regions when compared to the watch condition (Figure 3, Table 6), none of these regions were significantly more active during up-regulation than down-regulation. However, several regions were uniquely activated during down-regulation for negative emotion, including bilateral OFC and other right PFC and right parietal regions (Table 10). The opposite pattern was observed for positive emotion. No regions were significantly more active during down-regulation than up-regulation, whereas several regions were uniquely activated during up-regulation for positive emotion, including the medial orbito-frontal gyrus, additional medial and left prefrontal regions, as well as the anterior cingulate, thalamus, and caudate (Table 11).

These patterns were similar to those found in the direct comparison between activations associated with regulation of positive and negative emotion (Tables 5 and 8). Several regions were identified that were more active during the down-regulation of negative emotion

versus the down-regulation of positive emotion, but no regions were significantly more active for positive emotion in the reverse contrast. Similarly, several regions were more active during the up-regulation of positive emotion versus the up-regulation of negative emotion, but only a single, small cluster in the PFC was more active in the reverse contrast. This same pattern was observed when possible confounds between positive and negative stimuli, including arousal ratings and success ratings, were included as covariates in the analysis.

Activations unique to positive up-regulation were all left-lateralized or medial, with the exception of the right caudate, whereas activations unique to negative down-regulation were all right-lateralized, with the exception of OFC activation, which was bilateral. This lateralization may reflect the overall pattern for left-lateralized activation for up-regulation and right or bilateral activation for down-regulation, although it is also consistent with proposed hemispheric asymmetries in emotion processing that posit a greater role for the right hemisphere in processing of negative affect (Davidson et al., 2002; Heilman & Gilmore, 1998; Davidson, 1995). This same pattern of left-lateralized activations unique to up-regulation and right-lateralized activation unique to down-regulation was also observed by Ochsner et al. (2004) for negative emotion regulation, further suggesting that the lateralization reflects up- versus down-regulation rather than valence-specific effects. This previous study observed increase-specific activations for negative emotion in the left rostral medial prefrontal (BA 9/10) and posterior cingulate cortex (BA 23). Both of these increase-specific regions were identified for positive emotion in the current study, although increase-specific activations for negative emotion were not observed. The lack of unique activation in these regions for negative emotion was attributable here to left rostral PFC activation in both the increase > watch and the decrease > watch contrasts and the absence of posterior cingulate activation in either contrast.

Whereas the dorsal sector of the MPFC was activated commonly for all types of regulation tasks regardless of emotion type, the ventral part of the MPFC (BA 10), a region associated with self-referential processing and evaluation of internally generated information (Kelly, Macrae, Wyland, Inati, & Heatherton, 2002; Craik et al., 1999), and perceived similarity between self and others (Mitchell, Banaji, & Macrae, 2005), was uniquely activated while increasing positive emotion but not for any other types of regulation. This activation may reflect increased self-referential processing while subjects up-regulated positive emotion by imagining the scenes as more personally relevant.

In addition to regions exhibiting differential activity as a function of regulation condition, correlations between changes in on-line arousal ratings and regional brain activity revealed several regions whose activity tracked changes in subjective arousal (Tables 13 and 14), including prefrontal regions previously implicated in emotion regulation (Ochsner et al., 2004). Notably, activity in the insula was correlated with decreasing negative affect but not with changes in positive affect, consistent with the predicted specific relation of this region to negative affect (Table 13). Activity in the right LOFC (BA 47) was correlated with changes in emotional intensity due to voluntary emotion regulation for all contrasts where significant neural correlates were observed (no significant correlations were observed for the increase negative − watch negative contrast). The regulation-related activity observed in the right OFC related to changes in self-reported on-line arousal may reflect subjective awareness of emotional states and their intensity (Schirmer & Kotz, 2006).

Modulation of Amygdala Activity by Regulation

As predicted, voluntary emotion regulation modulated activity in the amygdala elicited by both negative and positive pictures, indicating that emotion regulation not only affected the subjectively reported experience of emotion but also activity in a key region mediating emotion processing. This pattern was more pronounced for positive pictures than for negative pictures. For positive pictures, activity in both the left and the right amygdala ROIs increased during the increase condition, and activity in the right amygdala ROI decreased during the decrease condition, compared to the watch condition. This is the first demonstration, to our knowledge, that emotion regulation can both increase and decrease activity in the amygdala for positive emotional stimuli, paralleling previous findings for regulation-related modulation of amygdala activity elicited by negative emotion stimuli (Ochsner et al., 2004).

The current findings are consistent with those of Beauregard et al. (2001) who reported that down-regulation of sexual arousal to visual sexually arousing stimuli was associated with decreased activity in the right amygdala in men, relative to viewing these stimuli without engaging in voluntary emotion regulation. The ROI results extend these previous findings by demonstrating that down-regulation decreases right amygdala activity for a wide variety of affectively positive visual stimuli, and that up-regulation can increase activity in this structure. The lack of a decrease in left amygdala activity for positive pictures associated with down-regulation in the current study is likely related to the absence of significant activity in the left amygdala for positive stimuli during the watch condition. Activity in the left amygdala ROI showed a trend ($p < .07$) of increasing from the decrease condition to the increase condition for negative pictures. Although the modulation effect for negative pictures was smaller in magnitude than that observed by Ochsner et al. (2004), the left-lateralization of the current finding is consistent with the increase in left amygdala activation associated with

up-regulation and a left-lateralized decrease in amygdala activation during down-regulation. As previously noted, negative pictures were rated higher on arousal than positive pictures, possibly contributing to greater difficulty in regulating reactions to negative pictures and weaker modulation effects in the amygdala. In addition, reactions to positive emotion stimuli may be intrinsically more malleable than reactions to negative emotion stimuli, possibly because negative emotion stimuli are typically associated with a greater degree of automatic processing (Morris, Ohman, & Dolan, 1999; Whalen et al., 1998).

Modulation of Ventral Striatum Activity by Positive Emotion Regulation

Consistent with previous reports demonstrating a role of the ventral striatum in reward processes (Montague & Berns, 2002) and in experiencing positive emotions (Hamann & Mao, 2002), activity in the ventral striatum showed a pattern of modulation consistent with regulation goals for positive emotion. When regulating positive emotion, up-regulation resulted in an increase in left and right ventral striatum activity, whereas down-regulation resulted in a nonsignificant decrease in activity in the left ventral striatum ROI, compared to the watch condition. When activity during up- and down-regulation of positive emotion was directly compared, activity in the ventral striatum was significantly greater during up-regulation. These results suggest that the ventral striatum is a modulatory target for the up-regulation of positive emotion, but leave open the question of whether down-regulation of positive emotion can modulate activity in the ventral striatum.

Future Directions and Conclusion

Only women were included in the current study because of evidence that women typically experience emotion more intensely (Fujita, Diener, & Sandvik, 1991), to increase comparability with the results from previous studies that have studied only women, and to avoid potential sex differences that might have tended to obscure the valence and regulation effects that were of primary interest. Additional study is needed to characterize the extent to which the results observed here also extend to men. Individual differences in genotype, personality, and other factors are increasingly being recognized as important influences on neural reactivity to emotional stimuli (Hamann & Canli, 2004). Correlations between individual difference measures and the brain responses of subjects in this study will be detailed in a separate report (Kim & Hamann, in preparation). Regarding clinical implications, a study of how the regulatory mechanisms examined here are affected in psychological disorders, such as depression and anxiety, can potentially further our understanding of the basic mechanisms underlying these disorders.

Although subjects were given examples of typical regulation strategies, and most subjects, in fact, used broadly similar strategies as indicated by postscan reports (e.g., increasing personal relevance), to increase the ecological validity and to maximize the effectiveness of the regulation manipulation, we allowed subjects to use whatever strategy worked best for them. Variability in strategies used may have influenced the current results, particularly for the down-regulation of positive emotion, where the most variability in strategy use was observed. Although self-rated regulation success and emotional arousal did not differ as function of specific strategy employed, it remains possible that this factor influenced patterns of brain activation. Further examination of how specific strategic factors alter the neural correlates of up-regulation and down-regulation will help to better characterize the regions that are commonly recruited by each type of regulation.

Because subjects were instructed not to increase or decrease their emotional responses by substituting an opposite emotion, regulation-related decreases and increases in emotional response most likely reflect decreases and increases in emotional arousal relative to a neutral baseline, rather than a reversal of emotional valence (e.g., from negative to positive affect). Further study will be needed to investigate the neural correlates associated with regulation strategies involving reappraisal by substituting opposing affective reactions. We also did not contrast regulation effects between different subcategories of emotion stimuli within a valence category, for example, between stimuli that primarily elicited disgust versus fear. A recent study reported that the neural correlates of down-regulating negative emotion differed depending on whether the stimuli depicted violations of moral rules, an effect that was observed even after arousal and other relevant stimulus factors had been equated (Harenski & Hamann, 2006). These findings suggest that the neural correlates of emotion regulation may differ in important ways according to other salient dimensions of emotional experience.

In conclusion, our findings indicate that voluntary up-regulation and down-regulation of positive and negative emotions engages prefrontal and cingulate regions involved in cognitive control and modulates activity in the amygdala, a key substrate for emotion processing. Regions involved in regulation of positive and negative emotion overlapped, but substantial differences were also found in cortical and subcortical responses during regulation, both between negative and positive emotion and between up-regulation and down-regulation. In summary, these findings help contribute to our understanding of the neural mechanisms underlying how individuals manage their own emotions, as they strive to accentuate the positive and eliminate the negative in their lives.

Reprint requests should be sent to Stephan Hamann, Psychology Department, 532 Kilgo Circle, NE, Emory University, Atlanta, GA 30322, or via e-mail: shamann@emory.edu.

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