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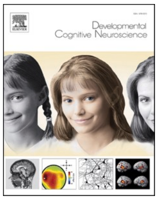

Hooked on a thought: Associations between rumination and neural responses to social rejection in adolescent girls

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ABSTRACT

Rumination is a significant risk factor for psychopathology in adolescent girls and is associated with heightened and prolonged physiological arousal following social rejection. However, no study has examined how rumination relates to neural responses to social rejection in adolescent girls; thus, the current study aimed to address this gap. Adolescent girls (N = 116; ages 16.95–19.09) self-reported on their rumination tendency and completed a social evaluation fMRI task where they received fictitious feedback (acceptance, rejection) from peers they liked or disliked. Rejection-related neural activity and subgenual anterior cingulate cortex (sgACC) connectivity were regressed on rumination, controlling for rejection sensitivity and depressive symptoms. Rumination was associated with distinctive neural responses following rejection from liked peers including increased neural activity in the precuneus, inferior parietal gyrus, dorsolateral prefrontal cortex, and supplementary motor area (SMA) and reduced sgACC connectivity with multiple regions including medial prefrontal cortex, precuneus and ventrolateral prefrontal cortex. Greater precuneus and SMA activity mediated the effect of rumination on slower response time to report emotional state after receiving rejection from liked peers. These findings provide clues for distinctive cognitive processes (e.g., mentalizing, conflict processing, memory encoding) following the receipt of rejection in girls with high levels of rumination.

1. Introduction

Rumination, a negative and perseverative thought pattern, is a risk factor for multiple forms of psychopathology including depression (Nolen-Hoeksema et al., 2007; McLaughlin and Nolen-Hoeksema, 2011), anxiety (McLaughlin and Nolen-Hoeksema, 2011), substance abuse (Grierson et al., 2016; Luca, 2019), self-injury (Ying et al., 2021), and disordered eating (Hilt et al., 2013). Rumination is also associated with sleep problems (Jose and Vierling, 2018; Palmer et al., 2018; Li et al., 2019), aggressive behavior (Peled and Moretti, 2007; McLaughlin et al., 2014; Li et al., 2021), and reports of peer victimization (McLaughlin and Nolen-Hoeksema, 2012) particularly during adolescence. Rumination and its maladaptive outcomes are more notable in girls than boys; girls report greater levels of rumination than boys (Peled and Moretti, 2007; Jose and Brown, 2008; Hamilton et al., 2015a) and rumination is more strongly associated with depression among girls compared with boys (Jose and Brown, 2008). Moreover, sex differences in depression symptoms in adolescents are partly mediated by rumination (Hankin, 2008). It is thus important to identify the contexts and neurocognitive mechanisms related to the developmentally-salient heightened levels of rumination in adolescent girls. In turn, such knowledge can inform new specificity for the content of clinical interventions to mitigate rumination-related mental health issues that often emerge among girls during adolescence and young adulthood (Solmi et al., 2021).

Experiences of negative social evaluation or social rejection (Nolen-Hoeksema et al., 2008) may be an important social context that elicits excessive and maladaptive thoughts about oneself particularly in high ruminators. One study found that participants assigned to a negative social evaluation condition, where confederates gave rejecting and critical nonverbal cues during a speech task, reported greater rumination about their poor performance and anxious feelings both 40 min and 3–5 days after the task than did participants in a non-evaluative condition (Zoccola et al., 2012). Other work has demonstrated that after

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listening to audio-recorded interpersonal criticism from a significant other, individuals with higher trait rumination showed poorer performance on a working memory task (Kaiser et al., 2015) suggesting lasting interference with cognitive functioning. Studies have also shown that healthy adults and adolescents with high dispositional rumination exhibit prolonged physiological responses following negative social evaluation including slow heart rate recovery (Aldao et al., 2014), prolonged duration of cortisol activation (Shull et al., 2016), and blunted diurnal decline of cortisol (Zoccola and Dickerson, 2015).

The link between rumination and rejection-related reactivity may be particularly apparent in girls during adolescence due to the developmentally-salient heightened social sensitivity (Somerville, 2013; Guyer et al., 2016; Schriber and Guyer, 2016; Sequeira et al., 2021), increased self-conscious emotions (Somerville et al., 2013), and increased rumination (Jose and Brown, 2008) in this developmental period. For example, research has found that adolescents exhibited greater biological responses (e.g., cortisol and alpha-amylase responses) when anticipating and receiving social evaluation compared to children (Stroud et al., 2009; van den Bos et al., 2014) potentially due to shifts in stress system reactivity that can accompany pubertal development (Guyer et al., 2016). In addition, studies that included participants in late childhood, adolescence, and emerging adulthood found age-related increases in the neural activity differentiating acceptance and rejection in emotion-related brain regions (Gunther Moor et al., 2010; Guyer et al., 2012), the tendency to change likability ratings for evaluators based on the given social feedback type (Rodman et al., 2017), and the tendency to denigrate others after receiving multiple negative social evaluations (Yoon et al., 2018), consistently indicating increased sensitivity to social evaluation during adolescence. Furthermore, sex differences in rumination (higher in girls vs. boys) have been linked to greater exposure to interpersonal stressors (e.g., fights with friends, romantic breakup) (Hamilton et al., 2015a). Relatedly, among girls with depression, those with a higher versus lower tendency to ruminate show higher levels of arousal (indicated by greater pupil dilation) in response to simulated peer rejection (Stone et al., 2016). Despite behavioral and physiological evidence that individual differences in rumination relate to responses to negative social evaluation, particularly in girls, little is known about rejection-related neural responses associated with rumination in adolescent girls.

Clues about brain regions associated with rumination come from a recent meta-analysis (Makovac et al., 2020) that identified key regions across 20 task-based fMRI studies, mostly of adults, that primarily used fMRI tasks involving rumination induction (e.g., recollection of arousing negative autobiographical memories, pain catastrophizing induction, angry rumination induction) or self-referential focus (e.g., judgment of whether a personality trait described oneself, visualization of words related to past/present/future concerns). Results of this meta-analysis indicated that people with greater levels of rumination show heightened neural activity in the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC)/precuneus, and subgenual anterior cingulate cortex (sgACC) relative to those with low levels of rumination. The mPFC and PCC/precuneus are hub regions of core default mode network (DMN) (Andrews-Hanna et al., 2014) known to be engaged during self-related processing such as retrieving self-knowledge (van der Meer et al., 2010), encoding self-relatedness (D`Argembeau, 2013), experiencing self-conscious emotion (Somerville et al., 2013), and retrieving autobiographical and episodic memory (Sajonz et al., 2010; Wen et al., 2020). The sgACC is a key region of the affective brain network involved in controlling and sustaining autonomic arousal (Dixon et al., 2017) and exacerbating negative affect (Rotge et al., 2015). Heightened reactivity of these three brain regions in high ruminators is in line with their tendency toward heightened self-focused attention (Brockmeyer et al., 2015; Kaiser et al., 2018), prolonged processing of negative information (Disner et al., 2011; Stone et al., 2016; Kaiser et al., 2018), and increased autonomic activity (Ottaviani et al., 2016). Although the majority of studies included in this meta-analysis used rumination induction tasks (Denson et al., 2009; Kross et al., 2009; Cooney et al., 2010; Fabiansson et al., 2012; Kowalski et al., 2019) or self-referential tasks (Marques et al., 2018; Nejad et al., 2019) that elicited neural activity when *retrieving* negative past events or self-relevant information, it is plausible that high ruminators also exhibit high activity in the same brain regions when *encountering* or *encoding* self-relevant and negative information, such as social rejection or evaluation. This expectation is supported by studies demonstrating recruitment of mPFC and PCC/precuneus activity during the successful encoding of self-relevant trait words (Dégeilh et al., 2015) and dynamic learning about the self, based on social evaluation from multiple others (Yoon et al., 2018). Furthermore, rejection-related activity in the sgACC has been linked to self-reported distress elicited by social rejection (Rotge et al., 2015; Mwilambwe-Tshilobo and Spreng, 2021) and prospective increases in depressive symptoms (Masten et al., 2011; Silk et al., 2022), indicating a role for the sgACC in negative emotion dysregulation like rumination.

In addition to neural activation, connectivity between brain regions underlying emotion- and self-related processing may relate to the propensity to ruminate. The recently proposed neurobiological model of rumination (Hamilton et al., 2015b) posits that a maladaptive pattern of thought may arise through the co-occurrence of the psychological processes engaged within core regions of the DMN (e.g., assigning value and applying an egocentric frame to internally represented stimuli) and those engaged by the sgACC (e.g., behavioral withdrawal driven by negative affect). Relatedly, resting-state functional connectivity (rsFC) studies have demonstrated that altered patterns of temporal dynamics of functional connectivity/co-activation of core DMN regions and a key region of the affective brain network (e.g., high variability of connectivity between MPFC and anterior insula, persistent coactivation of frontoinsular and DMN regions) are associated with biased attention toward self-relevant and negative stimuli (Kaiser et al., 2018) and trait rumination (Kaiser et al., 2018, 2019). Although previous studies examined the brain at rest with no task involved (Berman et al., 2011; Hamilton et al., 2011; Zhu et al., 2012), the relevance of rumination and the coupling neural response between affective brain regions and core DMN regions could also be present or even more prominent in the context of a self-relevant and salient event such as receiving negative social evaluation. To test sgACC-DMN connectivity, we planned to have sgACC as a seed region given its established role in generating negative affect after receiving social rejection (Rotge et al., 2015) and its expected influence on DMN to elicit self-focused attention following rejection (Fossati, 2019).

In the current study, we tested whether individual differences in rumination were associated with social rejection-related neural activity and connectivity in adolescent girls. Neural response to social rejection was elicited using the Chatroom fMRI Task (Guyer et al., 2012; Guyer et al., 2015), a social feedback task widely used with adolescents. In this task, at the first visit, participants were asked to classify half of the 60 adolescents' photographs into the peers that they wanted to chat with (liked peers) and another half of the photographs into the peers that they did not want to chat with (unliked peers). At the second visit, in the fMRI scanner, participants received feedback indicating whether each of 60 adolescents were interested in chatting with them (acceptance) or not (rejection) or did not rate their interest (not rated), and reported how receiving this social feedback made them feel. A previous study (Guyer et al., 2012) with the Chatroom fMRI task in a mixed-sex adolescent sample showed that participants' emotional responses were affected more strongly by feedback from liked peers than unliked peers, suggesting that a liked peer is a more salient stimulus type than an unliked peer. An examination of the association between rumination and neural responses to negative feedback with different saliency levels can reveal deeper insights into the specific context in which girls with greater rumination show distinctive responses. It is possible that girls with high levels of rumination show heightened neural sensitivity specifically to salient, self-relevant feedback. Alternatively, girls with high levels of rumination may exhibit neural sensitivity to even undervalued social rejection. Specifically, we hypothesized that girls who reported higher levels of rumination would show greater activity in the sgACC, mPFC, and PCC/precuneus and greater connectivity between the sgACC and core DMN regions (i.e., mPFC, PCC/precuneus) when receiving negative feedback from peers liked and/or unliked by participants.

In addition to testing these ROI-based hypotheses, we conducted whole-brain exploratory analyses to assess all brain regions engaged during bids of rejection delivered in this task. In sum, we conducted analyses of (1) neural activity to rejection from liked and unliked peers within a priori ROIs (i.e., sgACC, mPFC, PCC/precuneus) and across the whole brain, and (2) sgACC connectivity in response to rejection from liked and unliked peers within a priori ROIs (i.e., mPFC, PCC/precuneus) and across the whole brain. To identify the neural activity/connectivity uniquely explained by rumination, above and beyond the contribution of other variables closely related to rumination and neural response to social rejection (Kross et al., 2007; Silk et al., 2014), we controlled for rejection sensitivity (Pearson et al., 2010; Pearson et al., 2011), a trait characterized by heightened sensitivity to rejecting cues, and depressive symptoms, mental health problems often associated with ruminative tendency (Nolen-Hoeksema et al., 2008). To fully characterize neurocognitive processes associated with rumination, we further explored whether neural activity/connectivity associated with rumination explained the effect of rumination on distinctive behavioral responses measured during the task (e.g., emotional states, reaction time).

2. Materials and methods

2.1. Participants

Participants were 232 girls enrolled in the Pittsburgh Girls Study of Emotion (PGS-E) (Keenan et al., 2010), a substudy of the longitudinal Pittsburgh Girls Study (PGS), which collected a range of psychosocial functioning measures annually from childhood through young adulthood. The PGS study only included individuals with female sex assigned at birth. The PGS-E study began when girls were age 9 and included collection of neuroimaging data four times in late adolescence. As part of their annual PGS visit, girls completed self-reported questionnaires about rumination, rejection sensitivity, and depressive symptoms (mean age at PGS visit = 17.23 years, age range: 16.62 – 18.22 years). Then, as part of their PGS-E visit, girls completed the Chatroom fMRI task administered only in the substudy's second year of neuroimaging data collection (mean age at scan = 18.05 years, range of age at scan: 16.95 – 19.09 years). The PGS and PGS-E visits occurred within 1.41 – 18.96 months of each other. Of the 232 girls, 34 could not be reached to schedule them for the year 2 neuroimaging assessment, 31 opted out of the neuroimaging assessment, 22 were ineligible (e.g., currently pregnant, metal in the body, braces), and 14 did not complete the Chatroom fMRI task. Among the 131 remaining girls who completed the Chatroom fMRI scan, 15 were excluded from analyses due to excessive head motion (i.e., having greater than 15 % volumes of outliers with head movement, N = 8), abnormalities observed in the anatomical image (N = 1), poor data quality based on visual inspection of the preprocessed image (N = 1), missing all self-reported data (N = 1), and missing rejection sensitivity data (N = 4). Among participants with usable fMRI data, because only 3.3 % of participants had missing data for self-reported variables and as our data was missing completely at random (MCAR), we did a complete case analysis (i.e., including only the cases for which there were no missing values on any of the variables) rather than imputation to avoid data manipulation. MCAR was confirmed with Little's t-test drawing on three self-reported measures (i.e., rumination, rejection sensitivity, depressive symptoms) and four demographic measures (i.e., age at scan, age at self-report, race, public assistance) ($X^2(19) = 15.2$, $p = 0.71$). The final analysis sample was 116 girls, of whom 78 identified as Black (67 %), 31 as White (27 %), and 7 as another race or multi-racial (6 %). Written informed consent/assent was obtained from all participants and their caregivers. Participants were compensated monetarily for their participation. Study procedures were approved by the Human Research Protection Office at the University of Pittsburgh.

3. Measures

3.1. Self-reported measures

3.1.1. Rumination

The 7-item Rumination subscale of the Perfectionism Inventory (Hill et al., 2004) was used to assess participants' tendency to obsessively worry about past errors, less than perfect performance, or future mistakes (Hill et al., 2004). Example items include, "If I say or do something dumb I tend to think about it for the rest of the day," "When I make an error, I generally can't stop thinking about it," and "I spend a lot of time worrying about things I've done, or things I need to do." Participants rated each item from 1 = strongly disagree to 5 = strongly agree. In this sample, Cronbach's alpha was 0.95.

3.1.2. Rejection sensitivity

The Rejection Sensitivity Questionnaire (Berenson et al., 2009) was used to assess concerns and expectations about social rejection in response to nine hypothetical situations, measuring "the disposition to anxiously expect, readily perceive, and intensely react to rejection" (Downey et al., 2004). For example, in response to this situation, "You ask your parents or other family members to come to an occasion important to you." participants rated their rejection concern, "How concerned or anxious would you be over whether or not they would want to come?" (1 = very unconcerned, 6 = very concerned), and their rejection expectancy, "I would expect that they would want to come." (1 = very unlikely, 6 = very likely). Rejection sensitivity per situation was calculated by multiplying rejection concern and rejection expectancy subtracted from 7. Rejection sensitivity scores for all nine situations were averaged to calculate a total score. Cronbach's alpha was 0.8.

3.1.3. Depressive symptoms

Self-reported depressive symptom severity was obtained using the Adult Self-Report Inventory-4 (Gadow et al., 2004). The inventory assesses 10 symptoms of major depressive disorder (MDD) defined by DSM-IV (e.g., depressed mood, loss of interest in doing any activity, a sense of worthlessness), which has high validity, reliability, and clinical utility (Salcedo et al., 2018). Participants rated each item as 0 (*never*), 1 (*sometimes*), 2 (*often*), or 3 (*very often*). All items were summed for a total score; Cronbach's alpha was 0.89. Among the 116 participants, three participants met the DSM-IV criteria for MDD diagnosis (i.e., having one primary symptom of feeling depressed or loss of interest (i.e., scored 2 or 3) for two weeks and at least 5 other symptoms).

3.2. Chatroom fMRI task

The Chatroom task is an experimental paradigm that simulates social evaluation (Guyer et al., 2012, 2015). The task consists of a selection phase (out of scanner) and a feedback phase (in scanner) administered in two visits. Visits one and two were separated 16.49 days on average (*SD*: 28.96). Both phases of the task were administered using E-Prime software (Sharpsburg, PA).

3.2.1. Visit 1 (Selection Phase)

Participants were told they were participating in a nationwide study about how teenagers communicate with each other on the internet, and that they would chat online with a peer selected for them based on similar interests from among participants at the other study sites. To enhance believability, participants created an online profile describing their interests and were told they would have their photograph taken. Participants then completed the selection phase whereby they viewed 60 photographs of mid- to late-adolescents (30 boys, 30 girls) and then placed 30 peers into an "interested" (liked) and 30 into a "not interested" (unliked) onscreen bin. Peer photographs were taken from stimulus sets used in past studies (e.g., Guyer et al., 2012). Participants were told the other peers would indicate whether they wanted to chat with the participant using the same procedure.

3.2.2. *Visit 2 (Feedback Phase)*

During visit two, participants completed the feedback phase of the task while undergoing an MRI scan. Participants were told they would chat online at the end of the visit with the peer selected for them. The fMRI feedback task included 60 trials. On each trial, for 2 s, the photograph of each peer for whom participants had previously indicated their interest was displayed, and a reminder appeared about whether participants had judged the peer as one of interest (liked) or not (unliked). An inter-stimulus interval of 2, 4, 6, or 8 s was included in equal numbers per duration length across the 60 trials (i.e., 15 trials). Next, for 1 s, participants viewed feedback indicating whether the presented peer wanted to interact with the participants (i.e., acceptance feedback; "*He/she LIKED you*"), did not want to interact with the participants (i.e., rejection feedback; "*He/she DID NOT LIKE you*"), or did not rate their interest of the participants (i.e., "not rated" feedback; "*NOT RATED*"). We modified a previous version of the chatroom fMRI task (Guyer et al., 2012; Guyer et al., 2015) to include a "not rated" condition to have a neutral comparison event for use in fMRI analyses rather than a general baseline. Feedback types were pseudo-randomized with an equal number of trials (i.e., 15 trials) yielding 6 event types that combine participants' selections and peer feedback condition (i.e., acceptance/rejection/not rated from liked peers, acceptance/rejection/not rated from unliked peers). After feedback was displayed for 1 s, a rating bar was presented and participants indicated with an MRI response box, "How does this make you feel?" on a scale of 1 = very bad to 5 = great within a 3-second response duration. An inter-trial interval of 2, 4, 6, or 8 s was included in equal numbers per duration length across the 60 trials (i.e., 15 trials). After the fMRI scan, participants were debriefed and told that no social evaluations were actually performed and they would not chat with a peer at the end of the visit. No adverse reactions to the debriefing occurred.

3.2.3. *fMRI data acquisition*

During the Chatroom fMRI task, brain images were acquired with a Siemens 3 T Tim Trio scanner located at a university medical center located in a Northeastern U.S. city. Participants were given protective earplugs to wear and instructed to lay still in the scanner. Following localization scans, a high-resolution T1-weighted structural image was collected with the parameters of TR = 2300 ms, TE = 2.98 ms, flip angle = 9 degree, field of view (FOV) = 256 mm, 160 slices with 1.2 mm thickness, acquisition matrix = 256 × 240, voxel resolution = 1.0 × 1.0 × 1.2 mm^3 and used for co-registration and normalization with functional images. Functional images using T2 * -weighted gradient echo-planar imaging (EPI) were obtained using the following parameters: TR = 2000 ms, TE = 28 ms, flip angle = 90 degree, FOV = 205 mm, 39 slices with 3.1 mm thickness, acquisition matrix = 64 × 64, and voxel resolution = 3.2 × 3.2 × 3.1 $\text{mm}^{\mathbf{3}}$. A reference EPI scan was first acquired to visually inspect for artifacts (e.g., ghosting) and ensure adequate signal across the entire volume.

3.3. *Data analysis*

The current study focuses on neural responses to rejection feedback vs. not rated feedback, given that rumination involves perseverative thought patterns regarding self-relevant and negative content. However, to provide complete information associated with all components of the chatroom task, analyses and results regarding the association between rumination and neural and behavioral responses to acceptance feedback are provided in the supplementary information (see Supplementary Method 1 and Supplementary Result 1).

3.3.1. *Self-reported data*

We ran correlation analyses to test the relation between rumination and rejection sensitivity as well as rumination and depression in our sample. The purpose of these analyses was to confirm (1) the need to control for the two variables to exclude shared variance and assess unique contribution of rumination on neural activity/connectivity and (2) whether these variables are not too highly correlated (i.e., $r \geq 0.8$), which may risk multicollinearity problems (Shrestha, 2020).

3.3.2. *Behavioral data*

We ran four multiple regression analyses to explore the association between rumination and mean emotional response (i.e., rating for the question "How does this make you feel?") and mean RT after receiving rejection (vs. not rated) feedback from liked and unliked peers, controlling for the effect of rejection sensitivity and depressive symptoms.

3.3.3. *fMRI preprocessing*

Preprocessing and fMRI statistical analyses were implemented using SPM12. Functional images were realigned to the first volume to correct for head motion, and the mean functional image was co-registered to the structural image. The structural image was segmented and normalized to the Montreal Neurological Institute (MNI) template. The resulting warps were applied to the functional images for normalization. Images were smoothed using a Gaussian kernel with a 6 mm full width at half maximum. After preprocessing, head movement was further inspected using the Artifact Detection Toolbox (http://www.nitrc.org/projects/artifact_detect). For each participant, head movement outlier volumes (i.e., mean signal exceeding 4 standard deviations of the global mean and scan-to-scan movement exceeding 2 mm translation or 2 degree rotation in any direction) were identified to be included as nuisance regressors at the first-level fMRI analyses. Participants who had greater than 15 % volumes of outliers were excluded from statistical analyses.

3.4. *First-level fMRI analyses*

3.4.1. *Neural activation*

General Linear Models (GLMs) were estimated with the onset times of the following events and their duration convolved with the canonical hemodynamic response function: (1) reminder of peers that the participants deemed as liked (2 s), (2) reminder of peers that the participants deemed as unliked (2 s), (3) receipt of acceptance from liked peers (4 s), (4) receipt of rejection from liked peers (4 s), (5) receipt of "not rated" feedback from liked peers (4 s), (6) receipt of acceptance from unliked peers (4 s), (7) receipt of rejection from unliked peers (4 s), (8) receipt of "not rated" feedback from unliked peers (4 s). The 4 s duration for regressors of interest (3) to (8) included the onset of feedback (1 s) to the end of rating emotional response to the feedback (3 s). Nuisance regressors of head movement-outlier volumes were also included. Two contrast maps were obtained for rejection vs. not rated from liked peers (i.e., (4) – (5)) and rejection vs. not rated from unliked peers (i.e., (7) – (8)). We separately tested neural response to rejection from liked peers and unliked peers to gain insights into the specific context in which girls with higher rumination exhibit distinctive responses. We contrasted rejection with neutral feedback (baseline comparison) rather than acceptance feedback to clearly attribute individual differences in neural activity to (in)sensitivity to rejection, but not acceptance.

3.4.2. *Seed-based sgACC connectivity*

For this analysis, the focus was on connectivity specifically during peer rejection given our a priori hypotheses regarding rumination and sgACC connectivity during social rejection. Two GLMs for a generalized psychophysiological interaction (gPPI) analysis (McLaren et al., 2012) were estimated to examine functional connectivity of seed regions of the left and right sgACC following rejection from liked peers and rejection from unliked peers. The GLMs included the following regressors: (1) a physiological variable of time series of left or right sgACC defined by the

Automated Anatomical Labelling atlas 3 (AAL3) (Rolls et al., 2020), (2) psychological variables, which were 8 events included in the neural activation analysis, and (3) psychophysiological variables, which were the interactions between the physiological variable and the 8 psychological variables. Nuisance regressors of head movement-outlier volumes were included. The psychophysiological regressors of (1) rejection feedback from liked peers vs. “not rated” feedback from liked peers and (2) rejection feedback from unliked peers vs. “not rated” feedback from unliked peers were the contrasts of interest.

3.5. *Group-level fMRI analysis*

3.5.1. *Neural activity analysis*

To identify brain regions in which activity following rejection was uniquely explained by rumination rather than two other variables closely related to rumination (see significant associations in our sample described in Results), we ran two second-level multiple regression analyses where rumination, rejection sensitivity, and depressive symptoms were regressed on the contrast maps of rejection vs. not rated from liked peers and rejection vs. not rated from unliked peers.

We used the 3dClustSim function of Analysis of Functional NeuroImages (AFNI) for multiple comparison correction. To test our hypothesis (i.e., positive association between rumination and core DMN regions and sgACC activity), required cluster sizes were first estimated within the search volume of the union mask of core DMN regions and sgACC. The core DMN regions were defined by combining 12 parcels corresponding to PCC/precuneus and 12 parcels corresponding to mPFC within the Default-A network of Schaefer’s brain parcellation scheme (Schaefer et al., 2018) (see Supplementary Fig. 1A for core DMN mask). The sgACC was defined by combining the left and right sgACC defined by AAL3 (Rolls et al., 2020) (see Supplementary Fig. 1B for sgACC anatomical mask). The union mask was created by combining core DMN regions and sgACC using marsbar (Brett et al., 2002). Required cluster sizes for the whole brain were also estimated for whole-brain exploratory analysis (see Table 1 for required cluster sizes).

3.5.2. *sgACC connectivity analysis*

The same multiple regression analyses were conducted with the contrast maps of rejection vs. not rated from liked peers, rejection vs. not rated from unliked peers with the left and right sgACC seed regions obtained from gPPI analyses. To test our hypothesis (i.e., positive association between rumination and sgACC-core DMN connectivity), multiple comparison correction was first conducted with the search volume of the core DMN mask. Required cluster sizes for the whole brain analyses were then calculated (see Table 1 for required cluster sizes).

Table 1
The cluster size (in voxels) required for the brain maps of all the multiple regression analyses. We assumed that the cluster is defined if the faces or edges of voxels touch (i.e., NN2 option of 3dClustSim command). We used one-sided thresholding to estimate the required cluster size for the brain maps of the positive and negative association. For small volume correction (SVC) motivated by a priori hypothesis, we determined the cluster size required for surviving multiple comparison correction $\alpha < .0083$ (i.e., 0.05/6 (number of hypothesis)) with the initial uncorrected p-value $< .001$. For SVC of neural activity analyses, the union mask that combined core DMN regions (i.e., 24 parcels corresponding to the Default-A network of Schaefer’s brain parcellation scheme (Schaefer et al., 2018)) and the left and right sgACC defined by AAL3 (Rolls et al., 2020) was used. For SVC of sgACC connectivity analyses, the union mask that combined core DMN regions was used. For correction for exploratory whole brain analysis, we determined the cluster size required for surviving multiple comparison correction $\alpha < .05$ with the initial uncorrected p-value $< .001$. Cluster sizes with a decimal point were rounded up to the nearest integer. SVC, Small Volume Correction; WB, Whole Brain Analysis.

Analysis	SVC	WB
Neural activity following rejection from liked peers	45.6	74.9
Neural activity following rejection from unliked peers	50.4	99.3
left sgACC connectivity following rejection from liked peers	46.2	87.4
left sgACC connectivity following rejection from unliked peers	47.3	86.0
right sgACC connectivity following rejection from liked peers	43.3	89.5
right sgACC connectivity following rejection from unliked peers	47.4	77.2

3.5.3. *Multiple comparison correction for the number of analyses with hypotheses*

Because we had six analyses with hypotheses across the study (i.e., analyses examining neural activity following rejection from liked peers, neural activity following rejection from unliked peers, left sgACC connectivity following rejection from liked peers, left sgACC connectivity following rejection from unliked peers, right sgACC connectivity following rejection from liked peers, right sgACC connectivity following rejection from unliked peers), for small volume correction, we determined the cluster size required for surviving multiple comparison correction with the statistical threshold of $\alpha < .0083$ (i.e., 0.05/6) with the initial uncorrected p-value $< .001$. For the exploratory whole brain analysis for the same six analyses, we determined the cluster size required for surviving multiple comparison correction with the statistical threshold of $\alpha < .05$ with the initial uncorrected p-value $< .001$. Specific procedures for cluster correction are presented in Supplementary Note 2. Unthresholded statistical maps were uploaded to NeuroVault.org database and are available at https://neurovault.org/collections/SHFXELFH/.

3.5.4. *Treatment of outliers in neural activity and connectivity*

We planned to rerun all the fMRI analyses after excluding participants whose brain activity/connectivity was identified as an outlier (i.e., greater or less than 3 SD from the mean) across the majority of significant clusters identified in the initial analyses, assuming that they exhibited brain activity beyond typically seen levels. Because there was no participant who was identified as an outlier in more than 25 % of significant clusters, we did not rerun the analysis and results from the initial analyses were reported.

3.5.5. *Rumination-brain-behavior association*

If a significant association between both rumination and brain activity/connectivity and rumination and behavior during the task (i.e., emotional rating or RT following rejection (vs. not rated) from liked or unliked peers) was identified, we planned to explore rumination-brain-behavior associations in order to fully characterize high ruminators’ neurocognitive process during the task. Using correlational analyses, we first determined whether brain activity/connectivity significantly associated with rumination was also related to behavior during the task. If significant brain-behavior associations were found, we planned to test the rumination-brain-behavior association using mediation analyses with brain regions whose activity was associated with both rumination and behavior as mediators. The mediation analyses were implemented using a bootstrapping approach with 5000 samples using SPSS macros (Hayes, 2017). Rejection sensitivity and depressive symptoms were included as covariates in the mediation models.

4. Results

4.1. *Demographic and self-reported data*

Table 2 presents the descriptive statistics of demographic and self-reported data and associations among them. Consistent with previous literature and our expectation, self-reported rumination was moderately associated with depressive symptoms ($r = 0.4$, $p < .001$) and rejection sensitivity ($r = 0.34$, $p < .001$). This result confirms the need to include these two variables as covariates in regression models to measure neural activity and connectivity uniquely explained by rumination. It should be noted that because the correlation was moderate rather than high ($r < 0.8$), our regression estimates should be considered reliable and unaffected by multicollinearity.

Table 2
Descriptives and correlations of demographic and self-reported variables.

	Descriptive statistics		Age at questionnaires assessment[a]	Age at fMRI scan	Rumination	Rejection sensitivity	Depressive symptoms
	M (SD)	Min / Max	Bivariate correlation (r)				
Age at questionnaires assessment[a]	17.23 (0.35)	16.62 / 18.22					
Age at fMRI scan	18.05 (0.50)	16.95 / 19.09	0.76***				
Rumination	2.47 (0.99)	1 / 4.71	0.02	-0.01			
Rejection sensitivity	7.86 (3.03)	1 / 14.89	-0.15	-0.08	0.34***		
Depressive symptoms	5.85 (4.68)	0 / 28	-0.1	-0.14	0.40***	0.25**	
	N (Percentage)		One-way ANOVA (F statistics)				
Race/Ethnicity	White: 31 (26.72) Black: 78 (67.24) Others or multi-racial: 7 (6.03)		3.87*[b]	5.93*[c]	0.01	0.14	0.36
	N (Percentage)		Independent Sample T-Test (Welch's t)				
Public assistance[d]	Yes: 8 (7.21) No: 103 (92.79)		-0.50	0.03	0.04	-0.47	-0.53

Note: * $p < .05$, ** $p < .01$, *** $p < .001$

[a] Age at PGS visit when rumination, rejection sensitivity, and depressive symptoms were assessed.

[b] The effect was driven by the difference in White > Black (t = 2.81, df = 113, $p = 0.02$). White adolescents were older than Black adolescents at the time of questionnaires assessment.

[c] The effect was driven by the difference in White > Black (t = 3.49, df = 113, $p = 0.002$). White adolescents were older than Black adolescents at the time of fMRI data collection.

[d] This variable measures whether girls lived in household receiving some form of public assistance. Five participants were missing data for this variable.

4.2. Behavioral data

4.2.1. Emotional ratings

Rumination was not associated with emotional ratings following rejection vs. not rated from liked peers (b = −0.15, SE = 0.08, $p = 0.07$) and rejection vs. not rated from unliked peers (b = −0.08, SE = 0.07, $p = 0.24$). Results for the emotional ratings should be interpreted with caution due to a considerable amount of missing data (i.e., M = 39.32 % of trials per participant; SD = 30.09; range = 0 – 95) from a technical error.

4.2.2. Reaction time

Girls with greater levels of rumination showed slower RT to rejection vs. not rated from liked peers (b = 74.98, SE = 34.70, $p = 0.03$) but not to rejection vs. not rated from unliked peers (b = 0.69, SE = 31.37, $p = 0.98$). Among trials with missing emotional ratings, 140 trials (2.01 % of all trials across all participants) showed an RT value of 0. We excluded those trials from the RT analysis due to difficulty interpreting it as a meaningful response. Ten trials were further excluded as RT data were not recorded. Only a few trials were excluded in the analysis of RT (i.e., M = 2.01 % of trials per participant; SD = 4.41; range = 0 – 26.67).

4.2.3. Neural activation following rejection from liked peers

The multiple regression analysis with the search volume of core DMN regions and sgACC showed that rumination was positively associated with precuneus activity following rejection from liked peers (Fig. 1; statistics in Table 3).

The whole-brain regression analysis demonstrated that rumination was positively associated with activity of a large cluster of the precuneus, two regions within left inferior parietal gyrus (IPG), right IPG, left DLPFC, two regions within right DLPFC, and SMA following rejection from liked peers (Fig. 2; Table 3).

4.3. Neural activation following rejection from unliked peers

The same analysis of neural activity following rejection from unliked peers revealed non-significant results.

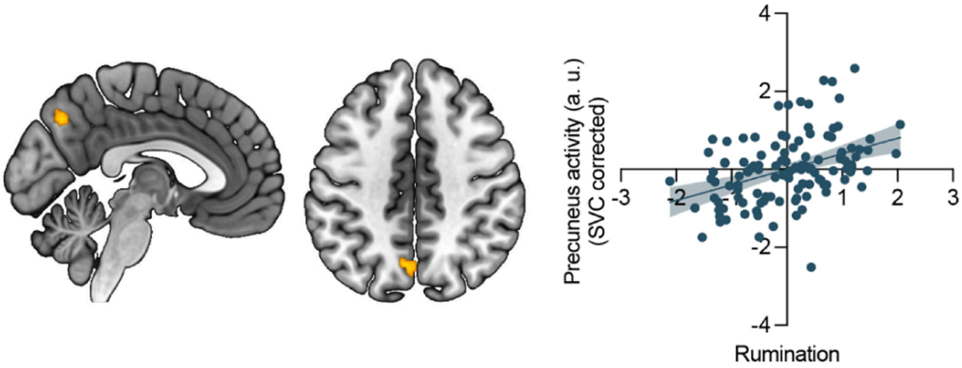

Fig. 1. Positive association between rumination and precuneus activity following rejection feedback from liked peers. The brain map depicts the significant result from multiple regression analysis with covariates of rejection sensitivity and depressive symptoms. Multiple comparison correction was conducted with the search volume that combines ROIs (i.e., sgACC and core DMN regions). The scatter plot depicts the partial regression plot demonstrating the association between rumination and precuneus activity, controlling for rejection sensitivity and depressive symptoms. The shaded area indicates the 95 % CI; SVC, Small Volume Correction; a. u., arbitrary unit.

Table 3
Brain regions in which neural activity and connectivity were significantly associated with rumination. Anatomical labels and the size of significant clusters are presented. Statistical values and MNI coordinates of peak voxels are presented. IPG, Inferior Parietal Gyrus; DLPFC, Dorsolateral Prefrontal Cortex; SMA, Supplementary Motor Area; pgACC, Pregenual Anterior Cingulate Cortex; MPFC, Medial Prefrontal Cortex; MOC, Middle Occipital Cortex; SPG, Superior Parietal Gyrus; VLPFC, Ventrolateral Prefrontal Cortex; IFG, Inferior Frontal Gyrus; ACC, Anterior Cingulate Cortex.

Anatomical Description	T-value	Cluster Size (voxels)	x	y	z
Neural activity following rejection from liked peers (SVC-corrected)					
Precuneus	5.38	75	-6	-68	42
Neural activity following rejection from liked peers (WB-corrected)					
Precuneus	5.46	585	-8	-68	42
IPG	5.07	127	-34	-52	38
	4.55	183	-44	-42	50
	4.51	201	48	-38	46
DLPFC (Middle Frontal Gyrus)	4.43	90	-24	12	62
	4.46	136	36	38	34
	4.02	103	32	18	56
SMA	4.29	106	-2	18	50
Left sgACC connectivity following rejection from liked peers (SVC-corrected)					
pgACC/MPFC	4.69	170	-8	44	-2
Precuneus	4.56	116	4	-58	16
Left sgACC connectivity following rejection from liked peers (WB-corrected)					
pgACC/MPFC	4.69	177	-8	44	-2
Precuenus	4.56	183	4	-58	16
MOC/SPG	4.66	436	28	-64	48
VLPFC (IFG, opercular part)	4.23	123	42	6	34
Right sgACC connectivity following rejection from liked peers (SVC-corrected)					
supracallosal ACC	4.06	59	-8	36	22

4.4. *sgACC connectivity following rejection from liked peers*

The functional connectivity analysis of the left sgACC seed with the search volume of core DMN regions showed that rumination was negatively associated with the connectivity between the left sgACC and the pgACC/mPFC and the precuneus following rejection from liked peers (Fig. 3A, top panel; Table 3). In the whole-brain regression analysis, rumination was negatively associated with the connectivity between the left sgACC and the large clusters of activity in the pgACC/mPFC and precuneus, middle occipital cortex/superior parietal gyrus (MOC/SPG) and posterior ventrolateral prefrontal cortex (vlPFC) (Fig. 3A, bottom panel; Table 3).

The functional connectivity analysis of the right sgACC seed with the search volume of core DMN regions revealed that rumination was negatively associated connectivity between the right sgACC and the supracallosal ACC (Fig. 3B; Table 3). The whole-brain regression analysis did not reveal any significant connectivity patterns associated with rumination.

4.5. *sgACC connectivity following rejection from unliked peers*

The same analysis of sgACC connectivity following rejection from unliked peers revealed non-significant results.

4.6. *Rumination-brain-behavior association*

Because rumination was associated with both brain activity/connectivity and slower RT following rejection (vs. not rated) from liked peers, we further explored whether RT was correlated with brain clusters significantly associated with rumination. The result showed that RT was positively associated with activity of precuneus identified in both small volume correction ([−6, −68, 42]) and whole brain correction ([−8, −68, 42]), one of the three IPG clusters ([−34, −52, 38]), one of the three DLPFC clusters ([32, 18, 56]) and SMA ([−2, 18, 50]) (see Supplementary Table 1 for statistics). Five mediation analyses with each of these brain regions as a mediator revealed that precuneus activity (identified in the whole-brain analysis) and SMA activity significantly mediated the effect of rumination on slower RT in response to rejection (vs. neutral) feedback from liked peers (see Fig. 4 and Supplementary Fig. 2 for statistics).

5. Discussion

This is the first study to examine self-reported rumination in association with rejection-related neural activity and connectivity in adolescent girls. When rejected by peers they liked, girls experiencing higher levels of rumination showed greater activity in the precuneus, IPL, DLPFC, and SMA and reduced sgACC connectivity with core DMN regions (i.e., pgACC/mPFC, supracallosal ACC, precuenus), posterior vlPFC, and a region encompassing MOC and SPC. A greater tendency to ruminate was associated with taking more time to report on one's emotional state in response to rejection from liked peers, and this effect was mediated by higher levels of precuneus and SMA activity. These results suggest that adolescent girls with a ruminative tendency exhibit distinctive patterns of neural processing of social rejection in affective, cognitive, and self-relevant circuitry. In our discussion, we interpret the observed rumination-related neural activity based on putative cognitive functions associated with these regions, slower RT of girls with higher levels of rumination observed during the task, and distinctive psychological processes of ruminators identified in previous studies. It is important to note that because the putative cognitive functions (e.g., mentalizing, emotion dysregulation) linked to these regions were not directly measured, we make a "weak reverse inference" (i.e., reverse inference is used not to claim strong conclusions but to generate promising hypotheses) (Calzavarini and Cevolani, 2022) on the cognitive functions underlying neural activity.

Consistent with our hypothesis, higher levels of rumination were associated with greater activity in the precuneus, a hub of the DMN implicated in self-relevant information processing. This result extends findings from a meta-analysis (Makovac et al., 2020) showing that precuneus and adjacent PCC activity are associated with adults' individual differences in rumination by demonstrating similar patterns in adolescent girls in the context of receiving social rejection, suggesting possible developmental stability in these processes from late adolescence to adulthood. Moreover, our result is consistent with findings from work showing that increased precuneus activity to threatening facial stimuli is associated with ruminative brooding (Peters et al., 2019). Based on consistent evidence across processes of autobiographical memory (Spreng et al., 2009), episodic memory (Kim, 2018), and self-referential processing (Northoff et al., 2006; Frewen et al., 2020), the precuneus/PCC has a central role in representing one's self-concept and generating a unitary sense of self (Parvizi et al., 2021; Davey and Harrison, 2022) by synthesizing self-relevant information received from the external environment (e.g., social evaluation) and pre-existing knowledge about the self (Yoon et al., 2018; Dohmatob et al., 2020; Lyu et al., 2021; Yeshurun et al., 2021). The precuneus/PCC is also a core region implicated in mentalizing (Fehlbaum et al., 2021), such as inferring others' intention and goals (Den Ouden et al., 2005; Van Overwalle and Baetens, 2009) and engaging in abstract forms of self-focus (Freton et al., 2014). Given evidence documenting functions of the precuneus, two interpretations of our finding of greater precuneus activity in girls with greater rumination are plausible. First, this pattern suggests that girls with a ruminative tendency have a propensity to deeply encode and internalize negative feedback as they represent their self-concept. Second, this pattern may reflect girls' attempts to analyze and overinterpret why peers, especially ones they liked, gave them negative feedback, which aligns with high ruminators' need to understand a situation and their propensity to ask "why" type questions (Watkins, 2004). Notably, within our a priori ROIs, we only found the effect of rumination in a core DMN region (i.e., precuneus), but not the sgACC, a brain region serving affect generation. This differentiation suggests that what uniquely characterizes girls with greater rumination

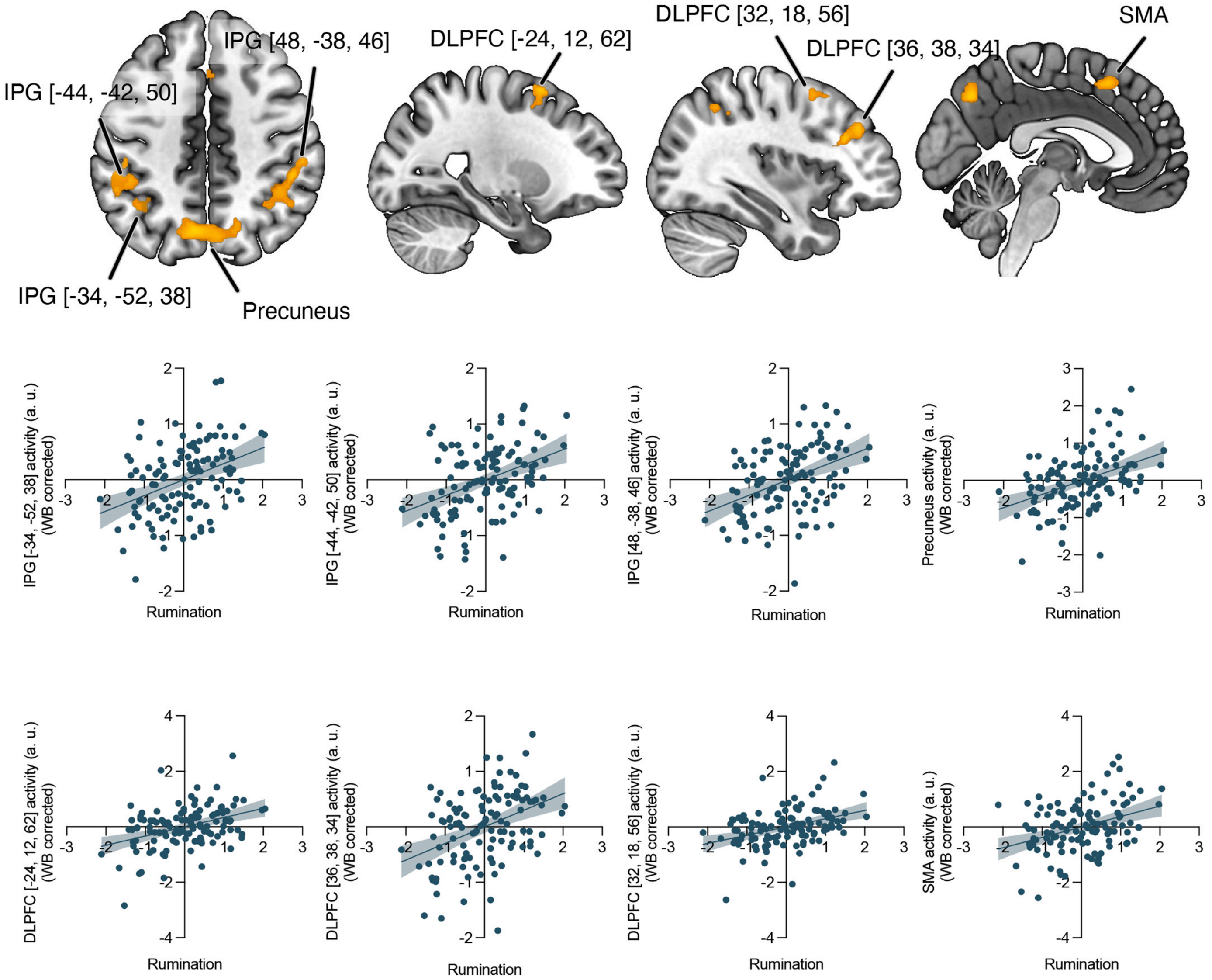

Fig. 2. Brain regions in which neural activity following rejection from liked peers showed a positive association with rumination. The brain map depicts the significant results from multiple regression analysis with the covariates of rejection sensitivity and depressive symptoms. Multiple comparison correction was applied to the whole brain. The scatter plots describe the partial regression plots demonstrating the association between rumination and several brain regions, controlling for rejection sensitivity and depressive symptoms. The shaded area indicates the 95 % CI; WB, Whole Brain; IPG, Inferior Parietal Gyrus; DLPFC, Dorsolateral Prefrontal Cortex; SMA, Supplementary Motor Area. a. u., arbitrary unit.

may be engaging in distinctive patterns of self-referential processing or mentalizing (e.g., deep integration of negative feedback into the self-concept and over-interpretation) rather than demonstrating distinctively high emotional reactivity immediately after negative social feedback. To clarify the function of the elevated rejection-related precuneus activity in girls showing high levels of rumination, future work should probe changes in participants' self-esteem (Eisenberger et al., 2011; Will et al., 2017) or ask participants whether they are thinking about the reason behind the social feedback, and then link brain activity to such self-reported responses.

The whole-brain analysis revealed that rumination was associated with heightened activity of the DLPFC, IPG, and SMA, regions that all correspond to the working memory network (Rottschy et al., 2012; Emch et al., 2019; Wang et al., 2019). This result suggests that girls with greater levels of rumination may allocate working memory resources to negative social feedback to a larger extent than girls with lower levels of rumination, which may interfere with performing cognitive tasks that demand working memory resources. This interpretation aligns with previous findings that rumination is associated with better recollection of negative words presented when encoding self-referent adjectives (Kuo et al., 2012), and that high ruminators respond more slowly on a working memory task following negative comments from a significant other, suggesting greater cognitive resources allocated to the criticism than to other aspects of the task at hand (Kaiser et al., 2015). Further studies are needed to directly test relations among rumination, activity of working memory network regions, and the interference of social rejection on subsequent memory task performance to fully confirm this interpretation.

Consistent with Kaiser et al. (2015), we found that girls with higher levels of rumination showed slower RT following rejection from liked peers, but the difference was that our task asked participants to report on their current emotional state as opposed to engaging in a working memory task as done in Kaiser et al. Interestingly, heightened SMA and precuneus activity to rejection from liked peers served as neural mediators that explained the effect of rumination on the slowed RT when reflecting on their current emotional state. Given the role of SMA (also called posterior MPFC) in conflict processing (Usami et al., 2013; Van der Molen et al., 2017; Wake et al., 2019), girls with higher levels of

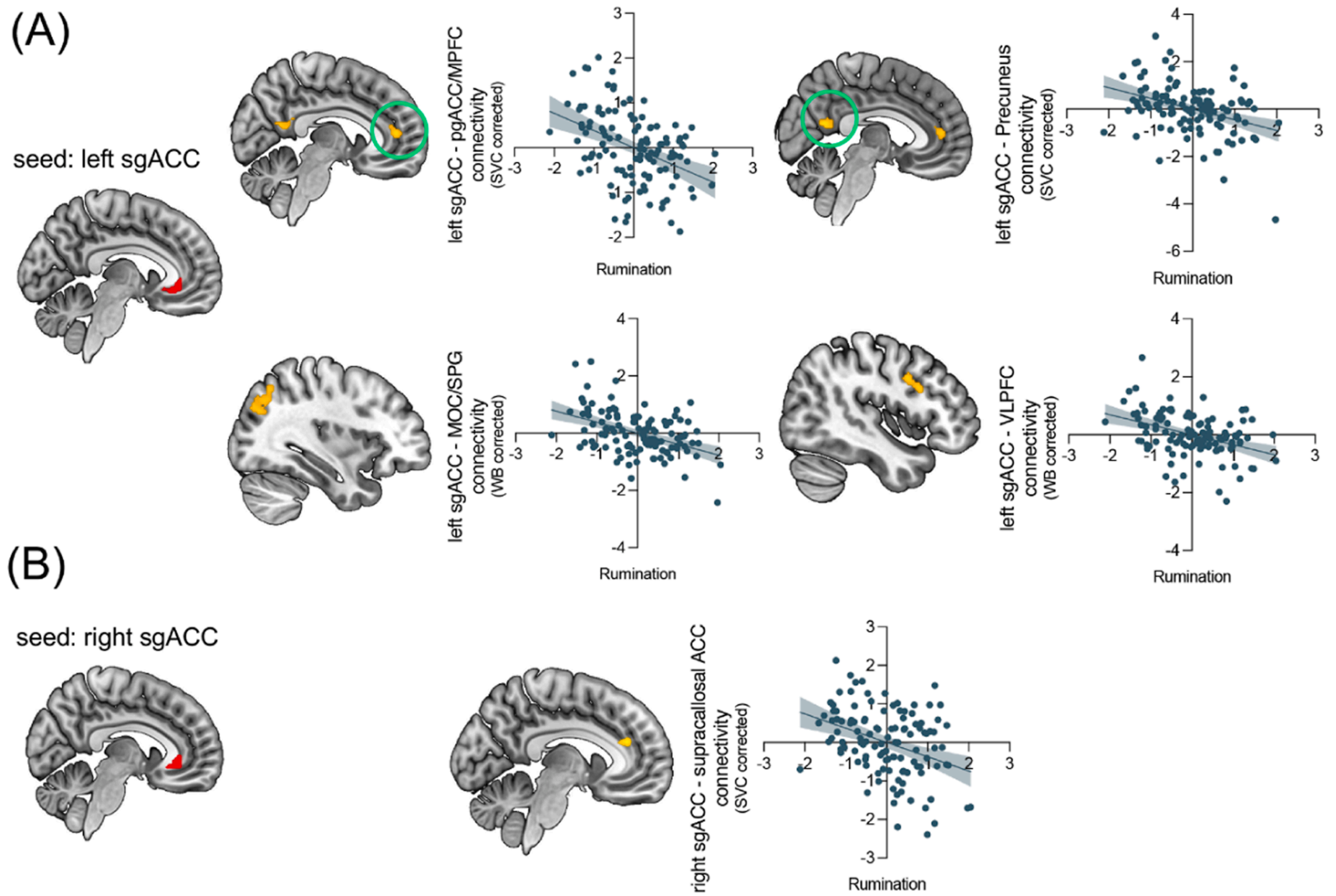

Fig. 3. Negative association between rumination and sgACC connectivity following rejection feedback from liked peers. (A) The results from gPPI analysis with the seed region of left sgACC. The ROI analysis with the search volume of core DMN regions found significant results in pgACC/mPFC and precuneus. The whole brain analysis found significant results in MOC/SPG and vlPFC, as well as in clusters of pgACC/mPFC and precuneus larger than the clusters identified from the ROI analysis. (B) The results from gPPI analysis with the seed region of right sgACC. ROI analysis with small volume correction within core DMN regions found significant results in supracallosal ACC. The scatter plot describes the partial regression plot demonstrating the association between rumination and sgACC connectivity, controlling for rejection sensitivity and depressive symptoms. The shaded area indicates the 95 % CI; SVC, Small Volume Correction; sgACC, Subgenual Anterior Cingulate Cortex; pgACC, Pregenual Anterior Cingulate Cortex; MPFC, Medial Prefrontal Cortex; MOC, Middle Occipital Cortex; SPG, Superior Parietal Gyrus; VLPFC, Ventrolateral Prefrontal Cortex; ACC, Anterior Cingulate Cortex; a. u., arbitrary unit.

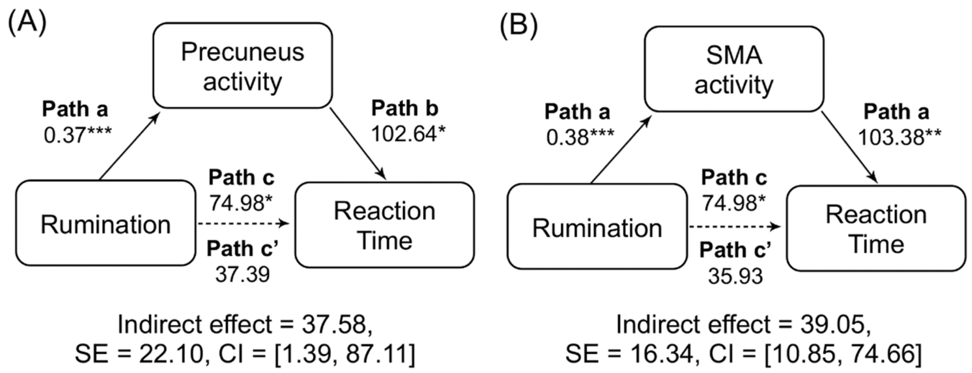

Fig. 4. Rumination-brain-behavior association when receiving rejection (vs. not rated) feedback from liked peers. (A) Precuneus activity identified in the whole brain analysis (k = 585, [−8, −68, −42]) significantly mediated the effect of rumination on slower reaction time following rejection (vs. not rated) from liked peers. (B) SMA activity (k = 106, [−2, 18, 50] significantly mediated the effect of rumination on slower reaction time following rejection (vs. not rated) from liked peers. SMA, Supplementary Motor Area; SE, standard error; CI, confidence interval.

rumination might have processed the rejection from liked peers as information that conflicted with their implicit or explicit standard to feel worthy which is to be accepted by others. This interpretation is supported by the fact that trait rumination is highly correlated with low self-esteem (Kolubinski et al., 2019) characterized by high reliance of one's self-worth on social evaluation (Will et al., 2020). Such conflict could have activated them to engage in analytical processing such as “why was this person not interested in me?” potentially supported by precuneus activity. This mental analysis might have elongated the time it took them to evaluate their feelings following the probe. Meanwhile, for girls with lower levels of rumination, rejection from liked peers might not have necessarily conflicted with their standards and thus required no mental analysis, allowing them to evaluate their feelings promptly.

Based on the functional connectivity analyses, we found that greater rumination was associated with *reduced* sgACC connectivity with core DMN regions (i.e., pgACC/mPFC, supracallosal ACC, precuneus) when being rejected from liked peers. This result contradicts our expectation that greater rumination would be associated with *greater* connectivity between sgACC with core DMN regions following rejection because of excessive pairing of emotional distress with self-processing (e.g., integrating a distress-eliciting event into self-concept), but nonetheless provides valuable insights into the relation between rumination and sgACC-DMN connectivity. It is possible that reduced sgACC-DMN connectivity following negative feedback reflects the difficulty in integrating emotional processing and positive self-referential cognitions, which may be related to the inability to preserve positive self-views when experiencing rejection via self-protective cognitions such as external attribution. Results of the current study that were opposite of the meta-analysis findings (Hamilton et al., 2015b) upon which our hypothesis was based could be attributed to differences in the context in which neural connectivity was measured and in the sample. While the current study measured neural connectivity following negative social feedback, the meta-analysis on neural connectivity associated with rumination was conducted with rsFC studies (Greicius et al., 2007; Berman et al., 2011; Gaffrey et al., 2012; Zhu et al., 2012; Sambataro et al., 2014). It is possible that increased sgACC-DMN connectivity serves an adaptive function (i.e., ability to preserve positive self-views when experiencing negative affect) in a self-threatening context, whereas it serves a maladaptive function (i.e., negative self-referential thoughts coupled with negative affect) in the absence of an immediate self-threatening context. While we could not directly probe this possibility because resting-state fMRI data was not collected in the PGS-E study, future work is needed to test the direction of the relation between rumination and sgACC-DMN connectivity in both self-threatening (via a task) and unconstrained (via rs-fMRI) contexts. Alternatively, because the samples of most studies included in the meta-analysis were adults with clinical depression (Greicius et al., 2007; Berman et al., 2011; Gaffrey et al., 2012; Zhu et al., 2012; Sambataro et al., 2014), and our sample was mostly adolescents without clinical disorders (except 3 who met criteria for MDD), sample differences may account for the opposite pattern of results.

In addition to core DMN regions, we found that rumination was negatively associated with sgACC connectivity with posterior vlPFC and a region encompassing MOC and SPL. The posterior vlPFC plays a critical role in inhibitory control in both affective and non-affective contexts, particularly in the early stages of inhibition (Cai et al., 2014) and is activated during the implicit regulation of negative emotion in adolescents (Pozzi et al., 2021). Relatedly, other work has found that adolescent girls with high levels of stress-reactive rumination exhibited disrupted connectivity between vlPFC and the amygdala during an implicit emotion regulation task (i.e., labeling emotions) administered following the experience of social exclusion (Fowler et al., 2017). The observed MOC/SPL cluster corresponds to the dorsal attention network and is implicated in the top-down modulation of attention (Hahn et al., 2006; Ciaramelli et al., 2008), attention allocation (Bentley et al., 2004; Cona et al., 2017; Abend et al., 2019), and attentional shift (Vandenberghe et al., 2001; Heinen et al., 2017). Taken together, reduced sgACC connectivity with core DMN regions, vlPFC, and MOC/SPL in girls with greater levels of trait rumination may suggest their reduced capacity to automatically downregulate emotion and shift attention away from arousal elicited by rejection with the goal of maintaining a positive sense of self.

Notably, the significant patterns of neural activation and sgACC connectivity associated with rumination were only observed when girls received negative feedback from peers they liked, and not when girls received negative feedback from peers they did not like. This observation suggests that distinctive cognitive processing of rejection in girls with high levels of rumination may be specific to events of high saliency and significance to the self. Our findings raise new questions for further investigation about the specific contexts of rejection events (e.g., social feedback vs. nonsocial feedback, peer feedback vs. parent feedback) that elicit distinctive cognitive processing in girls with high levels of rumination.

The present study was not without limitations. One drawback pertains to our rumination measure (i.e., Rumination Subscale of Perfectionism Inventory). Because the measure focuses on rumination regarding performance, it may have less relevance to reactivity to social evaluation. However, concern about imperfect performance is often derived from social expectations and other work confirms that our measure of rumination highly correlates with interpersonal sensitivity and fear of negative evaluation (Hill et al., 2004). Additionally, while participants received social feedback regarding one’s *likability* in the fMRI task, the perfectionism subscale assesses reactions to one’s *performance*. Nonetheless, performance referred to in this scale is non-specific and includes performance contexts such as public presentation and daily social behavior that could profoundly modulate one’s likability. Matching the stimuli used in the fMRI task and the target of rumination in a self-reported measure may reveal other patterns that would further characterize individual variability in neural reactivity to rumination-eliciting events. Future studies should measure rumination provoked by social feedback received during the fMRI task or add ecological momentary assessment (EMA) techniques to track daily receipt of social evaluation and subsequent rumination. A related limitation is that our findings may not generalize to all forms of rumination. Rumination is a heterogeneous and multi-faceted construct (Smith and Alloy, 2009), and our rumination measure primarily taps repetitiveness and difficulty of disengagement of thoughts about one’s behaviors. Separate studies are needed to test whether identified neural correlates are also associated with other measures (e.g., Ruminative Response Style (Nolen-Hoeksema et al., 2008)) or facets of rumination (e.g., intrusiveness, capture of attention). Third, the observed neural patterns may not necessarily reflect maladaptive cognitive functioning of high ruminators because our participants are from a community sample with relatively low rates of depression. Future studies should test whether the patterns we observed also exist in clinical samples. Additionally, future work should modify the fMRI task to include probes and questions about participants’ cognition and emotion upon receiving the feedback relevant to rumination to clarify the maladaptive psychological functions associated with neural activity. Lastly, there was considerable individual variability in the time gap between questionnaire data collection and scanning visits. In the context of this variability in assessment timing, neural activity was regressed on the mix of recently reported and past reported rumination, which could limit interpretations of the results particularly if trait rumination is not stable across time. Although our findings were maintained after adding the time gap as a covariate (except that the activity of a single DLPFC cluster emerged as an additional mediator between rumination and reaction time; see Supplementary Table 2; Supplementary Fig. 3) and the time gap was not associated with other covariates (see Supplementary Result 2), the findings should be replicated by collecting questionnaire and MRI data at the same time across participants.

Despite these limitations, the current study has notable strengths, including clear implications. First, we focused on a sample of adolescent girls, which is an important population with high vulnerability for developing depression and other forms of psychopathology for which rumination is a risk factor (Platt et al., 2021; Solmi et al., 2021). Second, our results contribute to broadening our understanding of developmentally-salient rejection-related neural mechanisms—rather than phenomenological or strictly autonomic physiological characteristics (Aldao et al., 2014; Stone et al., 2016)—associated with rumination in adolescents, which may lead to more sophisticated clinical neuroscience hypotheses. Third, our results contribute new information to the social, affective and developmental cognitive neuroscience literatures by focusing on individual differences in rumination in association with response to social feedback, thereby addressing a gap in knowledge about neural responses engaged when girls encoded salient, rumination-eliciting events. Finally, the results from our study have the potential to inform current practice using available interventions for high ruminators. For example, adolescents with high rumination can practice rumination-focused cognitive behavioral therapy (Watkins, 2018) by thinking "how can I make myself feel better?" rather than "why am I rejected?" in response to rejection from liked peers.

6. Conclusions

In conclusion, the current study identified social rejection-related neural activity and connectivity associated with rumination in adolescent girls, advancing the neurobiological model of rumination. Building on these findings by exploring cognitive strategies that yield reductions in rumination or attenuate the impact of rumination on processing of self-relevant social stimuli (e.g., cognitive reappraisal, attention modification) may lead to new approaches for supporting the mental health of adolescent girls.

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CRediT authorship contribution statement

Leehyun Yoon: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization; **Kate E. Keenan, Alison E. Hipwell, Erika E. Forbes:** Investigation, Resources, Data curation, Writing – review & editing, Project administration, Funding acquisition; **Amanda E. Guyer**: Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Unthresholded statistical maps were uploaded to NeuroVault.org database and are available at https://neurovault.org/collections/SHFXELFH/. Data will be freely distributed following a data use request protocol to qualified academic investigators for noncommercial research. Data will be shared in a format that protects the anonymity and privacy of participants.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dcn.2023.101320.

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