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Thumbs up or thumbs down: neural processing of social feedback and links to social motivation in adolescent girls

Megan M. Davis,[1] Haina H. Modi,[2] Haley V. Skymba,[2] Megan K. Finnegan,[2] Katherine Haigler,[3] Eva H. Telzer,[1] and Karen D. Rudolph[2]

[1]Department of Psychology and Neuroscience, University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA
[2]Department of Psychology, University of Illinois at Urbana-Champaign, Champaign, IL 61820, USA
[3]Human Development and Family Studies, Pennsylvania State University, State College, PA 16802, USA
Correspondence should be addressed to Megan M. Davis, Department of Psychology and Neuroscience, University of North Carolina at Chapel Hill, 235 E. Cameron Street, Chapel Hill, NC 27599, USA. E-mail: davismeg@unc.edu

Abstract

Adolescence is a period of rapid biological and psychological development, characterized by increasing emotional reactivity and risk-taking, especially in peer contexts. Theories of adolescent neural development suggest that the balance in sensitivity across neural threat, reward and regulatory systems contributes to these changes. Building on previous research, this study used a novel social feedback task to explore activation and functional connectivity in the context of social threat and reward in a sample of mid-adolescent girls ($n = 86$, $M_{age} = 16.32$). When receiving negative peer feedback, adolescents showed elevated activation in, and amygdala connectivity with, social processing regions [e.g. medial prefrontal cortex (mPFC) and temporoparietal junction (TPJ)]. When receiving positive feedback, adolescents showed elevated activation in social and reward (e.g. mPFC and ventromedial prefrontal cortex) processing regions and less striatum-cerebellum connectivity. To understand the psychological implications of neural activation and co-activation, we examined associations between neural processing of threat and reward and self-reported social goals. Avoidance goals predicted elevated amygdala and striatum connectivity with social processing regions [e.g. medial temporal gyrus (MTG)], whereas approach goals predicted deactivation in social processing regions (e.g. MTG/TPJ and precuneus), highlighting the importance of considering individual differences in sensitivity to social threat and reward in adolescence.

Key words: adolescence; neuroimaging; social goals; social evaluation

Adolescence is a period of significant physical, psychological and social change, with associated increases in emotional lability and impulsivity (Crone and Dahl, 2012; Romer *et al.*, 2017; Rapee *et al.*, 2019). Theories of adolescent neural development link heightened neural reactivity in threat avoidance and reward motivation systems, in conjunction with less effective regulatory control, to these increases in emotional distress and risk-taking during adolescence (Steinberg, 2008; Powers and Casey, 2015). In the present study, we developed a novel social feedback task (authors omitted for masked review) that allowed us to examine neural responses to peer evaluation of personally salient decisions. This task maps onto a common, but understudied, experience of adolescence, namely, receiving feedback about peer opinions, and can therefore provide insight into processing of daily peer encounters. This study extends current theory and research by exploring both neural activation and functional connectivity (FC) in the context of negative and positive peer feedback, allowing us to expand beyond knowledge about regional activation to understand integration across systems engaged in social feedback processing. Furthermore, this is the first study to examine how these patterns of neural processing differ as a function of individual differences in social avoidance and approach motivation, advancing our understanding of the psychological implications of social feedback processing in adolescents.

Adolescent neural sensitivity to threat and reward

The triadic neural systems model (Ernst *et al.*, 2006; Ernst, 2014) proposes that adolescent emotion and behavior are linked to the balance in sensitivity across three nodes of neural function: (a) an avoidance system, which processes threat and is centered in the amygdala; (b) a motivation system, which includes regions involved in reward processing [e.g. ventral striatum (VS), medial

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prefrontal cortex (mPFC) including the ventromedial PFC (vmPFC) and orbitofrontal cortex (OFC)]; and (c) a cognitive control system, which includes regions involved in multiple aspects of attention and inhibition [e.g. dorsolateral PFC (dlPFC)]. Relative activation in threat, reward and control regions and connectivity across these systems may help explain heightened negative affect and sensitivity to social reward, which are thought to lead to emotional distress and impulsive risk-taking as well as increased social reorientation and exploration during adolescence.

When viewing threatening images, adolescents are less effective than children and adults at regulating their affect and show heightened activation in the amygdala, a key region in the avoidance system (Hare *et al.*, 2008; McRae *et al.*, 2012). The threat of social exclusion or rejection may be especially salient for adolescents, who are particularly attuned to their social networks (O'Brien and Bierman, 1988; Knoll *et al.*, 2015). A growing body of research probes neural processing of social threat using tasks that evoke experiences of social exclusion, rejection or negative evaluation (Somerville *et al.*, 2006; Guyer *et al.*, 2009; Jarcho *et al.*, 2016). Consistent with the triadic systems model, these studies reveal that adolescents show elevated amygdala reactivity when anticipating evaluation from peers (Lau *et al.*, 2012) and that pre-adolescent children (Achterberg *et al.*, 2017) but not young adults (Achterberg *et al.*, 2016; van de Groep *et al.*, 2021) show elevated amygdala activation when receiving negative (relative to positive) peer feedback, suggesting developmental trends in these patterns. Expanding beyond this model, negative social evaluation and exclusion also activate regions involved in social processing and salience detection that are considered sensitive to the pain of social rejection [e.g. anterior cingulate cortex (ACC) and insula] in adolescent (Masten *et al.*, 2009; Will *et al.*, 2016) and young adult (Somerville *et al.*, 2006) samples. Social evaluation also activates regions involved in mentalizing about the self and others [e.g. temporoparietal junction (TPJ), posterior cingulate cortex (PCC) and superior temporal sulcus (STS)] in adolescents (Bolling *et al.*, 2011a) and young adults (Cassidy *et al.*, 2012), and activation in these regions is stronger in adolescents than adults in response to threat (McRae *et al.*, 2012). The mPFC, which is considered a node of the motivation system, also shows elevated activation to rejection in adolescents (Sebastian *et al.*, 2011) and to cues signaling social threat in addition to reward in children (Achterberg *et al.*, 2018) and young adults (van de Groep *et al.*, 2021) and thus may play a broader role in social status monitoring (Crone *et al.*, 2020).

Adolescence is also a stage of heightened reward seeking and reward reactivity (Steinberg, 2008; Telzer, 2016). Compared to adults, adolescents show both more activation in motivation system nodes (including the VS and OFC), and more willingness to take risks, in the presence of peers (Chein *et al.*, 2011). Adolescents are especially sensitive to *social* rewards, such as inclusion and positive peer evaluation (Galván, 2010; Quarmley *et al.*, 2019). Consistent with the triadic systems model, studies reveal elevated activation in the VS, mPFC and OFC in response to inclusion in adolescents (Gunther Moor *et al.*, 2010) and in response to positive feedback in pre-adolescents and adults (Achterberg *et al.*, 2016; 2018; van de Groep *et al.*, 2021). Expanding beyond this model, regions outside the motivation system that are involved in social processing and salience detection (e.g. ACC, insula) and mentalizing (superior temporal gyrus) show greater activation to peer acceptance than rejection in adolescents (Guyer *et al.*, 2012).

Although the triadic systems model emphasizes the importance of balance across the avoidance, motivation and cognitive control systems (Ernst, 2014), previous research on social threat and reward processing largely focuses on localized patterns of activation within discrete brain regions. To test assumptions of this model, it is important to examine whether nodes of the avoidance (e.g. amygdala) and motivation (e.g. VS) systems exhibit differences in patterns of FC with the PFC or other regions that may serve a regulatory function in social contexts (e.g. mentalizing regions) during social threat and reward processing.

Studies examining FC within the context of social threat reveal greater amygdala-ventrolateral PFC (vlPFC) connectivity during an emotion regulation task after (vs. before) rejection in adolescent girls (Miller *et al.*, 2019), as well as stronger connectivity within and across mentalizing (Schmälzle *et al.*, 2017) and social pain (Bolling *et al.*, 2011b) networks during social exclusion relative to inclusion. These findings indicate that social threat may elicit functional integration across threat and social processing networks. However, one study found less amygdala-mPFC and amygdala-ACC connectivity during exclusion relative to inclusion in adolescents (McIver *et al.*, 2019), highlighting the need for further examination of FC during social threat. Within the context of reward, connectivity studies (Robinson *et al.*, 2012), including those using monetary reward tasks (Cho *et al.*, 2013), suggest greater connectivity between VS and a diverse network of frontoparietal regions as well as the insula and other limbic structures across development. However, patterns of connectivity across both avoidance and motivation systems within a social context (which is especially salient during adolescence) remain to be explored.

This study built on previous research by using whole-brain analyses to examine neural responses to social threat and reward within the same social feedback task. Moreover, to test assumptions of the triadic systems model, which posits that communication across neural systems is integral to emotional experience and behavior, we used FC analyses to identify regions that show co-activation with key nodes of the avoidance (i.e. amygdala) and motivation (i.e. VS) systems during social threat and reward processing.

Individual differences in sensitivity to social threat and reward

To understand the psychological significance of neural activation to social feedback, we also examined associations with psychological indexes of social threat and reward motivation, as reflected in self-reported social goals. Social goal theory (e.g. Elliot *et al.*, 2006; Gable, 2006; Rudolph, 2021) distinguishes between performance-avoidance goals (i.e. demonstrating competence by minimizing negative social judgments) and performance-approach goals (i.e. demonstrating competence by gaining positive social judgments and prestige). Performance-avoidance goals are associated with more fear of negative evaluation (Jeanne Horst *et al.*, 2007) and a tendency to ignore or minimize conflict following peer aggression (Rudolph *et al.*, 2011), suggesting that youth with higher avoidance goals may be more reactive to the receipt of negative peer feedback. Performance-approach goals are associated with less prosocial behavior and more aggression (Rodkin *et al.*, 2013), and more disengagement when victimized (Rudolph *et al.*, 2011). Youth with higher approach goals thus may show both hyper-reactivity (e.g. aggression) and hypo-reactivity (e.g. disengagement) in the context of peer feedback.

Despite a lack of research on social avoidance goals, previous work examining the avoidance-related trait of behavioral inhibition (characterized by anxiety and withdrawal in novel social situations) suggests that behavioral inhibition predicts more activation to negative peer feedback in the right vlPFC in adolescents (Guyer *et al.*, 2015). Social reticence, a construct closely related to behavioral inhibition and characterized by hesitancy in social situations, predicts more insula and dorsal ACC activation and less insula-vmPFC connectivity when preadolescents anticipate feedback from unpredictable relative to nice peers (Jarcho *et al.*, 2016), suggesting that temperamental avoidance may predict more reactivity in, and less integration across, social and salience processing regions. Findings for reward processing have been more mixed, with behavioral inhibition predicting more activation of the caudate to positive peer feedback in adolescents (Guyer *et al.*, 2014) but less activation of the VS to monetary reward in young adults (Simon *et al.*, 2010).

Limited research exploring the approach-related trait of behavioral activation (characterized by the tendency to seek out rewarding situations) reveals that high behavioral activation predicts more activation in the VS and mPFC to monetary reward in young adults (Simon *et al.*, 2010; Kim *et al.*, 2015), suggesting that approach goals may be associated with greater neural reactivity to reward receipt. However, these studies involved a monetary reward and examined general approach motivation; motivation to demonstrate social competence, as in the case of high social performance-approach goals, may show different patterns of association with neural activation to social threat and reward.

Although theories of adolescent neural development implicate neural processes that may shape motivated behavior, studies have not yet examined how neural responses to social threat and reward differ as a function of social goals. Thus, the second aim of this study was to elucidate the psychological implications of neural sensitivity to social threat and reward by exploring how patterns of activation and connectivity are associated with individual differences in social avoidance and approach goals.

Study overview

This study explored neural activation and connectivity in threat avoidance and reward motivation systems using a novel social feedback task in which adolescents indicated their preferences in a variety of relevant daily life domains and received feedback indicating whether other teens ostensibly agreed or disagreed with their preferences or were neutral (i.e. half agreed and half disagreed). This task replicates realistic experiences of social threat and reward (finding out that other teens approve or disapprove of one's personal preferences) using a robust control (neutral feedback) and requiring minimal deception, making it well-suited to the study of social processing in adolescents.

We conducted whole-brain voxel-wise analyses to examine activation to negative and positive (*vs* neutral) feedback. Additionally, we conducted connectivity analyses using the amygdala seed region in the context of negative (*vs* neutral) feedback and the VS seed regions in the context of positive (*vs* neutral) feedback. To understand the psychological implications of neural processing of social threat and reward, we examined how activation and connectivity were associated with individual differences in social performance-avoidance and performance-approach goals. In line with previous studies, we hypothesized that negative feedback would be associated with more activation in regions involved in threat (i.e. amygdala) and social (e.g. mPFC, insula, ACC, and STS) processing, whereas positive feedback would be associated with more activation in regions involved in reward processing (e.g. VS, mPFC, and vmpFC). Drawing on the triadic neural systems model and informed by a limited number of studies examining FC in the context of social evaluation, we hypothesized greater amygdala connectivity with cognitive control system nodes (e.g. lateral PFC) and those involved in social processing (e.g. STS) in response to negative feedback and greater VS connectivity with cognitive control system nodes in response to positive feedback. We further sought to explore whether individual differences in social goals would predict variability in activation and connectivity, such that higher performance-avoidance goals would predict more activation and amygdala connectivity in regions involved in threat and social processing, especially in response to negative feedback, and performance-approach goals would predict more activation and VS connectivity in regions involved in social processing, especially in response to positive feedback. Our study focused on neural processing of feedback specifically in mid-adolescent girls. Mid-adolescence is characterized by elevated sensitivity to social threat and reward (Romer *et al.*, 2017) and increasingly complex social demands (Brown and Larson, 2009; Schriber and Guyer, 2016), especially for girls (Hankin *et al.*, 2007; Charbonneau *et al.*, 2009), highlighting the value of focusing on social processing in girls at this stage.

Method

Participants and procedures

Participants

Participants included 86 adolescent girls ($M_{age} = 16.32$, standard deviation = 0.84, range: 14.85–17.73) who completed the Social Feedback Task while undergoing a functional magnetic resonance imaging (fMRI) scan in the summer following 9th, 10th or 11th grade (see Supplementary Table S1 for additional demographic information). Of the 90 girls who completed the study, two were excluded due to issues with fMRI data collection and another two were excluded due to excessive movement during the scan, leaving a final sample of 86 girls.

Procedures

Participants attended a laboratory session in which they first completed several questionnaires, including a measure assessing social performance goals, and then completed fMRI tasks, including the Social Feedback Task. Participants were compensated $50 for completion of the study. Parents provided written consent, and adolescents provided written assent for all study procedures. All procedures were approved by the [omitted for masked review] Institutional Review Board.

Measures

Social feedback task

Adolescents completed the Social Feedback Task (authors omitted for masked review) during an fMRI scan (Figure 1). This task was composed of 60 trials lasting approximately 11–14 seconds. During the *Decision* phase, adolescents were shown two options from a variety of domains (e.g. music genres, school subjects and activities) and used a button press to indicate which one they preferred. In the *Anticipation* phase, adolescents were shown a screen, indicating that the computer was retrieving peer feedback. In the *Feedback* phase, participants received feedback indicating whether or not other teens who had completed the task ostensibly agreed

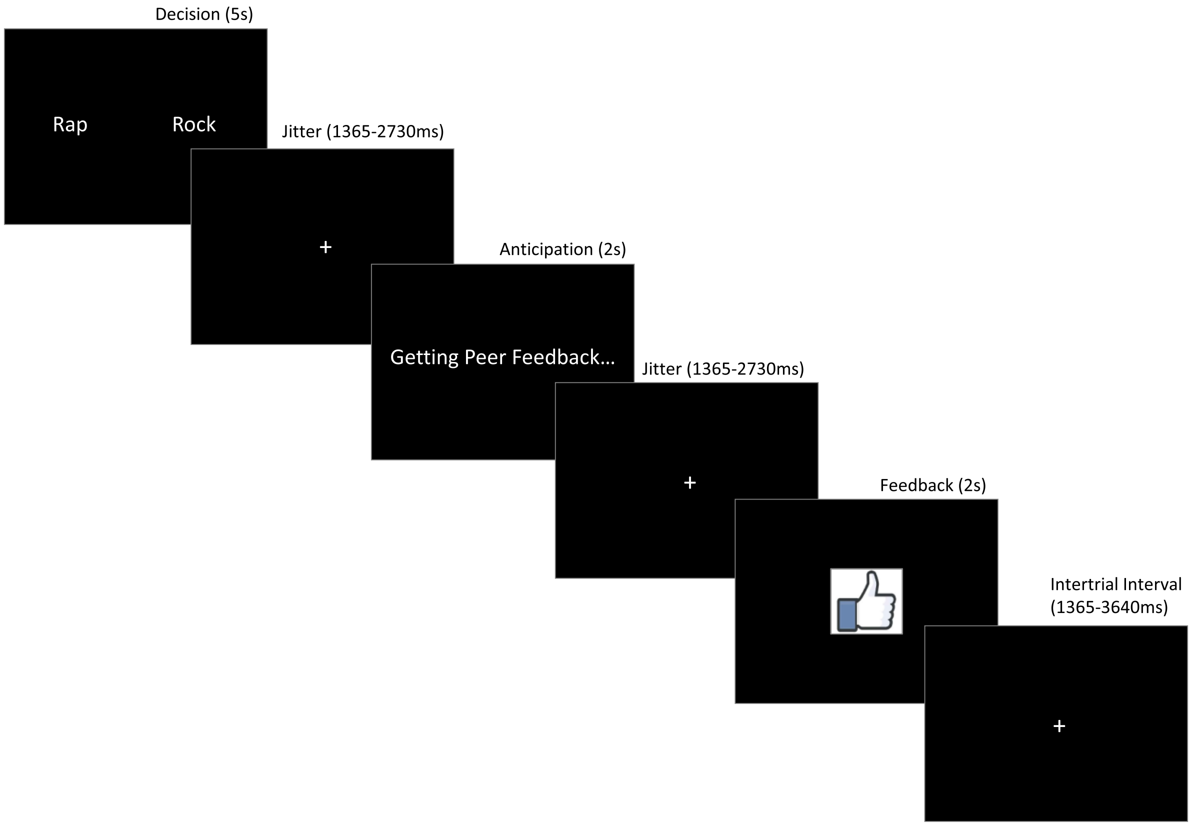

Fig. 1. Social feedback task design.

or disagreed with their choice. They saw a thumbs up (indicating that the majority of teens agreed with their choice), a thumbs down (indicating that the majority disagreed), or a thumb pointing to the side (indicating that roughly half of other teens agreed and half disagreed). In reality, the feedback was randomly generated so that adolescents saw 20 trials each of positive (thumbs up), negative (thumbs down) and neutral (sideways thumb) feedback, with the constraint that participants never saw more than two trials of any feedback type in a row. The present analyses focus on the *Feedback* phase of the task.

Social performance goals

Youth completed two subscales assessing social performance goals (Rudolph *et al.*, 2011): performance-avoidance, focused on demonstrating competence by avoiding negative peer judgments and performance-approach, focused on demonstrating competence by gaining positive peer judgments. Participants received the prompt ‘When I am around other kids…’ and responded on a 5-point scale (Not at All to Very Much). Scores were calculated as the mean of the items within each subscale; additional measure information and descriptive statistics are provided in Supplementary Table S2. Construct validity of the measure has been established in a community sample of youth (Rudolph *et al.*, 2011).

fMRI data acquisition and analysis

Functional neuroimaging data were collected using a 3 Tesla Siemens Trio MRI scanner. T2*-Weighted echoplanar images were collected during the task; structural scans consisted of a T2*-weighted, matched-bandwidth anatomical, high-resolution scan and a T1* magnetization-prepared rapid-acquisition gradient echo (MPRAGE) (see the Supplement for scanning parameters). The fMRI data were pre-processed using statistical parametric mapping (SPM8; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Images were spatially realigned to the mean to correct for head movement. Functional data were co-registered to the structural MPRAGE and transformed into standardized stereotactic space as defined by the Montreal Neurological Institute. Normalized functional data were smoothed using an 8-mm full-width-at-half-maximum Gaussian kernel to increase the signal-to-noise ratio. High-pass temporal filtering with a cutoff of 128 seconds was applied to remove low-frequency drift in the data. For each participant’s data, a general linear model (GLM) was created using regressors that corresponded to the entire duration of each phase (i.e. *Decision, Anticipation, and Feedback*) of the task. Trials with excessive head motion (over 2.5 mms absolute displacement in any direction) were de-weighted using a regressor of no interest in the GLM. Two participants were dropped from analyses due to head motion greater than 2.5 mm absolute displacement in over 25% of trials. In the remaining sample, overall motion was very low: only 0.22% of trials were censored across all included participants. Inter-trial intervals and trials in which participants did not respond were not explicitly modeled and are therefore included in the implicit baseline. For all analyses, Monte-Carlo simulations using Analysis of Functional NeuroImages (AFNI) updated (2016) 3dFWHMx and 3dClustSim programs were used to determine the cluster size necessary for a voxel-wise bi-sided threshold of $p < 0.005$ and a family-wise error rate of $p < 0.05$ for each analysis (Cox *et al.*, 2017). Smoothness was estimated with the -acf option, which used an average of individual-level autocorrelation function parameters

Table 1. Regions showing significant activation and amygdala connectivity in the negative feedback > neutral feedback contrast

Region label	k	t	x	y	z
Activation (negative > neutral)					
mPFC	2249	11.047	0	56	22
Left IFG (post-orbitalis extending into post-triangularis)	1164	9.156	−36	17	−17
Right IFG (post-orbitalis extending into post-triangularis)	322	7.663	30	17	−20
Left TPJ	226	5.923	−48	−61	28
Right dorsal caudate	66	5.382	12	5	16
Left calcarine gyrus	71	4.828	−12	−103	4
Right cerebellum	130	4.517	24	−85	−35
Right TPJ	82	4.436	48	−58	31
PCC	144	4.399	−3	−52	31
Right pSTS	75	3.905	60	−31	−5
Activation (neutral > negative)					
Left supramarginal gyrus	7541	−4.328	−57	−31	40
Right inferior temporal gyrus	7541	−9.408	54	−58	−11
Left dlPFC	1252	−7.165	−39	38	31
Middle cingulate cortex	185	−4.551	6	5	40
Right precentral gyrus	125	−3.666	33	−4	52
Amygdala connectivity (negative > neutral)					
Left dlPFC	158	4.683	−27	38	28
Left IFG (post-opercularis)	119	4.176	−45	8	19
Thalamus	80	3.955	−18	−16	13
Left TPJ	80	3.828	−60	−52	31
mPFC	128	3.429	−12	56	10
Amygdala connectivity (neutral > negative)					
No regions					

Notes: *k* refers to the number of voxels in each cluster; *t* refers to the peak activation in each cluster; x, y and z refer to Montreal Neurological Institute coordinates.

(obtained using each participant's residuals from the first-level model).

To compare activation to feedback receipt based on valence, separate regressors were created for positive (20 trials), negative (20 trials) and neutral (20 trials) feedback. Parameter estimates resulting from the GLM were then used to create linear contrasts. We used whole-brain voxel-wise one sample t-tests to assess neural activation during two contrasts: negative feedback > neutral feedback and positive feedback > neutral feedback.[1] In order to examine overlapping activation in the negative feedback > neutral feedback and positive feedback > neutral feedback contrasts, we conducted a conjunction analysis using 3dcalc in AFNI (Cox and Hyde, 1997). We used a logical AND approach (Nichols *et al.*, 2005), which requires that overlapping clusters exceed statistical threshold in the original contrasts and surpass a family-wise error rate of 0.05 in the conjunction analysis.

To assess differences in connectivity between regions during threat and reward processing (i.e. the interaction of physiological connectivity and psychological context; Friston *et al.*, 1997), we conducted psychophysiological interaction (PPI) analyses using the amygdala and VS as seed regions. The seed regions were created by combining across right and left anatomical regions as defined by the Harvard Oxford atlas (Frazier *et al.*, 2005). The gPPI toolbox in SPM8 (McLaren *et al.*, 2012) was used to (1) extract the time series from each region of interest to create the physiological variable, (2) convolve each trial type with the hemodynamic response function to create the psychological regressor and (3) multiply the physiological and psychological variables to create the interaction term. We explored functional connectivity using the amygdala seed region in the negative feedback > neutral feedback contrast and the VS seed region in the positive feedback > neutral feedback contrast.

To examine patterns of neural activation associated with youths' tendencies to avoid negative peer evaluation or seek out positive peer evaluation, we used scores on the social performance-avoidance and performance-approach subscales as predictors of activation (using whole-brain voxel-wise regression analyses) and connectivity (using PPI analyses) during the negative feedback > neutral feedback and positive feedback > neutral feedback contrasts. Social performance-avoidance and performance-approach scores were standardized and entered into whole-brain regressions in order to examine patterns of activation and connectivity associated with each goal type controlling for the other.

Results

Neural activation to negative social feedback

To examine neural processing of social threat, we compared activation to negative versus neutral feedback (Table 1). In response to negative (*vs* neutral) feedback, adolescents showed greater activation in the mPFC, bilateral TPJ, PCC, right posterior STS (pSTS), bilateral inferior frontal gyrus (IFG), dorsal caudate and cerebellum and showed less activation in the left supramarginal gyrus, right inferior temporal gyrus, left dlPFC, medial cingulate cortex and right pre-central gyrus (Figure 2). An exploratory analysis comparing negative to positive feedback revealed largely similar patterns, including increased activation in mPFC, bilateral IFG, TPJ, cerebellum and right caudate (Supplementary Table S3).

Amygdala connectivity during negative social feedback

We used a bilateral amygdala seed to examine functional connectivity to negative versus neutral feedback (Table 1). This analysis

[1] We chose the negative > neutral and positive > neutral feedback contrasts in order to separate processing of social threat and reward. Results from an additional exploratory analysis comparing negative *vs* positive feedback are presented in Supplementary Table S3.

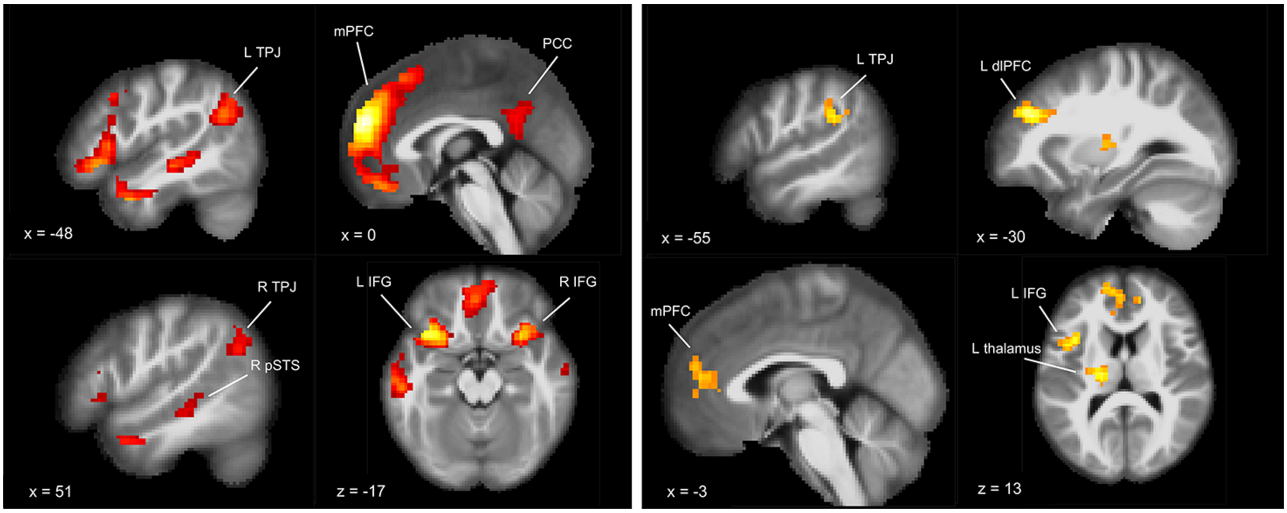

Fig. 2. Neural activation (left) and amygdala FC (right) to negative (*vs* neutral) feedback.
Note. dlPFC = dorsolateral prefrontal cortex.

Table 2. Regions showing significant activation and VS connectivity in the positive feedback > neutral feedback contrast

Region label	K	t	x	y	z
Activation (positive > neutral)					
Right cuneus	150	6.521	18	−97	16
Left cerebellum	165	6.056	−21	−91	−17
mPFC	211	3.978	−3	59	19
vmPFC	87	3.890	−6	44	−17
Activation (neutral > positive)					
Right inferior temporal gyrus	626	−6.115	57	−55	−8
Left inferior temporal gyrus	327	−5.539	−51	−49	−17
Right dlPFC	103	−4.339	48	41	13
Right inferior parietal lobule	165	−4.323	45	−37	55
Right IFG (post-opercularis)	255	−4.278	48	11	22
VS connectivity (positive > neutral)					
No regions					
VS connectivity (neutral > positive)					
Cerebellum	145	−4.0404	18	−58	−29

Notes: *k* refers to the number of voxels in each cluster; *t* refers to the peak activation in each cluster; *x*, *y* and *z* refer to Montreal Neurological Institute coordinates.

revealed greater FC between the amygdala and the left dlPFC, left IFG, thalamus, left TPJ and mPFC to negative (*vs* neutral) feedback (Figure 2).

Neural activation to positive social feedback

To examine neural processing of social reward, we compared activation to positive *vs* neutral feedback (Table 2). In response to positive (*vs* neutral) feedback, adolescents showed greater activation in the mPFC and vmPFC and nodes of the motivation system, as well as in the right cuneus and left cerebellum, and showed less activation in the bilateral inferior temporal gyrus, right dlPFC, right inferior parietal lobule and right IFG (Figure 3). An exploratory analysis comparing positive to negative feedback revealed greater activation to positive feedback in the striatum, the central node of the motivation system and several other regions including the left IFG, bilateral dlPFC, right precuneus, bilateral supramarginal gyrus, medical cingulate gyrus and bilateral cerebellum (Supplementary Table S3).

Conjunction analysis

In order to examine the overlap between patterns of activation to negative (*vs* neutral) and positive (*vs* neutral) feedback, we conducted a conjunction analysis of these two contrasts. Results of the conjunction analysis revealed an overlapping region within the mPFC that showed heightened activation to both negatively and positively valenced social feedback (Supplementary Figure S1).

VS connectivity during positive social feedback

We used a bilateral VS seed to examine FC to positive versus neutral feedback (Table 2). No regions showed greater VS connectivity, but the right cerebellum showed relatively less FC with the VS to positive (vs. neutral) feedback (Figure 3).

Patterns of neural activation associated with social performance goals

Whole brain regression analyses were conducted to examine associations between social performance goals and patterns of neural activation and co-activation to threat and reward. Separate analyses were conducted for social avoidance and social approach goals, controlling for the other goal type.

Social avoidance goals

When receiving negative (*vs* neutral) feedback, social avoidance goals were not associated with supra-threshold activation in individual regions but did predict relatively greater amygdala-left anterior middle temporal gyrus (MTG) connectivity.

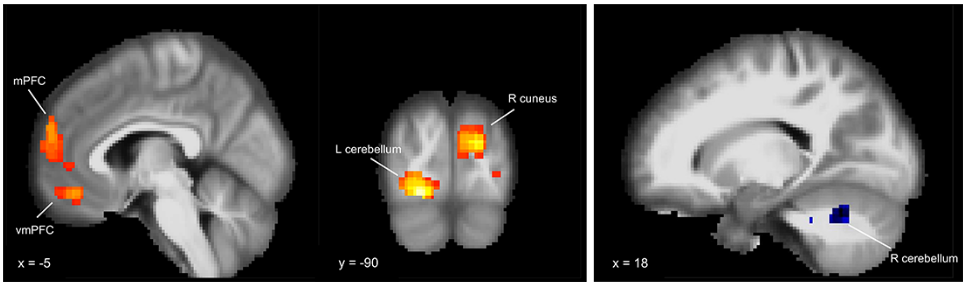

Fig. 3. Neural activation (left) and ventral striatum FC (right) to negative (*vs* neutral) feedback.

Table 3. Regions showing significant activation and FC in whole brain regressions with social performance-avoidance goals

Region label	*k*	t	x	y	z
Negative feedback					
Activation					
(negative > neutral)					
No regions					
Activation					
(neutral > negative)					
No regions					
Amygdala connectivity					
(negative > neutral)					
Left MTG	93	4.24	−51	2	−26
Amygdala connectivity					
(neutral > negative)					
No regions					
Positive feedback					
Activation					
(positive > neutral)					
No regions					
Activation					
(neutral > positive)					
No regions					
VS connectivity					
(positive > neutral)					
Left MTG	70	4.10	−51	−10	−11
Right cerebellum	82	3.37	15	−40	−44
VS connectivity					
(neutral > positive)					
No regions					

Notes: *k* refers to the number of voxels in each cluster; t refers to the peak activation in each cluster; x, y and z refer to Montreal Neurological Institute coordinates.

When receiving positive (*vs* neutral) feedback, social avoidance goals were not associated with supra-threshold activation in individual regions but were associated with relatively greater connectivity between the VS and both the left anterior MTG and right cerebellum (Table 3; Figure 4).

Social approach goals

When receiving negative (*vs* neutral) feedback, social approach goals were associated with less activation in the left precuneus, left medial frontal gyrus/dlPFC and right MTG/TPJ but were not associated with amygdala connectivity with any regions. When receiving positive (vs. neutral) feedback, social approach goals were associated with less activation in the left PCC, right parahippocampal gyrus and left precuneus and were associated with more VS-cerebellum connectivity and less VS-left IFG connectivity (Table 4; Figure 5).

Discussion

The triadic neural systems model (Ernst *et al.*, 2006; Ernst, 2014) proposes that elevated reactivity in avoidance and motivation systems, coupled with less downregulation by the PFC, contributes to increases in emotional lability, reward sensitivity, social exploration and risk-taking characteristic of adolescence. Drawing on this model, the present study used a novel social feedback task to explore activation and connectivity involving avoidance and motivation systems in response to social threat and reward in adolescent girls. Unique and overlapping findings for negative and positive feedback and associations with social goals highlight the importance of studying activation and co-activation across threat and reward processing systems within a social context.

Neural activation and FC in the context of social threat

Adolescents, compared to children and adults, show elevated emotional and neural reactivity to social threats, such as rejection and exclusion (McRae *et al.*, 2012). Contrary to hypotheses based on the triadic neural systems model, we did not find evidence of amygdala reactivity to negative feedback, which may suggest that receiving negative feedback in the context of this task was less immediately threatening than direct rejection. However, we did observe elevated reactivity to negative relative to neutral feedback across several regions involved in mentalizing about the self and others (e.g. mPFC, TPJ, pSTS, and PCC) as well as regions implicated in emotion processing (e.g. IFG and dorsal caudate) and the cerebellum. The mPFC (Amodio & Frith, 2006) and PCC (Johnson *et al.*, 2006; Leech and Sharp, 2014) are thought to play a role in monitoring one's own internal states, and the mPFC, TPJ and pSTS are activated when reasoning about others (van den Bos *et al.*, 2011; Patel *et al.*, 2019). During social monitoring, these regions also show increasing activation with age that is thought to reflect more in-depth processing of others' cognitive states (Bolling *et al.*, 2011a; Crone and Dahl, 2012). The IFG is often activated during emotion regulation (Frank *et al.*, 2014) and shows increasing activation with age (Vara *et al.*, 2014) in response to cognitive control demands. Although the cerebellum has typically not been the focus of studies on social-emotional processing, some research has found cerebellum hyper-reactivity to threat (e.g. Bolling *et al.*, 2011b), suggesting that patterns of cerebellar activation warrant further investigation.

In contrast to previous studies (e.g. Guyer *et al.*, 2009; Jarcho *et al.*, 2016; Achterberg *et al.*, 2017), we did not observe

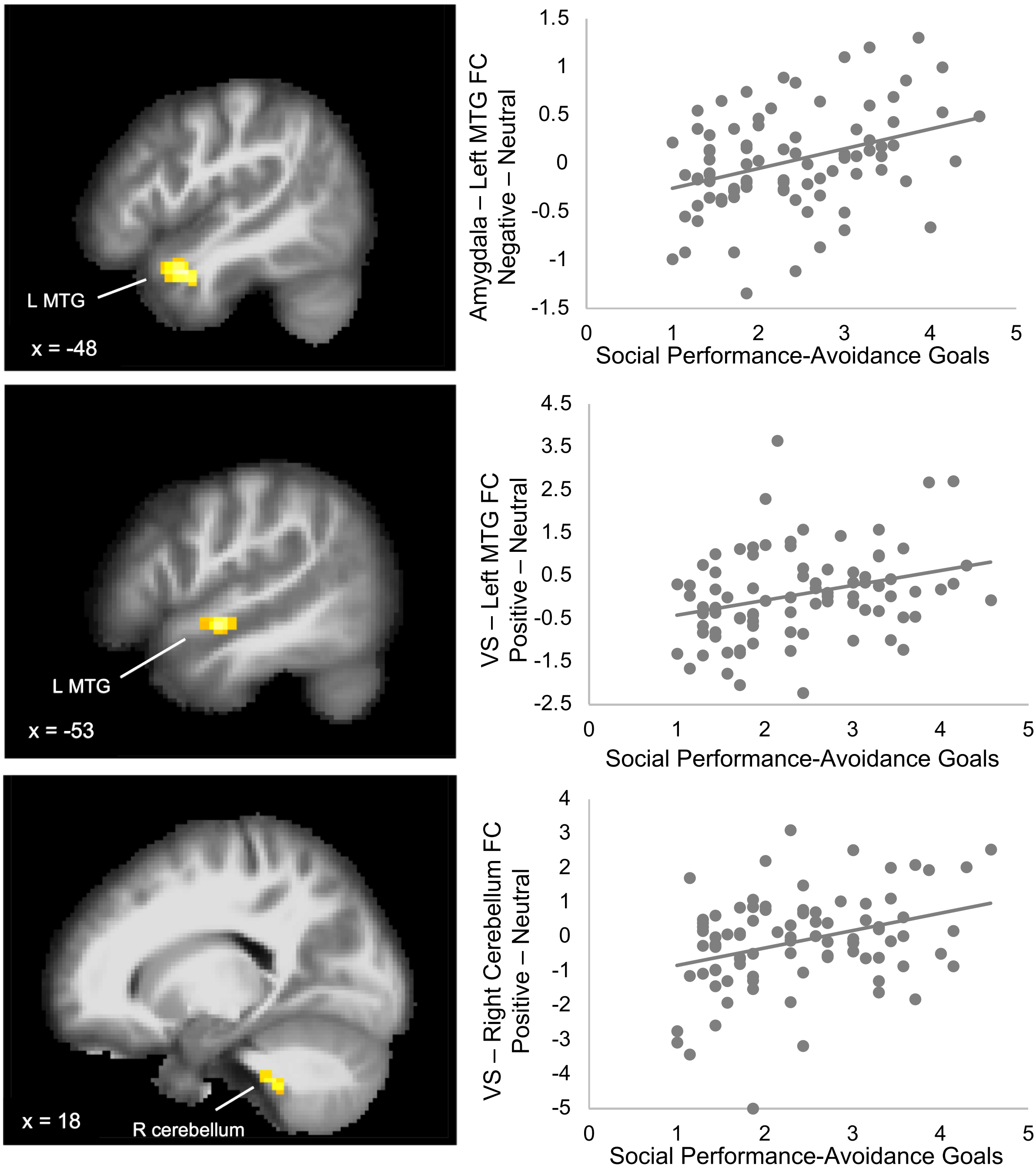

Fig. 4. Social performance-avoidance goals predicting amygdala (top) and VS (middle and bottom) FC.

increased activation in regions involved in salience detection (e.g. ACC and insula) in response to negative (*vs* neutral) feedback. This may result from differences in task design. Specifically, several previous social evaluation tasks have focused on global negative feedback about the individual, potentially eliciting more processing in regions involved in salience detection and social pain. The task used in the present study involved the receipt of feedback about specific preferences, which may lead to more mentalizing and other-focused processing. Interpreting negative peer feedback about specific preferences may require perspective taking in order to understand the discrepancy between one's own and others' views, which could explain the elevated activation we observed in regions involved in social processing. Patterns of activation observed when comparing negative to neutral feedback (e.g. heightened activation in mPFC, IFG, TPJ and cerebellum) remained largely the same when comparing negative to positive feedback (see Supplementary Table S3), suggesting that these patterns reflect enhanced reactivity to negative feedback rather than dampened reactivity to neutral feedback.

Connectivity analyses revealed greater amygdala connectivity with several regions that have been implicated in self-regulation (e.g. dlPFC and IFG) and mentalizing about others (TPJ and mPFC) during the receipt of negative relative to neutral feedback. These findings support hypotheses from the triadic neural systems model, which suggests that cooperation between avoidance and

Table 4. Regions showing significant activation and FC in whole brain regressions with social performance-approach goals

Region label	K	t	x	y	z
Negative feedback					
Activation					
(negative > neutral)					
No regions					
Activation					
(neutral > negative)					
Left precuneus	1443	−4.96	−9	−49	19
Left MFG/dlPFC	69	−3.98	−30	35	34
Right MTG/TPJ	63	−3.87	45	−64	13
Amygdala connectivity					
(negative > neutral)					
No regions					
Amygdala connectivity					
(neutral > negative)					
No regions					
Positive feedback					
Activation					
(positive > neutral)					
No regions					
Activation					
(neutral > positive)					
Left PCC	438	−5.32	−12	−46	19
Right temporal lobe/parahippocampal gyrus	85	−3.99	33	−34	25
Left precuneus	100	−3.88	−6	−64	40
VS connectivity					
(positive > neutral)					
Cerebellum	147	3.62	3	−61	−14
VS connectivity					
(neutral > positive)					
Left IFG (post-orbitalis)	152	−3.90	−48	35	1

Notes: *k* refers to the number of voxels in each cluster; *t* refers to the peak activation in each cluster; x, y and z refer to Montreal Neurological Institute coordinates. MFG = medial frontal gyrus.

cognitive control systems is implemented in the context of negative emotional states in order to promote emotion regulation. In the context of emotion regulation, the dlPFC and IFG show heightened activation (Goldin *et al.*, 2008; Frank *et al.*, 2014) and connectivity with the amygdala (Morawetz *et al.*, 2017). Patterns of greater activation and co-activation we observed may suggest more top-down control or may reflect a need to recruit greater prefrontal activation to effectively regulate amygdala reactivity (Nelson *et al.*, 2016) when receiving negative feedback. Similarly, greater amygdala connectivity with the TPJ and mPFC may suggest heightened social threat sensitivity or may reflect a process by which the emotional salience of negative feedback elicits social-cognitive processing in order to effectively adapt to the social environment.

Neural activation and FC in the context of social reward

Although social connection and approval are rewarding across the lifespan, adolescents are particularly reactive to reward (Telzer, 2016), especially in social domains (Quarmley *et al.*, 2019). In line with the triadic neural systems model, which implicates heightened activation in motivation system nodes in response to reward in adolescents, the present study found evidence of elevated reactivity to positive relative to neutral feedback in the mPFC and vmPFC (nodes of the motivation system) as well as in the cuneus and cerebellum. Interestingly, in this study, we did not find activation of the VS to the receipt of positive relative to neutral feedback, potentially because neutral feedback (which indicated that half of teens agreed with the participant's selection) was sufficiently rewarding to obscure any differences in VS activation between the receipt of positive and neutral feedback. However, the mPFC and vmPFC show more FC with the VS (Bostan and Strick, 2018; Camara *et al.*, 2009) and each other (Schmälzle *et al.*, 2017) in the context of reward (*vs* loss), suggesting that these regions may form a larger reward response network that is active when adolescents receive rewarding information. Furthermore, when comparing positive to negative feedback, we observed elevated activation in the striatum, as well as several other regions including dlPFC, precuneus and supramarginal gyrus, suggesting that receiving feedback indicating peer approval *vs* disapproval activated regions identified by the triadic neural systems model as playing a role in reward processing.

Contrary to expectations from the triadic neural systems model, we did not observe changes in FC between the VS and PFC during reward processing. However, FC analyses did reveal relatively less FC between the VS and right cerebellum during the receipt of positive relative to neutral feedback. This is in contrast to previous studies that have typically found stronger coupling of the VS and cerebellum to reward (e.g. Camara *et al.*, 2009). However, previous studies considered reactivity to a monetary reward, highlighting the importance of future research exploring FC within the context of social reward processing.

Overlap in social threat and social reward processing

Interestingly, conjunction analysis identified a region within the mPFC that showed greater activation to both negative and positive (*vs* neutral) feedback, a finding that aligns with previous research (Achterberg *et al.*, 2016) and may suggest a common neural mechanism of social-evaluative processing independent of feedback valence. The mPFC has been proposed to play a central role in integrating information about the self and others, particularly during adolescence, and preliminary evidence suggests that mPFC activation may reflect one pathway through which social experience shapes the development brain (Crone *et al.*, 2020). However, despite overlapping mPFC activation to both negative and positive (*vs* neutral) feedback, comparing negative to positive feedback, revealed greater mPFC activation to negative feedback, potentially because receiving feedback that others disagree with your preferences requires more mentalizing about discrepancies between one's own and others' opinions.

Individual differences in neural sensitivity to social threat and reward

Although a growing body of research examines neural responses to social threat and reward, the psychological implications of these response patterns are unclear. Accordingly, we sought to explore whether neural activation and co-activation to social threat and reward were associated with self-reported sensitivity to negative and positive social cues, as captured by social performance goals.

Social avoidance goals

Contrary to our hypothesis, social performance-avoidance goals did not predict neural activation to negative (relative to neutral) feedback within individual regions. However, avoidance goals did predict greater connectivity between the amygdala and the anterior MTG, a region implicated in social and semantic perception

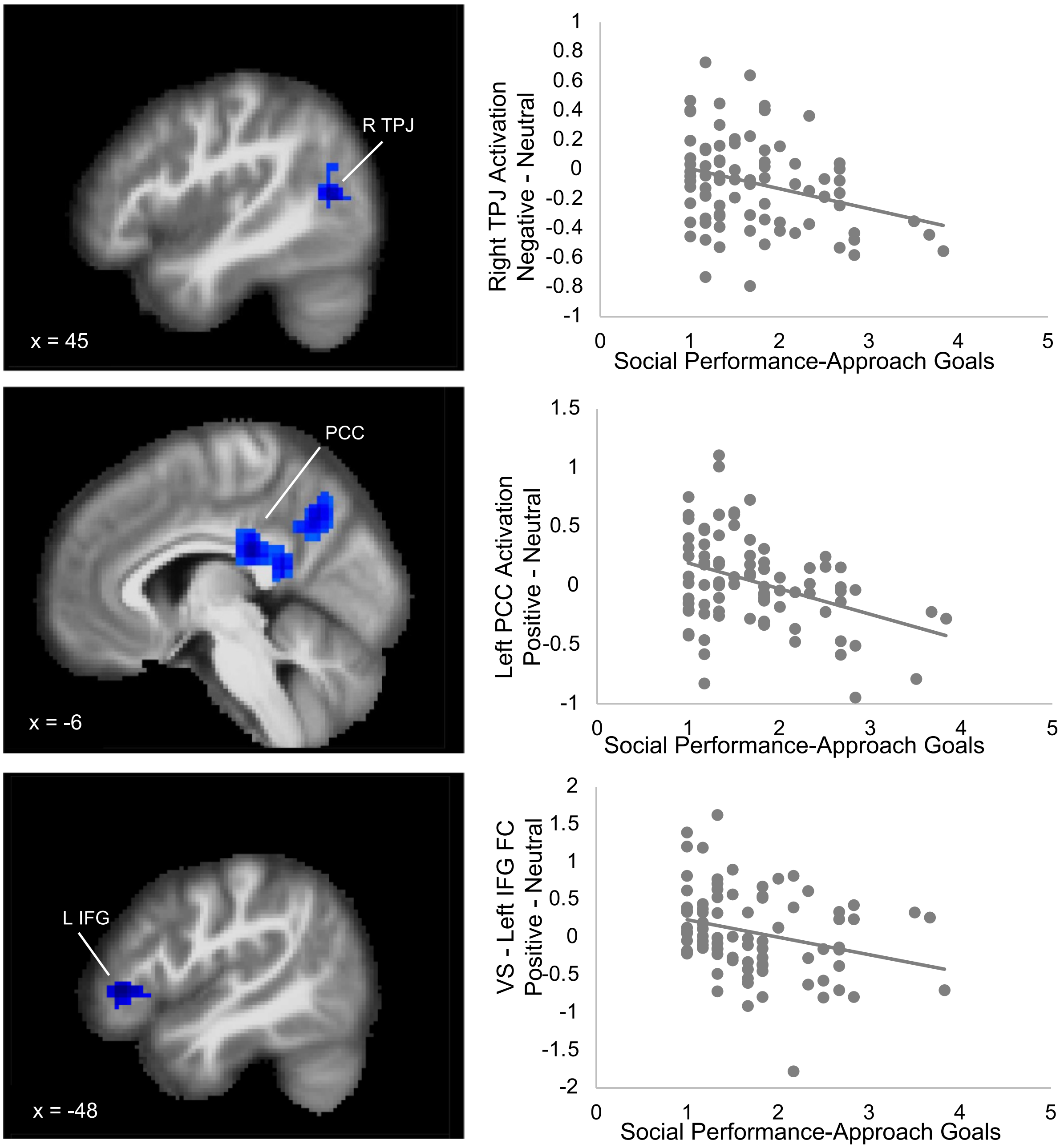

Fig. 5. Social performance-approach goals predicting neural activation (top and middle) and VS FC (bottom).

(Bonner and Price, 2013; Rice *et al.*, 2015). This co-activation between regions involved in threat processing and social perception may reflect a means through which these youth are more attuned to potentially socially threatening situations. Interestingly, similar results were found when adolescents received positive relative to neutral feedback: Social avoidance goals were not associated with activation within individual regions but were associated with more positive connectivity between the VS and both the MTG and cerebellum. Socially avoidant youth may not expect positive feedback, resulting in more communication between reward and social perceptual regions to process this unanticipated outcome. Overall, these results may reflect increased communication between regions involved in threat or reward and social processing in response to both negative and positive feedback that could allow socially avoidant youth to adjust their future behavior to ensure that peers do not perceive them as unpopular or unlikeable.

Social approach goals

Social performance-approach goals were associated with less activation to negative (vs. neutral) feedback in several regions implicated in social processing (TPJ and precuneus) and regulatory control (dlPFC). A similar pattern emerged when receiving positive relative to neutral feedback: Social approach goals were associated with less activation in the precuneus, PCC and parahippocampal gyrus, regions implicated in social-emotional reasoning. This pattern of results suggests that youth who are more motivated to demonstrate social competence or prestige may be less reactive to both negative and positive peer feedback, possibly because they are more focused on appearing socially competent than on incorporating peer feedback to increase their social skills. These findings suggest that youth higher in performance-approach goals may engage in less social reasoning in the peer context, in line with research suggesting that these youth emphasize self-interest rather than cooperation in the context of peer stress (Rudolph *et al.*, 2011) and use nonchalance coping strategies (e.g. portraying themselves as unbothered) to deal with peer problems (Shin and Ryan, 2012).

Although performance-approach goals did not predict amygdala connectivity during negative (*vs* neutral) feedback, they were associated with relatively less VS-IFG connectivity and relatively greater VS-cerebellum connectivity to positive (vs. neutral) feedback. Less coupling between the VS and IFG, a region involved in emotion regulation, could reflect downregulation of the VS by the IFG, consistent with the finding that social approach-oriented youth show blunted reactivity in social processing regions to positive and negative feedback. Although previous evidence links the VS to bilateral cerebellum and more medial regions of the PFC in response to reward (Bostan and Strick, 2018; Camara *et al.*, 2009), research exploring connections between the VS and other regions, including the IFG, warrants further exploration.

Contributions and limitations

The present study expanded on previous research exploring adolescent neural sensitivity to social evaluation (e.g. Guyer *et al.*, 2009; Jarcho *et al.*, 2016) using a novel social feedback task that assessed neural sensitivity to receiving peer feedback about personal preferences. This task requires minimal deception and measures reactivity to evaluation of personally salient opinions, making it ideally suited to the study of social sensitivity in adolescents, who often encounter, and report elevated concern about, peer judgments of their personal preferences in daily life and virtual settings (Magis-Weinberg *et al.*, 2021). Additionally, youth received positive, negative and neutral feedback within the same paradigm, allowing us to isolate reactivity based on the valence (positive or negative relative to neutral) of peer evaluation. Furthermore, we contributed to a limited research base exploring FC in the context of social threat and reward, allowing us to test implications of the triadic neural systems model that co-activation across avoidance and motivation systems would differ as a function of feedback valence. Finally, we provided the first evidence documenting links between neural reactivity and psychological indexes of social performance goals, illustrating the complexity of brain-behavior associations and providing insight into real-world implications of how adolescents process social cues.

Despite its contributions, the present study is not without limitations. Although the inclusion of separate positive, negative and neutral conditions is a strength, it is possible that our neutral condition was not completely valence neutral. Believing that half of previous participants agreed with their preferences may signal a high enough degree of acceptance to be rewarding, or even a high enough degree of rejection to be threatening, thereby reducing the contrast between either positive or negative and neutral feedback. Furthermore, youth likely vary in how they perceive the neutral condition, and those who perceive it as relatively more rewarding or threatening may differ in previous peer experiences and risk for later adverse outcomes.

Unlike other tasks designed to elicit neural reactivity to social feedback (e.g. Achterberg *et al.*, 2016), in this task, participants did not respond to the feedback they received or rate their emotional response to feedback of different valences. This task was developed to mimic the experience of receiving peer feedback about personal opinions, as often happens in situations in which youth do not have the chance to directly respond (e.g. on social media). Although we chose not to include affect ratings after each trial to maintain the feeling of sustained evaluation, having a participant response could benefit interpretability of observed patterns of neural activation. Finally, interpreting the psychological significance of observed patterns of activation and connectivity remains challenging. Although we observed greater connectivity between nodes of the avoidance (i.e. amygdala) and cognitive control (i.e. PFC) systems in response to negative feedback, participants in this task were not instructed to regulate their emotional responses to feedback; tasks that more directly probe cognitive control in the context of peer evaluation are warranted. In this study, we hypothesized that greater activation in and connectivity with nodes of the avoidance and motivation systems reflect heightened sensitivity to social threat and reward. This interpretation is bolstered by results showing heightened amygdala and VS connectivity with social processing regions among youth who are more concerned with avoiding negative peer judgments and dampened reactivity among youth who are more motivated to demonstrate competence and who show disengagement coping in the context of peer stress. However, in this study, we examined social avoidance and approach goals separately, and it is possible that different patterns might emerge when considering overall levels of social motivation (i.e. comparing youth high in both avoidance and approach goals *vs* those low in both goal types). Thus, future studies are needed to provide convergent validity of our task effects and to further probe the psychological and behavioral implications of neural responses to social threat and reward in adolescence.

Conclusion

This study explored neural sensitivity to social threat and reward in mid-adolescent girls using a novel social feedback task. Negative and positive feedback elicited overlapping and distinct patterns of activation and FC within and across avoidance and motivation systems and associated social processing regions. Furthermore, patterns of activation and co-activation differed as a function of social goals. These findings highlight the importance of studying both neural activation and connectivity in response to negative and positive social cues and identifying links between patterns of neural processing and individual differences in self-reported social tendencies.

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Conflict of interest

The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

Supplementary data

Supplementary data are available at *SCAN* online.

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