

Neural correlates of up-regulating positive emotions in fMRI and their link to affect in daily life

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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. Functional magnetic resonance imaging (fMRI) data were acquired from 63 healthy young participants (22 ± 1.6 years, 30 female), while they up-regulated their emotions to positive and neutral images or passively watched them. The same participants' daily affect and emotion regulation behavior was measured using experience sampling over 10 days. Focusing on the ventral striatum (VS), 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 affective valence 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 daily affect.

Key words: positive emotions; experience sampling; ventral striatum; affect; up-regulation

Our emotional experiences are characterized by ups and downs. While these changes depend on situations we encounter, we also influence how we feel by 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 *et al.*, 2008) and in daily life (Jose *et al.*, 2012) found that up-regulating positive emotions can enhance momentary levels of affect, less is known about the brain regions

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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 (Schultz *et al.*, 1997; Kringelbach and Berridge, 2009) and more generally in positive emotional responding, for example, to pleasant music (Blood and Zatorre, 2001), smiling faces (Vrticka *et al.*, 2011) or positive images (Sabatinelli *et al.*, 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). Such regulatory effects are usually ascribed to cognitive control processes in prefrontal and parietal regions (such as lateral and medial prefrontal as well as lateral parietal cortices), which in turn modulate activity in subcortical affect processing regions, such as the VS and the amygdala (Wager *et al.*, 2008; Ochsner *et al.*, 2012). Thus, to the extent that the up-regulation of positive emotions successfully enhances positive affective experiences, it should modulate activity in the VS.

Indeed, the few existing functional magnetic resonance imaging (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 (Kim and Hamann, 2007; Vrticka *et al.*, 2011; Greening *et al.*, 2014; Moutsiana *et al.*, 2014; Li *et al.*, 2018). 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 condition of ‘naturally’ viewing positive stimuli as a baseline. This way, one contrasts regulatory processes on the one hand and passive states on the other. To disentangle neural responses of the up-regulation of positive emotions from other regulatory processes, an ‘active’ control condition is needed. The up-regulation to neutral stimuli is such an active control condition, used 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 (Rutledge *et al.*, 2014; Eldar *et al.*, 2016). 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 and 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 *et al.*, 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 investigate an association between brain activation and moment-to-moment changes in affect—and to determine its generalizability (Araújo *et al.*, 2007)—it is beneficial to test individuals in the lab as well as their ‘natural habitat’. For example, Heller *et al.* (2015) investigated the link between reward and positive emotional states (cf. Eldar *et al.*, 2016) using a (rewarded) game and affect ratings in both the fMRI and in daily life. Their finding of a positive association between sustained reward-related VS activity and sustained positive affect in daily life suggests common pathways for affect-related brain activation (as measured in the lab) and the dynamics of emotional experience in daily life. Combining fMRI and daily life measures thus allows a better understanding of how neuroaffective processes relate to the experience of positive affect in daily life; thereby assessing the real-world relevance of lab-based neuroscientific findings. Assuming a similarity of behavior 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: (i) the VS is recruited more strongly when up-regulating to positive images compared to just watching them and to up-regulating to neutral images; (ii) higher VS activation is related to higher between-person levels of affect during up-regulation; and (iii) 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

A total of 77 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 (18.5–25 kg/m²) and standard MRI contraindications (e.g. metallic implants). Data from two participants were excluded due to technical issues (wrong MRI sequence parameters and crashing

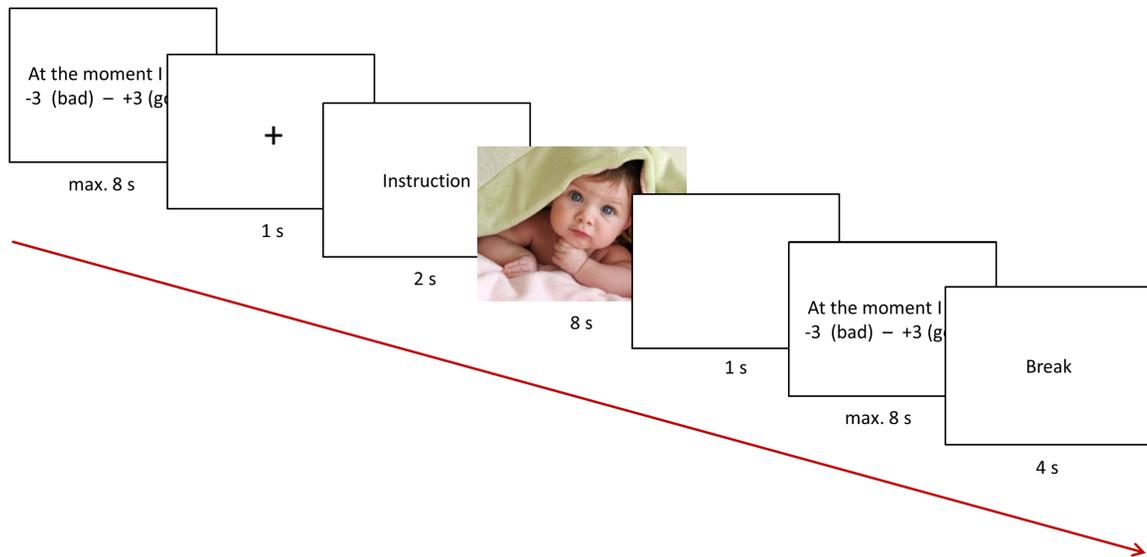


Fig. 1. Schematic of one trial in the emotion regulation task: (i) pre-image affect rating (trial continued when answer was given), (ii) fixation cross, (iii) instruction cue word ('Enhance' or 'Watch'), (iv) inter-stimulus interval, (v) post-image affect rating (trial continued when answer was given)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

task presentation) and two participants decided to terminate their participation. After a more detailed screening during the testing session, an additional 10 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

A total of 40 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 matched between conditions 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, see Supplement 1.2). No specific emotion regulation strategy was instructed, as we aimed to maximize the comparability with

the assessment in daily life, where people report using several emotion regulation strategies (Heij and 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 momentary affective valence ('At the moment I feel ...') on a scale from -3 ('bad') to $+3$ ('good'; see Figure 1) by using an MRI-compatible box with three buttons. The rating always started at ± 0 . The left button decreased and the right button increased the rating, while the middle button confirmed it. The currently chosen option was visually highlighted. After each fMRI session, participants were asked how much they engaged in up-regulation during the task and how strongly they used each of four different emotion regulation strategies (for details, see Supplementary Table S1).

Experience sampling in daily life

During the 10-day ESM phase (two periods of 5 days, separated by a 2-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 h. On average, participants answered on 54.5 beep-induced occasions ($SD=10.2$). At each occasion, we assessed momentary affective valence ['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, we differentiate between momentary self-reported affective valence during the fMRI task ($AffVal_{fMRI}$) and momentary self-reported affective valence during the ESM phase ($AffVal_{ESM}$).

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 Magnetization Prepared Rapid Gradient Echo (MPRAGE) 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). A total of 40 slices of 2.5 mm (0.5 mm gap) were obtained in interleaved order parallel to the anterior-posterior commissure line. A field map (TR=438, TE₁=5.19 ms, TE₂=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 et al., 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 (via interpolation), 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 Montreal Neurological Institute (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. This kernel size was chosen to parallel the study from which we obtained the VS mask (Rothkirch et al., 2014; see below) and because it fulfills the recommendation of at least twice the voxel dimension (Poldrack et al., 2011, p. 118). No participant had to be excluded due to head movement (cut-off, >0.3 mm of mean frame displacement; Power et al., 2012, 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 AffVal_{fMRI} during up-regulation to positive images compared to just watching them and to up-regulation to neutral images) was determined using the post-image AffVal_{fMRI} as the outcome variable with valence (Pos, Neu), instruction (Up, Watch), and their interaction as predictors (for full model, see Supplement 1.3). To determine trial-wise regulation success, the change in affect for each trial was calculated as the difference between the post- and pre-image AffVal_{fMRI}. The pre-image rating provides a trial-specific baseline, reflecting within-person changes in affect more directly (Augustine and Hemenover, 2009).

To test successful emotion regulation in daily life, momentary affect at each occasion (AffVal_{ESM}) was used as the outcome variable and the degree of emotion regulation as a predictor. To get a better proxy of the 'change' in AffVal_{ESM}, AffVal_{ESM} at the previous occasion was included as a lagged score as an additional predictor (for full model, see Supplement 1.3). 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 was specified for each participant to model the BOLD signal for each condition (using a canonical hemodynamic response function). Data were high-pass filtered (cut-off, 128 s) to remove low-frequency drifts. Autocorrelated residuals were accounted for by an autoregressive model, AR(1). The image (8 s),

the affect ratings (exact duration, max. 8 s), the instruction (2 s), the fixation cross (1 s) and the break (4 s) were all modeled with their respective duration as separate regressors. Besides these six regressors of interest, 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 right and left VS were conducted with a binary mask (total size, 208 voxels). This mask was based on coordinates from nine reward-related studies (Rothkirch et al., 2014 for more details), which were pooled and smoothed with a 3D Gaussian kernel of two standard deviations. Statistical parametric maps in the bilateral ROI were family-wise error (FWE)-corrected for multiple comparisons at $P < 0.05$.

VS ROI analyses were complemented by exploratory whole-brain analyses, for which cluster-extent based thresholding was used with $P < 0.001$ (uncorrected) at the voxel and $P < 0.05$ (FWE-corrected) at the cluster level. For each contrast, cluster extent thresholds k (ranging from 92 to 113 voxels) were estimated with the 'SPM Cluster Size Threshold' tool (version date: 12 January 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 AffVal_{fMRI}) and the BOLD signal, parametric analyses were conducted: changes in AffVal_{fMRI} were included as a parametric regressor at the first level, and a one-sample t -test was performed at the second.

All resulting t -maps are available on NeuroVault (Gorgolewski et al., 2015): 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 et al., 2011).

All (Pearson) correlations of the links between behavioral and neural measures were outlier-corrected (3 SD) and a (two-sided) α -level of 0.05 was used to determine statistical significance.

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 AffVal_{fMRI} 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-regulating positive emotions, we conducted a parametric analysis with changes in AffVal_{fMRI} for the PosUp condition only ($n=60$, as three participants showed no variance in their AffVal_{fMRI} in this condition). The use of a parametric regressor to account for within-person changes in affect during emotion regulation follows earlier studies that used a similar approach (e.g. Phan et al., 2005).

Relating VS activity and up-regulation in daily life. As a behavioral check, we correlated mean levels and variability of affect

from the laboratory and from daily life. That is, we extracted person-specific estimates of the random intercepts from our multilevel models of the lab-based and ESM data (leaving out any predictors), reflecting mean levels of $\text{AffVal}_{\text{fMRI}}$ and $\text{AffVal}_{\text{ESM}}$, respectively. Additionally, we computed within-person standard deviations of these affect measures. We then calculated the Pearson correlation coefficients between the means and standard deviations, respectively.

To test the hypothesis that greater VS activation occurring 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 $\text{AffVal}_{\text{ESM}}$ in relation to the degree of up-regulation) were then correlated with VS activity when up-regulating positive emotions (extracted parameter estimates from $\text{PosUp} > \text{PosWatch}$).

Emotion-related brain activity and its association with affect in daily life. To test which brain regions—beyond the VS—are associated with changes in affect during task performance, an exploratory parametric whole-brain analysis was conducted examining how trial-by-trial changes in $\text{AffVal}_{\text{fMRI}}$ relate to the BOLD signal. To increase comparability between affect measured in the laboratory and in daily life (no regulation instructions nor information on the affective valence of the exact situation in which affect ratings are provided in the latter), the parametric analysis included changes in affect across all conditions irrespective of instruction or stimulus valence (i.e. all trials of the up-regulate and watch condition, neutral and positive pictures). To explore how neurobehavioral associations in the lab relate to affective experiences in daily life, we extracted the mean parameter estimate for each participant from the parametric modulation analysis across all clusters that showed a significant positive relation with trial-by-trial changes in $\text{AffVal}_{\text{fMRI}}$. These parameter estimates, reflecting each participant's strength of the association between changes in $\text{AffVal}_{\text{fMRI}}$ and BOLD signal across the activated clusters, were then correlated with the person-specific estimates of the random intercepts from the linear-mixed model predicting $\text{AffVal}_{\text{ESM}}$ (i.e. mean levels of momentary affect in daily life).

Results

Behavioral results

For up-regulation during fMRI, a significant main effect of valence, $\beta = 0.76$, $P < 0.001$, and interaction effect, $\beta = 0.28$, $P < 0.001$, were found, but no significant main effect for instruction, $\beta = -0.04$, $P = 0.53$. Following up on the significant interaction, separate analyses were conducted for positive and neutral trials, keeping only instruction as a predictor. This showed that participants successfully up-regulated to positive, $\beta = 0.24$, $P < 0.001$, but not to neutral images, $\beta = -0.04$, $P = 0.52$, Figure 2; Supplementary Table S2.

In daily life, participants had a greater change in $\text{AffVal}_{\text{ESM}}$, the more strongly they up-regulated their positive emotions (significant main effect of the degree of emotion regulation, $\beta = 0.29$, $P < 0.001$, and $\text{AffVal}_{\text{ESM}}$ at the previous occasion, $\beta = 0.14$, $P < 0.001$; Supplementary Table S3).

FMRI results

VS activity during up-regulation. No significant voxels were found for the interaction ($[\text{PosUp} > \text{PosWatch}] > [\text{NeuUp} >$

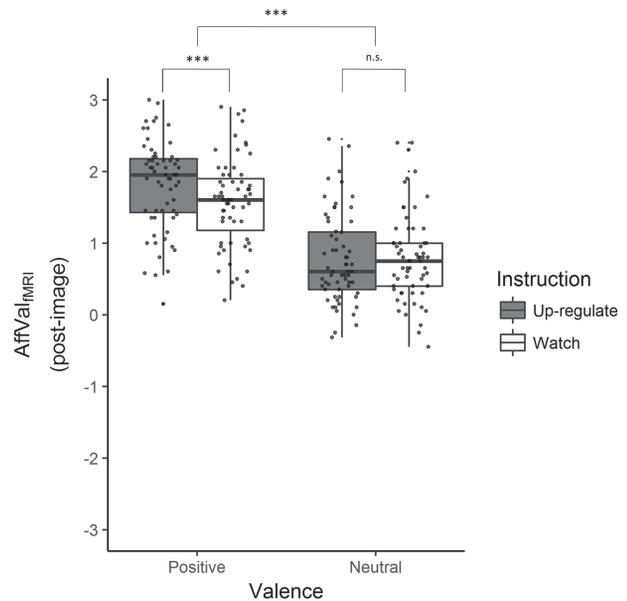


Fig. 2. Self-reported affective valence in the emotion regulation task in the fMRI. There was a significant main effect of valence and a significant valence-by-instruction interaction effect. That is, self-reported affective valence ($\text{AffVal}_{\text{fMRI}}$; post-image ratings) was more positive for positive compared to neutral images and more positive for up-regulating emotions to positive (vs passively watching them) compared to neutral images (vs passively watching them). No significant difference was observed for up-regulating neutral images vs passively watching them. Results are displayed as boxplots with median and first and third quartile. *** $P < 0.001$; n.s., not significant.

$\text{NeuWatch}]$ 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 $\text{PosUp} > \text{PosWatch}$ ($[-15, 0, -6]$, $T = 4.42$; $[15, 0, -6]$, $T = 4.54$) and $\text{NeuUp} > \text{NeuWatch}$ ($[-18, 3, -3]$, $T = 4.86$; $[15, 6, -3]$, $T = 5.92$). That is, there was higher activation in the VS while up-regulating to both positive and neutral images, as compared to just watching them.

VS activity and between-person differences in self-reported affective valence. Participants with stronger activation in the VS when up-regulating to positive images ($\text{PosUp} > \text{PosWatch}$) also reported more $\text{AffVal}_{\text{fMRI}}$ across trials, $r(61) = 0.28$, $P = 0.03$; Figure 3A).

VS activity and within-person changes in affect. Relatively greater trial-by-trial changes in $\text{AffVal}_{\text{fMRI}}$ 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).

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 to 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 ($\text{Pos} > \text{Neu}$) 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 ($\text{Up} > \text{Watch}$) yielded activation in a large cluster around the left supplemen-

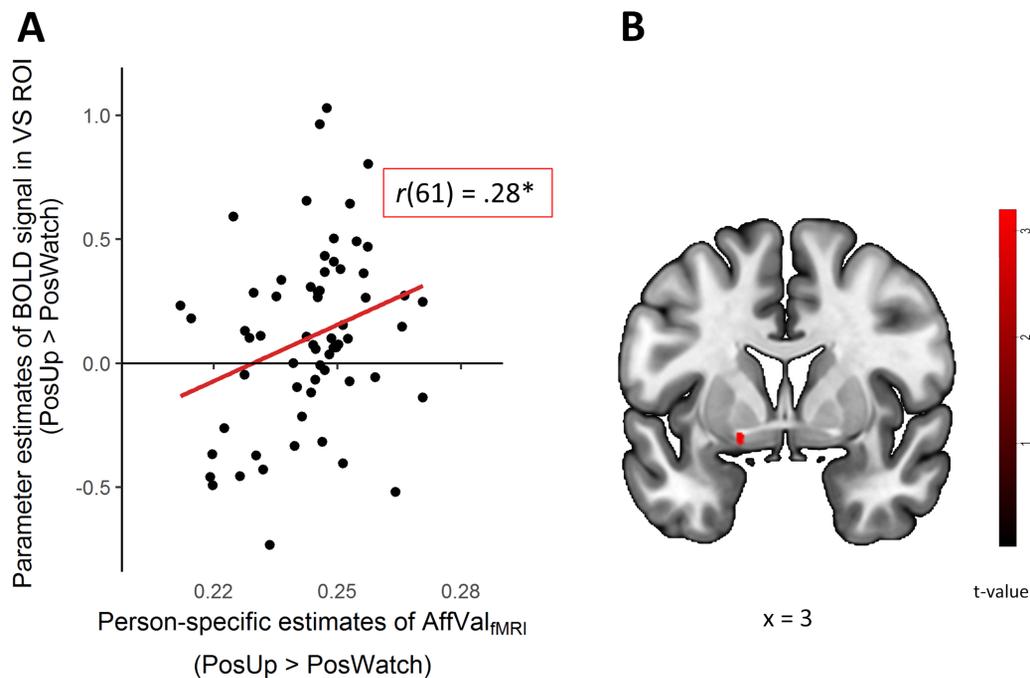


Fig. 3. Association of activity in the VS with between-person (i.e. across all trials) and within-person (i.e. trial-by-trial) differences in self-reported affective valence during the fMRI task (AffVal_{fMRI}). (A) Increased VS activity (mean activation across the entire ROI) was related to mean differences in AffVal_{fMRI} for the upregulation of emotions to positive images (PosUp), compared to passively watching them (PosWatch) and (B) positive association of changes in AffVal_{fMRI} in the left VS during PosUp (ROI analysis: $[-12, 6, -12]$, $T = 3.39$, $P < 0.05$, FWE-corrected). * $P < 0.05$.

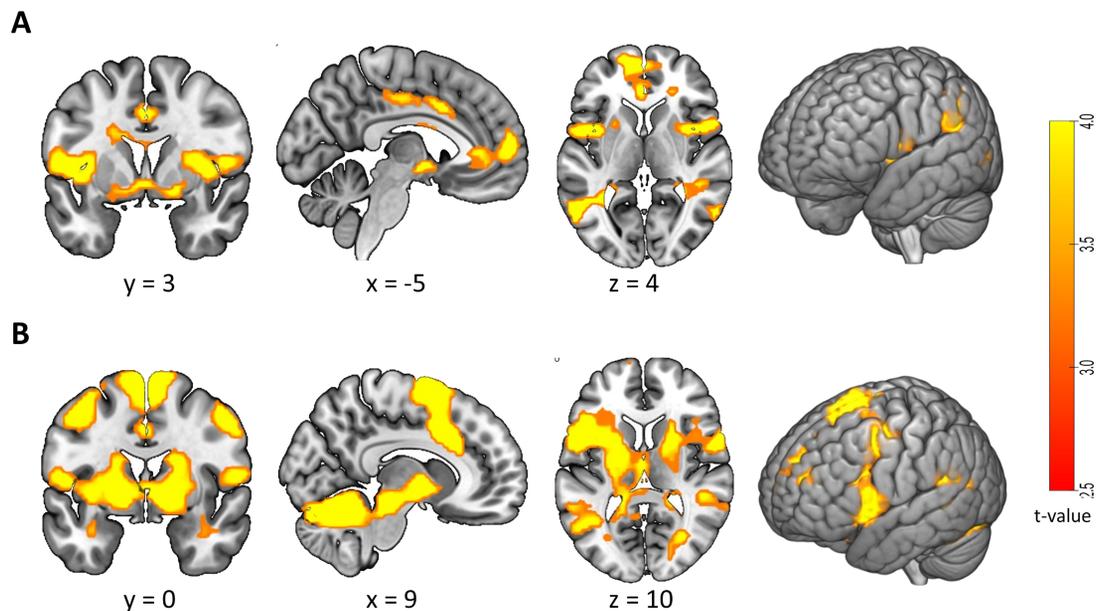


Fig. 4. Brain activation in the emotion regulation task (main effects). Regions of increased activation for the (A) main effect of valence (Positive > Neutral) and (B) main effect of instruction (Up > Watch). No significant voxels were found for the interaction. Threshold: $P < 0.001$ (uncorrected) at the voxel and $P < 0.05$ with FWE correction at the cluster level. For details, cf. Table 1. Coordinates are in MNI space.

tary motor area and in frontal, occipital and cerebellar clusters (Figure 4B, Table 1). Hypoactivation results (i.e. the inverse contrasts) are reported in the Supplement (Supplementary Table S4, Section 1.4, and Supplementary Figure S1).

Association of whole-brain activity and changes in affect. The exploratory analysis of associations between trial-by-trial changes in AffVal_{fMRI} 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 prefrontal cortex (PFC)’ and the psychological concepts ‘arousal’, ‘emotion’ and ‘valence’ for the

Table 1. Whole-brain analysis for the interaction, main effect of valence and main effect of instruction. For corresponding brain plots, see Figure 4. For the inverse contrasts, see Supplementary Table S4 and Supplementary Figure S1

Brain regions	Side	k	t	MNI coordinates		
				x	y	z
Interaction						
No significant voxels						
Positive > Neutral						
Supramarginal gyrus	R	502	7.70	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	4.40	30	-72	9

Note. Clusters labeled according to the anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). Threshold: $P < 0.001$ (uncorrected) at the voxel level and $P < 0.05$ with FWE correction at the cluster level.

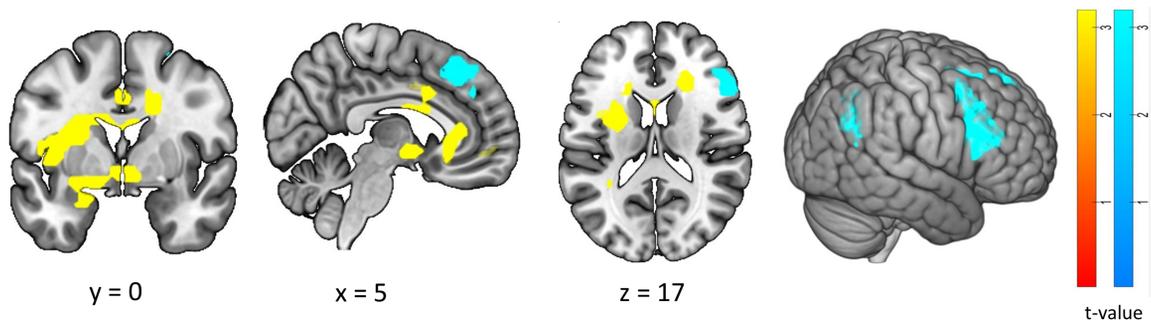


Fig. 5. Whole-brain parametric analysis with changes in affect. Regions in which the BOLD signal was positively (yellow) or negatively (blue) related to changes in self-reported affective valence (AffVal_{fMRI}) during image presentation in the fMRI task (across all conditions). Threshold: $P < 0.001$ (uncorrected) at the voxel level and $P < 0.05$ with FWE correction at the cluster level. For details, see Table 2.

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 AffVal_{fMRI} (for a full list of the first 25 entries and their correlation values, see Supplementary Table S5).

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

Affect in fMRI and in daily life. Participants who had higher means of AffVal_{fMRI} also had higher means of AffVal_{ESM}, $r(61) = 0.31$, $P = 0.01$, Supplementary Figure S2. Moreover, greater affect variability (within-person standard deviations) in the laboratory was associated with greater affect variability in daily life, $r(61) = .37$, $P = 0.003$, Supplementary 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 AffVal_{ESM} during up-regulation in daily life, $r(61) = 0.00$, $P = 0.97$.

Exploring whole-brain activity, changes in affect and affect in daily life. Parameter estimates from the whole-brain parametric analysis of trial-by-trial changes in AffVal_{fMRI} (from all clusters

that showed a significant positive association with AffVal_{fMRI}, cf. Figure 5) were significantly negatively correlated with mean AffVal_{ESM} in daily life, $r(59) = -0.32$, $P = 0.01$, Figure 6. That is, participants with lower daily affect showed a stronger association between changes in AffVal_{fMRI} and activation in these emotion-related regions.

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 (i) higher between-person differences in AffVal_{fMRI} and (ii) greater within-person changes in AffVal_{fMRI} 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 AffVal_{ESM} when up-regulating

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

Brain regions	Side	k	t	MNI coordinates		
				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: $P < 0.001$ (uncorrected) at the voxel level and $P < 0.05$ with FWE correction at the cluster level.

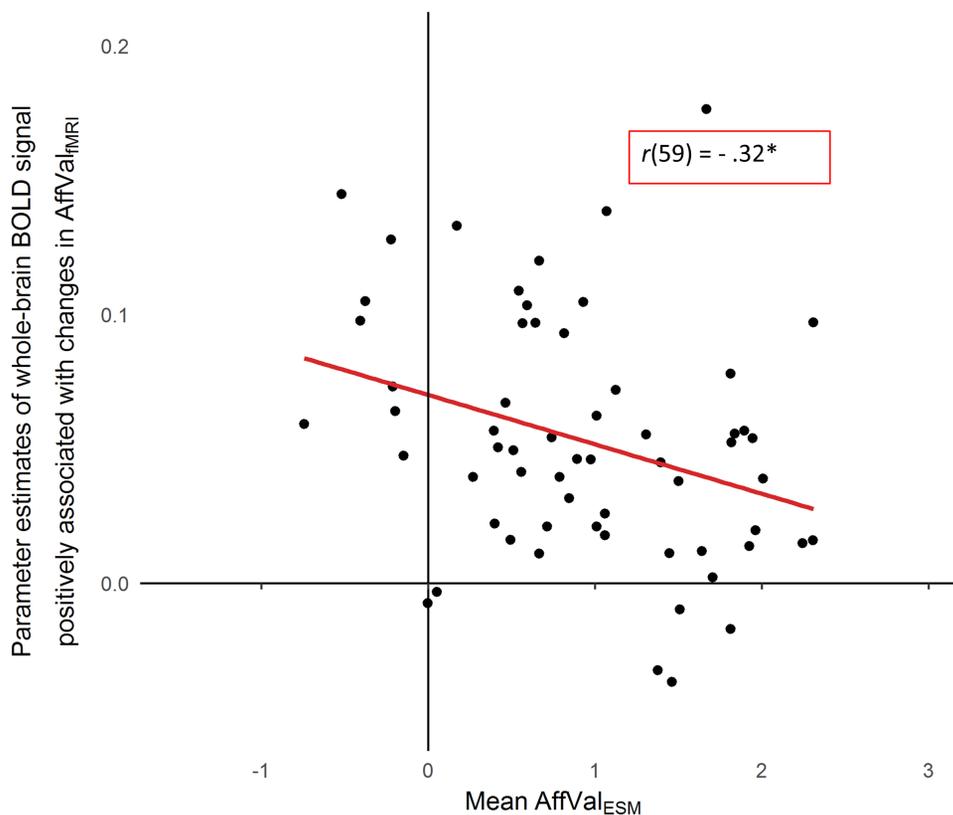


Fig. 6. Link between affect in daily life and emotion-related brain activation in the laboratory. Mean self-reported affective valence in daily life ($AffVal_{ESM}$) was negatively correlated with the BOLD signal in medial frontal and subcortical emotion-related regions that showed a significant positive association with self-reported affective valence during the fMRI task ($AffVal_{fMRI}$; whole-brain parametric analysis; see Table 2 and yellow clusters in Figure 5). * $P < 0.05$.

positive emotions in daily life. However, an exploratory (whole-brain) parametric analysis showed that the lower a participant's mean $AffVal_{ESM}$ in daily life, the stronger the involvement of a set of medial frontal and subcortical emotion-related brain regions (including the VS) in changing affect during the task in the laboratory.

Up-regulation to positive and neutral images

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' $AffVal_{fMRI}$. Thus, in

addition to the VS representing heightened positive experiences (Kringelbach and Berridge, 2009), it may serve another function during emotion regulation: VS activity may represent the general pursuit of an up-regulation goal (Ochsner et al., 2012). This notion is in line with the meta-analytic finding of increased VS activity during the up-regulation (as compared to the down-regulation) of 'both' positive and negative emotions (Morawetz et al., 2017).

Like a previous study (Greening et al., 2014), we found that increased activation in the VS was associated with more positive $AffVal_{fMRI}$ (across trials) 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 $\text{AffVal}_{\text{fMRI}}$ 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 and Cheavens, 2014) or intensity (Silvers et al., 2015b) of the emotion to be regulated.

Neural responses underlying changes in affect

Our data suggest that other brain regions and networks (in addition to the VS) also reflect changes in affective experiences. The whole-brain parametric analysis showed that changes in $\text{AffVal}_{\text{fMRI}}$ —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 et al., 2016).

Besides activation in these emotion-related regions, changes in $\text{AffVal}_{\text{fMRI}}$ were also associated with hypoactivation 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 et al., 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 repeatedly been shown to be active during cognitive reappraisal (Buhle et al., 2014) and associated with within-person changes in ‘negative’ affective experiences (Silvers et al., 2015a). In our study, similar prefrontal control regions were relatively ‘less’ recruited with positive changes in $\text{AffVal}_{\text{fMRI}}$. Two possible explanations for this finding are the following.

First, hypoactivation 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). During the up-regulation of positive emotions, an already existing affective experience is further intensified and regulatory efforts are suggested to be inversely proportional to the intensity of the affective experience to be regulated (Quoidbach et al., 2015). Hence, while the up-regulation of mild positive affect or 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), up-regulating (intense) positive emotions may simply mean ‘admitting more’ of an already existing emotional experience. Along these lines, participants are thought to regulate their positive emotions, as compared to regulating their negative emotions, more frequently and more successfully in their daily lives (Heiy and 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 hypoactivation in right fronto-parietal regions for the endogenous generation of positive emotions (besides activations in emotion-related regions; Engen et al., 2017). Thus, enhancing positive affective experiences may more strongly draw upon emotion generation than on alteration processes, compared to reducing negative affect (Silvers et al., 2015a;

see also [Supplementary Figure S3](#) and Supplement 1.5). 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 during up-regulation in fMRI and shifts in momentary affect when up-regulating in daily life was not supported by the data. Also the association between mean levels of self-reported affective valence and affect variability 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. For example, the capacity to change one’s emotional response upon instruction (as tested in the laboratory; Webb et al., 2012) possibly differs from the capacity to spontaneously regulate one’s emotions (as usually done in daily life).

Interestingly, in participants with lower mean affect in daily life (i.e. mean $\text{AffVal}_{\text{ESM}}$), more variance of changes in $\text{AffVal}_{\text{fMRI}}$ could be explained by 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 feeling worse in daily life 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 et al., 2011) and recent ESM findings from our group suggest that people with lower well-being benefit more (in terms of their momentary affect) from daily positive events (Grosse Rueschkamp et al., 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 similarity between laboratory/fMRI and daily life by, for example, having participants engage in spontaneous rather than instructed emotion regulation during fMRI or by instructing participants to use specific (comparable) strategies in both circumstances.

Second, when investigating affective processes, it is important to consider the timescale at which affective change occurs (Hollenstein et al., 2013). During fMRI, changes in affect are measured across seconds, whereas in daily life affective responses are assessed across minutes and hours. Thus, these two measures possibly capture different regulation processes (e.g. mood vs 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 hypoactivation 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 are available at SCAN online.

Conflict of interest

None declared.

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