

Neural Dynamics of Rejection Sensitivity

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Abstract

■ Rejection sensitivity (RS) is the tendency to anxiously expect, readily perceive, and intensely react to rejection. This study used functional magnetic resonance imaging to explore whether individual differences in RS are mediated by differential recruitment of brain regions involved in emotional appraisal and/or cognitive control. High and low RS participants were scanned while viewing either representational paintings depicting themes of rejection and acceptance or nonrepresentational control paintings matched for positive or negative valence, arousal and interest level. Across all participants, rejection versus acceptance images activated regions of the brain involved in processing affective stimuli (posterior cingulate, insula), and cognitive control (dorsal anterior cingulate cortex; medial frontal cortex). Low and high RS individuals' responses

to rejection versus acceptance images were not, however, identical. Low RS individuals displayed significantly more activity in left inferior and right dorsal frontal regions, and activity in these areas correlated negatively with participants' self-report distress ratings. In addition, control analyses revealed no effect of viewing negative versus positive images in any of the areas described above, suggesting that the aforementioned activations were involved in rejection-relevant processing rather than processing negatively valenced stimuli per se. Taken together, these findings suggest that responses in regions traditionally implicated in emotional processing and cognitive control are sensitive to rejection stimuli irrespective of RS, but that low RS individuals may activate prefrontal structures to regulate distress associated with viewing such images. ■

INTRODUCTION

Rejection is a common and potentially distressing human experience. Yet, people vary considerably in how they react to it. Some people respond to rejection with equanimity, remaining calm and composed in the face of challenging interpersonal threats. Others respond to rejection in ways that compromise their well-being and relationships. For example, they become angry, dejected, or withdrawn.

The rejection sensitivity (RS) model was introduced to explain why some individuals are more vulnerable to rejection experiences than others (Downey & Feldman, 1996). According to this theory, sensitivity to rejection cues, and subsequent overreactions, results from a natural learning process—high levels of RS develop as a result of early, prolonged, or acute rejection experiences with caregivers and significant others. Through such experiences, individuals learn to expect rejection in situations involving close others, and because these relationships are significant, the expectations people develop are laden with anxiety. Thus, anxious expectations of rejection characterize the high RS individual. These anxious expectations, in turn, lead high RS

individuals to display a heightened attentiveness to perceiving negativity in rejection-relevant cues and situations, and to display intense affective reactions to them (e.g., Levy, Ayduk, & Downey, 2001; Downey, Freitas, Michaelis, & Khouri, 1998).

A hallmark feature of RS is that the disposition becomes automatically activated in an *if...then...* manner by cues related to the concept of rejection, functioning to prepare the person to defend against the threat of rejection. Prior research has found, for example, that exposing high RS individuals to images that convey rejection themes (i.e., paintings depicting people who appear socially disconnected or lonely) or words associated with the concept of rejection (e.g., abandon, betray, exclude) leads to the activation of the defensively motivated RS schema and the negative thoughts, feelings, and physiological responses associated with it (Romero-Canyas & Downey, 2005; Downey, Mougios, Ayduk, London, & Shoda, 2004; Ayduk, Downey, Testa, Ying, & Shoda, 1999). This article examines the neural processes underlying the more intense distress-related affective responses that high RS people selectively show in response to rejection cues. Toward this end, we used functional magnetic resonance imaging (fMRI) to explore differences in brain activity between high and low RS individuals in response

to viewing rejection relevant and irrelevant stimuli evident in works of art.

Neural Regions Underlying RS: Candidate Areas

Cognitive neuroscience research suggests two possible relationships between individual differences in RS and patterns of neural activity in brain systems related to the generation and regulation of affect-driven responses that result from exposure to rejection-themed images.

First, because high RS individuals experience higher levels of distress when they are exposed to rejection cues than those lower in RS, they might demonstrate increased activity in brain regions involved in appraising the affective relevance of stimuli. Consistent with this hypothesis, prior work indicates that high, as compared to low, RS individuals experience more distress and show heightened startle responses when exposed to images conveying themes of rejection (Downey et al., 2004). This heightened threat response could be reflected in differential recruitment of a network of brain systems implicated in appraising the affective relevance of aversive stimuli, including the amygdala, insula, and various subregions of the cingulate cortex (Ochsner & Gross, 2004, 2005; Vogt, 2005; Eisenberger & Lieberman, 2004; Wager & Barrett, 2004; Ochsner & Barrett, 2001; Davidson & Irwin, 1999). Recent work has begun to show that activity in these regions may covary with individual differences in the way people process emotions and appraise stimuli as negative and threatening (Hamann & Canli, 2004; Phillips, Drevets, Rauch, & Lane, 2003). For example, insula activity correlates with awareness of anxiety-provoking body states and specific emotions, such as sadness (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Eugene et al., 2003), and increased amygdala activity has been found when individuals perceive threat in neutral faces (Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Donegan et al., 2003; Hart et al., 2000; Phelps et al., 2000; Birbaumer et al., 1998). Similarly, activity in the cingulate cortex has been shown to covary with awareness and experience of distress (e.g., Ochsner et al., 2006; Goldin et al., 2005; Ray et al., 2005; Coghill, McHaffie, & Yen, 2003; Eisenberger, Lieberman, & Williams, 2003) and specific subregions of the cingulate appear to be sensitive to rejection feedback. For example, Somerville, Heatherton, and Kelley (2006) recently demonstrated that although both ventral and dorsal regions of the ACC become active in response to overt rejection, the dorsal ACC (dACC) is sensitive specifically to expectancy violations (i.e., receiving feedback that is incongruent with one's expectations, regardless of feedback valence), whereas the ventral ACC (vACC) is sensitive specifically to whether one gets accepting as opposed to rejecting feedback.

A second possibility is that high RS individuals may show heightened reactivity to rejection cues because

they fail to adaptively regulate the emotional appraisals they generate in response to those cues. This hypothesis is motivated by three different behavioral and brain imaging findings. First, behavioral research indicates that high (relative to low) RS individuals show characteristic heightened reactivity to rejection cues and subsequent personal and interpersonal difficulties only if they also have low self-regulatory abilities (Ayduk et al., 2000). In addition, experimental evidence shows that when individuals who have been instructed to relive a rejection experience are instructed to appraise it in a cool, abstract manner, rather than in terms of its "hot," arousing features, they show less intense negative emotional responses, even if they are high in RS (Ayduk, Mischel, & Downey, 2002). Thus, behavioral evidence suggests that intense reactions to rejection may reflect a failure or inability to regulate emotions effectively.

Second, a growing number of studies have shown that instructing people to reappraise the meaning of aversive stimuli in less emotional terms (e.g., imagining that the blood on a corpse is ketchup) leads to decreases in distress, autonomic responses, startle reflex responses, and activity in affective appraisal systems such as the insula and amygdala (e.g., Harenski & Hamann, 2006; Kalisch et al., 2005; Phan, Fitzgerald, Nathan, & Tancer, 2005; Ochsner et al., 2004; Levesque et al., 2003; Ochsner, Bunge, Gross, & Gabrieli, 2002; Jackson, Malmstadt, Larson, & Davidson, 2000). These decreases depend upon increasing activation of left and right lateral prefrontal cortex (LPFC) regions thought to support the selection and application of reappraisal strategies, and of dACC regions that may monitor conflict between bottom-up appraisals of stimuli as aversive and top-down reappraisals of them as nonaversive (Ochsner & Gross, 2005; Ochsner et al., 2002, 2004; Jackson et al., 2003).¹

Third, a recent study conducted on the neural bases of social exclusion and its connection to self-report distress found increased activity in the insula, the right LPFC, and the dACC when participants perceived rejection by other players in an interactive computer game (Eisenberger et al., 2003). Whereas dACC activity correlated positively with distress ratings, prefrontal activity correlated negatively with both dACC activity and distress ratings, suggesting that interactions between prefrontal and cingulate cortices play a central role in regulating responses to rejection (Eisenberger & Lieberman, 2004). Because this study did not investigate whether individual differences in RS moderate PFC activity, however, it is unclear whether both low and high RS individuals will demonstrate this regulatory effect. It is possible, therefore, that high RS individuals' tendency to experience increased distress in response to rejection cues may be accompanied by a failure to recruit prefrontal regions involved in cognitively controlling such emotional responses (for a discussion, see Ochsner

& Gross, 2004, 2005). Consistent with this hypothesis, Hooley, Gruber, Scott, Hiller, and Yurgelun-Todd (2005) recently showed that individuals vulnerable to depression, for which RS is a risk factor (Ayduk, Downey, & Kim, 2001), displayed less dorsolateral prefrontal cortex (DLPFC) activity in response to maternal criticism as compared to maternal praise.

Overview of Present Study

The goal of this experiment was to examine the neural processes underlying high RS individuals' responses to rejection-related cues. As outlined above, we hypothesized that the increased levels of distress experienced by high RS individuals (relative to low RS individuals) when viewing rejection stimuli could be mediated by increased activity in neural systems related to affective appraisal and/or by a failure to recruit prefrontal regions involved in the cognitive control of emotion. To address these hypotheses, we modified for the fMRI scanner a study that used a startle paradigm to probe the emotional responses of high and low RS individuals to pictorial stimuli depicting rejection stimuli (Downey et al., 2004). This study design was based on Lang's work showing that phobic individuals showed a heightened emotional response to pictures relevant to their phobia (Lang, 1995; Lang, Bradley, & Cuthbert, 1990). Downey et al. (2004) recorded acoustic startle eye-blink magnitudes while high and low RS participants viewed rejection- and acceptance-themed representational works of art (respectively, selected paintings by Edward Hopper and August Renoir), as well as positively and negatively themed nonrepresentational works of art that served as controls for stimulus valence (respectively, selected paintings by Jean Miro and Mark Rothko). They found that high RS participants showed increased acoustic startle eye-blink magnitude only when viewing art that depicted rejection themes (i.e., Hopper paintings that conveyed a sense of loneliness or social disconnection; Downey et al., 2004), suggesting that it was the rejection content and neither the presence of social content per se nor the valence of images that mediated potentiated startle responses.

This paradigm was modified for scanning by (a) omitting startle noise bursts, which would be hard to detect in a noisy scanner environment and, more importantly, could induce motion-related activation artifacts, and (b) presenting the study stimuli using a blocked-design to enhance power of detecting significant differences in responses to rejection versus acceptance-themed art using fMRI. Participants were instructed to passively view the art used in order to observe how individual differences influenced participants' spontaneous evaluations of and responses to the study stimuli (for a similar approach, see Harenski & Hamann, 2006; Hamann & Canli, 2004; Jackson et al., 2003; Ochsner et al., 2002).

METHODS

Sample and Procedure

Twenty healthy right-handed participants (13 women, *M* age = 24.5 years) participated in the current study. Sixty-one percent were Caucasian, 12% were Asian, 12% were Middle Eastern, 6% were Hispanic, and 9% were from other ethnic backgrounds. They gave informed consent and were paid \$20 for their participation in the study in accordance with institutional guidelines. Participants were selected from a pool of 658 subjects who completed the Rejection Sensitivity Questionnaire (RSQ) as part of a battery of questionnaires administered to subjects participating in social psychology experiments unrelated to the present topic of study over the course of the past 4 years. Due to the present study's emphasis on exploring patterns of brain activation that distinguish low RS individuals from high RS individuals, only participants whose RSQ (described below) scores fell in the top or bottom 30th percentile of RSQ scores obtained in previous research were contacted via e-mail and invited to participate in this experiment, resulting in a total of 10 participants in each condition. The experiment took place over two sessions. During Session 1, participants completed a medical history questionnaire and handedness survey. During Session 2, participants were scanned while viewing rejection-relevant and -irrelevant stimuli (described below). Subsequent to scanning, participants rated the images they viewed while being scanned along a series of dimensions. They were then compensated.

Rejection Sensitivity Questionnaire

The RSQ assesses anxious expectations of rejection from significant or important others (Downey & Feldman, 1996; the measure is available at www.columbia.edu/cu/psychology/socialrelations). The measure consists of 18 items depicting hypothetical scenarios that ask participants to imagine themselves asking a significant other to do something for them (e.g., "You ask your boyfriend/girlfriend if he/she really loves you"). For each situation, participants are instructed to indicate how concerned or anxious they would be about the outcome, as well as how likely they think their significant others would respond to their requests with rejection. All ratings are made on a 6-point scale. Because the measure seeks to capture "hot" anxious expectations of rejection, RSQ scores are computed by first weighting the expected likelihood of rejection for each situation by the degree of anxiety, and then averaging these weighted scores across the 18 situations. The RSQ has been used extensively in prior research (see Pietrzak, Downey, & Ayduk, 2005, for review) and has been shown to have unique predictive utility, beyond conceptually and empirically related personality constructs, including depression, introversion, neuroticism, adult

attachment style, social anxiety, social avoidance, and self-esteem (Downey & Feldman, 1996). In this study, the mean RSQ score for participants in the low RS condition was 3.81 ($SD = 1.22$; range: 2.16–6.32); the mean RSQ score for participants in the high RS condition was 14.87 ($SD = 2.18$; range: 11.22–18.42). There were no significant gender or age differences between participants in each group. Data from two participants were excluded from the analyses due to excessive movement during scanning resulting in a total of nine participants in each condition.

Stimuli

The stimulus set consisted of representational paintings (i.e., paintings portraying people) depicting themes of rejection (by Edward Hopper) and acceptance (by August Renoir), as well as nonrepresentational paintings (i.e., abstract paintings) of either negative (by Mark Rothko) or positive valence (by Jean Miro). Four paintings from each artist constituted the stimulus set (the stimuli are available at www.columbia.edu/cu/psychology/socialrelations). The approach to developing a standardized set of slides intended to elicit particular types of emotional responses was modeled on that used by Lang and colleagues (e.g., Bradley, Cuthbert, & Lang, 1996; Lang, 1995) to develop the International Affective Picture System. Several artists were selected with the help of art experts because some of their art depicted the themes of specific interest (e.g., rejection, acceptance, nonrepresentational positive, nonrepresentational negative). Extensive pilot work yielded a final set of 4 artists and 16 specific paintings that were rated as depicting the themes of interest—rejection, acceptance, general positivity, or negativity, respectively—and that also allowed for a range of responses. Qualitative data obtained from 25 pilot participants who wrote about their thoughts and feelings as they viewed the 16 paintings confirmed that the selected paintings by Hopper evoked thoughts and feelings related to rejection (e.g., loneliness, social disconnection, and rejection); those by Renoir elicited thoughts and feelings related to acceptance (e.g., connected, social, romantic); those by Rothko elicited thoughts and feelings of general negativity (e.g., angry, scared, confused, physically lost), and those by Miro elicited thoughts and feelings that were generally positive (e.g., energetic, happy, bright, childlike). As described by Downey et al. (2004; pilot), a separate group of pilot participants ($n = 40$) rated on a 7-point scale the content of the slides along two dimensions, rejecting–accepting (How rejecting or accepting does this image seem to you?) and positive–negative (How positive or negative does this image seem to you?). Participants also rated the slides on level of interest (How interesting do you find this image?), and arousal (How aroused or calm does this image make you feel?). Ratings confirmed that Hopper paintings

depicted rejection themes and were negative in valence, whereas Renoir paintings depicted acceptance themes and were positive in valence. In addition, although the rejection-related Hopper paintings and the nonsocial, non-rejection-related Rothko paintings were both rated as highly negative, the Hopper images were rated as significantly more related to rejection. Likewise, although the Renoir and Miro paintings were both highly positive, the Renoir paintings were rated significantly more related to acceptance than were the Miro paintings. The Hopper paintings did not differ significantly from the other types in how arousing or intrinsically interesting participants rated them.

Behavioral Protocol

In the present study, the startle probe paradigm used by Downey et al. (2004) was modified for use in the fMRI. Participants viewed eight repetitions each of four types of stimulus blocks for a total of 32 block presentations. Each block was composed of a series of four trials lasting 4 sec each, with no interstimulus interval, for a total of 16 sec/block. All trials within a block presented either rejection (representational, negative), acceptance (representational, positive), negative (nonrepresentational negative), or positive images (nonrepresentational, positive). On each trial, participants were instructed to passively view each image and allow whatever thoughts they experienced to come to mind (for similar instructions, see Harenski & Hamann, 2006; Ochsner et al., 2002, 2004; Jackson et al., 2003). The order of rejection, acceptance, positive, and negative blocks was varied using a Latin Square permutation. Each sequence of blocks was separated by a 16-sec rest block in which participants were instructed to focus on a fixation cross that was presented in the center of the display. Stimulus delivery was controlled by Presentation software (Neurobehavioral Systems, <http://nbs.neuro-bs.com>) running on a PC laptop computer. Stimuli were displayed on a back-projection screen that could be viewed via a mirror mounted on the scanner head coil.

On completion of the scanning portion of the experiment, participants were asked if they had trouble following the task instructions, lost attention, or experienced drowsiness at any point. No participants indicated experiencing any problems. Participants then rated all stimuli on the following dimensions using 7-point scales: pleasant–unpleasant (“how pleasant–unpleasant does this image make you feel?”), secure–insecure (“how insecure–secure does this image make you feel?”), interest (“how interesting is this image to you?”), and arousal (“how aroused does this image make you feel?”). In this sample, participants’ average pleasant–unpleasant and secure–insecure ratings across all stimuli were highly correlated ($r = .78, p < .001$). They were therefore collapsed to provide a single index of distress.

fMRI Data Acquisition

Images were acquired with a GE 1.5-T scanner. Whole-brain functional data were acquired in 25 contiguous axial slices (4.5 mm thick, 1.5 × 1.5 mm in-plane resolution) parallel to the AC–PC line with a T2*-weighted EPI sequence (TR = 4000, TE = 60, flip angle = 60°, FoV = 190). Data were acquired in a single run of 165 volumes (660 sec). Structural data were acquired with a high-resolution T1-weighted SPGR scan (TR = 19, TE = 5, flip angle = 20°, FoV = 220) recording 124 slices at a slice thickness of 1.5 mm and in-plane resolution of 0.86 × 0.86 mm.

fMRI Data Analysis

Spatial preprocessing and statistical analyses were carried out with SPM2 software (Wellcome Department of Cognitive Neurology, University College London, UK, <http://www.fil.ion.ucl.ac.uk/spm/spm2.html>).

Preprocessing

Functional scans were spatially realigned to the first scan volume, and the structural image was coregistered to a mean image of the realigned functional scans. Normalization parameters were determined from warping the coregistered structural image to the Montreal Neurological Institute template T1 brain, and these parameters were applied to the functional scans, resampling the data at a 2-mm³ voxel size. Finally, the functional images were spatially smoothed with a Gaussian kernel of 9 mm³ full width at half maximum. The first three functional volumes were discarded from the analysis.

Primary Statistical Analyses

Using the general linear model framework (Friston et al., 1995), each experimental condition (REJ [Hopper: representational, negative], ACP [Renoir: representational, positive], NEG [Rothko: nonrepresentational, negative], POS [Miro: nonrepresentational, positive]) was modeled with a box-car function convolved with a canonical hemodynamic response function. In order to remove low-frequency confounds, data were high-pass filtered (128 sec). Temporal correlations were estimated using restricted maximum likelihood estimates of variance components using a first-order autoregressive model (AR-1), and the resulting nonsphericity was used to form maximum likelihood estimates of the activations. For each subject, voxelwise statistical parametric maps (SPM) were calculated to identify brain regions implicated in the processing of rejection-related stimuli (negative-representational paintings) compared with acceptance-related stimuli (positive-representational paintings), namely, a REJ > ACP contrast. This analysis controlled for the social themes in the rejection- and

acceptance-related stimuli because both sets of paintings (Hopper and Renoir) depicted people interacting. SPMs from each subject were then entered into group analyses, where participants were treated as random effects. To establish that brain regions identified in this manner were involved in rejection or social-threat processing, rather than in processing of negatively valenced stimuli per se, we carried out a control analysis by testing for an effect of NEG > POS (negative-nonrepresentational > positive nonrepresentational) in these functionally defined regions of interest (ROIs).

Rejection-related activation was assessed first across all subjects and then contrasted between groups. Based on previous findings cited in the Introduction, these analyses were carried out within a priori anatomical ROIs, consisting of the frontal and limbic lobes (as defined by the WFU pickatlas tool; www.rad.wfubmc.edu/fmri; Maldjian, Laurienti, Kraft, & Burdette, 2003). Within these a priori ROIs, we adopted a voxelwise statistical significance threshold of $p < .001$ (uncorrected) with a cluster threshold of 5 contiguous voxels (40 mm³). For correlating BOLD responses between different functional ROIs and behavioral data, beta values for peak voxel activations of each cluster were extracted via SPM2's "volume of interest" function and analyzed using SPSS software. Partial correlations were computed between extracted betas and participants' self-report distress ratings, while controlling for self-reports of arousal and interest in the painting. Arousal and interest were controlled for in these analyses in order to identify regions of brain activity that covaried specifically with distress experienced in response to viewing rejection-themed stimuli. Because we had specific hypotheses about the direction of the effects that would be observed between brain activity and participants' self-report distress ratings, one-tailed p values are reported for all correlational analyses.

Secondary Analyses

Because only two prior studies have directly examined the neural correlates of rejection in a healthy normal population (Somerville et al., 2006; Eisenberger et al., 2003), we thought it important to examine directly the relationship between our results and those of the previous studies. To address this issue, functional ROI analyses were conducted using eight clusters of activity observed by Eisenberger et al. (2003) when participants experienced social exclusion (three ROIs were in the dACC, four were in the right ventral LPFC [VLPFC], and one was in the insula) and two clusters of activity observed by Somerville et al. (2006) during a task that dissociated expectancy violation from social feedback (one ROI was in dACC and one was in vACC). Using Marsbar software (<http://marsbar.sourceforge.net/>), we extracted beta values from a 5-mm sphere around the peak-activated voxel for each cluster. We then

Table 1. Brain Regions Displaying Rejection > Acceptance Increases in Activation across All Subjects

Region	BA	MNI (x, y, z)	Z-score	Cluster
Middle Frontal G	46	-38 32 22	3.27	11
Middle Frontal G	46	48 38 18	3.26	8
Inferior Frontal G	47	46 18 -6	3.94	92
Dorsal ACC	32	8 16 34	3.46	23
	32	-16 10 38	3.44	36
Posterior Cingulate	31	-16 -64 14	4.42	44
	31	0 -48 34	3.53	126
	29	2 -56 10	3.40	47
Medial Frontal G	6	6 14 50	3.39	19
Precentral G	6	-30 -10 52	3.36	39
Parahippocampal	37	-22 -48 -10	4.44	175
Parahippocampal	37	22 -44 -12	4.25	87

For all activations: $p < .001$, uncorrected with an extent threshold of 5 voxels. BA = Brodmann's area; MNI (x, y, z) = Montreal Neurological Institute coordinates for peak activated voxel in cluster; Cluster = cluster size in voxels (1 voxel = 8 mm³); G = gyrus; ACC = anterior cingulate cortex.

computed: (1) Paired-sample t tests comparing betas for rejection trials and acceptance trials; (2) repeated-measures ANOVAs to test for possible group effects; and (3) correlations between self-report distress ratings and activation in the reject > accept contrasts, controlling for differences in overall levels of self-reported arousal and interest in paintings. Two-tailed p values are reported for all analyses because we did not have specific a priori hypotheses regarding how the present findings would

compare to those reported in Eisenberger et al. and Somerville et al.

RESULTS

Behavioral Results

Participants rated the Hopper and Rothko paintings significantly more distressing relative to the Renoir and Miro paintings ($t_s > 2.22$, $p_s < .05$). In addition, the Hopper paintings were rated more distressing than the Rothko paintings [$t(17) = 2.07$, $p < .05$], and, consistent with predictions, RS scores were positively correlated with participant's ratings of distress while viewing Hopper paintings, controlling for their distress while viewing Rothko ($r = .77$, $p < .001$). The paintings did not differ significantly from one another in terms of how interesting or arousing participants rated them (all $t_s < 1.50$, ns).

Neuroimaging Results

Responses to Rejection-themed vs. Acceptance-themed Stimuli

Activity during rejection and acceptance blocks was contrasted to identify regions related to exposure to rejection themes. Across both high and low RS participants, the REJ > ACP contrast identified significant clusters of activation in the posterior cingulate and dACC, medial frontal gyri, middle frontal gyri, right inferior frontal gyrus, precentral gyrus, and parahippocampal gyrus (see Table 1; Figure 1). We next examined whether activity in these areas was associated with participants' self-report ratings of distress while viewing the rejection-themed Hopper paintings. These analyses revealed a significant negative correlation between participants' dis-

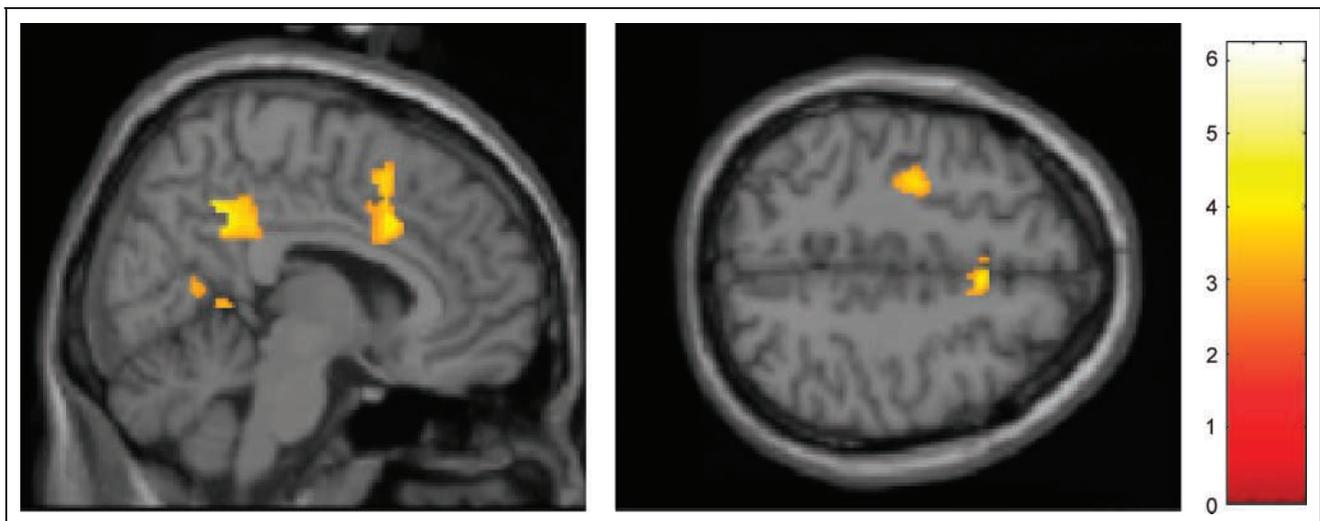


Figure 1. Increased activation across all subjects for rejection > acceptance contrast included foci in the dorsal anterior cingulate and posterior cingulate gyrus, as well as in the left precentral gyrus.

Table 2. Brain Regions of Increased Rejection > Acceptance Processing in Low versus High RS Subjects

Region	BA	MNI (x, y, z)	Z-score	Cluster
Inferior Frontal G	45	-38 26 10	3.46	7
Inferior Frontal G	9	-44 2 24	3.44	6
Superior Frontal G	6	18 8 62	3.66	7

For all activations: $p < .001$, uncorrected with an extent threshold of 5 voxels. BA = Brodmann's area; MNI (x, y, z) = Montreal Neurological Institute coordinates for peak activated voxel in cluster; Cluster = cluster size in voxels (1 voxel = 8 mm³); G = gyrus.

stress ratings and precentral gyrus activity ($[-30, -10, 52]$, $r = -.48, p < .05$). No other significant associations were observed.² In addition, the reverse contrast comparing activations in acceptance versus rejection-themed paintings (ACP > REJ) revealed no significant activations across the high and low RS groups.

To determine whether high and low RS individuals differed in their response to the rejection-themed Hopper paintings, an interaction contrast compared the effect of rejection versus acceptance (REJ > ACP) for low versus high RS groups. This analysis revealed greater activation in two clusters of the left LPFC and one cluster of activity in the right dorsal superior frontal gyrus (SFG) in low as compared to high RS participants (see Table 2; Figure 2). We then examined whether activity in these areas correlated with participants' self-reported distress while viewing the Hopper paintings. These analyses revealed significant negative correlations between activ-

ity in the SFG and one cluster of the left PFC and participants' distress ratings ($r = -.58, p < .05$; $r = -.45, p < .05$, respectively).

Control Analyses: Responses to Nonrepresentational Negative vs. Positive Paintings

To determine whether activity related to the rejection-themed art could be attributed to general differences in the negative valence of images, we performed control analyses testing for an effect of NEG > POS (i.e., negative nonrepresentational > positive nonrepresentational) in the regions activated in the REJ > ACP main effect and interaction (with RS group) contrasts. No significant activations were observed, even when dropping the statistical threshold to $p < .01$, uncorrected.

Secondary Analyses

To facilitate comparison of the present results with those of the only two prior published studies of social rejection (Somerville et al., 2006; Eisenberger et al., 2003), ROI analyses compared REJ and ACP activity in regions of ACC, PFC, and insula activated in those two studies. In general, ROI analyses performed on the Eisenberger et al. (2003) clusters were consistent with the results of our whole-brain analyses that identified similar, but not identical, regions of the ACC and PFC. Consistent with their findings, betas extracted from their functional ROIs (indexed below in Talairach coordinates) in the present study revealed greater levels of

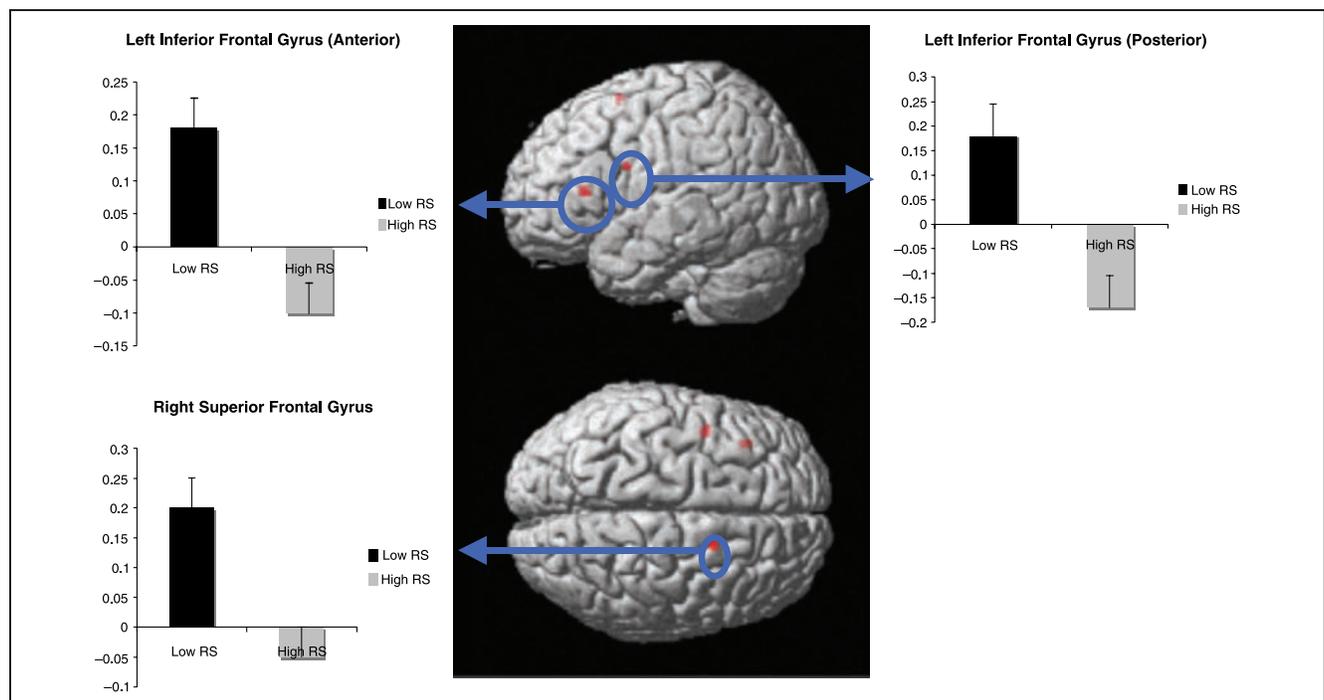


Figure 2. A between-group comparison shows that low RS subjects were distinguished from high RS subjects by increased activation primarily in the left LPFC, specifically along the inferior frontal gyrus, as well as in the right dorsal SFG.

activity in the REJ > ACP contrast for all participants in the VLPFC [$x = 37, y = 50, z = 1; t(17) = 2.83, p \leq .01; x = 30, y = 34, z = -3; t(17) = 2.83, p \leq .01; x = 34, y = 36, z = -3; t(17) = 2.58, p < .05$], dACC [$x = -6, y = 8, z = 45; t(17) = 2.70, p < .05$], and the insula [$x = 42, y = 16, z = 1; 2.28, p < .05$]. In addition, low RS individuals displayed significantly more activity in select clusters of the dACC [$x = -4, y = 31, z = 41; F(1, 16) = 4.86, p < .05$] and the right VPFC [$x = 34, y = 36, z = -3; F(1, 16) = 6.03, p < .05$] relative to high RS individuals.

Correlational analyses relating subjective reports of distress to brain activation revealed interesting differences between the results of the two studies. Contrary to the findings of Eisenberger et al. (2003), activity in the dACC ($x = -6, y = 8, z = 45$) correlated negatively with self-report distress ratings ($r = -.51, p < .05$) and positively ($x = -4, y = 31, z = 41$) with VLPFC activity ($x = 42, y = 27, z = -11, r = .71, p < .005; x = 37, y = 50, z = 1, r = .64, p < .01; x = 34, y = 36, z = -3; r = .70, p < .005$) in the present study. The only region positively correlated with self-report distress ratings in the current study was an insula region ($r = .48, p = .06$) that was not correlated with distress in Eisenberger et al.

In contrast to the functional ROI analyses conducted on the Eisenberger et al. (2003) clusters, no differences were observed either across or between groups in the dACC and vACC clusters reported in Somerville et al. (2006).

DISCUSSION

On the basis of prior behavioral research (Downey et al., 2004), we predicted that high RS individuals would differ from low RS individuals in their responses to viewing rejection as opposed to acceptance-themed images by showing either (a) increased activity in areas involved in emotional appraisal, (b) decreased activity in PFC regions related to cognitive control, or (c) some combination of the two. The present findings are most consistent with the second hypothesis. The only activations differentiating responses of high and low RS individuals to rejection-themed images were two clusters of activity in the left LPFC and one in the right SFG. This observation, combined with the fact that activity in these areas correlated negatively with self-report distress ratings, suggests that these regions may play a role in regulating responses to stimuli that convey themes of social rejection. This interpretation is consistent with prior research indicating that the LPFC plays a critical role in the top-down cognitive control of behavior in general (e.g., Egner & Hirsch, 2005a, 2005b; Miller & Cohen, 2001; MacDonald et al., 2000; Smith & Jonides, 1999) and the regulation of emotion in particular (Ochsner & Gross, 2004, 2005; Phan et al., 2005; Ochsner et al., 2002, 2004; Levesque et al., 2003; Davidson, 2002; Beauregard, Levesque, & Bourgouin, 2001). In this vein, it is note-

worthy that the activations observed here—when participants are free to appraise the meaning of stimuli in whatever way they choose—are very similar to those observed in studies when participants are instructed to down-regulate negative responses to aversive images by reappraising their meaning in “cool” unemotional ways (Ochsner et al., 2002, 2004).

In addition to characterizing a pattern of brain activity related to the regulation of rejection-related distress that distinguishes between high and low RS groups, the present study also identified a network of three regions (posterior cingulate, parahippocampal gyrus, and dACC/medial frontal cortex) that became activated across high and low RS groups in response to rejection versus acceptance images that was not associated with self-report ratings of distress. Prior work suggests three reasons why activations in these regions may have been observed. First, we observed activation of the posterior cingulate cortex to rejection-themed art, which is consistent with studies implicating this region in attention to, evaluation of, and individual differences in affective responses to aversive stimuli (Ochsner et al., 2006; Maddock, 1999), as well as self-referential and social cognitive processing more generally (Lieberman & Pfeifer, 2005; Nunez, Casey, Egner, Hare, & Hirsch, 2005; Ochsner et al., 2005). Second, bilateral activation of parahippocampal regions implicated in memory for episodic events in general and the encoding of complex visual scenes in particular (Davachi, Mitchell, & Wagner, 2003; Epstein & Kanwisher, 1998) was observed. This activity may reflect greater attention to and encoding of the perceptual aspects of rejection-themed visual images. Third, mid-dorsal ACC activity was observed in combination with LPFC regions for low RS individuals in response to rejection images. This finding is consistent with emerging theory and findings, which suggest that the ACC may function as a general purpose “alarm” system that recruits the DLPFC to respond to, and help interpret, goal-incongruent events (Eisenberger et al., 2003; Ochsner & Barrett, 2001; Gehring & Knight, 2000) such as rejection, which violate social motives and expectancies for affiliation and bonding (Somerville et al., 2006; Eisenberger & Lieberman, 2004). As discussed above, additional recruitment of LPFC regions by low RS individuals may be important for interpreting rejection-related events in ways that minimize personal distress, perhaps by evaluating whether the rejection cues are self-relevant or from people who matter.

It is important to consider the relationship between the present findings and those of the only two prior studies to date that have examined the relationship between the neural bases of perceived rejection and self-report distress in healthy normal adults (Somerville et al., 2006; Eisenberger et al., 2003). The present findings were similar to Eisenberger et al. (2003) in that the (a) critical whole-brain contrasts of rejection as opposed to acceptance stimuli show activation of the dorsal and mid

cingulate cortex in concert with the LPFC (the latter, only for low RS individuals) and (b) functional ROI analyses conducted on the areas identified in the study of Eisenberger et al. revealed significant levels of activity among both low and high RS individuals in the insula, dACC, and PFC in response to rejection versus acceptance images. That such similar patterns of activity were observed in both studies despite the fact that different paradigms and stimuli were used to activate rejection concerns suggests that these regions may be critical mediators of distress associated with exposure to rejection cues.

Despite these similarities, the present findings differ from those reported in Eisenberger et al. (2003) in three ways. First, a broader network of activations was observed in the present study in response to rejection stimuli. Second, the insula correlated positively with self-report distress ratings in the present study, whereas no correlations were observed between this region and distress ratings in Eisenberger et al. Third, in the present study, right VLPFC and dACC activity were positively correlated, and dACC activity and self-report distress ratings were negatively correlated, whereas the opposite was true for both sets of correlations in Eisenberger et al. These differences may have resulted from the fact that the different tasks used to manipulate rejection in each study may have recruited different processes or some processes more strongly.

The present findings also show interesting similarities and differences compared to those of Somerville et al. (2006). On one hand, dACC activity was found in both studies. On the other hand, the specific foci of dACC activity in the two studies differed, and we observed no rejection-related or RS-related activity in the specific dACC or vACC regions identified by Somerville et al. These differences may be attributable, at least in part, to cross-study variability in experimental tasks and participant behavior. However, because Somerville et al. did not collect self-report ratings of either acceptance or distress, it is difficult to determine whether the discrepant results are attributable to differences in the affective responses experienced by each study's participants or some other difference between the tasks.

That being said, salient task differences between the two studies suggest another possibility. The dACC region observed by Somerville et al. (2006) was activated not just when participants received rejection feedback from someone they liked (or thought would like them too), but when they rejected others as well (i.e., they did not like someone who liked them). This suggests that their dACC activation may be related to conflict or expectancy violation—as Somerville et al. suggested—whereas the more posterior focus observed here may be more related to experienced distress (Vogt, 2005). Similarly, the vACC region observed by Somerville et al., but not here, was activated more for acceptance than for rejection feedback, that is, when others indicated liking

for a participant. This is consistent with findings that the vACC and the associated MPFC respond to rewarding feedback of various kinds (e.g., Knutson, Fong, Adams, Varner, & Hommer, 2001; Elliott, Dolan, & Frith, 2000; Elliott, Friston, & Dolan, 2000), which was absent in the present study.

Taken together, the results of the three extant studies of social rejection are compatible with suggestions that the cingulate cortex may be composed of multiple subregions that carry out related, but distinct, computations (Vogt, 2005; Eisenberger & Lieberman, 2004; Bush, Luu, & Posner, 2000). It is not yet clear, however, whether and how differences in the presence or absence of interpersonal feedback, level of experienced acceptance or distress, and violations of expectancy may recruit similar or different neural mechanisms.

Future Directions

These findings raise a number of questions about the psychological and neural processes underlying the experience of social rejection, suggesting new directions for research. One question concerns what process is reflected by the increased level of LPFC activity demonstrated by low RS individuals in response to rejection cues. As noted above, prior research has shown that similar areas of LPFC play a role in enabling individuals to reappraise the meaning of negative affect inducing stimuli to reduce their emotional impact (Ochsner et al., 2004, 2005). However, because the present study did not include a comparison condition in which participants were instructed to reappraise the meaning of the paintings they viewed, it is unclear whether the increased levels of activity observed in this area reflect participants' attempts to reappraise the images, or instead reflect some other cognitive process. Assuming that the LPFC activity does reflect reappraisal, it is not possible to distinguish whether the relative inactivity of high RS individuals in this area reflects a failure to reappraise the rejection images or a reduced capacity for doing so. Given prior work indicating that high RS individuals can regulate negative emotional responses to rejection when instructed accordingly (Ayduk et al., 2002), the latter possibility—that they lack the ability to reappraise negative experiences—seems unlikely. Instead, it seems more probable that high RS individuals lack the ability to adaptively implement the appropriate emotion-regulatory strategies when they are most needed, that is, when the possibility of rejection exists. A key question for future research is to understand how such difficulties arise and whether they can be reduced.

A second issue raised by the current findings concerns the role that the amygdala plays in distinguishing the responses of high and low RS individuals to rejection. In the present study, no differences were observed in amygdala activity between high and low RS individuals in response to rejection stimuli. Failure to observe such

heightened levels of amygdala activity was surprising given our prior work indicating that high RS individuals display greater startle responses to rejection stimuli and the well-known finding that the amygdala plays a critical role in mediating the startle reflex circuit in both humans and animals (Davis, 1992). One explanation for why such group differences in amygdala activity were not observed concerns the way the Downey et al. (2004) startle paradigm was modified for use with fMRI in the current experiment. Specifically, whereas a blocked design was used in the present study, in the experiment of Downey et al., each stimulus was randomly presented only once. Thus, the amygdala may have habituated to the stimuli used in the present experiment through repeated exposure, as is often observed with face stimuli (Fischer et al., 2003; Hart et al., 2000; Breiter et al., 1996). This interpretation is consistent with positron emission tomography and fMRI studies of animal phobia, which reveal amygdala activity among animal phobics in response to phobic stimuli only when event-related designs are used (Straube, Mentzel, & Miltner, 2006; Dilger et al., 2003), which are less susceptible to habituation effects. It is also possible that group differences in amygdala activity were not observed because of noisy signal in dropout-sensitive regions that are difficult to detect with a relatively small sample. Future research should address the discrepancy between the findings of the current study and the findings suggested by the startle research using larger samples with event-related designs that are less susceptible to habituation.

The present findings also raise a question concerning how different kinds of rejection experiences relate to one another in terms of their underlying neural dynamics. In the present study, rejection concerns were activated by exposing individuals to paintings that portrayed rejection scenes. However, in both the real world and the laboratory, there are many ways in which rejection-related distress can be triggered. For example, a person can be provided with feedback from a valued person or group indicating that they are not wanted or disliked (cf. Somerville et al., 2006; Eisenberger et al., 2003). It is also possible that rejection-related distress may be triggered on the basis of perceptual properties of rejection cues alone (i.e., viewing the face of a former romantic partner who rejected you), similar to the way recent research has demonstrated that stereotyping can become accessible by simply viewing faces of out-group members (e.g., Lieberman et al., 2005; Hart et al., 2000; Phelps et al., 2000). As research on the neural basis of rejection moves forward, it will become important to understand how different ways of manipulating rejection compare to one another in terms of the patterns of neural activation they elicit.

Finally, it is important to acknowledge that the present study used a stratified sample and had a relatively small number of participants per condition. Both of these factors limit the generalizability of the present findings.

Conclusion

This study examined the neural systems underlying responses to social rejection cues and how these responses vary with the personality disposition of rejection sensitivity, the disposition to anxiously expect rejection. Our findings indicate that a critical difference distinguishing between low and high RS individuals may be the latter group's failure or inability to activate top-down cognitive control to regulate responses to rejection. Although many important questions regarding the neural bases of rejection sensitivity remain unanswered, the present study is a first step toward achieving a more complete understanding of the mechanisms that underlie failures of social functioning and their deleterious consequences for mental and physical health.

Acknowledgments

This research was supported by a National Institutes of Mental Health grant (RO1 MH069703) to Geraldine Downey, a National Institutes of Mental Health grant (RO1 MH076137) to Kevin Ochsner and the Columbia University Academic Quality Fund.

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Notes

1. This theorizing is consistent with current neural models of attention regulation (Botvinick, Braver, Barch, Carter, & Cohen, 2001), which posit that the dACC monitors processing conflicts (Carter et al., 1998, 2000; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999) and recruits (dorsal) LPFC regions to resolve them by engaging top-down cognitive control processes (Egner & Hirsch, 2005a, 2005b; Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000).
2. In order to examine whether any additional associations existed between self-report distress ratings and brain activity associated with processing rejection versus acceptance stimuli, we regressed participants' distress ratings into whole-brain analyses as part of an exploratory analysis. The results of this analysis, reported here for the sake of completeness, revealed four additional significant correlations. Specifically, distress ratings correlated negatively with activity in parahippocampal gyrus ($x = -18, y = -26, z = -10$), thalamus ($x = 20, y = -32, z = 2$), and putamen ($x = -26, y = 2, z = 8; x = -28, y = -20, z = 2$), and positively with a small cluster of activity in the occipital lobe ($x = -2, y = -92, z = 12$).

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