Neural Correlates of Up-Regulating Positive Emotions in fMRI and Their Link to Affect in Daily Life

Journal:	*Social Cognitive and Affective Neuroscience*
Manuscript ID	SCAN-19-025
Manuscript Type:	Original Manuscript
Date Submitted by the Author:	22-Jan-2019

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Acknowledgments

We thank Jennifer Spiegel and Sandy Hannibal for their help acquiring the data, Deniz Kumral for her assistance in quality assessment of the MRI data, Karsten Mueller for methodological advice, and Lorenz Deserno for helpful comments on the manuscript. Johanna M. Grosse Rueschkamp is a pre-doctoral fellow of the International Max Planck Research School on the Life Course (LIFE, www.imprs-life.mpg.de).

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Abstract

Emotion regulation is typically used to down-regulate negative or up-regulate positive emotions. While there is considerable evidence for the neural correlates of the former, less is known about the neural correlates of the latter – and how they are associated with emotion regulation and affect in daily life. From 63 healthy young participants (22±1.6 years, 30 female), fMRI data was acquired while they up-regulated their emotions to positive and neutral images or passively watched them. From the same participants, daily affect and emotion regulation behavior were measured using experience-sampling over 10 days. Focusing on the ventral striatum (VS), which was previously associated with positive affective processing, we found increased activation during the up-regulation to both positive and neutral images. VS activation for the former positively correlated with between- and within-person differences in self-reported affect during fMRI but was not significantly associated with up-regulation in daily life. However, participants with lower daily affect showed a stronger association between changes in affect and activation in emotion-related (medial frontal and subcortical) regions – including the VS. These results support the involvement of the VS in up-regulating positive emotions and suggest a neurobehavioral link between emotion-related brain activation and emotions in daily life.

197 words

Keywords: positive emotions, experience-sampling, ventral striatum, affect, up-regulation

Total word count: 4,853

Our emotional experiences are characterized by ups and downs. While these changes depend on situations we encounter, we also influence how we feel through deliberately up- or down-regulating our emotions. There are different motivations to do so, but, in general, people are pro-hedonically motivated, that is, they want to maintain or increase their positive and decrease their negative emotions (Riediger et al., 2009). Previous neuroimaging studies have mainly focused on the down-regulation of negative emotions and identified brain regions or networks supporting this type of regulation: Most often, “cognitive control” regions in prefrontal and parietal cortices have been shown to modulate subcortical regions involved in emotional responding (e.g., amygdala; Buhle et al., 2014). However, people can also pursue pro-hedonic goals by enhancing positive emotions. While behavioral studies in the laboratory (Giuliani, McRae, & Gross, 2008) and in daily life (Jose, Lim, & Bryant, 2012) found that up-regulating positive emotions can enhance momentary levels of affect, less is known about the brain regions underlying this form of emotion regulation and the heightened experience of affect.

One of the brain structures suggested to be involved in – particularly positive – affective processing is the ventral striatum (VS). The VS has been implicated specifically in reward-related behavior (Kringelbach & Berridge, 2009; Schultz, Dayan, & Montague, 1997) and more generally in positive emotional responding, for example, to pleasant music (Blood & Zatorre, 2001), smiling faces (Vrticka, Sander, & Vuilleumier, 2011), or positive images (Sabatinelli, Bradley, Lang, Costa, & Versace, 2007). Furthermore, VS activity can be modulated through emotion regulation, for example by cognitive reappraisal, which can increase positive emotions in negative contexts (Doré et al., 2017). Thus, to the extent that the up-regulation of positive emotions successfully enhances positive affective experiences, it should also modulate activity in the VS.

Indeed, the few existing fMRI studies that examined the up-regulation of positive emotions reported increased activation in the VS – along with activation in medial and lateral prefrontal areas (similar to the down-regulation of negative emotion), the temporal lobe, and the anterior cingulate (Greening, Osuch, Williamson, & Mitchell, 2014; Kim & Hamann, 2007; Li et al., 2018; Moutsiana et al., 2014; Vrticka et al., 2011). In one of these studies, increased VS activity was related to behavioral measures of regulation success, that is, higher positive affect during up-regulating compared to just watching positive stimuli (Greening et al., 2014). However, several aspects of the role of the VS during the up-regulation of positive emotions remain unknown:

First, previous studies that found increased activation in the VS during the up-regulation of positive emotions used a passive baseline condition of "naturally" viewing positive stimuli as a control condition. However, to disentangle neural responses of affect-related up-regulation from more general regulatory efforts, an "active" control condition is needed; such as the up-regulation to neutral stimuli, which are thought to induce minimal affect (Gasper, 2018). Based on reports that the VS supports the heightened experience of positive affect during emotion regulation (e.g., Doré et al., 2017), we hypothesized stronger VS activation during the up-regulation to positive than to neutral stimuli, as the latter should not lead to changes in momentary affect.

Second, while activation in the VS has been related to between-person differences in the ability to up-regulate positive emotions (i.e., individuals with more activation have higher positive affect; Greening et al., 2014), it is important to also consider variability *within* individuals. A relation between VS activity and within-person changes in affect would indicate that, in addition to being persistently activated across contexts, the VS also reflects more subtle moment-to-moment changes in affect during the up-regulation of positive emotions. Such dynamic changes in affective states have also been associated with reward-related learning processes in the VS (Eldar, Rutledge, Dolan, & Niv, 2016; Rutledge, Skandali, Dayan, & Dolan, 2014). For example, exaggerated reward expectations during heightened positive affective states lead to decreases in positive affect. Lower affective states then facilitate increases in positive affective experiences through adjusted reward expectations (Eldar & Niv, 2015; Eldar et al., 2016). Combined with the relation between VS activity and differences in affect during the up-regulation of positive emotions (e.g., Greening, 2014), we hypothesized that activation in the VS also reflects within-person changes in affect during the up-regulation of positive emotions. Understanding the neural responses that support these brief changes in affect is particularly relevant considering the unpredictability of everyday-life situations. Ever-changing contexts and an individual's interaction with them naturally result in varying regulatory efforts and varying affective states.

To test an association between brain activation and moment-to-moment changes in affect – and to determine its generalizability (Araújo, Davids, & Passos, 2007) – it is beneficial to (also) test individuals in their "natural habitat". Studies that combined laboratory and daily-life measures found, for example, that reward-related VS activity was positively related to positive affect during a smartphone game in daily life (Heller et al., 2015). Assuming a similarity of behaviour in- and outside the laboratory, we expected that increased VS activity during emotion regulation in the fMRI also relates to changes in momentary affect when up-regulating positive emotions in daily life.

Taken together, in the present study, we investigated the neurobehavioral associations of the up-regulation of positive emotions during fMRI and in daily life. First, a standard emotion regulation paradigm was used to measure neural and behavioral responses while participants were instructed to up-regulate their affect to positive and neutral images during fMRI – compared to passively watching them. Given its above mentioned involvement in positive affective processing, the present study focused on the role of the VS for the heightened experience of affect during the up-regulation of positive emotions. We tested three hypotheses: (1) The VS is recruited more strongly when up-regulating to positive images compared to just watching them and to up-regulating to neutral images; (2) higher VS activation is related to higher between-person levels of affect during up-regulation; (3) higher

VS activation is related to higher within-person changes in affect during up-regulation (i.e., on a trial-by-trial basis).

Second, participants completed an additional 10 days of smartphone-based experience-sampling in their daily lives, during which they reported their momentary affect and degree of regulating positive emotions. Given the small empirical basis with a similar approach, we explored whether stronger activation in the VS during instructed up-regulation in the laboratory is related to higher changes in momentary affect when up-regulating in daily life.

Materials and Methods

Participants

Seventy-seven healthy participants between 18 and 25 years (*M*=22, *SD*=1.6, 39 women) were recruited through mailing lists and online ads. Exclusion criteria were current psychiatric or neurological disorders, an above normal body mass index (18.5 to 25 kg/m^2), and standard MRI contraindications (e.g., metallic implants). Data from two participants were excluded due to technical issues (wrong MRI sequence parameters and crashing task presentation) and two participants decided to terminate their participation. After a more detailed screening during the testing session, an additional ten participants were excluded because of a history of neurological or psychiatric diagnoses. Hence, 63 participants (*M*=22, *SD*=1.6, 30 women) entered the analyses.

Procedure

The experiment comprised two phases, an fMRI and an experience-sampling method (ESM) phase, the order of which was counterbalanced across participants (49% fMRI first). During the ESM introductory session, participants received smartphones and completed trait questionnaires (not relevant for the current research question; Supplement 1.1). During fMRI, an emotion regulation task and a reward-learning task (the results of which will be presented elsewhere) were performed. Both tasks were practiced beforehand outside the scanner.

Participant reimbursement ranged from 44.50 to 90 Euros, depending on the performance in the reward learning task and the number of completed ESM measurement occasions. The study was approved by the ethics committee of the medical faculty at the University of Leipzig.

Emotion regulation task in the MRI

Forty positive (Pos; valence: *M*=7.09, *SD*=0.34; arousal: *M*=4.59, *SD*=0.72) and 40 neutral images (Neu; valence: *M*=5.29, *SD*=0.17; arousal: *M*=3.15, *SD*=0.40) were chosen as stimuli from the Emotional Picture Set (EmoPicS; Wessa et al., 2010) based on the normative ratings (9-point Self-Assessment Manikins: 1=sad/calm, 9=happy/excited) and between conditions matched for number of persons depicted, social interactions, close-up images and eye contact. Participants were instructed to either up-regulate their emotions ("deliberately intensify the emotions you are experiencing"; Up) or to passively watch ("experience the emotions naturally as they come and go"; Watch) indicated by the cue words "Enhance" or "Watch" (for exact wording in German, Supplement 1.2). No specific emotion regulation strategy was instructed with the aim to maximize the comparability with the assessment in daily life, where people report using several emotion regulation strategies (Heiy & Cheavens, 2014). Each of the four experimental conditions (PosUp, PosWatch, NeuUp, NeuWatch) had 20 trials, split into two runs of 40 trials each. For each participant, images were randomly assigned to the four conditions and the trial order was pseudo-randomized with the constraint of maximally three consecutive trials from the same condition. Before and after each image, participants rated their current affect ("At the moment I feel") on a scale from -3 ("bad") to +3 ("good"; see Figure 1).

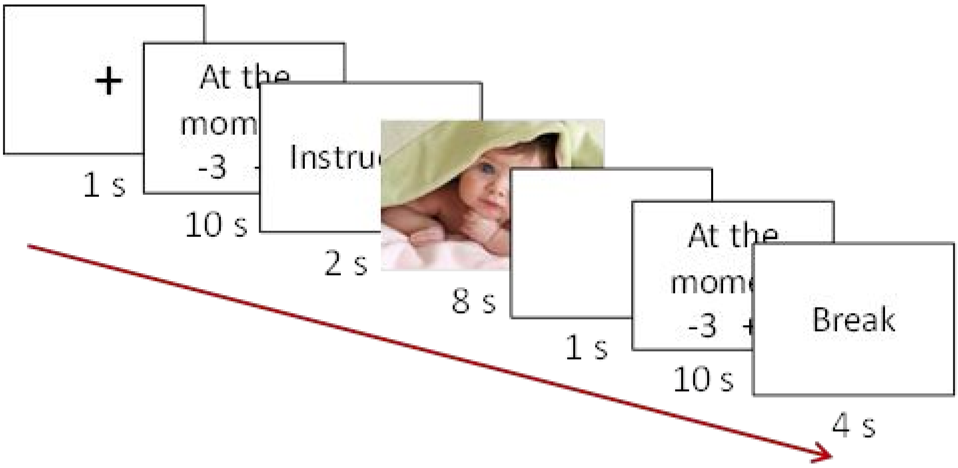

Figure 1. Schematic of one trial in the emotion regulation task: (i) fixation cross, (ii) pre-image affect rating (trial continued when answer was given), (iii) instruction cue word (“Enhance” or “Watch”), (iv) inter-stimulus interval, (v) post-image affect rating (trial continued when answer was given), and (vi) short break.

Experience-sampling in daily life

During the 10-day ESM phase (two periods of five days, separated by a two-day break), participants answered questions on a smartphone (Huawei Ascend G330), which beeped six times per day at pseudo-random time points (between 45 and 195 min apart) within 12 hours. On average, participants answered on 54.5 beep-induced occasions (*SD*=10.2). At each occasion, we assessed momentary affect (“At the moment I feel”, scale: -3 (“bad”) to +3 (“good”)) and the degree of emotion regulation (“I tried to intensify my pleasant feelings”; scale: 0 (“not at all”) to +6 (“very much”)) since the last occasion. In the following, “momentary affect” refers to ratings during the ESM phase and “self-reported affect” refers to ratings during the fMRI task.

MRI acquisition and processing

MRI was performed at the Berlin Center for Advanced Neuroimaging using a 3-T Siemens Tim Trio MRI (Siemens, Erlangen, Germany) with a standard 12-channel head coil. T1-weighted images were acquired with an MPRAGE pulse sequence (TR=1900 ms, TE=2.52 ms, FOV=256 mm, 192 slices, flip angle=9°, voxel size=1 mm isotropic).

Functional images were acquired using a T2*-weighted gradient-echo echo-planar imaging (EPI) sequence (TR=2090 ms, TE=22 ms, flip angle=90°, FOV=192 mm, voxel size=3 mm isotropic). Forty slices of 2.5 mm (0.5 mm gap) were obtained in interleaved order parallel to the anterior-posterior commissure (AC-PC) line. A field map (TR=438, TE_1=5.19 ms, TE_2=7.65 ms, flip angle=60°, FOV=192 mm) was acquired (before the EPI sequence) for distortion correction. The experiment was presented on an MR-compatible screen (NordicNeuroLab, Bergen, Norway) using OpenSesame 3.0.6 (Mathôt, Schreij, & Theeuwes, 2012). MR images were processed and analyzed using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/software/spm12/). First, four dummy scans, acquired at the beginning of each run, were excluded. FMRI preprocessing consisted of slice time correction, realignment to the mean EPI, co-registration of the T1-weighted image to the mean EPI, segmentation into three tissue classes (GM, WM, CSF), and normalization to MNI space (3 mm isotropic voxels) with the IXI555 template (from 555 healthy subjects; www.brain-development.org) plus spatial smoothing (with an 8-mm full-width-at-half-maximum Gaussian kernel) using DARTEL. No participant had to be excluded due to head movement (cut-off: >0.3 mm of mean frame displacement; Power, Barnes, Snyder, Schlaggar, & Petersen, 2012; Power, Schlaggar, & Petersen, 2015).

Statistical Analyses

Behavioral analyses. As a manipulation check, we first tested successful emotion regulation during fMRI and in daily life using linear-mixed modeling. Successful up-regulation of positive emotions during fMRI (i.e., higher levels of self-reported affect during up-regulation to positive images compared to just watching them and to up-regulation to neutral images) was determined using the post-image affect rating as the outcome variable with valence (Pos, Neu), instruction (Up, Watch), and their interaction as predictors. Follow-up analyses were conducted on positive and neutral trials separately, only with instruction as a predictor. To determine trial-wise regulation success, the change in affect for each trial was calculated as the difference between the post- and pre-image self-reported affect. The pre-image rating provides a trial-specific baseline, reflecting within-person changes in affect more directly (Augustine & Hemenover, 2009).

To test successful emotion regulation in daily life, momentary affect at each occasion was used as the outcome variable and the degree of emotion regulation as a predictor. To get a better proxy of the *change* in momentary affect, affect at the previous occasion was included as a lagged score as an additional predictor. Measures from these analyses were used for hypothesis-specific tests of a relation between neural activation and differences in affect (see below).

fMRI – first and second-level analyses. At the first level, a general linear model (GLM) was specified for each participant to model the BOLD signal for each condition (using a canonical hemodynamic response function). The six motion parameters were entered as regressors of no interest. At the second (i.e., group) level, random effects analysis was performed. According to our hypotheses, region-of-interest (ROI) analyses of the VS were conducted using a binarized mask based on coordinates from 9 reward-related studies (Rothkirch, Schmack, Deserno, Darmohray, & Sterzer, 2014 for more details) and family-wise error (FWE) corrected for multiple comparisons at p<.05.

VS ROI analyses were complemented by exploratory whole-brain analyses, for which cluster-extent based thresholding was used with p<.001 (uncorrected) at the voxel- and p<.05 (FWE-corrected) at the cluster-level. For each contrast, cluster extent thresholds k (ranging from 92 to 113 voxels) were estimated with the tool "SPM Cluster Size Threshold" (version date: 12 Jan 2016; https://github.com/CyclotronResearchCentre/SPM_ClusterSizeThreshold). To test for an association between dynamic within-person changes in affect (i.e., trial-by-trial changes in affect) and BOLD signal, parametric analyses were conducted: changes in affect were included as a parametric regressor at the first and a one-sample t-test was performed at the level.

All resulting t-maps are available on NeuroVault (Gorgolewski et al., 2015): https://neurovault.org/collections/MAZDXCZW/. To psychologically interpret the results of the exploratory whole-brain analysis in a data-driven way, the respective t-maps were compared (using NeuroVault's *decode* function) with terms of the online database Neurosynth, which contains activations and associated (psychological, anatomical) labels from 14,371 studies (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011).

All (Pearson) correlations of the link between behavioral and neural measures were outlier-corrected (3 *SD*) and to determine statistical significance, a (two-sided) α-level of .05 was used.

VS activity during up-regulation. To examine whether the VS is particularly activated during the up-regulation to positive images, compared to just watching them and to up-regulating neutral images, the interaction of valence and instruction ((PosUp>PosWatch)>(NeuUp>NeuWatch)), their two main effects (Pos>Neu and Up>Watch), and – given the study's focus on regulation effects – the simple effects PosUp>PosWatch and NeuUp>NeuWatch were analyzed in the VS.

Next, the hypothesis was tested that increased activation in the VS is related to higher between-person levels of affect when up-regulating positive emotions (i.e., successful up-regulation). For this, VS activity of the PosUp>PosWatch contrast was correlated with person-specific estimates of the random slopes from the linear-mixed model of the behavioral data (positive trials only), which represent average levels of affect during PosUp vs. PosWatch.

To test whether increased activation in the VS is related to greater within-person (i.e., trial-by-trial) changes in affect when up-upregulating positive emotions, we conducted a parametric analysis with changes in affect for the PosUp condition only (*n*=60, as three participants showed no variance in their self-reported affect in this condition).

Relating VS activity and up-regulation in daily life. As a behavioral check, laboratory measures of affect (i.e., mean self-reported affect of pre- and post-image ratings across all trials) were correlated with affect in daily life (i.e., mean momentary affect across all occasions).

To test the hypothesis that greater VS activation when instructed to up-regulate during fMRI is related to higher changes in momentary affect when up-regulating in daily life, person-specific estimates of the random slopes were extracted from the linear-mixed model of the ESM data. These estimates (i.e., each person's change in momentary affect in relation to the degree of up-regulation), were then correlated with VS activity when up-regulating positive emotions (extracted parameter estimates from PosUp>PosWatch).

Emotion-related brain activity and its association affect in daily life. To test which brain regions – beyond the VS – are associated with changes in affect, an exploratory parametric whole-brain analysis was conducted. To increase comparability between affect measured in the laboratory and in daily life (where there are no regulation instructions and events are not categorized by valence), this analysis included changes in affect across all conditions (i.e., trials) irrespective of instruction or stimulus valence. To test the link to between-person differences affective experience in daily life (Hamann & Canli, 2004), parametric effects from all significant clusters of this analysis were extracted and correlated with the participants' mean momentary affect over all measurement occasions during the ESM phase.

Results

Behavioral results

For up-regulation during fMRI, a significant interaction (β=0.28, p<.001) and main effect of valence (β=0.76, p<.001) but no significant main effect for instruction (β=-0.04, p=0.53) were found. Follow-up analyses showed that participants successfully up-regulated to positive (β=0.24, p<.001) but not to neutral images (β=-0.04, p=0.52, Figure 2).

In daily life, participants had a greater change in momentary affect, the stronger they up-regulated their positive emotions (significant main effect of the degree of emotion regulation, $\beta=0.29$, $p<.001$, and affect at the previous occasion, $\beta=0.14$, $p<.001$; Table S2).

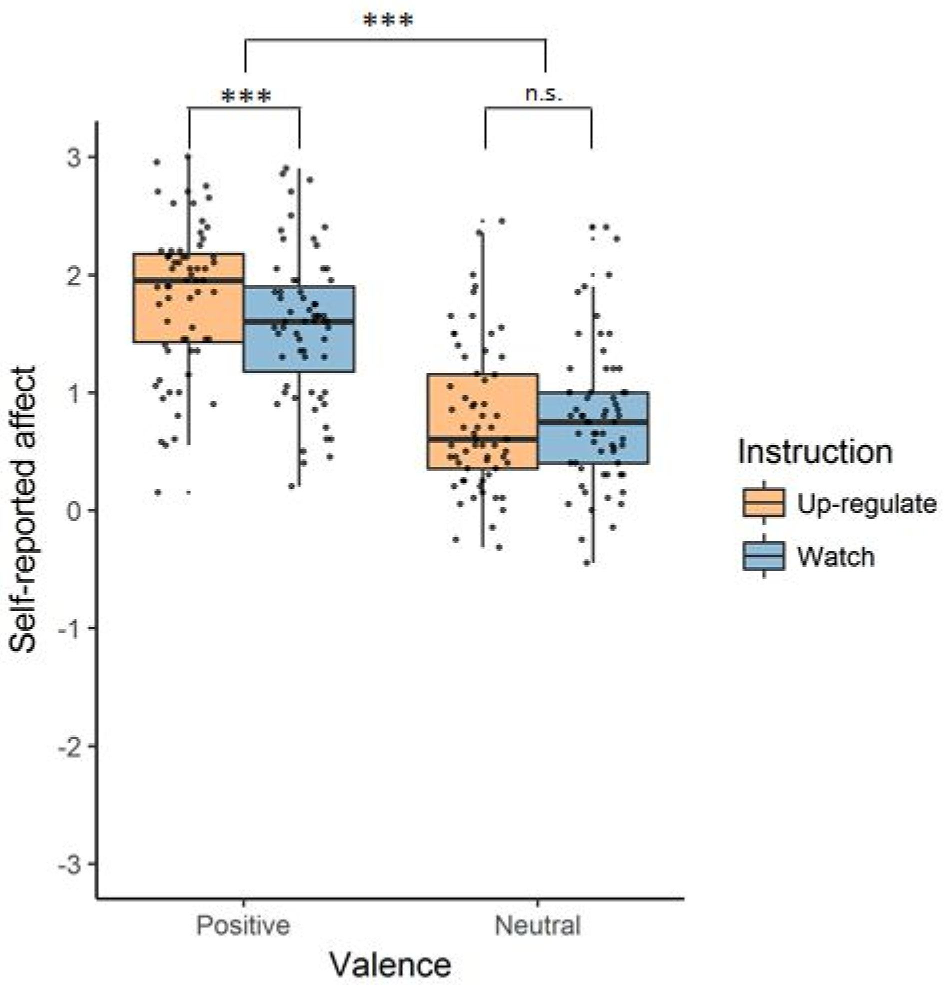

Figure 2. Self-reported affect in the emotion regulation task in the fMRI. There was a significant main effect of valence and a significant valence-by-instruction interaction effect, that is, higher self-reported affect for positive versus neutral images and for up-regulating emotions to positive images versus passively watching them. No significant difference was observed for up-regulating to neutral images versus passively watching them. Results are displayed as boxplots with median and first and third quartile. ***=$p<.001$; n.s.=not significant.

fMRI results

VS activity during up-regulation. No significant voxels were found for the interaction ((PosUp>PosWatch)>(NeuUp>NeuWatch)) in the VS, which would have indicated higher activation specifically for the up-regulation to positive images, compared to passively watching them and the up-regulation of neutral images. However, in bilateral VS, main effects of valence ([-12, 3, -9], T=4.0; [18, 0, -9], T=4.6) and instruction ([-15, 0, -6], T=5.44; [15, 3, -3], T=6.47; [-9, 18, 0], T=3.13) were significant. Follow-up analyses showed significant activation in the bilateral VS for the simple effects PosUp>PosWatch ([-15, 0, -6], T=4.42; [15, 0, -6], T=4.54) and NeuUp>NeuWatch ([-18, 3, -3], T=4.86; [15, 6, -3], T=5.92). That is, there was higher activation in the VS while up-regulating to both positive and neutral images, compared to just watching them.

VS activity and between-person differences in self-reported affect. Participants with stronger activation in the VS when up-regulating to positive images (PosUp>PosWatch) also reported higher average levels of affect (r(63)=0.28, p=.03; Figure 3A).

VS activity and within-person changes in affect. Relatively greater trial-by-trial changes in affect were related to increased engagement of the VS during the up-regulation of positive emotions, as shown by parametric increases in the left VS (PosUp condition; [-12, 6, -12], T=3.39, Figure 3B).

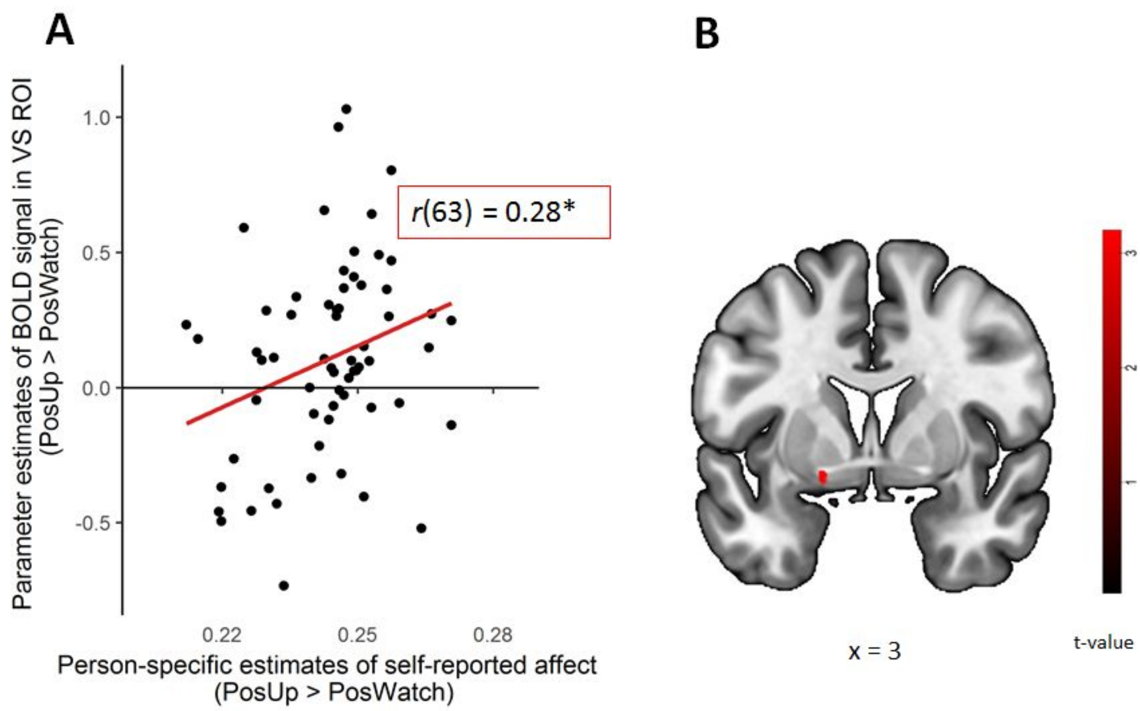

Figure 3. Association of activity in the ventral striatum (VS) with between-person (i.e., average) and within-person (i.e., trial-by-trial) differences in self-reported affect. (A) Increased VS activity (mean activation across the entire region-of-interest, ROI) was related to mean differences in self-reported affect for the up-regulation of emotions to positive images (PosUp), compared to passively watching them (PosWatch) and (B) positive association of changes in self-reported affect in the left VS during PosUp (ROI analysis: [-12, 6, -12], T=3.39, p=.05, FWE-corrected). *=p<.05

Whole-brain activity during up-regulation. In the exploratory whole-brain analysis of increased activation during the up-regulation specifically of positive images (compared to just watching them and the up-regulation to neutral images, i.e., the interaction of valence and instruction), no voxels survived multiple-comparison correction. The main effect of valence (Pos>Neu) showed widespread activation in lateral and medial temporal, frontal, and parietal cortices and in subcortical areas (Figure 4A, Table 1). The main effect of instruction (Up>Watch) yielded activation in a large cluster around the left supplementary motor area and in frontal, occipital, and cerebellar clusters (Figure 4B, Table 1). Deactivation results (i.e., the inverse contrasts) are reported in the Supplement (Table S3, section 1.3, and Figure S1).

Table 1.
Whole-brain analysis for the interaction, main effect of valence, and main effect of instruction. For corresponding brain plots, cf. Figure 4. For the inverse contrasts, cf. Table S3 and Figure S1.

				MNI coordinates		
Brain regions	Side	k	t	*x*	*y*	*z*
Interaction						
no significant voxels						
Positive>Neutral						
Supramarginal gyrus	R	502	7.7	66	-39	27
Supramarginal gyrus	L	318	7.23	-60	-36	30
Middle temporal gyrus	L	277	6.94	-60	-60	3
Inferior occipital	R	147	6.73	42	-84	-9
Superior frontal gyrus	L	441	5.89	-15	60	3
Precuneus	R	192	5.61	21	-42	12
Insula	L	676	5.55	-42	6	0
Rolandic operculum	R	248	5.34	51	6	6
Midcingulate gyrus	L	339	5.18	-12	-24	42
Up-regulate>Watch						
Supplementary motor area	L	10731	7.54	-9	15	69
Middle frontal gyrus	R	163	6.69	51	0	51
Calcarine sulcus	R	132	4.4	30	-72	9

Note. Clusters labeled according to the anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). Threshold: p<.001 (uncorrected) at the voxel- and p<.05 with family-wise error (FWE) correction at the cluster-level.

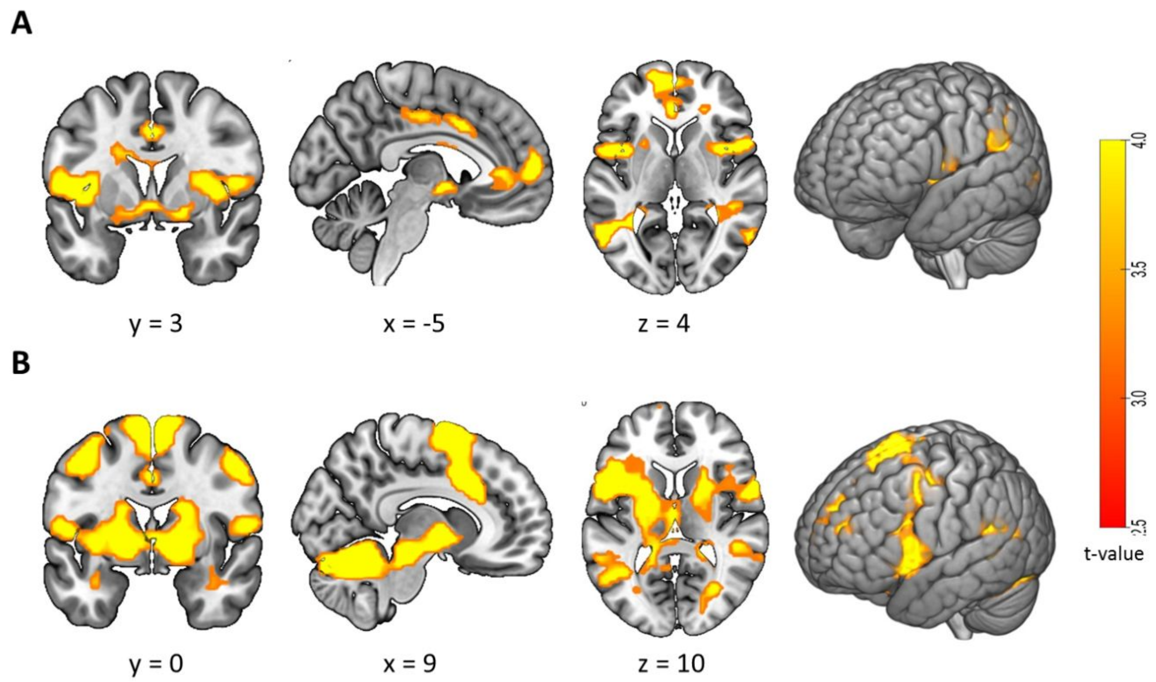

Figure 4. Brain activation in the emotion regulation task (main effects). Regions of increased activation for the (A) main effect of valence (Positive>Neutral) and (B) main effect of instruction (Up>Watch). No significant voxels were found for the interaction. Threshold: p<.001 (uncorrected) at the voxel- and p<0.05 with family-wise error (FWE) correction at the cluster-level. For details cf. Table 1. Coordinates are in MNI space.

Association of whole-brain activity and changes in affect. The exploratory analysis of associations between trial-by-trial changes in affect across all conditions and activation across the whole brain showed significantly positive correlations in widespread regions around medial frontal and subcortical areas and significantly negative correlations in lateral parietal but also in medial and lateral frontal areas, extending into the left insula (Figure 5, Table 2). The Neurosynth analysis mainly associated these regions with the anatomical labels *amygdala, hippocampus*, *ventromedial PFC* and the psychological concepts *arousal*, *emotion*, and *valence* for the positive association with changes in affect and with *inferior frontal, parietal, dorsolateral*, and *working memory, task,* and *comprehension* for the negative association with changes in self-reported affect (for a full list of the first 25 entries and their correlation values, see Table S4).

Table 2.
Whole-brain parametric analysis with changes in affect. For corresponding brain plots, cf. Figure 5.

				MNI coordinates		
Brain regions	Side	k	t	*x*	*y*	*z*
Increased activation						
Anterior cingulate gyrus	R	1010	5.77	18	33	3
Caudate nucleus	R	210	5.49	6	3	-6
Hippocampus	L	148	5.4	-27	-36	0
Middle occipital gyrus	L	119	4.45	-39	-60	0
Decreased activation						
Middle frontal gyrus	R	765	5.44	45	18	45
Inferior frontal gyrus, pars orbitalis	L	115	4.91	-39	18	-12
Angular gyrus	R	219	4.57	54	-57	33

Note. Clusters labeled according to the anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). Threshold: p<.001 (uncorrected) at the voxel- and p<.05 with family-wise error (FWE) correction at the cluster-level.

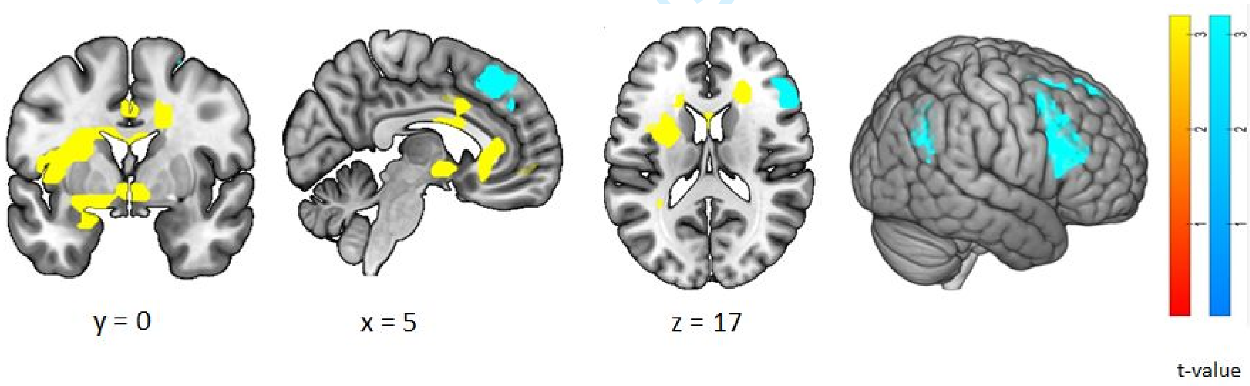

Figure 5. Whole-brain parametric analysis with changes in affect. Regions in which the BOLD signal was positively (yellow) or negatively (blue) related to changes in self-reported affect during image presentation in the emotion regulation task (across all conditions). Threshold: p<.001 (uncorrected) at the voxel- and p<.05 with family-wise error (FWE) correction at the cluster-level. For details cf. Table 2.

Neurobehavioral associations of up-regulation in fMRI and in daily life

Participants who had higher average affect in the laboratory also had higher affect in daily life ($r(63)=0.31$, $p=.01$, Figure S2).

Relation between VS activity and up-regulation in daily life. The association between VS activity during the up-regulation of positive emotions (PosUp>PosWatch) during fMRI was not related to the change in momentary affect during up-regulation in daily life ($r(63)=0.00$, $p=.97$).

Exploring whole-brain activity, changes in affect, and affect in daily life. Participants with lower average affect in daily life (mean-momentary affect during the ESM phase) had a stronger association between the engagement of emotion-related regions (across the whole brain) and changes in affect during the emotion regulation task ($r(61)=-0.30$, $p=.02$, Figure 6).

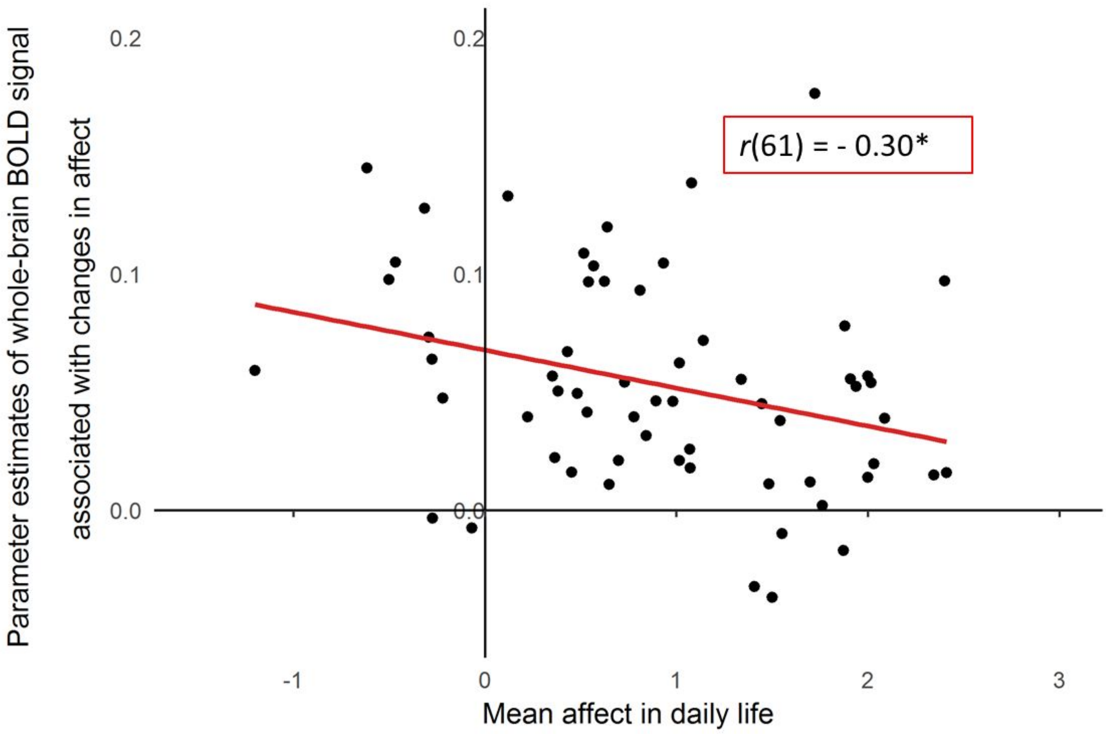

Figure 6. Link between affect in daily life and emotion-related brain activation in the laboratory. Mean momentary affect during the ESM phase was negatively correlated with the BOLD signal in medial frontal and subcortical emotion-related regions that showed a

significant association with changes in affect (whole-brain parametric analysis; cf. Table 2 and yellow clusters in Figure 5). *p<.05

Discussion

This study investigated neurobehavioral associations of the up-regulation of positive emotions during fMRI and their relation to emotion regulation and affect in daily life. Specifically, we tested the involvement of the VS in the experience of affect during the up-regulation of positive emotions. We found that VS activation was increased during the up-regulation to images, relative to passively watching them, irrespective of their content's valence (positive or neutral). For positive images, increased VS activity was related to (1) higher between-person differences in self-reported affect and (2) greater within-person changes in affect during up-regulation. This shows that the VS is not only activated persistently across contexts but also tracks within-person changes in affect – suggesting a central role for the VS in the up-regulation of positive emotions. Against our hypothesis, VS activity was not significantly related to changes in momentary affect when up-regulating positive emotions in daily life. However, an exploratory (whole-brain) parametric analysis showed that the lower a participant's general affect in daily life, the stronger the involvement of a set of medial frontal and subcortical emotion-related brain regions (including the VS) in changing the affect during the task in the laboratory.

VS activity during the up-regulation of positive emotions

We did not find the VS to be uniquely activated during the up-regulation to positive images but also during the up-regulation to neutral images. Behaviorally, however, the up-regulation to neutral images did not change participants' affect. Thus, in addition to the VS representing heightened positive experiences (Kringelbach & Berridge, 2009), it may serve another function during emotion regulation: VS activity may represent the general pursuit of an up-regulation goal (Ochsner, Silvers, & Buhle, 2012). This idea is in line with the metaanalytic finding of increased VS activity during the up-regulation (as compared to the down-regulation) of *both* positive and negative emotions (Morawetz, Bode, Derntl, & Heekeren, 2017).

Like in a previous study (Greening et al., 2014), we found that increased activation in the VS was associated with higher average levels of self-reported affect when up-regulating positive emotions. Hence, the strength of VS recruitment can be considered a neural indicator of between-person differences in the ability to up-regulate positive emotions. We additionally found that increased activation in the VS was associated with greater moment-to-moment changes in affect during the up-regulation of positive emotions. Thus, the VS seems to be sensitive to varying regulatory efforts that may result from factors such as the specific type (Heiy & Cheavens, 2014) or intensity (Silvers, Weber, Wager, & Ochsner, 2015) of the emotion to be regulated.

Neural responses underlying changes in affect

Our data suggest other brain regions and networks (in addition to the VS) to reflect changes in affective experiences. The whole-brain parametric analysis showed that changes in affect – also an index of successfully up-regulating positive emotions – were associated with activation in several brain regions that have been implicated in affective functioning, such as amygdala, hippocampus, ventromedial PFC, and striatum (cf. our Neurosynth decoding results). This finding aligns with the 'affective workspace hypothesis' that affective experiences rely on a flexible set of brain regions generally implicated in affective processing rather than on single brain regions representing positivity or negativity (Lindquist, Satpute, Wager, Weber, & Barrett, 2016).

Next to activation in these emotion-related regions, changes in affect were also associated with *deactivation* of a fronto-parietal network, comprising lateral parietal and medial as well as lateral prefrontal cortices, which has previously been related to goal-directed cognition in general (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010) and the cognitive control of emotions in particular (Ochsner et al., 2012). Studied mainly in the context of the down-regulation of negative emotions, this network has been repeatedly shown active during cognitive reappraisal (Buhle et al., 2014) and associated with within-person changes in *negative* affective experiences (Silvers, Wager, Weber, & Ochsner, 2015). In our study, similar prefrontal control regions were relatively *less* recruited with positive changes in affect. Two possible explanations for this finding are:

First, deactivation in these prefrontal regions might indicate that increasing one's positive affect (e.g., during the up-regulation of positive emotions) is less cognitively challenging and involves less cognitive control ("less suppression") of subcortical emotion regions than, for example, the active down-regulation of negative emotions, as suggested previously (Morawetz et al., 2017). Put differently, the down-regulation of negative emotions may require (more) cognitive effort to change an emotional response (e.g., by altering its meaning through reappraisal; Buhle et al., 2014) while the up-regulation of positive emotions may simply mean "admitting more" of an already existing emotional experience. Along these lines, participants find it easier to regulate their positive than their negative emotions (Kim & Hamann, 2007) and they do so more successfully in their daily lives (Heiy & Cheavens, 2014).

Second, the present finding suggests that enhancing momentary affective experiences might initiate distinct processes compared to other forms of emotion regulation. A recent study found (beside activations in emotion-related regions) deactivation in right fronto-parietal regions for the endogenous generation of positive emotions (Engen, Kanske, & Singer, 2017). Thus, enhancing positive affective experiences may more strongly draw upon emotion generation rather than alteration processes, compared to decreasing negative affect (Silvers, Wager, et al., 2015; see also Figure S3 and Supplement 1.4). In sum, the fronto-parietal control network seems to be relevant for the management of both positive and negative affective experiences.

Relating neurobehavioral associations with emotion regulation and affect in daily life

The hypothesized link between VS activity related to changes in affect during fMRI and shifts in momentary affect when up-regulating in daily life was not supported by the data. Also the association between average levels of affect during fMRI and daily life was relatively weak in our study. This may be due to methodological constraints that limit the comparability between measures from the laboratory and the real world. It could be, for example, that the capacity to change one's emotional response upon instruction (as tested in the laboratory; Webb, Miles, & Sheeran, 2012), differs from the capacity to spontaneously regulate one's emotions (as usually done in daily life).

Interestingly, in participants with lower average affect in daily life, more variance of changes in affect could be explained with activation in a network of emotion-related brain regions (including the VS). This could indicate that the lower one's affect, the more this "core set" is involved in pro-hedonically changing one's affective states. Speculatively, such changes could reflect reward-related processes: that is, people with lower average affect have lower expectations of positive events, which leads to higher reward-prediction errors and higher mood (Eldar et al., 2016; Rutledge et al., 2014). Fittingly, a meta-analysis found activation in a similar affective network during the experience of reward as opposed to loss (Liu, Hairston, Schrier, & Fan, 2011) and recent ESM findings by our group suggest that people with lower well-being benefit more (in terms of their momentary affect) from daily positive events (Grosse Rueschkamp, Kuppens, Riediger, Blanke, & Brose, 2018).

Limitations and further directions

There are several limitations: First, as partly discussed above, there are inherent differences between emotion regulation in laboratory-based tasks and in daily life (e.g., standardized stimuli vs. idiosyncratic events or instructed vs. spontaneous emotion regulation). Future studies could aim at establishing a greater parallelism by, for example, having participants engage in spontaneous rather than instructed emotion regulation during fMRI or by experimentally manipulating daily events (cf. Koval & Kuppens, 2012).

Second, when investigating affective processes, it is important to consider the time-scale at which affective change occurs (Hollenstein, Lichtwarck-Aschoff, & Potworowski, 2013). During fMRI, changes in affect are measured over seconds, whereas in daily life affective responses are assessed over minutes and hours. Thus, these two measures possibly capture different regulation processes (e.g., mood versus affect regulation).

Conclusion

By enhancing our positive emotional experiences, we can substantially improve the way we feel. This study highlights the relevance of the VS during the up-regulation of positive emotions by showing that not only between-person differences but also dynamic within-person changes in affect are supported by VS activity. The present findings further suggest that the ability to enhance one’s positive experiences might rely less on cognitive control processes, as indicated by the relative deactivation in a fronto-parietal network, and more on the capacity to endogenously generate emotions. Finally, people who tend to feel worse in daily life show a stronger link between neural activation in emotion-related regions (including the VS) and changes in their affective experiences. Together, these findings emphasize the role of the VS for positive affect and underline the importance of including both laboratory and daily life measures in the study of emotion.

Supplementary data

Supplementary data is submitted together with this manuscript.

Conflict of Interest

None declared.

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Supplementary material

1. Methods

1.1. Questionnaires

Big-Five Inventory (Lang & Lüdtke, 2005)

Satisfaction with Life Scale; (Diener, Emmons, Larsen, & Griffin, 1985)

Positive and Negatvie Affect Scale (Watson, Clark, & Tellegen, 1988)

Cognitive Emotion Regulation Questionnaire (Garnefski, Kraaij, & Spinhoven, 2001)

WHO-5 questionnaire (World Health Organization, 1998)

Emotion Regulation Profile-Revised (Nelis, Quoidbach, Hansenne, & Mikolajczak, 2011)

Dispositional Positive Emotion Scales (Shiota, Keltner, & John, 2006)

Hypomanic Personality Scale (Eckblad & Chapman, 1986)

1.2. Emotion regulation instructions during fMRI

original German wording

„Willkommen bei dieser Studie.

Sie werden verschiedene Bilder sehen, die unterschiedliche Emotionen hervorrufen können. Vor jedem Bild erhalten Sie eine Anleitung, was Sie tun sollen. Diese lautet entweder 'VERSTÄRKEN oder 'ANSEHEN'.

Wenn Sie die Anleitung 'VERSTÄRKEN' sehen, versuchen Sie bitte, willentlich Ihre Gefühle zu verstärken, die Sie haben wenn Sie die Bilder sehen und welche die dargestellte Szene in Ihnen auslöst. Versuchen Sie also, Ihre Gefühle so intensiv wie möglich zu erleben.

Wenn die Anleitung 'ANSEHEN' lautet,

möchten wir Sie bitten, Ihre Gedanken und Gefühle einfach kommen und gehen zu lassen, so wie das natürlicherweise passiert.

Vor und nach jedem Bild werden Sie gefragt, wie Sie sich gerade fühlen. Bitte bewerten Sie Ihre Gefühle auf einer Skala von +3 (gut) bis -3 (schlecht), indem Sie mit der linken und rechten Pfeiltaste das entsprechende Kästchen wählen und dann mit der unteren Pfeiltaste Ihre Antwort einloggen.

Bitte antworten Sie spontan ohne langes Nachdenken. Sie haben max. 10 Sekunden Zeit um eine Antwort zu geben.

Nach einer kurzen Pause werden Sie dann ein weiteres Mal nach Ihren Gefühlen gefragt. Wenn Sie noch Fragen haben, stellen Sie diese bitte jetzt dem Versuchsleiter."

Free English translation

„Welcome to this study.

You will see different images that can evoke different emotions. Before each image you will receive an instruction about what you should do. This can be either "INCREASE" or "WATCH".

If you see the instruction „INCREASE", please try to voluntarily increase your feelings, which you experience while viewing the images and which the depicted scene evokes in you. That is, try to experience your feelings as intensely as possible.

If the instruction is „WATCH", we kindly ask you to just let your feelings and thoughts come and go, as it naturally happens.

Before and after each image you will be asked how you currently feel. Please rate your feelings on a scale from +3 (good) to -3 (bad) by choosing the corresponding box with the left and right button and then confirming your answer with the middle button.

Please answer spontaneously without thinking too long. You have maximally 10 seconds to give an answer.

After a short break you will be asked once more about your feelings. If you have questions, please ask the experimenter now."

Table S1.

Results from the linear mixed-effects model predicting change in affect and affect in the emotion regulation task

Variable	Self-reported affect (post-image)		Change in affect (post – pre-image rating)	
	Estimate	*SE*	Estimate	*SE*
Fixed Effects				
Intercept	0.81***	0.08	-0.30***	0.06
Valence	0.76***	0.07	0.79***	0.09
Instruction	-0.04	0.06	-0.09	0.06
Valence x Instruction	0.28***	0.08	0.29**	0.09
Random Effects				
Within-person	1.34		1.94	
Between-person				
Intercept	0.32		0.10	
Valence slope	0.19		0.30	
Instruction slope	0.07		0.05	
Valence x Instruction slope	0.12		0.14	

***=*p*<.001 **=*p*<.01

Table S2.

Results from the linear mixed-effects model predicting affect when up-regulating positive emotions in daily life

Variable	Momentary affect	
	Estimate	*SE*
Fixed Effects		
Intercept	0.92***	0.11
Affect at previous occasion	0.14***	0.02
Degree of emotion regulation	0.29***	0.03
Random Effects		
Within-person	2.37	
Between-person		
Intercept	0.69	
Affect at previous occasion slope	0.01	
Degree of emotion regulation slope	0.02	

***=*p*<.001 **=*p*<.01

Table S3.

Whole-brain analysis for the interaction, main effect of valence, and main effect of instruction.

				MNI coordinates		
Brain regions	Side	k	t	*x*	*y*	*z*
Interaction: deactivation						
Medial frontal gyrus	R	144	4.92	6	48	42
Neutral > Positive						
Fusiform gyrus	L	6489	18.67	-27	-54	-9
Inferior frontal gyrus, pars triangularis	L	595	8.13	-54	24	21
Inferior frontal gyrus, pars triangularis	R	431	8.02	54	27	27
Supplementary motor area	L	227	5.39	-12	18	66
Middle frontal gyrus	R	307	5.25	24	15	48
Watch > Up-regulate						
Inferior parietal lobe	R	399	5.8	45	-51	54
Middle frontal gyrus	R	247	5.52	27	15	54

Note. Clusters labeled according to the anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). Threshold: p<.001 (uncorrected) at the voxel- and p< .05 with family-wise error (FWE) correction at the cluster-level

1.3. Deactivation for interaction: Follow-up analyses

Extracted parameter estimates from the cluster [6, 48, 42] showed a significant valence by instruction interaction, $F(1, 62)=19.5$, $p<.001$. Pairwise comparisons showed a significant difference ($t(62)=-4.57$, $p<.001$) between NeuUp (mean $b=0.21$) and PosUp (mean $b=0.04$) as well as ($t(62)=4.05$, $p<.001$) between NeuUp and NeuWatch (mean $b=0.04$; Figure 3), suggesting that activation in this cluster was driven by *increased* activation in NeuUp.

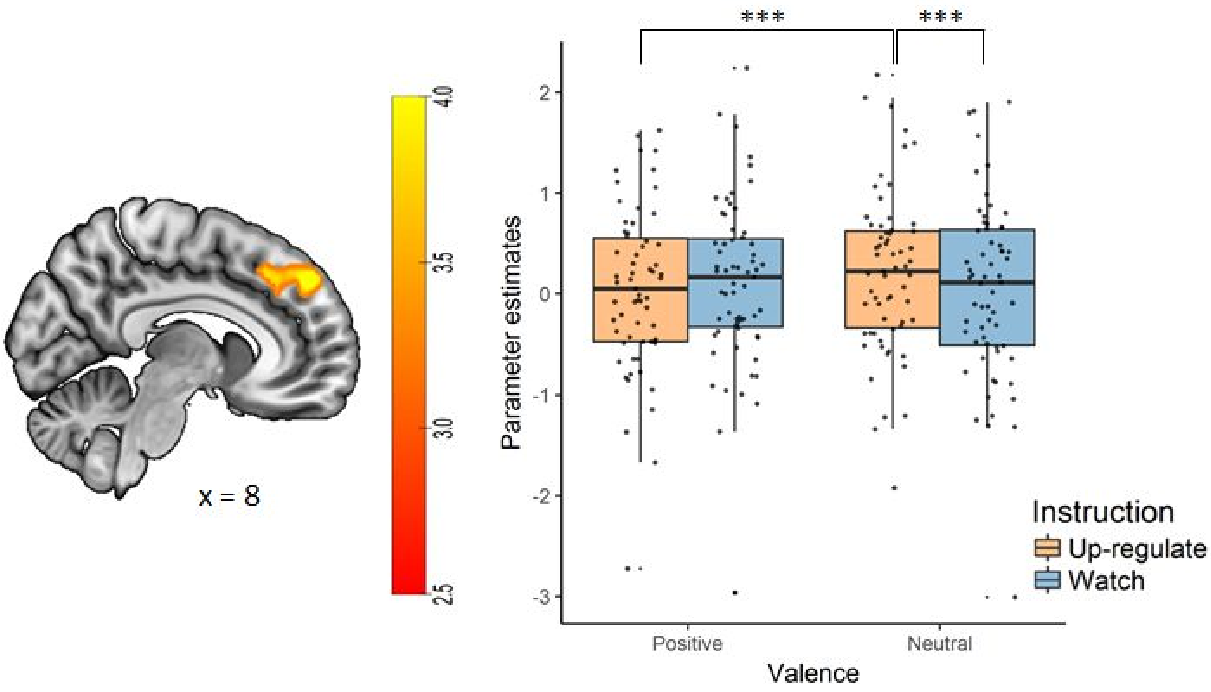

Figure S1. Brain activation in the emotion regulation task (inverse interaction). Decreased brain activation was found in the right dorsomedial prefrontal gyrus for the interaction of valence and instruction. Follow-up analyses indicate that there was significantly less activation for up-regulating to positive images and passively watching neutral images than for up-regulating to neutral images. (No significant voxels were found for the main interaction contrast, cf. Table 1.) Threshold: $p<.001$ (uncorrected) at the voxel- and $p<.05$ with family-wise error (FWE) correction at the cluster-level. ***=$p<.001$

Table S4.
Neurosynth terms that show an association with activation in brain regions that are parametrically modulated by changes in affect

Neurosynth term	r
Increased activation	
amygdala	0.190
fa	0.151
hippocampus	0.149
vmpfc	0.147
amygdala hippocampus	0.138
neutral	0.136
arousal	0.135
faces	0.135
ventromedial	0.134
ventromedial prefrontal	0.133
callosum	0.131
corpus callosum	0.131
corpus	0.130
cortex vmpfc	0.129
amygdala response	0.127
emotion	0.124
putamen	0.123
emotional	0.122
hippocampal	0.120
valence	0.120
cingulate cortex	0.117
fearful	0.117
pain	0.116
limbic	0.116
reactivity	0.115
Decreased activation	
frontal	0.258
working memory	0.218
working	0.216
inferior frontal	0.211
task	0.206
parietal	0.202
inferior	0.196
comprehension	0.189
sentences	0.181
sentence	0.171
demands	0.169
linguistic	0.166
tasks	0.164
dorsolateral	0.161
language	0.160
parietal cortex	0.157
frontoparietal	0.156
fronto parietal	0.155
prefrontal	0.154

frontal gyrus	0.154
theory mind	0.148
syntactic	0.143
mind tom	0.142
speaker	0.138
semantic	0.130

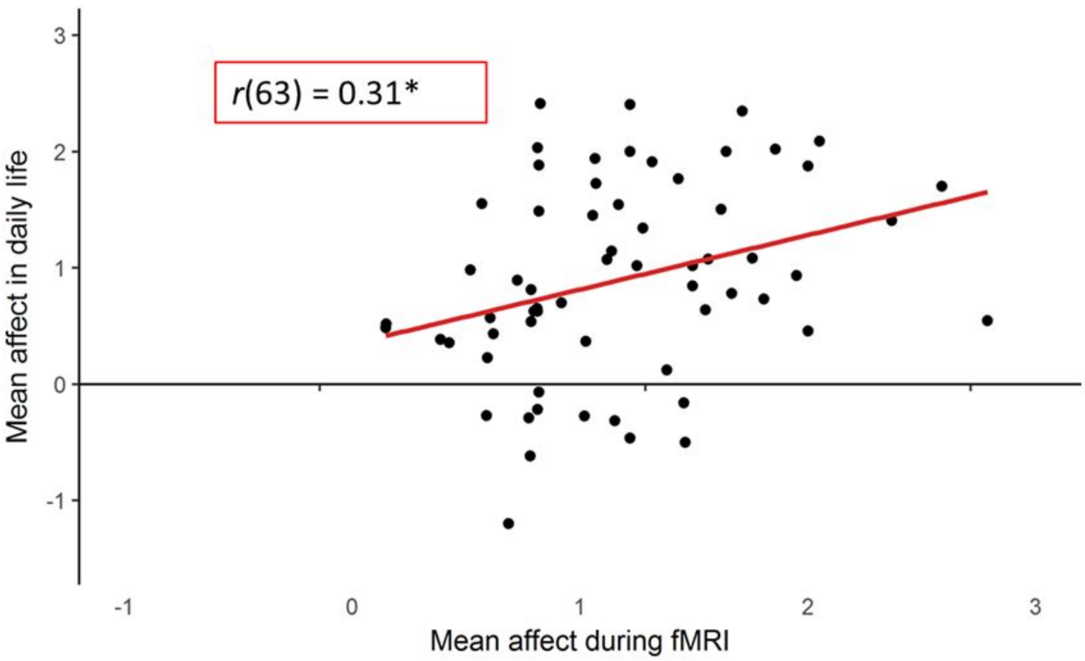

Figure S2. Association between mean affect during fMRI and mean affect in daily life. Mean self-reported affect during fMRI was positively correlated with mean momentary affect in daily life. *=p <.05.

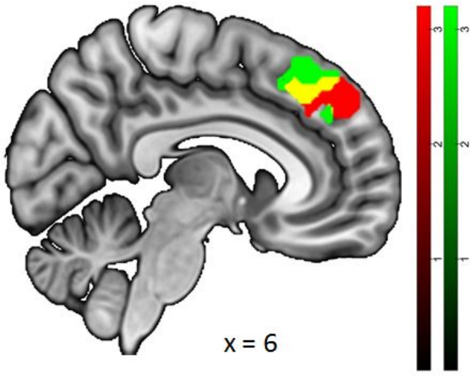

Figure S3. Overlap between brain activation in the emotion regulation task (inverse interaction) and in the whole-brain parametric analysis with changes in affect. The BOLD signal that was *negatively* correlated with changes in affect (green; whole-brain parametric analysis across all conditions, see also Table 2 and Figure 5) partially overlaps (yellow) with *deactivation* for the interaction of valence and instruction (red; whole-brain analysis, [6, 48, 42], T=4.92, see also Table S2). Threshold: $p<.001$ (uncorrected) at the voxel- and $p<.05$ with family-wise error (FWE) correction at the cluster-level. ***=$p<.001$

1.4. Deactivation for interaction and deactivation of whole-brain parametric analysis

In its medial part, the fronto-parietal network overlapped with the *deactivation* of the dorsomedial prefrontal cortex (dmPFC) cluster found in the interaction of valence and instruction (see above and Figure S3 for the overlap). As this cluster was solely deactivated during the up-regulation of positive emotions, it further supports the idea that successful up-regulation of positive emotions, at least partly, depends on the deactivation of prefrontal control systems. However, if one understands the deactivation of the dmPFC cluster as a significant *increase* in activation for the up-regulation to neutral images, this cluster could indicate that, similar to the regulation of negative emotions, regulatory efforts to neutral images require auxiliary cognitive functions (Miller & Cohen, 2001). However, these seem to be dissociated from changes in affect, as indicated by the behavioral data and the whole-brain parametric analysis.

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