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Authors

Parrish, Michael H
Dutcher, Janine M
Muscatell, Keely A
et al.

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Frontostriatal functional connectivity underlies self-enhancement during social evaluation

Michael H. Parrish,[1] Janine M. Dutcher,[2] Keely A. Muscatell,[3] Tristen K. Inagaki,[4] Mona Moieni,[1] Michael R. Irwin,[5] and Naomi I. Eisenberger[1]

[1]Department of Psychology, University of California, Los Angeles, CA 90095, USA
[2]Department of Psychology, Carnegie Mellon University, Pittsburgh, PA 15213, USA
[3]Department of Psychology and Neuroscience, The University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA
[4]Department of Psychology, San Diego State University, San Diego, CA 92182, USA
[5]Norman Cousins Center for Psychoneuroimmunology, Semel Institute for Neuroscience and Human Behavior and Department of Psychiatry and Biobehavioral Science, University of California, Los Angeles, CA 90095, USA
Correspondence should be addressed to Michael H. Parrish, Department of Psychology, University of California, 5566 Pritzker Hall, Los Angeles, CA 90095-1563, USA. E-mail: mparrish@ucla.edu.

Abstract

Self-enhancement, the tendency to view oneself positively, is a pervasive social motive widely investigated in the psychological sciences. Relatively little is known about the neurocognitive mechanisms underlying this motive, specifically in social-evaluative situations. To investigate whether positive emotion regulation circuitry, circuitry involved in modulating positive affect, relates to the self-enhancement motive in social contexts, we conducted an functional magnetic resonance imaging (fMRI) study in a healthy young adult sample. We hypothesized that self-enhancement indices (state and trait self-esteem) would relate to greater functional connectivity between right ventrolateral prefrontal cortex (RVLPFC), a region implicated in emotion regulation, and the ventral striatum (VS), a region associated with reward-related affect, during a social feedback task. Following social evaluation, participants experienced stable or decreased state self-esteem. Results showed that stable state self-esteem from pre- to post-scan and higher trait self-esteem related to greater RVLPFC–VS connectivity during positive evaluation. Stable-state self-esteem also related to greater RVLPFC–VS connectivity during negative evaluation. Moreover, RVLPFC activation during all types of feedback processing and left VS activation during negative feedback processing was greater for participants with stable-state self-esteem. These findings implicate neurocognitive mechanisms underlying emotion regulation in the self-enhancement motive and highlight a pathway through which self-enhancement may restore feelings of self-worth during threatening situations.

Key words: self-enhancement; fMRI; ventral striatum; emotion regulation

Self-enhancement, the tendency to view oneself favorably, is a core human social motive and is found, in some form, within all cultures (Sedikides and Gregg, 2008; Fiske, 2018). Across several countries, individuals have been shown to self-enhance on personality traits deemed personally relevant to themselves or their cultures more broadly (Sedikides *et al.*, 2003). Importantly, the universality and primacy of self-enhancement have been confirmed by a large-scale meta-analysis using over 500 diverse, independent samples (Mezulis *et al.*, 2004). Indeed, self-enhancement may be a pervasive part of human nature because enhancing personal attributes or values has evolved as a useful cognitive adaptation to protect one's self-view from the challenging or stressful events we face daily (Alicke, 1985; Taylor and Sherman, 2008). Attesting to its importance, research into self-enhancement as a coping strategy has been one of the most widely studied topics in social and personality psychology and has been a mainstay in psychology since the days of Freud (Alicke and

Sedikides, 2011). However, despite the steady stream of research on the topic of self-enhancement in social and personality psychology to date, research has yet to reach a consensus about the psychological or neural mechanisms underlying self-enhancement. The current study focuses on using neuroimaging to explore whether emotion regulation circuitry is critical for self-enhancement. Given the importance of characterizing disruptions in these emotion regulation neural mechanisms in psychological disorders, such as depression, the current research results have the potential to highlight possible targets for future investigations and interventions in translational and clinical neuroscience.

Behavioral studies in social psychology suggest a strong link between self-enhancement-related processes and emotion regulation mechanisms. These studies point to an important role for self-enhancing strategies in increasing positive affect in particular. Some researchers have even speculated that mood regulation

and restoration of positive affect is the primary functional benefit of self-enhancement (Tesser, 2000; Sedikides and Gregg, 2008). For example, behavioral research suggests that individuals with positive self-views engage in regulatory processes in order to 'savor' or enhance positive feelings in the context of self-relevant events (Bryant, 1989, 2003; Wood *et al.*, 2003, 2005). Specifically, following the description of positive and personally relevant events, individuals with greater self-enhancing tendencies tended to enjoy and magnify their success (Wood *et al.*, 2003), whereas individuals with less self-enhancing tendencies tended to mute or dampen the positive feelings associated with the events. In addition, related research shows that self-serving judgments about the desirability or favorability of one's own qualities are used strategically to regulate affective experience to improve negative mood (Roese and Olson, 2016). For example, in response to failures, self-enhancers often seek opportunities to repair mood by increasing positive affect (e.g. watching comedic videos) and improving self-related feelings (e.g. reinterpreting feedback in a self-serving manner; Heimpel *et al.*, 2002; Alicke and Sedikides, 2009). Relatedly, self-enhancers tend to report overly optimistic attitudes about others' future perceptions of their own behaviors when facing the threat of social evaluation (Preuss and Alicke, 2009). Moreover, individuals with self-enhancing tendencies often maintain an inflated self-image in the face of adversity by using positive affirmations of their personal values (Taylor and Armor, 1996; Taylor and Sherman, 2008), suggesting that self-related positive affect may be upregulated in response to threat. Taken together, these studies suggest that the mechanisms of self-enhancement are most likely rooted in the mechanisms of domain-general positive emotion regulation, specifically regulatory mechanisms that increase positive affect.

Neuroscience approaches can be utilized to investigate whether emotion regulation-related neural mechanisms underlie individual differences in self-enhancement. Concerning the specific regulatory mechanisms that might account for self-enhancement effects, both upregulation and downregulation of positive affect have been tied to ventral striatum (VS) functioning (Kim and Hamann, 2007; Wager *et al.*, 2008; Greening *et al.*, 2014). More specifically, connectivity between ventrolateral prefrontal cortex (VLPFC) and VS may be an important regulatory circuit implicated in positive reappraisal (Wager *et al.*, 2008). Research has shown that the effect of right VLPFC (RVLPFC) activation on emotion regulation outcomes is mediated in part by reward-related VS activation (Wager *et al.*, 2008). Taken together, previous research in psychology and neuroscience points to an important role for positive emotion regulation circuitry, specifically circuits involved in modulating reward-related activity, in maintaining favorable self-views and motivational processes which underlie them.

To date, however, few studies have focused on the neural underpinnings of self-enhancement effects and those that have, have mostly focused on self-referential processes rather than positive emotion regulation mechanisms (Beer and Hughes, 2011; Hughes and Beer, 2012a, 2012b; Chavez and Heatherton, 2015). Specifically, in most earlier neuroimaging studies examining self-enhancement, participants were instructed to rate a personality trait adjective's self-relatedness or explicitly compare themselves to their peers (Beer and Hughes, 2010; Beer, 2014). Although this is a well-known method for assessing the presence of self-enhancement, this task may be less similar to the real-life situations in which self-enhancement processes are engaged, such as in response to evaluative feedback, and thus may be less likely to recruit emotion regulatory processes. This may be

one of the multiple reasons why previous investigations have yet to find reliable associations between self-enhancement effects and activity in either reward-related regions or positive emotion regulation circuitry (Beer and Hughes, 2011; Kuzmanovic *et al.*, 2016; Chavez *et al.*, 2017; Flagan *et al.*, 2017; Izuma *et al.*, 2018). Thus, neuroimaging research employing naturalistic tasks which simulate real-life situations in which self-enhancing processes are utilized, such as in response to social evaluative feedback, is critically needed.

In order to examine a possible circuit-level neural correlate of self-enhancement, we administered an experimental fMRI task in which subjects would have a chance to self-enhance in response to receiving positive and negative feedback from others. Participants completed an fMRI scan in which they received feedback about how an evaluator ostensibly rated their personality and opinions. A third of the feedback they received was positive, a third was neutral, and a third was negative. They were told that this feedback came from a peer (who was actually a confederate) who listened to a previously recorded audio interview in which the participant discussed themselves. Prior to the scan, participants completed standard questionnaire measures of trait self-esteem. Before and after the evaluative task in the scanner, participants indicated their state self-esteem, and we calculated whether subjects showed a drop in their state self-esteem from pre- to post-task or whether their state self-esteem remained stable (did not change). Based on prior work (Eisenberger *et al.*, 2011) and since subjects received considerable negative feedback during the task, we did not expect state self-esteem to increase. Individuals who maintained a stable level of state self-esteem in response to this evaluative task were inferred to have been more likely to engage in self-enhancement processes during the task itself than those who showed a drop in state self-esteem.

To examine whether emotion regulation circuitry plays a role in the act of self-enhancement, we examined whether RVLFPC–VS functional connectivity positively related to indices of self-enhancement (i.e. trait and state self-esteem). We hypothesized that stronger functional connectivity in the RVLFPC–VS circuit in response to positive and negative evaluative feedback would be related to stable levels of state self-esteem, as well as relatively higher levels of trait self-esteem.

Methods
Participants

Fifty participants (23 female; M = 23.36 years, range: 18–47 years) provided data for the present study. Participants were recruited from University of California, Los Angeles (UCLA) and the surrounding community. The study generally represented standard UCLA demographics: 48% White, 28% Asian/Pacific Islander, 16% Latino/Chicano, 2% Black/African American and 6% other. In total, 115 participants were originally enrolled in a larger study (ClinicalTrials.gov identifier NCT01671150) for which this current study was a follow-up investigation. The purpose of the larger study was to examine effects of inflammation on social and affective responses, and thus half of the full sample of participants received an injection of an inflammatory challenge (0.8 ng/kg endotoxin; Moieni *et al.*, 2015). All participants incorporated into the present follow-up investigation were a part of the placebo control group and therefore did not receive the inflammatory drug. Neural responses to this task as a function of the inflammatory challenge have been reported previously (e.g. Muscatell

et al., 2016). This paper focuses specifically on how functional connectivity related to individual differences in trait self-esteem and changes in state self-esteem from before to after the evaluative task in subjects in the placebo condition only.

Procedure

Potential participants were excluded during phone screening and in-person screening due to contraindications for the MRI environment (e.g. metallic implants, left-handedness and claustrophobia) and history of neurological or psychiatric disorders (through the Structured Clinical Interview for DSM-IV Axis I Disorders (SCID)). They were also excluded if they had a history of physical health problems (e.g. allergies, autoimmune disease, Body Mass Index (BMI) greater than 30, current prescription or recreational drug use). All participants provided written informed consent. The UCLA Institutional Review Board (IRB) approved all study procedures. Complete procedures for the study session have been explained in full elsewhere (Moieni *et al.*, 2015). On the experiment day, participants arrived at the UCLA Clinical and Translational Research Center, where a nurse inserted a catheter into the dominant forearm for hourly blood draws and a catheter into the opposite forearm for continuous saline flush and drug (placebo) administration. Following administration of the drug/placebo, participants completed an audio-recorded interview during which they were asked about their personal characteristics and opinions for about 10 min (e.g. 'What makes you happy?', 'What is your best quality?', 'What is your greatest shortcoming?' and 'What are you most afraid of?'). During the MRI scan, participants were informed that evaluators would listen to and form impressions of them based on their interview and that participants would rate how they felt in response.

fMRI social feedback task

Upon arrival at the MRI scanning center, participants met two other individuals (actually confederates; one male, one female) with whom they believed they would be interacting during the MRI tasks. Specifically, for the present task, participants were told that while they were in the MRI scanner, the evaluators would be seated in the scanner control room and listen to the participant's interview. They would provide feedback about how the participant came across in the interview. In reality, participants in the scanner viewed the computer screen displaying an array of adjective 'buttons' (i.e. 'interesting' 'modest' and 'boring') and watched a pre-recorded video of a cursor moving around the screen, which they were led to believe was the real-time display of the confederate's feedback on their interview. The number of feedback adjectives selected was equally divided into a positive category (e.g. 'intelligent'), a neutral category (e.g. 'practical'), and a negative category (e.g. 'annoying'). Participants watched as a new adjective button was selected every 10–12 s. During the entirety of the scan, participants received fifteen each of positive, neutral, and negative feedback selections. All feedback was presented in a pseudorandom order with the constraint that no more than two adjectives of the same valence were presented consecutively. Following the experimental session, participants were promptly debriefed in a funneled manner and informed of the true purpose of the task. No participants reported suspicion prior to debriefing about the true purpose of the task.

State self-esteem measure

Participants rated their state self-esteem before starting the scan and again immediately after completing the scanning session. Based on previous studies (Leary *et al.*, 1998), participants rated their state self-esteem by judging 'how they felt right now' on a 4-point Likert scale from 1 (really bad) to 4 (really good). First, difference scores were calculated by subtracting pre-session state self-esteem from post-session state self-esteem. Then, participants were grouped based on whether they showed a decline in state self-esteem ($n = 19$) or remained stable in state esteem ($n = 20$) from before to after the social feedback categorized as either stable (no change) or declined (1–2 point change). No participants showed an increase in state self-esteem.

Trait self-esteem measure

Trait self-esteem was measured approximately 2 h before the scanning session using the Rosenberg Self-Esteem Scale (Rosenberg, 1965). This measure is the most widely used measure for global self-worth and has been shown to have good internal consistency and construct validity. This scale assesses self-views with items such as 'I feel that I have a number of good qualities'. Ratings are on a 4-point Likert scale from 1 (strongly agree) to 4 (strongly disagree).

MRI data collection

Imaging data were acquired from a Siemens 3 T Tim Trio MRI scanner at the UCLA Staglin IMHRO Center for Cognitive Neuroscience. A high-resolution T1-weighted echo-planar imaging volume (spin-echo, repetition time = 5000 ms; echo time = 33 ms; matrix size 128 × 128; 36 axial slices; field-of-view = 20 cm; 3 mm thick, skip 1 mm) and T2-weighted, matched-bandwidth anatomical scan (slice thickness = 3 mm, gap = 1 mm, 36 slices, TR = 5000 ms, TE = 34 ms, flip angle = 90°, matrix size 128 × 128, FOV = 20 cm) were obtained for each participant. Afterward, a functional scan was acquired which lasted 8 min, 38 s (echo planar T2-weighted gradient-echo, TR = 2000 ms, TE = 25 ms, flip angle = 90°, matrix size 64 × 64, 36 axial slices, FOV = 20 cm; 3 mm thick, skip 1 mm).

MRI preprocessing

MRI data were preprocessed with the Statistical Parametric Mapping software (SPM8; Wellcome Department of Cognitive Neurology, London, UK). The pipeline for preprocessing incorporated functional realignment to correct for head movement, co-registration of the functional to the structural images, spatial normalization of functional and structural images to Montreal Neurologic Institute (MNI) space (resampled at 3 mm isotropic), and spatial smoothing using an 8-mm Gaussian kernel, full width at half maximum, to increase signal-to-noise ratio. The feedback task was modeled as a block design. The presentation of each feedback word (positive, negative or neutral trait adjectives) and the subsequent 10 s were modeled as a block.

Functional connectivity analyses

Functional connectivity analyses were conducted with the CONN toolbox (nitrc.org/projects/conn) implemented through MATLAB and SPM8 software. The preprocessed functional and structural data were entered into the toolbox. Confounding variables distorting functional connectivity values were removed through the CONN CompCor algorithm for physiological noise and temporal filtering was applied ($f > 0.008$ Hz). Realignment parameters (representing head movement) produced during preprocessing were also entered in the toolbox as nuisance covariates to be removed from statistical analyses. For the functional data

collected during the social feedback task, condition onsets and durations (10 s for each block) were specified in the toolbox so that the blood oxygenation level dependent (BOLD) time series could be appropriately divided into task-specific blocks.

For the main statistical tests of interest, we conducted region of interest (ROI)-to-ROI generalized psychophysiological interactions (gPPI) analyses to determine functional connectivity (i.e. temporal correlations) between the RVLPFC and both left and right VS. For these analyses, we chose ROIs implicated in previous studies of emotion regulation (Frank *et al.*, 2014). The RVLPFC ROI was generated by creating a spherical volume centered on peak coordinates in right inferior frontal gyrus (MNI 45, 22, 4) from a previous meta-analysis on the neural correlates of cognitive emotion regulation (Frank *et al.*, 2014). The right and left VS ROIs were structurally defined using the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer *et al.*, 2002). The ventral parts of the right and left caudate nucleus and putamen from the atlas were constrained at x between 0 and –24, y between 4 and 18, and z between 0 and –12 for the left ROI and x between 0 and 24, y between 4 and 18, and z between 0 and –12 for the right ROI (based on ROIs from Inagaki and Eisenberger, 2012). Thus, we constrained the ROI to the ventral parts of the caudate nucleus and putamen to create this VS ROI.

Within the ROIs, the BOLD activation time series was averaged across all voxels. Functional connectivity (gPPI parameter estimates) values were computed on each individual's feedback condition time series from these ROIs at the single-subject level. These connectivity values provide a measure of the statistical dependence of the ROIs' BOLD activation time series. Connectivity values underwent Fisher's r-to-Z transformation to ensure assumptions of normality. This procedure was completed to generate task-evoked absolute connectivity measures for each of the three social feedback conditions. Relative connectivity measures were generated by taking the difference between connectivity values produced by the positive trials *vs* the neutral trials and the negative trials *vs* the neutral trials. In other words, they should be interpreted as the difference in the functional coupling between these neural regions (i.e. RVLPFC and VS) between these conditions. These gPPI parameter estimate values were imported into SPSS v23 for further statistical analyses. We first examined differences in RVLPFC–VS connectivity during positive (*vs* neutral) feedback between stable and decreased state self-esteem groups by performing independent samples t-tests and Mann–Whitney U tests due to concerns about data normality and outliers. We then performed the same analyses for RVLPFC–VS connectivity during negative (*vs* neutral) feedback. To examine correlations between trait self-esteem and RVLPFC–VS connectivity, we computed Pearson's correlations and Spearman's rank correlations between trait self-esteem and RVLPFC–VS connectivity during positive (*vs* neutral) feedback as well as during negative (*vs* neutral) feedback.

Exploratory follow-up whole-brain connectivity analyses

Given the possibility of other regions' regulatory influences on VS functioning, we conducted exploratory whole-brain analyses with the left VS (LVS) as seed ROI. Independent samples t-tests were conducted to analyze state self-esteem group differences, and regression analyses were conducted to assess correlations with trait self-esteem. Standard statistical thresholding was applied (P < 0.001 voxel-level, uncorrected; P < 0.05 cluster-level false discovery rate (FDR)-corrected).

Exploratory follow-up univariate analyses

To better characterize the RVLPFC–VS circuitry and its response to the social evaluation task, we additionally extracted parameter estimates from the original univariate activation analyses (for preprocessing steps, see Muscatell *et al.*, 2016). Specifically, we extracted parameter estimates for the RVLPFC and LVS since their functional connectivity was shown to relate to self-enhancement indices significantly. These ROI parameter estimates were computed individually for each feedback condition (compared to implicit baseline) using the Marsbar SPM toolbox (www.nitrc.org/projects/marsbar). To first characterize differences between the feedback conditions, we conducted paired samples t-tests and Wilcoxon signed-rank tests. Independent samples t-tests and Mann–Whitney U tests were conducted to compare state self-esteem group differences, and Pearson's and Spearman's rank correlations were conducted to determine associations between these neural measures and trait self-esteem.

Results

RVLPFC–VS functional connectivity during feedback processing

Relationships with changes in state self-esteem

To examine whether subjects with stable state self-esteem were engaging in greater self-enhancement processes, we examined whether those who maintained stable state self-esteem in response to both positive and negative feedback showed greater RVLPFC–VS functional connectivity than those who showed a drop in state self-esteem.

First, concerning neural activity to positive (*vs* neutral) feedback, we found that the stable state self-esteem group showed significantly greater positive connectivity between RVLPFC and LVS compared to the group that showed decreases in state self-esteem [t(37) = 2.948, P = 0.003; Figure 1A]. Nonparametric statistical testing was additionally used due to concerns about data normality and outliers. A Mann–Whitney U test also revealed that the stable self-esteem group showed significantly greater positive connectivity than the decreased self-esteem group (U = 278.00, P = 0.007). Results indicated that functional connectivity between the RVLPFC and the right VS (RVS) was not significantly different between stable and decreased state self-esteem groups [t(37) = 0.35, P > 0.05; U = 181.00, P > 0.05].

We next examined neural activity to negative (*vs* neutral) feedback. Similar to what was observed in response to positive feedback, the stable state self-esteem group, relative to the decreased self-esteem group, showed significantly greater positive RVLPFC–LVS connectivity during negative (*vs* neutral) feedback [t(37) = 1.70, P = 0.049; U = 130.00, P = 0.046, Figure 1B]. Again, no differences between groups were found for functional connectivity between the RVLPFC and the RVS [t(37) = 0.59, P > 0.05; U = 219.00, P > 0.05].
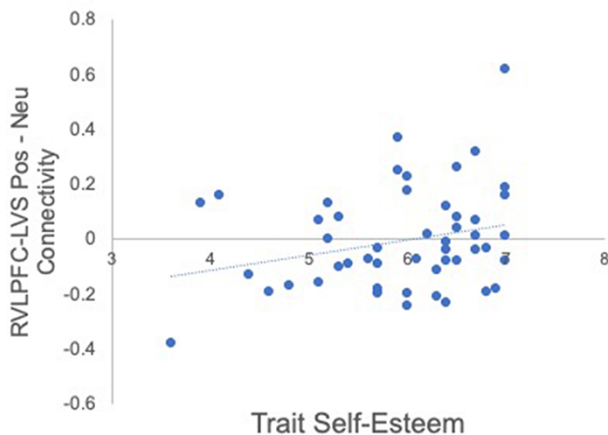
Relationships with trait self-esteem

First, upon examination of state self-esteem group differences, we found there to be no difference between the groups with respect to trait self-esteem [t(37) = 0.105, P > 0.05]. We next examined the relationship between trait self-esteem and RVLPFC–VS connectivity in response to both positive and negative feedback across the entire sample. Here, we found that, in response to positive (*vs* neutral) feedback, trait self-esteem significantly correlated with RVLPFC–LVS connectivity [r(48) = 0.257, P = 0.036; Figure 2], such that individuals with higher trait self-esteem showed greater
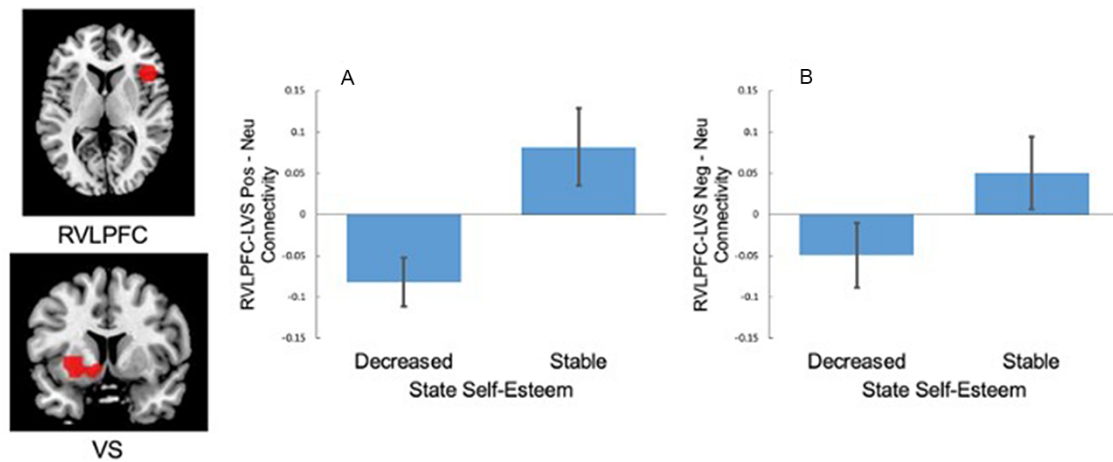
Fig. 1. Bar graphs depicting difference in RVLPFC–LVS functional connectivity during positive *vs* neutral (left, A) and negative *vs* neutral social feedback (right, B) between stable and decreased state self-esteem groups.

Fig. 2. Scatterplot depicting the significant relationship between trait self-esteem and RVLPFC–LVS functional connectivity during positive *vs* neutral social feedback.

positive connectivity in the positive feedback condition relative to the neutral condition. These results remained the same when using a Spearman's rank correlation analysis [$\rho(48) = 0.238$, $P = 0.048$]. However, this same significant relationship did not hold for RVLPFC connectivity with the RVS [$r(48) = 0.181$, $P = 0.104$; $\rho(48) = 0.187$, $P = 0.097$].

Finally, when examining functional connectivity during negative (*vs* neutral) feedback, trait self-esteem was not significantly positively correlated with either RVLPFC–LVS connectivity [$r(48) = 0.120$, $P > 0.05$; $\rho(48) = 0.131$, $P > 0.05$] or RVLPFC–RVS functional connectivity [$r(48) = 0.143$, $P > 0.05$; $\rho(48) = 0.084$, $P = 0.282$].

Exploratory follow-up whole-brain connectivity results

No clusters of differential LVS connectivity between state self-esteem groups survived statistical corrections. No clusters of differential LVS connectivity correlating with trait self-esteem survived statistical corrections.

Exploratory follow-up activation results

As a result of finding significant associations between RVLPFC–LVS connectivity and self-enhancement measures, we further explored whether either of these region's activation levels showed

a similar pattern of results. First, we examined whether there were differences in either RVLPFC or LVS activation across the feedback conditions. For RVLPFC, activation was significantly greater for negative compared to neutral [$t(49) = 2.39$, $P = 0.011$; $W = 927.00$, $P = 0.003$] and positive feedback processing [$t(49) = 3.23$, $P = 0.001$; $W = 312.00$, $P = 0.001$] as well as significantly greater for neutral compared to positive feedback processing [$t(49) = 1.92$, $P = 0.031$; $W = 459.00$, $P = 0.043$]. For LVS, activation was significantly stronger for negative compared to positive feedback processing [$t(49) = 2.29$, $P = 0.013$; $W = 156.00$, $P = 0.002$] and neutral compared to positive feedback processing [$t(49) = 3.51$, $P < 0.001$; $W = 330.00$, $P = 0.002$]; there was no significant difference between negative and neutral feedback processing [$t(49) = 0.612$, $P = 0.272$; $W = 637.00$, $P = 0.500$].

Moreover, when examining differences between those whose state self-esteem remained stable *vs* those whose state self-esteem decreased as a function of the task, we found that RVLPFC activation was greater for stable self-esteem participants (compared to those with decreased self-esteem) in response to positive [$t(37) = 1.581$, $P = 0.061$; $U = 125.00$, $P = 0.035$], neutral [$t(37) = 1.856$, $P = 0.036$; $U = 119.00$, $P = 0.023$] and negative [$t(37) = 2.122$, $P = 0.020$; $U = 115.00$, $P = 0.018$] feedback. While LVS activation during positive [$t(37) = 0.973$, $P = 0.168$; $U = 119.00$, $P = 0.175$] and neutral [$t(37) = 1.167$, $P = 0.125$; $U = 155.00$, $P = 0.168$] feedback did not significantly differ between state self-esteem groups at standard thresholds, we found some evidence for LVS activation during negative feedback processing to be stronger for the stable (*vs* decreased) self-esteem group [$t(37) = 1.696$, $P = 0.049$; $U = 140.00$, $P = 0.083$; Figure 3], consistent with the idea that this region might be involved in self-enhancement in response to threat. Analyses of relationships with trait self-esteem and RVLPFC and LVS activation yielded non-significant results ($P > 0.05$).

Discussion

The goal of the present research was to examine whether measures of self-enhancement were related to functioning within neural circuitry previously linked to emotion regulation, particularly regulatory processes implicated in increasing positive affect. In particular, we investigated whether frontostriatal functional connectivity during a social evaluation task positively related to changes in state self-esteem in response to socially evaluative

RVLPFC Activation
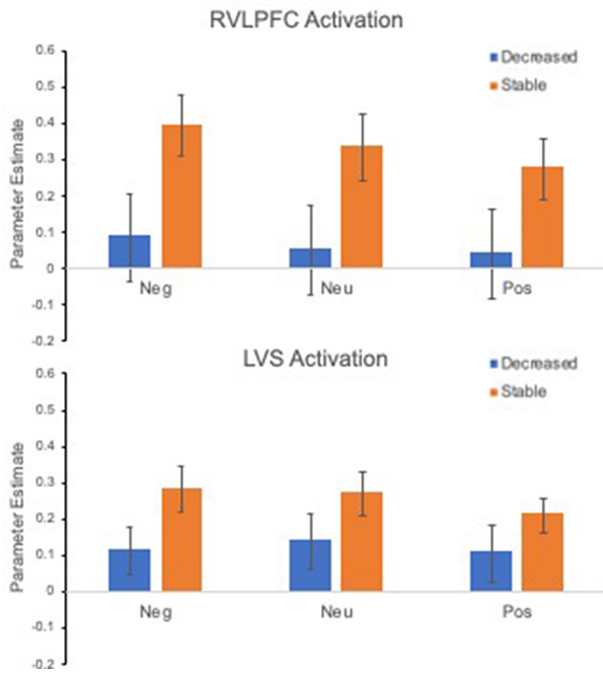
LVS Activation

Fig. 3. Bar graphs depicting differences in RVLPFC activation (top) and LVS activity (bottom) during negative, neutral, and positive feedback conditions as a function of stable and decreased state self-esteem groups.

feedback as well as individual differences in trait self-esteem. The current research builds upon earlier findings by examining self-enhancing tendencies with a functional connectivity approach, using a more naturalistic behavioral task and targeting a previously unexamined measure of neural circuit functioning linked to emotion regulation, namely connectivity between RVLPFC and the VS.

Results indicated that individuals with greater positive connectivity between RVLFPC and LVS during positive and negative feedback showed more stable state self-esteem than those whose self-esteem decreased in response to the evaluative feedback. In addition, greater positive connectivity between RVLFPC and LVS during positive (*vs* neutral) feedback was associated with higher levels of trait self-esteem. Additionally, follow-up exploratory activation analyses revealed that RVLPFC and LVS activation were most active to negative feedback conditions. Moreover, RVLPFC activation during all feedback conditions was greater for individuals who maintained stable state self-esteem than those who showed decreased state self-esteem. Additionally, VS activation in response to negative feedback was greater for individuals who maintained stable self-esteem than those who showed a decrease in self-esteem. These findings align with research demonstrating the importance of self-enhancement as a coping mechanism which may serve to upregulate or restore positive affect in reaction to threatening situations.

It is important to note that, based on the presumed role of the VS in responding to positive feedback, it might be expected that the VS would be most active to positive instead of negative feedback, as we observed here. While this could seemingly call into question the role of reward processing for this region during the task, it is possible that the LVS is generally involved in the motivation-related reward processes needed to maintain adaptive emotion regulation during the task. Indeed,

this account of the LVS in motivation-related reward processes, such as self-enhancement, is consistent with the finding that (i) LVS activity was greater in response to negative and neutral feedback compared to positive feedback (e.g. negative and neutral feedback would require more self-enhancement to regulate) and (ii) those with more stable (*vs* decreased) state self-esteem showed greater LVS activity in response to negative feedback specifically. Considering this account, the motivational processes underpinned by LVS functioning could thus be needed to maintain stable self-worth in response to negative feedback. Whether or not this circuitry is definitively involved in the motivational aspects of self-enhancement needs to be a focus of future research.

To date, the vast majority of social and affective neuroscience research on emotion regulation has focused on downregulating negative emotions. The current set of results point to the possibility that self-enhancement may be important, not only for decreasing negative affect but for increasing positive affect as well, in order to restore feeling of self-worth in response to critical social evaluation. The present results, which emphasize the importance of functional connectivity between RVLPFC and VS, align with evidence showing that these regions are important for regulating positive affect. For example, both upregulation and downregulation of positive affect have been linked to VS activity (Kim and Hamann, 2007; Wager *et al.*, 2008; Greening *et al.*, 2014). Critically, RVLPFC activity has also been shown to directly correlate with subjective ratings of increased positive affect during emotion regulation tasks (Kim and Hamann, 2007). This is notable given that most emotion regulation research has focused on the role of the RVLPFC in regulating negative affect. The current study highlights the RVLPFC–VS circuitry as another important neural pathway involved in regulating emotional well-being and self-worth.

In addition, the present results are well-aligned with social psychology behavioral research, emphasizing the importance of upregulating positive affect for maintenance of self-enhancing tendencies. For example, behavioral studies suggest individuals maintain positive self-views by engaging regulatory processes in order to 'savor' or enhance positive feelings in the context of self-relevant events (Bryant, 1989, 2003; Wood *et al.*, 2003, 2005). Notably, self-enhancing individuals have been shown to enjoy and magnify their success (Wood *et al.*, 2003), whereas individuals with less self-enhancing tendencies fail to amplify the positive feelings associated with the event. Moreover, self-enhancement occurs in contexts of social-evaluative threats or aversive events as well (Taylor and Armor, 1996; Rudman *et al.*, 2007; Taylor and Sherman, 2008; Preuss and Alicke, 2009). Taken together, separate lines of previous research in both social psychology and neuroscience have emphasized the importance of positive emotion regulatory processes for supporting well-being and self-worth; however, the current neuroimaging study is novel in its approach by demonstrating the importance of these processes for self-enhancement in a more naturalistic setting in which emotion regulation was not explicitly prompted.

While prior neuroimaging investigations into self-enhancement processes have been informative, many previous studies have not utilized experimental paradigms simulating naturalistic social evaluative situations (c.f., Hughes and Beer, 2012b). This may be one of the reasons for the previous lack of evidence linking functioning of the VS and regulatory circuits to self-positivity biases and self-enhancing behaviors. For example, most investigations into neural correlates of self-positivity biases,

such as the 'above average effect' (participants rating themselves more positively than statistically possible), have failed to reveal consistent activation in reward-related regions. Specifically, activation in VS has shown no association with some measures, while interestingly, ventromedial prefrontal cortex (VMPFC) has been shown to negatively correlate with self-enhancing behavior in some research (Beer and Hughes, 2010). Alternatively, other research has shown that measures of self-enhancement in reaction to specific threat conditions do indeed correlate with VMPFC activity (Hughes and Beer, 2012b). Hence, additional work is needed to further clarify the neural correlates of self-enhancement in response to self-threatening situations.

The current study may have multiple methodological advantages in comparison to prior studies. First, the experimental paradigm leverages a naturalistic behavioral task with a high degree of psychological realism; that is, participants believed that the social evaluative feedback was from similar peers and, as a result, their levels of state self-esteem fluctuated as they would in real-life situations. Second, our functional connectivity approach allowed us to target regulatory processes unobtrusively while not explicitly prompting conscious emotion regulation. These combined advantages allowed us to effectively examine the functioning of a putative positive emotional regulatory neural mechanism as it likely occurs in response to real-world social evaluation.

Our pattern of neural findings, suggesting the importance of upregulating positive affect for self-worth, also reinforces the significance of similar findings in the clinical neuroscience of emotion regulation. Research shows that greater frontostriatal connectivity relates to greater self-reported positive affect among depressed patients, whereas a lack of frontostriatal connectivity is associated with depressive symptoms (Heller *et al.*, 2013). Healthy profiles of functional connectivity between lateral PFC and VS are sustained over time in healthy adults (Heller *et al.*, 2009). However, depressed patients who are unable to sustain lateral PFC–striatum connectivity experience reduced positive affect. Research also shows that greater lateral PFC–VS connectivity is associated with lower levels of trait anhedonia in healthy adults (Keller *et al.*, 2013). Importantly, tasks involving naturalistic mood induction link positive affect in healthy adults with frontostriatal connectivity (Admon and Pizzagalli, 2015). Finding frontostriatal connectivity to be related to self-enhancement seems quite reasonable in the light of the findings focused on clinical disorders and health and emotional well-being. Given our results, findings showing that depressed patients have lower levels of frontostriatal functioning may also suggest that an inability to generate a sense of self-worth in depression is associated with connectivity in this circuit. Future research should explore this interesting potential direction.

While the pattern of observed results generally matched our prior hypotheses, a few noteworthy exceptions and study limitations are worth highlighting. First, although we predicted that trait self-esteem would be correlated with RVLPFC–VS functional connectivity in response to both positive (*vs* neutral) and negative (*vs* neutral) feedback, results showed trait self-esteem only correlated with connectivity in response to positive (*vs* neutral) feedback and did not correlate with univariate activation responses in RVLPFC or VS. Although it is not clear why, the fact that trait self-esteem did not correlate with connectivity to negative feedback could mean trait self-esteem maintenance may relate more to increasing positive affect (or savoring the experience) following positive experiences rather than increasing positive affect after negative experiences.

Second, we found hemispheric laterality effects, such that the main set of significant associations was primarily found for the left VS. This is somewhat unexpected given that there is a lack of definitive evidence for hemispheric specialization in VS functioning in the context of self-enhancement-related processes. Regardless, prior studies targeting the RVLPFC–VS pathway to investigate the neural correlates of emotion regulation success have also found unexpected hemispheric differences. In particular, Wager *et al.* (2008) using a voxelwise mediation analysis found that the relationship between RVLPFC activity and emotion reappraisal success was specifically mediated by a cluster of activity within the LVS. It remains to be seen whether there will be definitive evidence for the specific involvement of RVLPFC–LVS circuit functioning in future neuroimaging studies on the topic of self-enhancement.

Third, the current investigation may have suffered from statistical power issues. Despite positive results, the current set of analyses was not planned based on an a priori power analysis. This is particularly pertinent to consider for the results of correlational analyses. Past research into neuroimaging best practices has indicated that sample sizes significantly larger than this ($n > 100$) are required to produce reliable estimates of correlational results concerning individual differences across contexts (Dubois and Adolphs, 2016; Elliott *et al.*, 2018). Given this significant limitation, future researchers should aim to replicate these findings. We warn against overinterpretation of these present results until replication has been conducted.

Fourth, while we believe that differences in RVLPFC–VS functional connectivity may be reflecting differences in positive emotion regulation in response to experimental stimuli, we lacked multiple convergent measures to confirm this interpretation definitively. Nonetheless, multiple studies investigating similar neural circuitry have found direct associations between frontostriatal functioning and positive affect (Heller *et al.*, 2009; Keller *et al.*, 2013; Admon and Pizzagalli, 2015). Moreover, previous researchers have also directly linked frontostriatal functioning to more active forms of explicit emotion regulation (Kim and Hamann, 2007; Wager *et al.*, 2008; Greening *et al.*, 2014). Further research is needed to definitively confirm associations between dynamic changes in self-worth, positive mood and PFC–VS connectivity.

In summary, the present study results on self-enhancement inform current areas of research linking positive emotion regulation mechanisms (e.g. mechanisms involved in generating feelings of self-worth) to the functional interactions between the PFC and striatum. Using a task simulating naturalistic social interaction, the current study showed that neural circuits connecting regulatory-related PFC and reward-related VS regions are likely involved in generating feelings of self-worth in response to threatening or challenging social feedback. Our findings support prior research demonstrating that the self-enhancement motive is underpinned by emotional regulation mechanisms which upregulate or restore positive affect in social-evaluative contexts. These results may have implications for clinical disorders such as depression, given that these disorders have been consistently linked with reduced functioning within frontostriatal circuits and are characterized by impaired self-esteem. Lastly, these findings underscore the importance of examining social processes with multiple types of functional neuroimaging measures (e.g. functional connectivity) and with paradigms more closely approximating the real-world situations in which these social processes emerge.

Conflict of interest

None declared.

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