PAPER

Neural responses to witnessing peer rejection after being socially excluded: fMRI as a window into adolescents' emotional processing

Carrie L. Masten,[1] Naomi I. Eisenberger,[2] Jennifer H. Pfeifer[3] and Mirella Dapretto[4,5,6,7]

1. Department of Psychology and Human Development, Vanderbilt University, USA
2. Department of Psychology, University of University of California, Los Angeles, USA
3. Department of Psychology, University of Oregon, USA
4. Ahmanson-Lovelace Brain Mapping Center, University of California, Los Angeles, USA
5. Interdepartmental Neuroscience Program, University of California, Los Angeles, USA
6. Department of Psychiatry and Biobehavioral Sciences, University of California, Los Angeles, USA
7. FPR-UCLA Center for Culture, Brain and Development, University of California, Los Angeles, USA

Abstract

During adolescence, concerns about peer rejection and acceptance become increasingly common. Adolescents regularly experience peer rejection firsthand and witness these behaviors among their peers. In the current study, neuroimaging techniques were employed to conduct a preliminary investigation of the affective and cognitive processes involved in witnessing peer acceptance and rejection – specifically when these witnessed events occur in the immediate aftermath of a firsthand experience with rejection. During an fMRI scan, 23 adolescents underwent a simulated experience of firsthand peer rejection. Then, immediately following this experience they watched as another adolescent was ostensibly first accepted and then rejected. Findings indicated that in the immediate aftermath of being rejected by peers, adolescents displayed neural activity consistent with distress when they saw another peer being accepted, and neural activity consistent with emotion regulation and mentalizing (e.g. perspective-taking) processes when they saw another peer being rejected. Furthermore, individuals displaying a heightened sensitivity to firsthand rejection were more likely to show neural activity consistent with distress when observing a peer being accepted. Findings are discussed in terms of how witnessing others being accepted or rejected relates to adolescents' interpretations of both firsthand and observed experiences with peers. In addition, the potential impact that witnessed events might have on the broader perpetuation of bullying at this age is also considered.

Introduction

Adolescence is a time when the importance of peer relationships rapidly increases. When young adolescents make the transition to middle school, it is common to spend more time with peers, place greater value on peers' approval, and be more concerned about peer acceptance (Brown, 2004; Brown & Larson, 2009). As the importance of peers increases, peer rejection and bullying become increasingly prevalent (e.g. Brown, 2004) and have negative effects on psychological adjustment

(Arseneault, Bowes & Shakoor, 2010; Brendgen & Vitaro, 2008; Flanagan, Erath & Bierman, 2008; Isaacs, Hodges & Salmivalli, 2008; Kaltiala-Heino, Frojd & Marttunen, 2010; Rigby, 2000, 2003; Trentacosta & Shaw, 2009). Moreover, adolescents are affected not only by personal experiences with rejection, but also by the larger environment in which rejection is common (Janes & Olson, 2000; Nishina & Juvonen, 2005). Indeed, the majority of adolescents witness peer rejection on a regular basis (Rivers, Poteat, Noret & Ashurst, 2009), and they observe peer rejection just as often as they

Address for correspondence: Carrie L. Masten, Department of Psychology and Human Development, Peabody College, 230 Appleton Place, Vanderbilt University, Nashville, TN 37203-5721, USA; e-mail: carrie.masten@gmail.com

experience this treatment firsthand (Nishina & Juvonen, 2005). Thus, frequent experience with rejection is common for the majority of adolescents, regardless of their social status or the extent to which they experience peer rejection firsthand.

Witnessing the peer interactions of others is likely to impact adolescents in many ways that potentially influence how they respond to peer rejection and bullying. In some cases, comparing the rejection or acceptance of others to one's firsthand experiences with peers might alter how adolescents interpret and respond to their firsthand experiences, as would be predicted by social comparison theory (Festinger, 1954). In other words, witnessing others being rejected might prove beneficial insofar as it mitigates one's own hurt feelings about a firsthand experience with peer rejection. For example, for an individual who frequently experiences rejection, witnessing others' rejection might promote the belief that rejection is a common event and reduce feelings of injustice (i.e. 'this happens to everyone, it isn't just me'; see Brannon & Brock, 2001; Ditto & Jemmott, 1989). This, in turn, might instill the belief that one's past experiences of being rejected were not necessarily personal, which could help reduce self-blame. Conversely, seeing others getting accepted or included might enhance feelings of distress about one's recent rejection, because it signals that one's experience of being rejected was indeed personal. Thus, affective responses to firsthand peer rejection might be moderated (i.e. either enhanced or reduced) by the experience of witnessing others being rejected or accepted by peers.

More broadly, if adolescents are frequently witnessing peer rejection and other forms of bullying on a regular basis, this might also impact their beliefs about, and tolerance of, bullying behaviors more generally. For example, if adolescents see others being harassed or victimized on a regular basis, some degree of habituation and/or desensitization might occur, as suggested by desensitization theory (see Engelhardt, Bartholow, Kerr & Bushman, 2011; Rule & Ferguson, 1986). So, to the extent that adolescents feel less distressed about their own firsthand experiences of peer rejection as a result of seeing the rejection of others, there may be some long-term comfort in knowing that these events are commonplace. In other words, if witnessing the ridicule of classmates is both frequent and in some cases comforting (i.e. to the degree that it mitigates the affective consequences of being rejected oneself), this may eventually lead to an implicit acceptance of bullying behaviors that contributes to the perpetuation of these behaviors over time. Thus, understanding how observed peer interactions impact affective processing among adolescents could also provide new insight on how bullying becomes mainstream and relatively acceptable at this particular age (see also Dijkstra, Lindenberg & Veenstra, 2008).

Despite the potential links between witnessing others' peer interactions and adolescents' responses to their own firsthand experiences, as well as broader implications for understanding bullying behaviors during adolescence more generally, there is a dearth of research on this topic. In addition, the mechanisms via which witnessing others' experiences might moderate one's own affective processes are poorly understood. Prior studies that have examined adolescents' experiences witnessing peer rejection have typically relied on self-reports. Although these self-reports have often been collected in clever ways that minimize bias (i.e. daily reports of peer-related events and affect; Nishina & Juvonen, 2005), additional techniques are warranted.

Here, our goal was to use fMRI to examine one particular way in which witnessing another person's interactions with peers might relate to one's own affective processing. Specifically, we examined adolescents' affective responses (indexed by brain activity) while observing another adolescent being included (versus excluded) by peers, immediately following a firsthand experience of peer exclusion. fMRI is particularly useful in this case, because it permits the examination of neural activity underlying affective processes in the moment that social interactions are occurring. In other words, with fMRI we can gain insight into how affective responses might vary when an individual is witnessing a peer being accepted versus rejected, and examine how these affective responses relate to a particular individual's sensitivity to rejection more broadly. Thus, neuroimaging is an ideal tool with which to expand our knowledge of how witnessing peer interactions impacts adolescents' affective processes.

A handful of previous studies have used neuroimaging techniques to examine both firsthand (Crowley, Wu., Molfese & Mayes, 2010; Masten, Eisenberger, Borofsky, Pfeifer, McNealy, Mazziotta & Dapretto, 2009, Masten, Colich, Rudie, Bookheimer, Eisenberger & Dapretto, 2011a; Masten, Eisenberger, Borofsky, McNealy, Pfeifer & Dapretto, 2011b; Sebastian, Roiser, Tan, Viding, Wood & Blakemore, 2010) and observed (Masten, Eisenberger, Pfeifer, Colich & Dapretto, in press; Masten, Eisenberger, Pfeifer & Dapretto, 2010a) experiences of peer rejection among adolescents. Thus, we have begun to identify some of the neural regions involved in the affective and cognitive processes involved in experiencing and witnessing peer rejection at this age. Although none of these previous studies examined neural activity involved in both firsthand and observed experiences of peer rejection within the same individuals, they provide a useful framework.

In our previous examination of firsthand peer rejection – in which we focused specifically on peer exclusion, we found that both the subgenual anterior cingulate cortex (subACC) and the anterior insula (AI) displayed heightened activity during peer exclusion compared to inclusion, particularly to the extent that adolescents reported being more distressed by the exclusion experience (Masten *et al*., 2009). As a whole, this work is consistent with other research on adolescents linking insula activity to experiences of social exclusion (Crowley *et al*., 2010) and peer evaluation (Guyer, McClure-Tone, Shiffrin, Pine & Nelson, 2009), and anterior cingulate activity (in both Brodmann Areas 24 and 32) to experiences of relational aggression (Baird, Silver & Veague, 2010). In addition, it is consistent with prior research in adults that has linked the AI to a wide array of affective processing, including distress responses to social exclusion in particular (Eisenberger, Lieberman & Williams, 2003; DeWall, MacDonald, Webster, Masten, Baumeister, Powell, Combs, Schurtz, Stillman, Tice & Eisenberger, 2010; Kross, Heimdal, Olsnes, Olofson & Aarstad, 2007; Masten, Telzer & Eisenberger, 2011d) and other types of aversive stimuli (e.g. Phan, Wager, Taylor & Liberzon, 2004), as well as research which has linked the subACC with affective responses to rejection-related processes (e.g. Burklund, Eisenberger & Lieberman, 2007) and atypical functioning in depressed populations (e.g. Chen, Ridler, Suckling, Williams, Fu, Merlo-Pich & Bullmore, 2007; Keedwell, Drapier, Surguladze, Giampietro, Brammer & Phillips, 2008).

Our previous work also demonstrated that when adolescents felt less distressed during peer exclusion (versus inclusion) they displayed greater activity in the ventral striatum (VS) and ventrolateral prefrontal cortex (VLPFC; Masten *et al*., 2009; Masten *et al*., 2011a). These findings are consistent with previous research that has linked the VS to emotion regulatory processes in adults (Wager, Davidson, Hughes, Lindquist & Ochsner, 2008) and adolescents (Pfeifer, Masten, Moore, Oswald, Iacoboni, Mazziotta & Dapretto, 2011) and the VLPFC to a variety of emotion regulation processes (Hariri, Bookheimer & Mazziotta, 2000; Lieberman, Jarcho & Satpute, 2004; Lieberman, Eisenberger, Crockett, Tom, Pfeifer & Way, 2007; Petrovic & Ingvar, 2002), including the regulation of distress resulting from social exclusion in adults (e.g. Eisenberger *et al*., 2003) and experiences of relational aggression in adolescents (Baird *et al*., 2010). Finally, this previous work also examined the relationship between self-reported rejection sensitivity and neural responses to firsthand peer exclusion. Findings revealed that adolescents reporting higher levels of rejection sensitivity displayed greater levels of neural activity consistent with affective/distress processing (i.e. dACC) and mentalizing (i.e. precuneus; Masten *et al*., 2009).

In terms of witnessing peer rejection, our prior work has indicated that adolescents display greater activity during observed peer exclusion (versus inclusion) in the dorsomedial prefrontal cortex (DMPFC), the medial prefrontal cortex (MPFC), and the precuneus (Masten *et al*., 2010a). More generally, these three regions have been linked to a larger neural network involved in 'mentalizing' – a term which broadly includes making judgments about the thoughts, intentions, and feelings of others – and there is growing evidence that the MPFC is particularly important for adolescents' understanding of others' perspectives, affect and social emotions (e.g. Burnett, Bird, Moll, Frith & Blakemore, 2009; Pfeifer, Masten, Borofsky, Dapretto, Fuligni & Lieberman, 2009; Sebastian, Fontaine, Bird, Blakemore, De Brito, McCrory & Viding, 2012; Wang, Lee, Sigman & Dapretto, 2006). In addition to the DMPFC, MPFC and precuneus, this larger mentalizing network is commonly thought to include the posterior superior temporal sulcus (pSTS), the temporal parietal junction (TPJ), the posterior cingulate cortex (PCC), and the temporal poles, and these regions within the mentalizing network have been linked to a variety of cognitive abilities that let individuals understand others' mental states and emotions (Beer & Hughes, 2010; Frith & Frith, 1999, 2003, 2006; Hynes, Baird & Grafton, 2006; Mitchell, Banaji & Macrae, 2005; Saxe, 2006; Sebastian *et al*., 2012; Singer, 2006). Thus, in the case of peer rejection specifically, activity in this mentalizing network might reflect a variety of underlying cognitive processes – for example, efforts to understand why the rejection is occurring or how the victim is feeling, feelings of empathy for the victim, or reasoning about the perpetrators' motives for rejecting the victim.

Finally, additional prior research examining empathic and vicarious experiences has also indicated that there is likely overlap between some of the brain regions linked to peer rejection and the brain regions that are involved in 'mirroring' others' emotions (i.e. the more affective component of empathy in which observers share the emotional experiences of others). For example, the anterior insula is activated by both direct and observed experiences of disgust (Wicker, Keysers, Plailly, Royet, Gallese & Rizzolatti, 2003), and the dACC and anterior insula are activated by direct and observed physical pain in adults (Botvinick, Jha, Bylsma, Fabian, Solomon & Prkachin, 2005; Jackson, Bruney, Meltzoff & Decety, 2005; Morrison, Lloyd, Di Pellegrino & Roberts, 2004; Singer, Seymour, O'Doherty, Kaube, Dolan & Frith, 2004; Singer, Seymour, O'Doherty, Stephan, Dolan & Frith, 2006) and children (Decety, Michalska &

Akitsuki, 2008). The insula is also activated among children when they both observe and make emotional face expressions (Pfeifer, Iacoboni, Mazziotta & Dapretto, 2008). These studies provide additional support for the notion that experiences of peer exclusion and experiences involving empathy and vicarious emotions share similar neural substrates and likely interact in interesting ways.

In the current study we aimed to examine the experience of witnessing peer inclusion and exclusion, immediately following an experience of firsthand exclusion, and we focused primarily on these regions known to be involved in firsthand and observed peer rejection from prior work. During an fMRI scan, we first simulated an experience of firsthand peer exclusion to elicit the affective responses associated with peer rejection (neural responses to firsthand exclusion for the current sample are published elsewhere; Masten *et al.*, 2009). Then, in the immediate aftermath of this firsthand exclusion, the participant observed a new adolescent ostensibly being included, and then excluded, by the same two players who had excluded the participant previously. Neural activity during this observed Cyberball was the focus of the current analyses. Specifically, we were interested in examining two primary research questions. First, what affective processes are involved in witnessing the acceptance versus rejection of another adolescent, immediately following a firsthand experience of peer rejection? Second, how do individual differences in rejection sensitivity relate to adolescents' affective states when they are witnessing this peer acceptance versus rejection? Given that adolescents vary in terms of both their neural sensitivity to peer rejection and their subjective sensitivity to peer rejection (Downey & Feldman, 1996; Masten *et al.*, 2009), we examined how neural activity during observed peer acceptance versus rejection related to two different indices of rejection sensitivity: (a) neural sensitivity in response to the distress of firsthand peer rejection, and (b) self-reported rejection sensitivity.

First, we hypothesized that adolescents would display more neural activity consistent with distress (i.e. greater activity in the subACC and AI) when they watched another adolescent being included compared to when they saw him or her being excluded. In other words, we expected that adolescents might feel worse when they saw that it was 'just them' who had been excluded. In contrast, when the participant saw a new adolescent being excluded (compared to included) by the same two peers that excluded the participant previously, we expected participants to display more activity in regions previously linked with emotion regulation (e.g. VLPFC and VS), because then the rejection would likely be perceived as more 'common' and not personal. Of

course, in many cases seeing a peer being excluded might induce distress in an adolescent witness – either due to empathy and vicarious distress felt for the victim, or because witnessing exclusion might remind the adolescent of their own prior rejection experiences. However, since adolescents in the current study observed a peer being included and then excluded immediately following a firsthand experience of exclusion, we expected their responses to these witnessed events to specifically relate to their interpretation of their own previous rejection (i.e. was it personal, or are the players just mean to everyone?), and not necessarily reflect their responses when they observe peers being rejected in other types of context.

Next, when watching someone else interacting with peers, we also expected to see neural activity in regions linked to mentalizing. However, it was less clear whether we would see more activity consistent with mentalizing while observing someone being included, or while observing someone being excluded. One possibility is that we would see more neural activity consistent with mentalizing during observed inclusion (versus exclusion) when adolescents are feeling worse about their own rejection and potentially trying harder to understand the perpetrators' reasons for excluding them. However, an alternative possibility is that we would see more neural activity consistent with mentalizing during observed exclusion (versus inclusion), when adolescents are likely feeling comforted by the apparent impersonal nature of the exclusion and feeling relieved that they now understand why they were excluded (i.e. 'they do this to everyone'). Finally, of course, a third possibility is that adolescents might display activity consistent with mentalizing similarly during both observed exclusion and inclusion. Thus, our goal was to use neuroimaging to gain insight into these possibilities.

Our last hypothesis was that among adolescents displaying heightened sensitivity to rejection (i.e. either more neural activity consistent with distress during firsthand rejection or higher self-reported rejection sensitivity), there would be greater neural activity in affective/distress regions while witnessing another person's inclusion versus exclusion. In other words, since previous research has indicated that adolescents who are highly sensitive to rejection show more neural activity consistent with distress (e.g. dACC; Masten *et al.*, 2009), we expected that these adolescents would also feel more hurt when they saw someone else getting included right after they had just been excluded – likely because it would indicate that their firsthand rejection was indeed personal and thus more distressing. In addition, since previous work has also revealed more activity in mentalizing-related regions among adolescents who are

highly sensitive to rejection during firsthand rejection (e.g. precuneus; Masten *et al.*, 2009), we also explored whether we would see similar neural activity consistent with mentalizing in these adolescents as they were observing a peer being included following a firsthand experience of rejection.

Method

Participants

Participants included an ethnically and socioeconomically diverse sample of 23 adolescents (14 females) from the greater Los Angeles area. All participants had attended at least one year of middle school and ranged in age from 12.4 to 13.6 years old ($M = 13.0$); boys and girls did not differ in terms of their mean age. This age range was chosen based on previous research characterizing the middle school transition as a time of heightened salience of peer relationships resulting from both concern about peer acceptance as well as increased prevalence of both firsthand and observed experiences of peer rejection (e.g. Brown, 2004). Participants came from a variety of ethnic backgrounds, including 52% Caucasian, 26% Latino, 9% African-American, 9% Asian, and 4% Native American. Ethnic distributions for boys and girls were similar; 78% of boys were Caucasian and 22% were Latino, while 50% of girls were Caucasian, 29% were half-Caucasian, and 21% were Latino, African-American

or Asian. Participants were recruited through mass mailings, summer camps, and fliers distributed in the community. All participants and parents provided assent/consent to participate in the study, which was approved by UCLA's Institutional Review Board. This sample is identical to that examined in Masten *et al.* (2009), and overlaps with the sample examined in Masten *et al.* (2011b). However, all analyses and findings described below are new and have not been reported previously.

The Cyberball task

To simulate firsthand and observed peer rejection during an fMRI scan, we used the game 'Cyberball' (Figure 1A). Cyberball is an animated experimental paradigm that simulates a real interactive experience of social exclusion (Williams, Cheung & Choi, 2000; Williams, Govan, Croker, Tynan, Cruickshank & Lam, 2002). It has been used successfully in previous neuroimaging studies to simulate the experience of peer rejection among adolescents (Masten *et al.*, 2009, Masten *et al.*, 2011a; Masten *et al.*, 2011b; Sebastian *et al.*, 2010) and adults (e.g. DeWall *et al.*, 2010; DeWall, Masten, Powell, Combs, Schurtz & Eisenberger, 2012; Eisenberger *et al.*, 2003; Eisenberger, Gable & Lieberman, 2007; Masten *et al.*, 2011d; Masten, Telzer, Fuligni, Lieberman & Eisenberger, 2010b), as well as the experience of observing another person being rejected among adolescents (Masten *et al.*, 2010a) and adults (Masten, Morelli & Eisenberger, 2011c). We chose this simulated
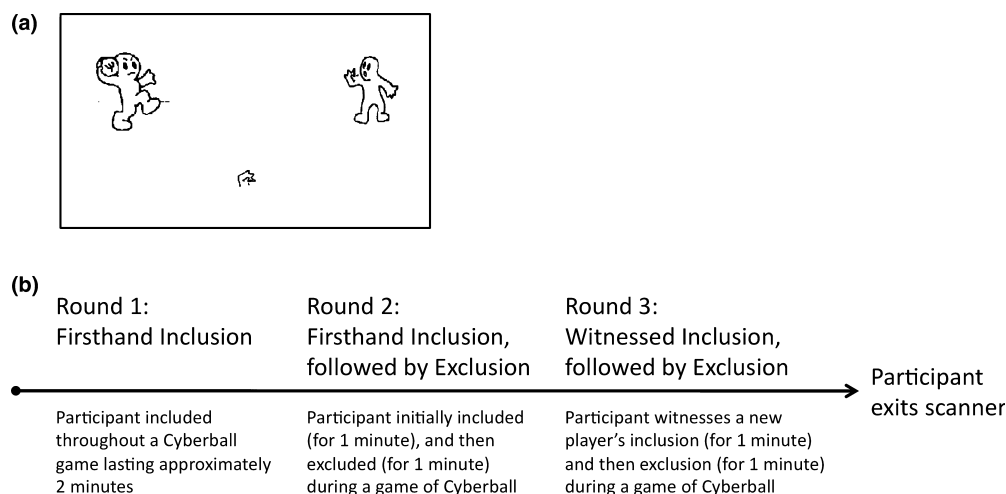
Figure 1   *Panel A depicts a still shot of the animated Cyberball game that was viewed by participants. During firsthand inclusion and exclusion in the first two rounds, participants controlled the 'hand' at the bottom of the screen. During witnessed inclusion and exclusion in round three, participants were told that a new player was controlling the hand and playing with the same two people that the participant had played with previously. Panel B depicts the order of the task events. Each round of Cyberball occurred during a separate functional scan. Data collected during Round 3 ('Witnessed Inclusion, followed by Exclusion') was examined in all neuroimaging analyses.*

experience of social exclusion as a proxy for peer rejection based on research indicating that during early adolescence, isolating peers from social groups is one of the dominant methods used to reject peers (Coie, Dodge & Kupersmidt, 1990).

Firsthand Cyberball

Participants first played the Cyberball game with two players that they believed were real adolescent peers. Cyberball consists of a simple ball-tossing game, and participants were told that they would play this game via the Internet with two other adolescents in scanners at other institutions, to examine coordinated neural activity. These other 'players' were not real and were just part of the computer paradigm. On a screen displayed through fMRI-compatible goggles, participants saw cartoon images representing these other players, and a cartoon image of their own 'hand' that they controlled using a button-box. Throughout the game the ball is thrown back and forth among the three players, with the participant choosing the recipient of their own throws, and the throws of the other two 'players' determined by the pre-set program. Participants completed two different rounds of firsthand Cyberball during two fMRI scans: one in which they were 'included' throughout the game, and one in which they were 'excluded' by the other players (Figure 1B). Throughout the inclusion round, the computerized players were equally likely to throw the ball to the participant or the other player. During the exclusion round, the players stopped throwing the ball to the participant after the participant had received a total of 10 throws, and the participant just watched the remainder of the game. Each round of Cyberball consisted of 60 ball tosses in total, including all the participants' tosses as well as the tosses of the two simulated players. Thus, the exclusion portion of the second round, following the participant's first 10 throws, consisted of half the total number of ball tosses and lasted for approximately half of the round or about 60 seconds (depending on the time that it took each participant to throw the ball after having received it).

Witnessed Cyberball

After actually playing the game, participants *observed* a game of Cyberball during a third scan (Figure 1B), in which they believed they were watching a new adolescent player (who was their age and gender) playing with the same two peers who had previously excluded the participant in the preceding game. This 'new player' was first included, and then ultimately excluded, just as the participant was previously. The observed game of Cyberball was presented on a screen displayed through fMRI-compatible goggles. Participants saw cartoon images representing the three players that they were observing. Although they believed they were watching a live interaction occurring via the Internet, they were actually watching a prerecorded video. Throughout the game, the participant watched as the ball was thrown back and forth among the three players (the 'new player' and the two players that excluded the participant previously). For the first half of the game (approximately 30 tosses), all three players received the ball an equal amount. Then, during the second half of the game, the new player was excluded by the other two players, and did not receive any more throws for the duration of the game. The exclusion of the new player very closely mirrored the exclusion of the participant in the preceding Cyberball game (i.e. exclusion occurred approximately half-way through the game).

Throughout the playing and observation of the Cyberball games, extensive measures were taken to maintain the believability of the cover story and to ensure that participants believed that they were playing with and/or observing real adolescents (e.g. between runs, participants were asked to wait for a short time while one of the 'players' had their goggles adjusted). Upon exiting the scanner, participants completed questionnaires and were fully debriefed about the deception involved in the study. During this debriefing session, participants were probed to determine whether they had believed the manipulation. Three of the 23 participants expressed suspicions about whether the other players were real after being scanned, and two participants thought that there might have been computer glitches that caused certain players to be excluded. The remaining 18 participants believed the deception and did not indicate that they were suspicious prior to being debriefed.

Behavioral measures

Manipulation check

A manipulation check was administered to ensure that participants were engaged throughout both the firsthand and observed games of Cyberball, and were aware of their own exclusion, as well as that of the observed player. Following completion of Cyberball, participants were asked how often they (or the new player during the observed round) received the ball during the game.

Distress resulting from firsthand rejection

Following completion of the scan, adolescents completed the Need-Threat Scale (NTS; Williams *et al.*, 2000;

Williams *et al.*, 2002) to measure distress associated with the firsthand exclusion. The NTS assesses 12 subjectively experienced consequences of being excluded during the game (e.g. 'I felt rejected', 'I felt invisible'), on a scale ranging from 1 = 'not at all' to 5 = 'very much'.

Rejection sensitivity

In addition, earlier in the day that participants underwent the fMRI scan, they also completed the Rejection Sensitivity Questionnaire for Children (RSQ; Downey & Feldman, 1996), interspersed with other questionnaires unrelated to the current study. The RSQ assesses the importance of being socially accepted as well as anxiety and beliefs about the likelihood of being accepted, on a scale ranging from 1 = 'not at all anxious'/'expect to be accepted', to 6 = 'very anxious'/'expect to be rejected'.

fMRI data acquisition

Images were collected using a Siemens Allegra 3-Tesla MRI scanner. Adolescents were given extensive instructions to decrease motion, and head motion was restrained with foam padding and surgical tape. One of the subjects originally recruited for the study was excluded due to motion in excess of 1.5 mm, resulting in the final sample of 23 participants described above. The Cyberball task was presented on a computer screen, which was projected through scanner-compatible goggles.

For each participant, an initial 2D spin-echo image (TR = 4000 ms, TE = 40 ms, matrix size 256 × 256, 4-mm thick, 1-mm gap) in the sagittal plane was acquired to enable prescription of slices obtained in structural and functional scans. In addition, a high-resolution structural scan (echo planar T2-weighted spin-echo, TR = 4000 ms, TE = 54 ms, matrix size 128 × 128, FOV = 20 cm, 36 slices, 1.56-mm in-plane resolution, 3-mm thick) coplanar with the functional scans was obtained for functional image registration during fMRI analysis preprocessing. The observed game of Cyberball was completed during one functional scan lasting 2 minutes, 48 seconds (echo planar T2*-weighted gradient-echo, TR = 2000 ms, TE = 25 ms, flip angle = 90°, matrix size 64 × 64, 36 axial slices, FOV = 20 cm; 3-mm thick, skip 1 mm).

Data analysis

All neuroimaging data were preprocessed and analyzed using Statistical Parametric Mapping (SPM5; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Preprocessing for each indi-

vidual's images included image realignment to correct for head motion, normalization into a standard stereotactic space as defined by the Montreal Neurological Institute and the International Consortium for Brain Mapping, and spatial smoothing using an 8-mm Gaussian kernel, full width at half maximum, to increase the signal-to-noise ratio. Cyberball was modeled as a block design. The observed game of Cyberball was modeled as a run with each period of inclusion and exclusion modeled as a block within the run for a total of one observed inclusion block, and one observed exclusion block. A high pass filter was applied at twice the length of each condition block (120 seconds for observed exclusion, 240 seconds for observed inclusion), to reduce noise due to temporal drift. After modeling the Cyberball paradigm, linear contrasts were calculated for each planned condition comparison for each participant. These individual contrast images were then used in whole-brain, group-level, random-effects analyses across all participants.

Whole-brain, main effect analyses

To examine what neural regions were more active when participants were observing an adolescent being included (by the two peers who had previously excluded the participant), we performed a group-level test at each voxel across the entire brain volume that examined the direct comparison between observed inclusion and observed exclusion. In addition, we also examined the reverse contrast – observed exclusion compared to observed inclusion.

Whole-brain, regression analyses

Next, we sought to examine whether adolescents displaying heightened sensitivity to rejection (i.e. either more neural activity consistent with distress during firsthand rejection or higher self-reported rejection sensitivity) would display greater neural activity in affective/distress regions while witnessing another person's inclusion versus exclusion. First, we examined whether participants' neural sensitivity to distress during their preceding firsthand experience of exclusion related to differential activity during their subsequent observation of inclusion compared to exclusion. To do this, we extracted parameter estimates from the specific clusters within the subACC (−6 22 −12) and AI (−46 8 −4) that were previously found (via whole-brain regressions conducted in SPM5) to display significantly greater activity during firsthand exclusion to the extent that participants were more distressed by firsthand exclusion (see Masten *et al.*, 2009, for details of how these clusters

were identified). Then, we conducted a whole-brain regression analysis examining how these parameter estimates related to subsequent brain activity during observed inclusion compared to observed exclusion. Finally, we conducted an additional whole-brain regression analysis examining correlations between participants' self-reported rejection sensitivity (i.e. RSQ scores) and their neural activity during observed inclusion compared to observed exclusion. Reported correlational findings reflect the specific clusters of activation in which heightened sensitivity to rejection (i.e. either greater activity in clusters displaying heightened sensitivity to distress during the preceding firsthand experience of exclusion, or greater RSQ scores) significantly related to the difference in activity during observed inclusion compared to observed exclusion.

Thresholding for whole-brain analyses was determined according to recommendations set forth by Lieberman and Cunningham (2009) to minimize both Type I and Type II errors. For a priori defined regions previously found to be involved in our processes of interest, analyses were thresholded at $p < .005$ for magnitude, with a minimum cluster size threshold of 10 voxels. This threshold is consistent with that employed in our previous examination of the current sample (Masten *et al.*, 2009), is typical of studies examining activity in a priori defined regions, and is comparable to a corrected threshold of $p < .05$ (see Lieberman & Cunningham, 2009, for a complete discussion of appropriate thresholding in these types of fMRI investigation). These a priori defined regions included those previously found to be involved in: (a) the distress of both peer rejection during adolescence (i.e. subACC, AI; Masten *et al.*, 2009; Masten *et al.*, 2011a; Masten *et al.*, 2011b) and socially threatening stimuli more generally (i.e. dorsal ACC, amygdala) (e.g. Davis & Whalen, 2001; DeWall *et al.*, 2010; Eisenberger *et al.*, 2003; Masten *et al.*, 2011d), (b) regions previously found to be involved in distress regulation specifically during social exclusion experiences among adolescents and adults (i.e. VLPFC, VS; rostral ACC; Masten *et al.*, 2009; Masten *et al.*, 2011a; Masten *et al.*, 2011b Petrovic & Ingvar, 2002; Phelps, Delgado, Nearing & LeDoux, 2004), and (c) regions underlying the mentalizing processes thought to be engaged when viewing others interacting with peers (i.e. DMPFC, MPFC, TPJ, PCC, precuneus, temporal poles; Beer & Hughes, 2010; Frith & Frith, 1999, 2003, 2006; Hynes *et al.*, 2006; Masten *et al.*, 2010a; Masten *et al.*, 2011c; Mitchell *et al.*, 2005; Singer, 2006). All other brain regions were examined at the same threshold but with FDR-correction applied in SPM5, as recommended for exploratory whole-brain examination. All coordinates are reported in Montreal Neurological Institute (MNI) format.

Results

Behavioral results

Manipulation check

During the Cyberball game when the participant experienced firsthand exclusion, they reported getting the ball an average of 27% of the time. When observing the game of Cyberball during which they saw another adolescent being excluded, participants similarly reported that the excluded adolescent received the ball an average of 27% of the time. Thus, participants noticed that exclusion occurred in both cases, and believed that they were excluded the same amount as the observed adolescent. In addition, this similarity between the estimates of how much the ball was received in the firsthand and witnessed games also suggests that the participants remained engaged in the task (and were thus able to accurately estimate the number of ball tosses) even when they were no longer playing the game.

Descriptive information

In terms of participants' distress following their experience of firsthand rejection, participants' mean NTS score was 2.90 ($SD = .73$) and ranged from 1.58 to 4.50 out of a possible 5; these scores did not differ by gender. Participants' average scores for self-reported rejection sensitivity ($M = 2.78$, $SD = .58$) ranged from 1.42 to 3.58 out of a possible 6. The mean for boys' rejection sensitivity ($M = 3.11$) was slightly higher than for girls ($M = 2.57$; $F = 5.71$, $p < .05$). Additional results for these subjective measures of distress and rejection sensitivity in this group of participants – including their relationships with brain activity during firsthand exclusion – have been reported previously (see Masten *et al.*, 2009).

Neuroimaging results

Neural activity during observed inclusion versus observed exclusion

First we performed a whole-brain analysis to examine adolescents' neural activity when they observed a new player being included in Cyberball (compared to observing this new player being excluded) by the same two individuals that had excluded the participant in the preceding game. This contrast revealed greater activity primarily in neural regions previously linked with the distress and pain of peer rejection. Specifically, there were significant clusters of activity in the right AI and
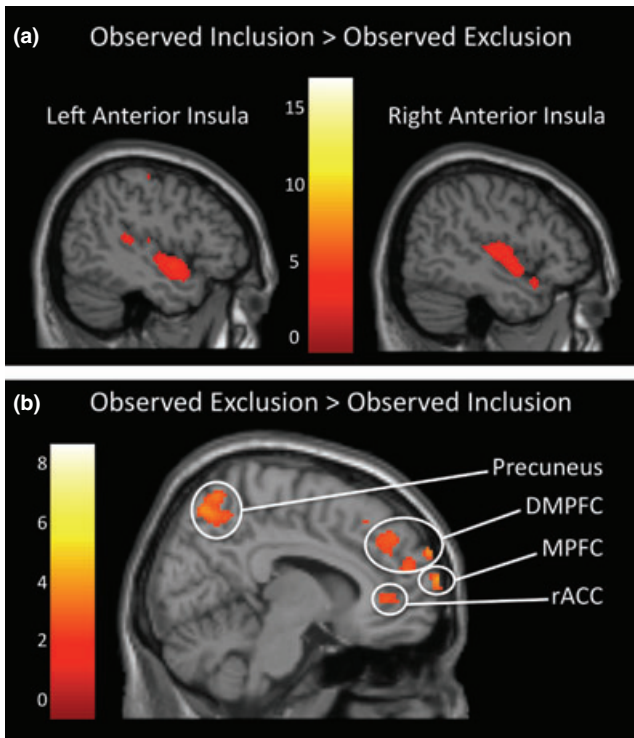
Figure 2 *Panel A depicts activity during observed inclusion versus exclusion in the left anterior insula (−46 0 −8) with extension into the temporal lobe, and right anterior insula (48 0 −6). Panel B depicts activity during observed exclusion versus inclusion in the precuneus (10 −68 56), dorsomedial prefrontal cortex (DMPFC; 6 56 22, 10 66 30), medial prefrontal cortex (MPFC; 10 72 14), and rostral anterior cingulate cortex (rACC; 16 40 −2).*

Table 1 *Regions activated during observed inclusion vs. observed exclusion (A), and during observed exclusion vs. observed inclusion (B)*

Anatomical region	BA		x	y	z	t	k	p
(A) Observed Inclusion>Observed Exclusion								
AI		L	−46	0	−8	6.04	641	<.0001
		R	48	0	−6	4.57	1393	<.0001
		R	40	14	−18	4.10	1393	<.0005
sub/rACC	24		0	36	−2	3.60	16	<.001
dACC	32	L	−6	8	46	5.75	1334	<.0001
Amygdala		L	−12	−6	−18	4.64	47	<.0001
		R	32	−10	−26	4.17	99	<.0005
VLPFC	46	L	−54	34	12	4.03	20	<.0005
Cerebellum*		L	−4	−40	−6	19.51	1543	<.0001
Caudate*			0	10	12	11.76	674	<.0001
Uncus*	28	L	−18	−16	−32	6.07	76	<.0001
Postcent.	3	R	22	−32	86	5.81	111	<.0001
Gyrus*	3	L	−30	−30	80	5.18	20	<.0001
	43	R	68	−18	16	5.68	187	<.0001
STG*	38	L	−34	8	−24	5.66	41	<.0001
	22/42	L	−66	−32	14	4.56	10	<.0001
	41/42	L	−54	−26	12	4.32	11	<.0005
Precent.	4	R	34	−20	78	4.83	30	<.0001
Gyrus*	4	L	−18	−28	82	4.76	23	<.0001
	6	R	18	−8	82	4.80	13	<.0001
(B) Observed Exclusion>Observed Inclusion								
DMPFC	9	R	6	56	22	3.79	314	<.001
	9	R	10	66	30	4.18	33	<.0005
MPFC	10	R	10	72	14	4.35	47	<.0005
	10	L	−4	56	16	3.60	314	<.001
precuneus	7	R	10	−68	56	4.15	751	<.0005
rACC	32/24	R	16	40	−2	3.67	689	<.001
MFG/	10/47	R	32	62	−8	4.93	689	<.0001
VLPFC	10/47	L	−38	56	−6	4.27	432	<.0005
Occ. Lobe*	19	L	−48	−78	2	8.78	68	<.0001
ITG/Occ. Lobe*	37/19	R	50	−66	−2	7.92	178	<.0001
IPL*	40	R	52	−56	48	6.54	12	<.0001

Note: Regions marked with a star (*) are those that were not the primary focus of this investigation but that were still significant at $p < .005$, 10 voxels (FDR-corrected). All other regions (e.g. regions previously linked with distress, emotion regulation and mentalizing) are listed at $p < .005$, 10 voxels. BA refers to putative Brodmann's Area; L and R refer to left and right hemispheres; x, y, and z refer to MNI coordinates; t refers to the t-score at those coordinates (local maxima); k refers to the number of voxels in each cluster. The following abbreviations are used for the names of specific regions: anterior insula (AI), subgenual anterior cingulate cortex (subACC), rostral anterior cingulate cortex (rACC), dorsal anterior cingulate cortex (dACC), ventrolateral prefrontal cortex (VLPFC), postcentral (Postcent.), superior temporal gyrus (STG), precentral (Precent.), dorsomedial prefrontal cortex (DMPFC), medial prefrontal cortex (MPFC), occipital (Occ.), inferior temporal gyrus (ITG), and inferior parietal lobule (IPL).

the left AI (with some extension into the temporal lobe; see Figure 2A), the subACC, the dACC, and the amygdala (see Table 1A). Interestingly, participants also displayed differential activity in neural regions previously linked with distress regulation during peer rejection – including both the VLPFC and VS – when they were observing this new player being included vs. excluded (see details of all activations in Table 1A).

Neural activity during observed exclusion versus observed inclusion

During the reverse contrast – neural activity while observing a new player being excluded (versus included) by the same two peers who had excluded the participant previously – we found evidence of heightened activity in regions previously linked with mentalizing and empathy, including the DMPFC, MPFC and precuneus (see Figure 2B). In addition, we found heightened activity

in regions previously linked with distress regulation during peer rejection, including the rACC (see Figure 2B) and a region that included the VLPFC but which was primarily located in the middle frontal gyrus (MFG), with some extension into the inferior frontal gyrus (see details of all activations in Table 1B). In

contrast, there was no differential activity in areas previously linked with distress or social pain while observing exclusion compared to inclusion.
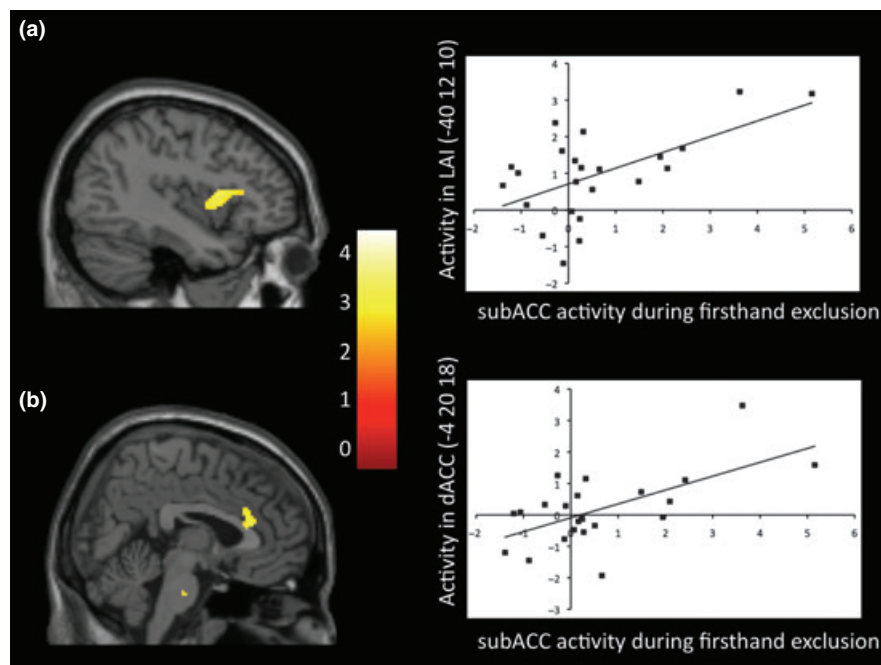
Activity during observed inclusion versus exclusion associated with neural sensitivity to firsthand peer rejection

Next a whole-brain regression analysis was performed to identify how adolescents' neural sensitivity to firsthand peer rejection – specifically, brain activity in the subACC and AI that was positively correlated with self-reported distress during a prior experience of peer rejection – related to their brain activity while subsequently observing a new adolescent being included (versus excluded). First, this analysis revealed that greater neural sensitivity to distress in the subACC during firsthand rejection was associated with more neural activity consistent with distress during subsequent observation of a peer being included (versus excluded). Specifically, there were significant clusters of activity in the right and left AI (see Figure 3A), the dACC (see Figure 3B), and the amygdala (see Table 2A). Similarly, greater neural sensitivity to distress displayed in the AI during firsthand rejection was also associated with greater activity during observed inclusion versus exclusion in the AI and dACC (see Table 2A). In addition, distress-related activity in

the AI during firsthand rejection also related to greater activity in regions previously linked with mentalizing, including the MPFC, right and left TPJ, precuneus and PCC, as well as regions involved in distress regulation, including the VLPFC and rACC (see details of all activations in Table 2A). Distress-related neural activity during firsthand rejection did not negatively correlate with any brain activity during observed inclusion versus exclusion.

Activity during observed inclusion versus exclusion associated with self-reported rejection sensitivity

Finally, we performed an additional whole-brain regression analysis to identify how adolescents' self-reported rejection sensitivity related to their neural activity when observing a peer being included (versus excluded) following a firsthand experience of peer rejection. Participants who reported being more sensitive to rejection displayed greater neural activity during observed inclusion versus exclusion in the subACC – a region previously linked with the distress of peer rejection (see Figure 4), as well as in the VLPFC and precuneus – regions commonly linked with distress regulation and mentalizing, respectively. Details of these and other significant activations are listed in Table 2B. Self-reported rejection sensitivity did not negatively
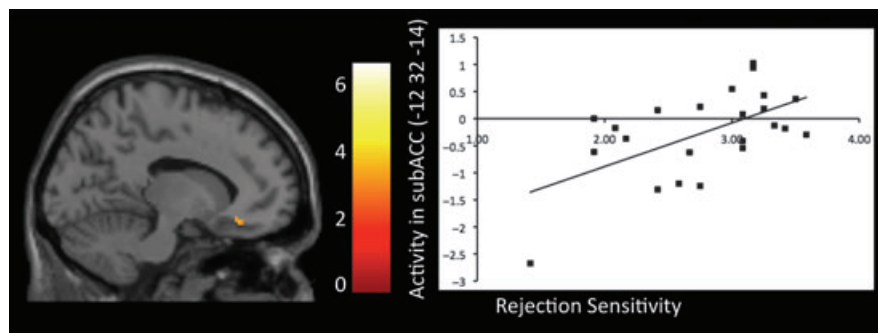

Figure 3 *Activity during observed inclusion versus exclusion in the left anterior insula (LAI; Panel A) and dorsal anterior cingulate cortex (dACC; Panel B) that is positively related to distress-related activity displayed in the subgenual anterior cingulate cortex (subACC) during firsthand exclusion versus inclusion.*

Table 2 *Regions activated during observed inclusion vs. observed exclusion that correlated significantly with: (A) distress-related activity in the subACC and AI during firsthand exclusion vs. inclusion and (B) self-reported rejection sensitivity*

Anatomical region	BA		x	y	z	t	r	k	p
(A) Positive associations with distress-related subACC activity during firsthand exclusion									
AI		L	−40	12	10	3.62	.62	251	<.001
		R	54	−2	0	3.23	.58	15	<.005
dACC	24	L	−4	20	18	3.71	.63	411	<.001
Amygdala		L	−30	4	−22	4.76	.72	42	<.0001
Positive associations with distress-related AI activity during firsthand exclusion									
AI		L	−46	4	6	3.64	.62	59	<.001
		R	42	20	8	3.67	.63	87	<.001
dACC	24/32	R	4	24	24	3.77	.64	899	<.001
	32	L	−12	26	24	4.03	.66	899	<.0005
d/rACC	32	L	−4	40	20	4.33	.69	899	<.0005
MPFC/rACC	32	R	12	40	6	3.67	.63	93	<.001
MPFC/ALPFC	10	R	26	60	6	3.88	.65	400	<.0005
precuneus	7	R	8	−62	58	4.65	.71	1652	<.0001
PCC	31	R	6	−48	38	3.69	.63	1652	<.001
TPJ	40	L	−44	−32	22	5.88	.79	287	<.0001
	40	R	44	−32	24	7.01	.84	450	<.0001
VLPFC	45/46	R	42	36	4	3.67	.63	52	<.001
	44/46	L	−38	44	2	3.37	.59	45	<.005
(B) Positive associations with self-reported rejection sensitivity									
subACC	25/11	L	−12	32	−14	3.34	.59	14	<.005
VLPFC	46/10	R	40	58	14	3.88	.65	29	<.0005
precuneus	7		0	−56	52	2.95	.54	40	<.005

Note: All regions are listed at *p* < .005, 10 voxels. BA refers to putative Brodmann's Area; L and R refer to left and right hemispheres; x, y, and z refer to MNI coordinates; *t* refers to the *t*-score at those coordinates (local maxima); *r* refers to the correlation coefficient representing the strength of the association between each regressor and activity in the specified region; *k* refers to the number of voxels in each cluster. There were no regions in which activity during observed inclusion versus observed exclusion was negatively associated with any of these regressors. The following abbreviations are used for the names of specific regions: anterior insula (AI), dorsal anterior cingulate cortex (dACC), rostral anterior cingulate cortex (rACC), medial prefrontal cortex (MPFC), anterolateral prefrontal cortex (ALPFC), posterior cingulate cortex (PCC), temporal parietal junction (TPJ), ventrolateral prefrontal cortex (VLPFC), and subgenual anterior cingulate cortex (subACC).

Figure 4 *Activity during observed inclusion versus exclusion in the subgenual anterior cingulate cortex (subACC) that is positively related to participants' self-reported rejection sensitivity. Note: if the apparent outlier (which is not a true statistical outlier) in this figure it removed, this relationship remains significant.*

correlate with any regions during observed inclusion versus exclusion.

Discussion

This study aimed to examine neural activity among adolescents watching another person being accepted or rejected by peers, immediately following a firsthand experience of peer rejection. As a whole, findings suggest that when adolescents witness others' interactions with peers, their previous firsthand experiences with rejection are related to their responses to these witnessed events, and these observations may alter adolescents' emotional processing as they are dealing with their own previous experiences being rejected. Here, we discuss the potential

meaning of these findings for understanding how interactions that adolescents observe in their immediate social environment might influence their reactions to peer rejection more generally. In addition, we speculate about the implications of these findings for understanding how observing positive and negative peer interactions on a regular basis might contribute to the perpetuation of bullying behaviors at this age. Specifically, we focus our discussion on brain regions that were of particular interest in this investigation because of their prior links with peer-related processes, including both firsthand and witnessed peer rejection in adolescents and adults. However, future research will undoubtedly provide additional, new insights about other regions identified in this study that may also be key neural substrates of adolescents' experiences with their peers.

First, in terms of neural responses to observed peer inclusion (versus exclusion), we found that adolescents displayed greater activity in the subACC and bilateral AI – neural regions previously linked with the distress of peer rejection among adolescents (Crowley *et al.*, 2010; Masten *et al.*, 2009; Masten *et al.*, 2011a; Masten *et al.*, 2011b), as well as the dACC and amygdala – regions also linked with social exclusion and threat processing (e.g. Davis & Whalen, 2001; DeWall *et al.*, 2010; Eisenberger *et al.*, 2003; Masten *et al.*, 2011d). This is consistent with our hypothesis and supports the notion that adolescents may feel more hurt or distressed when they perceive their rejection experiences as personal or 'just them'. In fact, after being rejected by others, seeing someone else being accepted might increase feelings of self-blame and enhance victims' feelings of distress resulting from their rejection. Interestingly, participants also displayed differential activity during observed inclusion versus exclusion in both the VLPFC and VS, regions linked to distress regulation in previous studies examining firsthand peer rejection (e.g. Masten *et al.*, 2009). Although this was not expected, it is possible that activity in these regions reflects a greater effort to inhibit the negative emotions that might be elicited when adolescents infer that their own rejection was indeed personal, and thus more hurtful.

Next, we examined participants' responses while they were watching another adolescent being excluded (compared to included) by the same two peers that had previously excluded the participant. We hypothesized that they would likely feel less distress and show more neural activity consistent with emotion regulation. Interestingly, in this case adolescents did show activity in frontal regions associated with distress regulation. However, this activity was in more medial regions (MFG, rACC) that were distinct from those found during observed inclusion versus exclusion (described

above). Thus, greater activity in these medial regions could reflect a heightened ability to recruit regulatory resources, specifically in situations where an impersonal explanation for one's rejection is available (i.e. 'others are also being rejected, it is not just me'). Alternatively, observed inclusion (versus exclusion) and observed exclusion (versus inclusion) may also elicit different types of regulatory processes (e.g. inhibition versus attribution), which could explain why different frontal regions are activated by each of these experiences. Furthermore, activity in MFG and rACC during observed exclusion (versus inclusion) could also reflect other cognitive processes beyond emotion regulation. Future work will be useful in teasing apart the various inhibitory, attributional, and other cognitive processes that are occurring when adolescents are observing these different types of social interaction and regulating their resulting emotional responses.

Interestingly, in terms of neural activity consistent with mentalizing processes, we found that adolescents displayed greater activity in the DMPFC, MPFC and precuneus, specifically when they were watching someone being excluded compared to included. Thus, it is possible that seeing others being excluded (more so than seeing them being included) leads adolescents to think about the thoughts and feelings of the individuals that they are observing. Perhaps, when adolescents have just experienced firsthand peer rejection, seeing another person being treated the same way might give adolescents insight into the minds of the excluders (i.e. 'they are mean, they do this to everyone'). Alternatively, heightened neural activity consistent with mentalizing during observed exclusion could also indicate that participants are understanding the perspective of the adolescent who is being excluded, or even feeling empathic towards the excluded player – a possibility consistent with prior work showing neural activity consistent with empathic processing during observed exclusion in adolescents (Masten *et al.*, 2010a). Given the shared plights of the participant and the observed victim, the participant might feel similar to the victim and show more neural activity consistent with empathy and mentalizing as a result (see also Cialdini, Brown, Lewis, Luce & Neuberg, 1997; Masten *et al.*, 2011c; Meyer, Masten, Ma, Wang, Shi, Eisenberger & Han, 2012).

Our next hypothesis was that, following a firsthand experience of being rejected, there would be more neural activity consistent with distress during witnessed peer acceptance versus rejection among adolescents with a heightened sensitivity to rejection. First, our results indicated that adolescents who displayed greater distress-related subACC and AI activity during firsthand peer exclusion also showed more neural activity consistent

with distress (i.e. more dACC, AI and amygdala activity) when they subsequently witnessed another adolescent being included. Similarly, adolescents who reported being more sensitive to rejection displayed greater activity during observed inclusion versus exclusion in the subACC – a region specifically linked with the distress of firsthand peer rejection. Together, these findings build on our prior work linking rejection sensitivity with more neural activity consistent with distress (i.e. greater dACC activity) during firsthand peer exclusion (Masten *et al.*, 2009), and further suggest that adolescents who are more sensitive (as indexed by either their neural responses or by their self-report) to peer rejection may also feel more hurt when they see others being accepted by peers – particularly when they see this in the aftermath of a firsthand rejection experience.

Next, adolescents who displayed more neural activity consistent with distress during firsthand rejection, and adolescents who reported being more sensitive to peer rejection, also displayed differential activity within the mentalizing network while they witnessed another peer being included versus excluded – a finding that extends our prior work linking rejection sensitivity to heightened activity in the mentalizing network in the context of peer rejection (Masten *et al.*, 2009). It is possible that these adolescents were more likely to be thinking about the thoughts and intentions of the players that they were watching, and this mentalizing may have contributed to greater hurt feelings in these individuals. This possibility is supported by other data from our lab showing that individuals who report lower social status more broadly (i.e. who may perceive social interactions similarly to those who are highly sensitive to rejection) also display more neural activity consistent with mentalizing in social situations (Muscatell, Morelli, Falk, Way, Pfeifer, Lieberman, Dapretto & Eisenberger, 2012). Of course, this suggestion goes beyond the current data, and future studies will be needed to directly investigate the cognitive reasoning that may accompany or exacerbate the distress that results from firsthand and witnessed peer interactions at this age.

As a whole, these data address one particular situation in which observing others being accepted or rejected might influence an adolescent's affective processing – specifically in the moments immediately following a firsthand experience of peer rejection when the adolescent is likely still recovering and/or making sense of his or her own experience of being rejected. However, on a larger scale, we believe that these data may also provide some insight into the processes via which bullying behaviors may come to be condoned and perpetuated more generally at this age. In other words, witnessing peer rejection and other forms of bullying on a regular

basis may impact individuals' affective and cognitive processing in a way that eventually alters their implicit beliefs about, and tolerance of, bullying behaviors more generally. Of course, witnessing peer rejection and bullying is known to be anxiety-provoking among adolescents (Janes & Olson, 2000; Nishina & Juvonen, 2005). However, the current data suggest that in certain situations witnessing others being accepted might also induce distress, and conversely, witnessing others being rejected might reduce distress. For example, when adolescents have recently experienced negative treatment by peers, their responses to witnessed peer rejection and their perception and interpretation of their own firsthand rejection are likely to be related. To this end, if adolescents witness peer rejection frequently and find it to have a mitigating effect with regard to their own negative affect, an implicit acceptance of bullying behaviors might grow over time and eventually contribute to the perpetuation of bullying behaviors at this age. Additional research on this topic will continue to increase our understanding of how witnessing peer interactions might contribute to the mainstream status of bullying at this particular age.

Findings in the current study should be considered in light of some limitations. First, this study did not directly assess adolescents' specific beliefs or attributions about either their firsthand or witnessed experiences of peer exclusion and inclusion. Thus, our interpretations of these data in terms of adolescents' perceptions about their interactions with their peers are speculative and will need to be examined in future work. Given that previous neuroimaging work has shown that manipulating individuals' attributions for social exclusion significantly moderates distress-related neural responses to exclusion (e.g. Masten *et al.*, 2011d), additional investigation specifically within the context of adolescent peer rejection is clearly warranted. In addition, future studies should examine how social status might influence our observed patterns. For example, if information was collected regarding participants' social status or their prior experience with peer rejection, this could provide insight into how firsthand and observed social interactions impact adolescents' emotional processing in their real lives.

Next, in this study, we only examined one sequence in which firsthand and witnessed peer events might actually occur – firsthand exclusion, followed by observed inclusion and exclusion. Of course, it would likely be impossible to examine several different sequences using a within-subjects design, without altering the qualitative meaning of each event, as well as the ecological validity of the task. Nevertheless, it would be intriguing for future studies to investigate how firsthand and witnessed peer events impact each other when they are experienced

as part of other sequences typical of adolescents' daily lives (e.g. witnessed exclusion followed by firsthand exclusion). Examining patterns of mediation among adolescents' subjective and neural responses to these various events as well as their rejection sensitivity would be a particularly fruitful direction for these investigations.

Related to this issue, since this study did not include counterbalancing or a true baseline condition (e.g. resting, or watching a ball without social context), we cannot conclude whether our observed differences in activity are due to increased or decreased engagement of specific regions, and we cannot rule out the possibility that order effects or habituation impacted our findings. Future studies could employ a between-subjects design to explore some of these issues; for example, comparing data similar to those included in the current analyses to a separate data set from a control group who witnessed two consecutive inclusion games would allow more conclusive interpretation of the findings. Nevertheless, in the current investigation we deliberately kept the Cyberball games very short to ensure participants' continued engagement and minimize the risk of habituation. In addition, the significant main effects of observed exclusion verses observed inclusion (see Table 1B) provide evidence that there was not an *overall* decrease in activity at the end of the task (i.e. during observed exclusion) that could account for the areas of heightened activity during observed inclusion versus observed exclusion.

Also related to task design, since all participants experienced firsthand exclusion prior to observing a peer in this study, it was not possible to conclusively determine the effect that firsthand exclusion had on subsequent neural responses during the observation phases of the task. Thus, the insights generated by these data regarding how firsthand and observed peer interactions might interact and influence adolescents' responses to these events will benefit from future studies with experimental designs permitting more conclusive identification of causal effects. Finally, neural activity displayed during observed inclusion may have included residual activity from the preceding experience of firsthand exclusion. However, since adolescents displayed a somewhat different and more extensive network of affective/pain-related activity during observed inclusion versus observed exclusion (i.e. AI, subACC, dACC, amygdala) than we previously observed during firsthand exclusion (i.e. AI, subACC; Masten *et al.*, 2009), our current finding of heightened neural activity consistent with distress during observed inclusion cannot be attributed to potential 'left-over' activity from adolescents' previous firsthand experiences.

In summary, the current study provides an important, preliminary step toward understanding the interplay between adolescents' firsthand experiences with peers and the peer-related events that they witness in their daily social environment. Moreover, we have provided new evidence that individuals who are particularly sensitive to negative peer interactions may be most affected when they witness the acceptance and/or rejection of others. In particular, this investigation has permitted the formation of new insights about brain regions previously linked to peer rejection, and has also revealed additional regions, which – despite being beyond the scope of the current discussion – will undoubtedly provide useful groundwork for future examinations and eventually contribute to a more complete understanding of adolescent peer rejection. Ultimately, this line of work may contribute to our understanding of bullying behaviors in adolescence more generally, and increase knowledge of how individuals navigate the complex social interactions that characterize the adolescent period.

Acknowledgements

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