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Associations Among Pubertal Development, Empathic Ability, and Neural Responses While Witnessing Peer Rejection in Adolescence

Carrie L. Masten
Vanderbilt University

Naomi I. Eisenberger
University of California, Los Angeles

Jennifer H. Pfeifer
University of Oregon

Natalie L. Colich
Stanford University

Mirella Dapretto
University of California, Los Angeles

Links among concurrent and longitudinal changes in pubertal development and empathic ability from ages 10 to 13 and neural responses while witnessing peer rejection at age 13 were examined in 16 participants. More advanced pubertal development at age 13, and greater longitudinal increases in pubertal development, related to increased activity in regions underlying cognitive aspects of empathy. Likewise, at age 13 greater perspective taking related to activity in cognitive empathy-related regions; however, affective components of empathy (empathic concern and personal distress) were associated with activity in both cognitive and affective pain-related regions. Longitudinal increases in empathic ability related to cognitive and affective empathy-related circuitry. Findings provide preliminary evidence that physical and cognitive-emotional development relate to adolescents' neural responses when witnessing peer rejection.

In adolescence, peer relationships take on new importance as youth spend more time with peers and place more value on peer belonging (Brown, 2004). Unfortunately, due to the high value placed on maintaining peer relationships, peer rejection and bullying become increasingly prevalent at this age (Brown, 2004), and are associated with many negative outcomes (Arseneault, Bowes, & Shakoor, 2010; Brendgen & Vitaro, 2008; Isaacs, Hodges, & Salmivalli, 2008; Lev-Wiesel, Nuttman-Shwartz, & Sternberg, 2006; Prinstein, Sheah, & Guyer, 2005). Furthermore, it is not just increases in firsthand experiences of peer rejection that adolescents worry about. Even adolescents who are not themselves rejected by others are still exposed to, and impacted by, the peer rejection they see happening to others (Janes & Olson, 2000; Nishina & Juvonen, 2005). In fact, most adolescents witness peer rejection on a regular basis in their daily environment (Rivers, Poteat, Noret, & Ashurst, 2009) and observe peer rejection and bullying at least as often as they experience it firsthand (Nishina & Juvonen, 2005).

Recently, neuroimaging techniques have been used to examine adolescents' emotional responses and empathy when they witness others being rejected (Masten, Eisenberger, Pfeifer, & Dapretto, 2010, 2012). Functional magnetic resonance imaging (fMRI) is particularly useful because it permits the

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Correspondence concerning this article should be addressed to Carrie L. Masten, Psychology and Human Development, Vanderbilt University, 230 Appleton Place, Peabody #552, Nashville, TN 37203. Electronic mail may be sent to carrie.masten@gmail.com.

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study of processes underlying peer interactions as they are occurring, rather than relying solely on retrospective self-reports or observer ratings, which are limited in their ability to tap in-the-moment processes. In addition, fMRI has the potential to disentangle simultaneous, distinct processes that co-occur when a social interaction is being observed, which together create an individuals' overall subjective experience. Furthermore, fMRI is also particularly useful for studying social developmental processes because it allows examination of how social contexts or individual differences might alter underlying affective and cognitive processes. In other words, it can help reveal how certain developmental constructs (e.g., pubertal development or empathic processing) might modulate affective and cognitive neural processes engaged during peer-related events. Thus, this method provides a unique perspective when trying to understand correlates of adolescent behavior (see also Masten & Eisenberger, 2009; Pfeifer & Blakemore, 2012).

Prior work has shown that affective and cognitive neural processes may impact how individuals subjectively experience the observation of peer exclusion (details in the next section). However, as major social changes in adolescence (i.e., increased peer rejection) coincide with many physical and cognitive changes (see Nelson, Leibenluft, McClure, & Pine, 2005; Steinberg, 2004, 2007), neural processes underlying peer interactions are likely related to ongoing physical and cognitive emotional development across this transitional period. For example, structural and functional reorganization of neural networks involved in social and empathic processes occur during puberty and are thought to interact with social and behavioral changes at this age (Blakemore, 2008; Blakemore, Burnett, & Dahl, 2010; Bramen et al., 2011; Decety, 2010; Nelson et al., 2005). Moreover, hormonal changes precipitated by puberty are thought to be one of the most important influences driving social reorientation in adolescence (e.g., Forbes & Dahl, 2010) and are therefore likely to have direct links with the neural underpinnings of adolescent social processes. Thus, the goal of this study was to build on prior research by examining how longitudinal changes across the transition to adolescence in two developmental indices—pubertal development, an indicator of physical change, and empathic ability, an indicator of both cognitive (i.e., perspective taking) and emotional (i.e., empathic concern, personal distress) change—relate to adolescents' neural responses when they witness peer rejection.

The Cognitive and Affective Components of Empathy

Research examining the processes underlying empathy has typically focused on two different aspects of empathic experiences (e.g., Baron-Cohen, 2003; Eisenberg, 2000; Eisenberg, Spinrad, & Sadovsky, 2006). First, there are the cognitive abilities that enable people to understand the mental states of other (skills often termed *mentalizing*; Frith, Leslie, & Morton, 1991). Second, there is the affective dimension of empathy, which allows people to share or "mirror" the emotions and pain of others. Recently, neuroimaging research has indicated that two different neural networks underlie the cognitive and affective components of empathy (Decety, 2010; Decety & Meyer, 2008; Shamay-Tsoory, Aharon-Peretz, & Perry, 2009; Singer, 2006; Singer & Lamm, 2009). Typically, the cognitive component of empathy is thought to rely on the "mentalizing network"—a network of regions that are associated with various aspects of mentalizing, including the posterior superior temporal sulcus (pSTS), the temp oral poles, the precuneus and posterior cingulate cortex (PCC), the temporal–parietal junction (TPJ), and the medial and dorsomedial prefrontal cortex (MPFC–DMPFC; Frith & Frith, 1999, 2003, 2006; Mitchell, Banaji, & Macrae, 2005; Saxe, 2006; Singer, 2006). In contrast, the neural regions underlying the affective component of empathy are thought to be those that are activated during both firsthand and vicarious affective experiences. For example, the anterior insula is activated by both direct and observed experiences of disgust (Wicker et al., 2003), the amygdala is activated during direct and observed fear (Whalen et al., 2001), and the dACC and anterior insula are activated by direct and observed physical pain in adults (Botvinick et al., 2005; Jackson, Bruney, Meltzoff, & Decety, 2005; Morrison, Lloyd, Di Pellegrino, & Roberts, 2004; Singer et al., 2004; Singer et al., 2006) and children (Decety, Michalska, & Akitsuki, 2008). Both the insula and amygdala are also activated among children when they both observe and make emotional face expressions (Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008).

Neural Correlates of Witnessing Social Exclusion

A few studies have examined the neural correlates of empathy-related processes engaged while observing social exclusion specifically. In adults, viewing exclusion (vs. inclusion) activates regions in the mentalizing network (DMPFC, MPFC, VMPFC, precuneus; Masten, Morelli, & Eisenberger, 2011). The affective pain network (dACC, AI) is also activated during observed exclusion in individuals reporting high levels of empathy (Masten et al., 2011), and among friends of the excluded victim (Beeney, Franklin, Levy, & Adams, 2011; Meyer et al., 2012)—suggesting that sharing the affective experience of the victim might depend on feelings of closeness or similarity to the victim or being able to relate to him or her more. In terms of adolescents, a recent study demonstrated that 13-year-olds also display activity in the mentalizing network (DMPFC, MPFC, precuneus, pSTS) when viewing peer exclusion (Masten et al., 2010). Interestingly, in this study, there was no evidence of affective pain processes even in adolescents who reported being more empathic. However, we used a single unidimensional empathy measure in this early study, which may not have been sensitive enough to separately index cognitive and affective components of empathy, or their respective associations with distinct networks of brain activity.

Pubertal Development and Changes in Empathic Ability in Adolescence

To understand adolescents' neural responses when they witness negative interactions among their peers, it is crucial to consider the many developmental factors that might modulate individuals' responses. First, it is commonly hypothesized that many of the social changes occurring in adolescence—including the increasing salience of peers—coincide with early stages of pubertal development, and occur as a result of puberty-related hormonal changes (Blakemore et al., 2010; Forbes & Dahl, 2010; Nelson et al., 2005; Steinberg, 2004, 2007). Next, youth also make significant strides in terms of empathic ability as they transition to adolescence (Eisenberg, Miller, Shell, McNally, & Shea, 1991), which is not surprising given increased time spent with peers and concern about peer acceptance. In fact, given known links between empathy and successful social communication (Denham, Renwick-DeBardi, & Hewes, 1994; de Vignemont & Singer, 2006; Zahn-Waxler, Cole, Welsh, & Fox, 1995; Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman, 1992), empathic ability may continue to develop in adolescence precisely because of the increased need for empathy-related skills that facilitate successful peer interactions (Eisenberg & Morris, 2004; Eisenberg, Morris, McDonald, & Spinrad, 2009). Although there has been a shortage of empirical work examining direct links between puberty and empathy, recent research has linked pubertal development with: assessment of others' opinions and feelings (Burnett, Thompson, Bird, & Blakemore, 2010)—a skill that becomes particularly important in adolescence when the perceived opinions of peers are highly salient (Brown, 2004); heightened stress due to social evaluation (Gunnar, Wewerka, Frenn, Long, & Griggs, 2009; Sumter, Bokhorst, Miers, Van Pelt, & Westenberg, 2010); increased sensation seeking (Martin et al., 2002) and emotional reactivity (Silk et al., 2009; Spear, 2009); as well as greater "mentalizing" ability (Keulers, Evers, Stiers, & Jolles, 2010). It is likely also associated with increasing interest in, and efforts to interact with, peers (Forbes & Dahl, 2010). In fact, Forbes and Dahl (2010) posit that puberty-related hormonal increases are a major catalyst underlying adolescents' ability and motivation to maintain peer relations. Thus, it is crucial to examine how pubertal factors relate to peer interactions and social cognitive advances at this age.

In terms of brain development, a significant degree of structural reorganization and functional changes are thought to occur concurrently with puberty and relate to the social changes that accompany adolescence (Blakemore, 2008; Blakemore et al., 2010; Bramen et al., 2011; Nelson et al., 2005). Similarly, many of the regions linked to both the cognitive and affective components of empathy undergo significant structural and functional change across the adolescent transition (Blakemore, 2008; Blakemore et al., 2010; Decety, 2010; Nelson et al., 2005). To our knowledge, interrelated influences of puberty and empathy on neural processing have not yet been examined. However, pubertal development has been linked with prefrontal cortical activity during reward processing (Forbes et al., 2010), as well as both limbic and prefrontal cortical activity during facial emotion processing (Moore et al., 2012). Thus, pubertal development appears to be associated with activity in some of the same neural networks that are involved in both cognitive and affective aspects of empathy. Together, this research indicates that pubertal development and increasing empathic ability likely have important, interrelated links with adolescents' social experiences at behavioral and neural levels.

Clearly, understanding the roles of pubertal development and empathic ability is crucial to understanding adolescents' social interactions. Moreover, witnessing peer rejection is a particularly common type of peer interaction in adolescence that depends on relatively advanced cognitive abilities and higher order cortical function for its understanding. Thus, it is important to examine how pubertal development and empathic ability relate to adolescents' responses when they witness these peer encounters. So far, there is limited research on this topic—particularly with regard to how these constructs are represented at the neural level. Additionally, little is known about how changes in pubertal development and empathic ability across the transition to adolescence are associated with neural functioning in the context of witnessing peer rejection.

The goal of this study was to examine how two developmental indices—pubertal development and empathic ability, measured both concurrently (at age 13) and longitudinally across the adolescent transition (from ages 10 to 13)—might be related to adolescent's neural responses when they witnessed peer rejection (i.e., a neural index of their empathy for peers) at age 13. In particular, we measured pubertal development via self-reports of physical appearance and maturation. In addition, we used three separate dimensions of empathic ability—empathic concern, personal distress, and perspective taking (instead of the single dimension examined in Masten et al., 2010)—because dimensions of empathy that are more cognitively or affectively focused might differentially relate to activity in mentalizing or affective pain regions. We also measured *concurrent* self-reports, as well as *longitudinal increases* across the adolescent transition for both pubertal development and empathic ability, to examine: (a) current status (i.e., the level of development achieved) and (b) changes (i.e., the amount of development occurring during the transition) for each of these measures, in relation to neural responses to peers.

Measuring longitudinal increases was of particular interest given recent literature focusing on *velocity* of change as a key predictor of social emotional outcomes in adolescence. For example, there is wide variation in the rate at which youth progress through puberty (e.g., Mendle, Harden, Brooks-Gunn, & Graber, 2010), and because puberty is itself a stressful life transition that all youth must face (see Ge et al., 2003), physiological or cognitive changes occurring at a faster than average rate might result in a need for especially rapid adjustment to new social demands and experiences. Indeed, accelerated pubertal change or "pubertal tempo" (i.e., a larger degree of pubertal maturation across a specific time frame) has been linked to depressive symptoms in adolescence, particularly for boys (Ge et al., 2003; Mendle et al., 2010).

Hypotheses

First, based on previous developmental research, we predicted that pubertal development and empathic ability would be positively associated with each other both at age 13 and across the adolescent transition (from ages 10 to 13).

In terms of neural associations, we hypothesized that adolescents who reported more advanced pubertal development at age 13 would display greater activity in regions associated with mentalizing and affective pain processing while seeing another adolescent being excluded. In addition, we explored whether longitudinal increases in pubertal development from ages 10 to 13 might also relate to greater neural responses suggestive of empathy for an excluded peer (in both mentalizing and affective pain-related regions) at age 13. Although prior work on this topic is limited, we speculated that rapid physical change coinciding with the social contextual changes that characterize the adolescent transition (e.g., greater peer orientation, middle school transition) might relate to enhanced sensitivity to peers' emotions. In other words, because emotional advances are known to accompany pubertal change (Burnett et al., 2010; Forbes & Dahl, 2010; Keulers et al., 2010), one possibility is that rapid pubertal development—during the precise period when peer importance increases—might relate to similarly accelerated increases in peer salience and emotional understanding.

In terms of empathic ability, we expected that greater empathic ability at age 13 would, in general, relate to more cognitive and affective empathy-related neural activity during observed peer exclusion. Specifically, however, we expected that higher perspective taking scores would relate to more neural evidence of mentalizing, while empathic concern and personal distress would relate to more neural evidence of affective pain processing. Regarding longitudinal changes in empathic ability, we expected positive associations between increasing empathic ability from ages 10 to 13 and neural evidence of both mentalizing and affective pain processes at age 13. But, as the high salience of peers at this age might increase anxiety about negative peer interactions (i.e., more personal distress), or more concern for others who are observed being negatively treated (i.e., greater empathic concern), we expected that increases in these affective dimensions of empathic ability in particular might relate to corresponding increases in neural activity related to affective components of empathy during observed peer exclusion.

Finally, given that pubertal changes, increasing social cognitive skills, and neural functioning during peer interactions are likely to be meaningfully interrelated during adolescence, exploratory mediation analyses were conducted to derive clues about the possible directionality of the relations among these variables. Specifically, we tested two mediation pathways. First, given the commonly posited theory that functional reorganization of the brain accompanies puberty and relates to subsequent social changes (Blakemore, 2008; Blakemore et al., 2010; Bramen et al., 2011; Nelson et al., 2005), we examined if a neural mechanism (increased responses during observed exclusion) might help explain the positive relation between pubertal development and empathic ability. Next, as emotional and cognitive advances are known to accompany puberty and relate to emerging patterns of brain function (Burnett et al., 2010; Forbes & Dahl, 2010; Keulers et al., 2010), we examined whether a cognitive-emotional mechanism (increasing empathic abilities) might help explain the positive relation between pubertal development and neural responses to observed peer exclusion.

Method

Participants

An ethnically and socioeconomically diverse sample of 16 typically developing youth (nine females) completed data collection at two time points separated by 3 years (M = 3.17 years, SD = .29). To examine the effect of pubertal status unconfounded by age, we recruited participants in an extremely narrow age range. At Time Point 1, participants were 10 years old (M = 10.07 years old, SD = .30), and at Time Point 2, they were 13 years old (M = 13.17 years old, SD = .29) and had attended at least 1 year of middle school. Participants came from a range of ethnic backgrounds—62% Caucasian, 19% Asian, 13% Latino (including one individual who reported being Latino and Native American), 6% African American—and socioeconomic backgrounds; maternal education ranged from high school diploma to advanced graduate degrees (Mdn = bachelor's degree), and total household income ranged from less than \$25,000 to greater than \$400,000 (Mdn = \$65,000–\$80,000). The study was initially presented to participants and their parents as a longitudinal examination of adolescent brain development, and recruitment was performed via mass mailings, summer camps, and fliers distributed in the Greater Los Angeles area so as to obtain a sample that was as representative as possible. Participants had no history of psychiatric, neurological, or medical disorders. All participants and parents provided assent or consent, which was approved by UCLA's Institutional Review Board.

This sample is identical to that examined (at age 13 only) in Masten et al. (2010), but all analyses and findings are unique from those reported previously.

Overview of Procedures and Task

The goal of this study was to examine how participants' neural responses to witnessing peer rejection related to their concurrent pubertal development and empathic ability, as well as their longitudinal changes in these variables across the 3-year period preceding the witnessed event (i.e., from ages 10 to 13)—a period thought to span the transition to adolescence. Thus, participants completed self-reports of both pubertal development and empathic ability at age 10 and again at age 13 (see details in the next section). Then, at age 13 (and at least 1 day after the completion of the self-reports), participants underwent fMRI while they believed they were observing another adolescent (who was their same age and gender) being socially excluded by others. To simulate this exclusion, participants observed two rounds of the computer task "Cyberball" (Williams, Cheung, & Choi, 2000; Williams et al., 2002), during which three "players" (who were actually computer programmed) ostensibly played a ball-tossing game together. On their screen, participants could see three icons representing each "player," and they watched as the icons (supposedly controlled by the players) passed the ball back and forth. Prior to the scan, the experimenter explained that the purpose of the study was to examine neural activity during the observation of social interaction. Participants were then told that three individuals their age had volunteered to play the game via the Internet during their scan, and they were given the first names and genders of these "previous participants" (one male, one female, and a third player, who was to be "excluded" by the first two, whose gender matched that of the participant). Participants were instructed to watch the game closely and think about what the players might be thinking or feeling, how they were treating each other, and what strategies they might have for deciding the recipient of each ball toss. In the first round, participants observed all players being included in the game equally (60 throws total). In the second round, one player was excluded by the others after being included for 10 throws and was left out for the rest of the game. Exclusion was used as a proxy for peer rejection based on evidence that isolating peers from social groups is a common way of rejecting peers in adolescence (Coie, Dodge, & Kupersmidt, 1990).

Evidence of Task Validity

Cyberball has elicited feelings of distress and empathy for observed victims of exclusion in prior neuroimaging studies (Beeney et al., 2011; Masten et al., 2010; Masten et al., 2011; Meyer et al., 2012). In addition, careful measures taken in this study support Cyberball's ecological validity.

Evidence from previous literature. First, previously published data (Masten et al., 2010) provide evidence for the effectiveness of Cyberball. After watching the exclusion round of Cyberball, participants reported their state empathy (i.e., how much it hurt to watch the victim being excluded). These reports of state empathy indicated that participants experienced empathic feelings as they watched the exclusion. Next, participants wrote e-mails to the excluded victims, which were later coded for evidence of prosocial behavior (e.g., offering support or comfort). Participants displayed moderate amounts of prosocial behavior, again suggesting that they were concerned for and wanted to help the observed victim (see Masten et al., 2010, for details).

Cover story. In this study, extensive efforts were made to maintain the cover story. Participants were told that the "players" were real kids who had already participated in the study. Participants were even given the chance to volunteer to be a player in a future participant's game. Researchers also pretended to call the players to establish their Internet connections, and once during the scan participants were told to wait while one of the players used the restroom.

Manipulation check. Participants completed a manipulation check to ensure that they noticed the social exclusion during Cyberball. After the scan, they were asked to answer several yes or no questions about whether specific events happened during the game (e.g., "One player was treated unfairly," "All the players participated in the game the same amount"). They were told that this was necessary "because each set of players acts differently." All participants included in this study indicated that one player had been left out during the second round of the game.

Debriefing. After collection of all measures, participants were thoroughly debriefed about the deception in the study. They were also questioned to make sure that they believed that they were observing real people during the scan. All participants reported believing the cover story.

Self-Report Measures

Pubertal development. Participants completed the Pubertal Development Scale (PDS; Petersen, Crockett, Richards, & Boxer, 1988) at ages 10 and 13. On the PDS, participants self-report their visible development of secondary sexual characteristics (e.g., growth spurt, pubic hair, etc.) using a scale from 1 (*no development*) to 4 (*development already completed*) for five items. The PDS has shown good reliability (αs = .68 to .83) and validity (e.g., correlations with physician ratings: rs = .61 to .67; correlations with the sexual maturity scale—another self-report puberty measure; see Duke, Litt, & Gross, 1980; Morris & Udry, 1980; rs = .72 to .80) in prior samples of early adolescents (see Brooks-Gunn, Warren, Rosso, & Gargiulo, 1987; Petersen et al., 1988). Reliability in the current sample was also good (α = .81). Participants' composite PDS scores at age 13 reflect their concurrent pubertal development. Scores at age 13, after controlling for scores at age 10, reflect changes in participants' pubertal development during the 3 years preceding the scan. To control for scores at age 10, residualized scores for age 13 were calculated, such that the group-level variance in scores at age 13 that was explained by scores at age 10 was removed.

Empathic ability. To obtain indices of distinct aspects of empathy that tapped both mentalizing and affective pain processes, at ages 10 and 13 participants completed three subscales of the Interpersonal Reactivity Index (IRI; Davis, 1983, 1996) measuring: (a) empathic concern—a type of affective empathy (e.g., "When I see someone being taken advantage of, I feel kind of protective toward them"), (b) personal distress—another type of affective empathy (e.g., "I sometimes feel helpless when I am in the middle of a very emotional situation"), and (c) perspective taking—a type of cognitive empathy (e.g., "I try to look at everybody's side of an argument before I make a decision"). Each of these subscales contains seven items that are rated using a scale ranging from 1 (*does not describe me at all*) to 5 (*describes me very well*). The IRI subscales have demonstrated satisfactory internal reliabilities (ranging from .71 to .77) and test–retest reliabilities (ranging from .62 to .71) in prior samples (Davis, 1983), as well as expected associations with related psychological variables, supporting their validity (see Davis, 1983). Satisfactory reliability was also found in the current sample (empathic concern: α = .79; personal distress: α = .74; perspective taking: α = .79). Subscale scores at age 13 reflect 3 dimensions of participants' concurrent empathic ability. Scores at age 13, after controlling for scores at age 10, reflect changes in these dimensions during the 3 years preceding the scan.

fMRI Data Acquisition and Analysis

Data acquisition. Using a Siemens Allegra 3-Tesla MRI scanner, images were collected during functional scans lasting 2 min, 48 s (echo planar T2*-weighted gradient-echo, TR = 2000 ms, TE = 25 ms, flip angle = 90°, matrix size 64 × 64, 36 axial slices, FOV = 20 cm; 3 mm thick, skip 1 mm) for each round of Cyberball, and during 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) to enable functional image registration.

Data analysis. Neuroimaging data were preprocessed and analyzed using SPM5 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK), and ROI extraction was performed with the Marsbar toolbox in SPM (http://marsbar.sourceforge.net). Preprocessing included image realignment to correct for head motion, normalization into a standard stereotactic space defined by the Montreal Neurological Institute and the International Consortium for Brain Mapping by averaging 152 brains, and spatial smoothing with an 8 mm Gaussian kernel, full width at half maximum, to increase signal-to-noise ratio.

A block design was used. Each round of Cyberball was modeled as a run with inclusion and exclusion conditions modeled as blocks in the run. Linear contrasts were calculated for each condition comparison for each participant, and used in whole-brain, random-effects analyses.

To examine relations between brain activity during observed exclusion versus inclusion and self-report measures, we used whole-brain and region of interest (ROI) regression analyses. The purpose of the whole-brain analyses was to look at the entire brain volume for any areas in which individuals' brain activity while witnessing peer exclusion related to pubertal development and empathic ability. Specifically, this analysis identified significant clusters of activation representing the particular areas of the brain in which the difference in activity during observed exclusion versus inclusion among our participants, significantly related to their individual differences in concurrent and longitudinal self-reports. In contrast, the purpose of the ROI analyses was to examine the relation between each self-report measure and the average activity during observed exclusion versus inclusion within specific regions identified ahead of time as being meaningful for our task (see ROI definition in the following section). In other words, ROI analyses allowed us to identify whether the average amount of activity displayed by participants, during observed exclusion versus inclusion, in specific a priori–defined brain regions, significantly related to their individual differences in concurrent and longitudinal self-reports.

Thus, overall we examined how differences in neural activity during observed exclusion versus inclusion at age 13, across the whole brain and in a priori–defined ROIs, correlated with: (a) concurrent pubertal development, (b) longitudinal changes in pubertal development from ages 10 to 13, (c) concurrent empathic ability (i.e., empathic concern, personal distress, and perspective taking IRI subscale scores), and (d) longitudinal changes in empathic ability (i.e., changes in empathic concern, personal distress, and perspective taking) from ages 10 to 13.

Whole brain analyses. First, we examined the whole brain to localize areas of activity that were most associated with pubertal development and empathic ability. For each regressor (i.e., self-report measure), we performed one correlational test (the results of which are reported as both t values and r values), which revealed the specific brain areas in which the regressor was significantly associated with the difference in activity between observed exclusion and inclusion. Because standard whole brain analysis software only permits the identification of clusters of activity above a specified threshold, nonsignificant results are not reported as part of our results.

Consistent with Masten et al. (2010), whole brain analyses were thresholded at $p < .005$ for magnitude (uncorrected, minimum cluster size = 10 voxels), for all a priori–defined regions in mentalizing networks (DMPFC, MPFC, TPJ, pSTS, PCC, temporal poles, precuneus), and affective pain networks (dACC, AI, amygdala, subACC; Masten et al., 2009). Other regions were examined at an FDR-corrected threshold ($p < .05$; see Lieberman & Cunningham, 2009). Coordinates are reported in Montreal Neurological Institute (MNI) format.

ROI analyses. Next, we examined adolescents' pubertal development and empathic ability in relation to brain activity during observed exclusion versus inclusion in a set of a priori defined ROIs. These ROIs were functionally defined (using the Marsbar toolbox) as the clusters of activity in the mentalizing network that were found to be significantly more active during the main effect of observed exclusion compared with inclusion in this sample of adolescents (see Masten et al., 2010). Specifically, these ROIs included: one region in the DMPFC (peak voxel [12 44 50]), $t(15) = 4.76$, $p = .0005$, $k = 194$ voxels; two regions in the MPFC (peak voxel [16 70 12]), $t(15) = 3.22$, $p = .005$, $k = 13$ voxels, and (peak voxel [14 46 14]), $t(15) = 3.96$, $p = .001$, $k = 54$ voxels; two regions in the precuneus (peak voxel [10 −66 48]), $t(15) = 4.18$, $p = .0005$, $k = 433$ voxels, and (peak voxel [−12 −62 50]), $t(15) = 3.61$, $p = .005$, $k = 22$ voxels; and one region in the pSTS (peak voxel [58 −44 20]), $t(15) = 3.53$, $p = .005$, $k = 311$ voxels (Masten et al., 2010). Mean parameter estimates for each participant (which model the amplitude of the BOLD response during observed exclusion vs. inclusion) were then extracted and averaged across all voxels in each ROI. Standard software (SPSS 16.0; SPSS, Chicago, IL) was used to conduct regressions to determine whether these parameter estimates were related to each self-reported variable of interest. A standard statistical threshold of $p < .05$ was used for these ROI analyses; based on a priori hypotheses, all tests were one-tailed.

Exploratory mediation analyses. Exploratory mediation analyses were conducted to look at potential directional relations among pubertal development, empathic ability, and neural responses to observed peer rejection. As traditional mediation tests can be biased when used with small samples (Preacher & Hayes, 2008), we employed a bootstrapping method (scripted in SPSS; Preacher & Hayes, 2004) with bias-corrected confidence intervals to more accurately interrogate the significance of these mediational models (Preacher & Hayes, 2004; Shrout & Bolger, 2002). Bootstrap analyses and estimates were based on 2,000 bootstrap samples.

Results

Results for Self-Reported Variables

Descriptive information. As expected, participants' PDS scores reflected significantly greater pubertal development at age 13 (range = 1.20 to 3.40, $M = 2.47$, $SD = .71$) compared to age 10 (range = 1.00 to 1.80, $M = 1.41$, $SD = .28$), $t(15) = 6.32$, $p < .001$. In terms of empathic ability, participants showed significant increases in empathic concern from age 10 (range = 2.00 to 4.43, $M = 3.24$, $SD = .60$) to age 13 (range = 2.29 to 4.43, $M = 3.51$, $SD = .57$), $t(15) = 1.90$, $p < .05$, but their reports of personal distress (age 10: range = 2.00 to 3.00, $M = 2.60$, $SD = .37$; age 13: range = 1.57 to 4.43, $M = 2.69$, $SD = .68$), $t(15) = .42$, *ns*, and perspective taking (age 10: range = 1.57 to 4.50, $M = 3.17$, $SD = .69$; age 13: range = 2.00 to 4.29, $M = 2.90$, $SD = .55$), $t(15) = -1.01$, *ns*, did not significantly change across time.

Gender differences. Given that our sample size was not large enough to meaningfully examine gender differences, gender differences in pubertal development and empathic ability (examined using a series of one-way analyses of variance) are reported here for descriptive purposes only. We do not focus on gender differences in the remainder of the results; however, it is worth noting that controlling for gender did not meaningfully change any of our reported findings.

Boys and girls reported statistically equivalent pubertal development at age 10 (boys: $M = 1.46$, $SD = .28$; girls: $M = 1.38$, $SD = .29$), $F(1, 14) = .31$, *ns*; however, girls reported higher levels by age 13 (boys: $M = 2.09$, $SD = .61$; girls: $M = 2.77$, $SD = .66$), $F(1, 14) = 4.51$, $p = .05$, and greater changes in pubertal development from ages 10 to 13, $F(1, 14) = 6.97$, $p < .01$. In terms of empathic ability, boys reported marginally higher empathic concern than girls at age 10 (boys: $M = 3.49$, $SD = .79$; girls: $M = 3.05$, $SD = .34$), $F(1, 14) = 2.34$, $p = .07$, but girls reported marginally higher empathic concern than boys at age 13 (boys: $M = 3.27$, $SD = .74$; girls: $M = 3.70$, $SD = .33$), $F(1, 14) = 2.51$, $p = .07$, as well as greater changes in empathic concern from ages 10 to 13, $F(1, 14) = 13.47$, $p < .005$. Although girls and boys reported similar personal distress at age 10 (boys: $M = 2.49$, $SD = .26$; girls: $M = 2.69$, $SD = .43$), $F(1, 14) = 1.21$, *ns*, girls reported significantly higher personal distress by age 13 (boys: $M = 2.18$ $SD = .43$; girls: $M = 3.08$ $SD = .57$), $F(1, 14) = 11.80$, $p < .005$, and greater changes in personal distress from ages 10 to 13, $F(1, 14) = 12.58$, $p < .005$. Girls and boys did not differ in their reports of perspective taking at either time point: age 10 (boys: $M = 3.40$, $SD = .71$; girls: $M = 2.98$, $SD = .65$), $F(1, 14) = 1.47$, *ns*, and age 13 (boys: $M = 2.86$, $SD = .77$; girls: $M = 2.94$, $SD = .34$), $F(1, 14) = .09$, *ns*, and there was no gender difference in the degree to which perspective-taking ability changed from ages 10 to 13, $F(1, 14) = .02$, *ns*.

Associations among self-report variables. Intercorrelations of self-report variables are displayed in Table 1. At age 13, pubertal development was positively related to personal distress and marginally related to empathic concern. The relation between pubertal development and perspective taking was positive but not significant. In terms of relations among the dimensions of empathic ability, empathic concern was significantly related to per-

Table 1
Intercorrelations of Self-Reported Pubertal Development and Three Dimensions of Empathic Ability

	1	2	3	4
1. Pubertal development	—	.38†	.42*	.31
2. Empathic concern	.50*	—	.32	.55*
3. Personal distress	.57*	.47**	—	−.02
4. Perspective taking	.12	.28	−.08	—

Note. Values above the diagonal represent correlations among self-report variables measured at age 13. Values below the diagonal represent correlations among increases in self-report variables measured from ages 10 to 13. All correlations presented included 14 *df*.
$^{\dagger}p < .10$. $^{*}p \le .05$. $^{**}p \le .01$.

spective taking at age 13 but not personal distress, and perspective taking and personal distress were not related. In terms of the associations among longitudinal changes, increases in puberty from ages 10 to 13 related to increases in empathic concern and personal distress, but not perspective taking. Increases in empathic concern were significantly related to increases in personal distress but not perspective taking, and increases in perspective taking and personal distress were not related.

Neuroimaging Results: Associations With Pubertal Development

First, we examined if (a) adolescents' concurrent pubertal status at age 13 and (b) their changes in pubertal development from ages 10 to 13, were associated with neural activity during observed exclusion versus inclusion at age 13, in regions linked to mentalizing and affective pain processing. We examined correlations across the entire brain, and in a priori–defined ROIs.

Whole brain analyses. Adolescents with greater pubertal development at age 13 showed more activity in regions linked to mentalizing processes, as they watched exclusion versus inclusion. Specifically, they showed greater activity in the bilateral DMPFC (2 58 38; −8 46 28), PCC/precuneus (10 −56 44), bilateral TPJ (48 −50 30; −42 −60 40), and temporal pole (42 20 −32; 52 −2 −34 with anterior spread covering inferior temporal gyrus and temporal pole). Table 2(a) lists details of activations. There were no associations between pubertal development at age 13 and activity during observed exclusion versus inclusion in affective pain network regions and no negative correlations between pubertal developmental at age 13 and brain activity.

Among adolescents who showed greater increases in pubertal development from ages 10 to 13, there was more differential activity during observed exclusion compared to inclusion in two areas of the DMPFC (−10 46 28; −4 60 36; see online Figure S1A) and in the temporal pole (46 −8 −34 with anterior spread covering inferior temporal gyrus and temporal pole). Table 2(b) lists details of activations. There were no associations between changes in pubertal development from ages 10 to 13 and activity during observed exclusion versus inclusion in affective pain network regions, and no negative correlations between increases in pubertal developmental and brain activity.

ROI analyses. Adolescents with greater pubertal development at age 13 showed a marginally greater difference in activity during observed exclusion versus inclusion in one precuneus ROI (10 −66 48), $r(14) = .41$, $p = .056$, in the pSTS ROI, $r(14) = .37$, $p = .082$, and in one MPFC ROI (16 70 12), $r(14) = .36$, $p = .083$. The links between pubertal development at age 13 and activity in the other ROIs were in the expected positive direction but

Table 2
Brain Activity During Observed Exclusion Versus Inclusion Correlated With: (a) Concurrent and (b) Changes in Pubertal Development

	(a) Concurrent puberty						(b) Changes in puberty					
Region	BA		[*x y z*]	*t*(14)	*r*	*p*	BA		[*x y z*]	*t*(14)	*r*	*p*
DMPFC	8	R	[2 58 38]	4.61	.78	<.0005	9	L	[−4 60 36]	3.96	.73	<.001
	9	L	[−8 46 28]	3.70	.70	<.005	9	L	[−10 46 28]	3.52	.69	<.005
PCC	7	R	[10 −56 44]	3.76	.71	<.005						
TPJ	40	R	[48 −50 30]	3.50	.68	<.005						
	40	L	[−42 −60 40]	4.52	.77	<.0005						
Temporal pole	38	R	[42 20 −32]	3.60	.69	<.005						
Temporal pole–ITG	21	R	[52 −2 −34]	4.58	.77	<.0005	21	R	[46 −8 −34]	4.03	.73	<.001

Note. BA = Brodmann's Area; L–R = left–right hemisphere; *x y z* = MNI coordinates; *t* = *t* score of local maxima; *r* = correlations between regressors and brain activity; DMPFC = dorsomedial prefrontal cortex; PCC = posterior cingulate cortex; TPJ = temporal–parietal junction; ITG = inferior temporal gyrus.

not significant. In terms of changes in puberty from ages 10 to 13, there were no associations with brain activity during observed exclusion versus inclusion in any ROIs.

Neuroimaging Results: Associations With Indices of Empathic Ability

Next, we examined if (a) adolescents' concurrent empathic ability (empathic concern, personal distress, and perspective taking IRI subscale scores at age 13) and (b) their changes in this empathic ability from ages 10 to 13, were associated with neural activity during observed exclusion versus inclusion at age 13, in regions involved in mentalizing and affective pain processing. We examined correlations across the entire brain, and in a priori–defined ROIs.

Whole brain analyses. Adolescents with greater empathic concern at age 13 displayed more activity during observed exclusion versus inclusion in regions previously linked with mentalizing—specifically, the bilateral DMPFC (4 54 42; −20 44 38), the MPFC (20 68 12), and the TPJ (−40 −52 40), as well as in a region previously linked with affective pain processing—the AI (44 30 −10). Adolescents with greater personal distress at age 13 also displayed more activity during observed exclusion versus inclusion in two areas of the DMPFC (−2 64 30; −4 54 44), and in the bilateral AI (36 20 −6; −38 14 −10). Adolescents with greater perspective-taking ability at age 13 showed more activity during observed exclusion versus inclusion in two mentalizing regions—the MPFC (2 68 4) and precuneus (4 −70 64), but showed no differential activity in any affective pain-related regions. Table 3(a) lists details of activations. There were no negative correlations between IRI subscale scores at age 13 and brain activity.

In terms of changes in empathic ability from ages 10 to 13, adolescents with greater increases in empathic concern showed more differential activity during observed exclusion versus inclusion in a network of regions involved in mentalizing,

Table 3

Brain Activity During Observed Exclusion Versus Inclusion Correlated With (a) Concurrent and (b) Changes in Empathic Ability

	(a) Concurrent empathy ability						(b) Changes in empathic ability					
Region	BA		[*x y z*]	*t*(14)	*r*	*p*	BA		[*x y z*]	*t*(14)	*r*	*p*
Empathic concern subscale of IRI												
DMPFC	8	R	[4 54 42]	4.70	.78	<.0005	8	R	[10 44 42]	9.01	.92	<.0001
	8	L	[−20 44 38]	4.39	.76	<.0005	8	R	[4 54 42]	5.00	.80	<.0001
MPFC	10	R	[20 68 12]	4.26	.75	<.0005	10	L	[−2 66 2]	4.19	.75	<.0005
							10	L	[−2 66 24]	4.08	.74	<.001
TPJ	40	L	[−40 −52 40]	3.85	.72	<.001	40	R	[54 −52 38]	4.53	.77	<.0005
							40	L	[−44 −50 40]	3.39	.67	<.005
Temporal pole							38	R	[44 12 −36]	3.13	.64	<.005
							38/47	L	[−36 20 −28]	5.02	.80	<.0001
AI		R	[44 30 −10]	4.85	.79	<.0005		R	[44 24 −10]	8.65	.92	<.0001
								L	[−42 14 −14]	4.39	.76	<.0005
SubACC							25/11	L	[−8 30 −12]	3.30	.66	<.005
Personal distress subscale of IRI												
DMPFC	9	L	[−2 64 30]	4.21	.75	<.0005	9	L	[−2 64 30]	4.33	.76	<.0005
	8	L	[−4 54 44]	3.94	.73	<.001	8	L	[−4 54 48]	4.06	.74	<.001
AI		R	[36 20 −6]	3.29	.66	<.005		R	[36 20 −6]	3.29	.66	<.005
		L	[−38 14 −10]	3.39	.67	<.005		L	[−40 12 −12]	3.34	.67	<.005
								L	[−36 32 −14]	3.46	.68	<.005
Perspective taking subscale of IRI												
MPFC	10	R	[2 68 4]	3.82	.71	<.001						
Precuneus	7	R	[4 −70 64]	3.17	.65	<.005	7	R	[2 −68 64]	3.52	.69	<.005
TPJ							40	L	[−40 −52 44]	4.11	.74	<.001
AI								R	[50 6 6]	3.53	.69	<.005

Note. BA = Brodmann's Area; L–R = left–right hemisphere; *x y z* = MNI coordinates; *t* = *t* score of local maxima; *r* = correlations between regressors and brain activity; DMPFC = dorsomedial prefrontal cortex; MPFC = medial prefrontal cortex; TPJ = temporal–parietal junction; AI = anterior insula; subACC = subgenual anterior cingulate cortex.

including: two areas in the DMPFC (10 44 42; 4 54 42; see online Figure S1B), two areas in the MPFC (−2 66 2; −2 66 24), two areas in the temporal poles (44 12 −36; −36 20 −28), and the bilateral TPJ (54 −52 38; −44 −50 40). These adolescents also displayed greater activity in affective pain-related regions, including bilateral AI (44 24 −10; −42 14 −14) and subACC (−8 30 −12). Adolescents with greater increases in personal distress from ages 10 to 13 showed more activity during observed exclusion versus inclusion in regions associated with mentalizing (DMPFC: −2 64 30; −4 54 48; see online Figure S1C) and affective pain processing (AI: 36 20 −6; −40 12 −12; −36 32 −14). Finally, adolescents with greater increases in perspective taking from ages 10 to 13 showed more activity during observed exclusion versus inclusion in regions linked to mentalizing (precuneus: 2 −68 64; TPJ: −40 −52 44) and affective pain processing (AI: 50 6 6). Table 3(b) lists details of activations. There were no negative correlations between changes in IRI scores and brain activity.

ROI analyses. Adolescents with greater empathic concern at age 13 displayed more activity during observed exclusion versus inclusion in the DMPFC, $r(14) = .55$, $p < .05$, and in one of the MPFC (16 70 12), $r(14) = .61$, $p < .01$, ROIs. This association was not significant for the other ROIs. There were no significant associations between brain activity in any of the ROIs and adolescents' personal distress or perspective-taking ability at age 13.

Next, adolescents with greater increases in empathic concern from ages 10 to 13 displayed more activity during observed exclusion versus inclusion in the DMPFC, $r(14) = .66$, $p < .005$; pSTS, $r(14) = .44$, $p < .05$; and one of the MPFC, [16 70 12], $r(14) = .64$, $p < .005$, ROIs. The relations between increases in empathic concern and activity in the other ROIs were in the expected positive direction, but not significant. There were no significant links between ROI activity and increases in adolescents' personal distress or perspective taking from ages 10 to 13.

Results of Exploratory Mediation Analyses

After separately examining how pubertal development and empathic ability each related to neural responses to observed exclusion, we performed mediational tests to explore possible interrelations among these three variables. For these analyses, we focused on empathic concern as our index of empathic ability because it was found to be the most consistently linked to pubertal development and neural activity in the analyses above (i.e., personal distress did not relate to any ROIs, and perspective taking did not relate to any ROIs or pubertal development). We also used estimated neural activity from ROIs (rather than estimates extracted from whole brain analyses) in these mediation tests, so that indices of neural activity would be independent from the measures of pubertal development and empathic ability. Moreover, we focused on ROIs that we identified as being the most likely candidates for mediation based on the above analyses. Specifically, we chose the MPFC (16 70 12) ROI when testing concurrent relations among puberty, empathic concern, and neural activity at age 13, as well as both the MPFC (16 70 12) and pSTS ROIs when testing relations among neural activity at age 13 and longitudinal increases in pubertal development and empathic concern from ages 10 to 13. These ROIs were identified as likely candidates for mediation because they had meaningful positive associations with each of the two other variables included in each model. As the bootstrapping method is specifically designed to permit exploration of significant mediation in small samples that are unlikely to yield p values meeting traditional standards of significance, we used a more liberal threshold of $p < .20$ to identify ROIs that had "meaningful" positive relations with the other variables. The MPFC (16 70 12) was the only ROI showing a meaningful positive relation with both pubertal development ($r = .36$, $p = .08$) and empathic concern ($r = .61$, $p < .01$) at age 13. The MPFC (16 70 12) and pSTS were the only ROIs showing meaningful positive relations with both increases in pubertal development (MPFC: $r = .29$, $p = .14$; pSTS: $r = .36$, $p = .08$) and increases in empathic concern (MPFC: $r = .64$, $p < .005$; pSTS: $r = .44$, $p < .05$) from ages 10 to 13.

First, we examined if a neural mechanism (i.e., increased MPFC or pSTS while observing peer exclusion) might help explain the positive relation between pubertal development and empathic concern. However, none of these models reached significance. Next, we examined whether a cognitive mechanism (i.e., increasing empathic concern) might help explain the positive relation between pubertal development and neural responses to observed peer exclusion. For concurrent relations at age 13, we found no significant mediation. Interestingly, however, we did find that increases in empathic concern from ages 10 to 13 significantly mediated the link between increases in pubertal development from ages 10 to 13 and MPFC activity during observed peer exclusion at age 13 (95% CI

[.02, .81], $p < .05$). Of course, these mediation tests are only preliminary due to the small sample size tested. But, these findings provide initial support for the notion that increasing empathic concern across the transition to adolescence might help explain the positive link between pubertal development across this transition and adolescents' MPFC responses to observed peer exclusion.

Discussion

The findings in this investigation provide new information about how two important indices of adolescent development—pubertal development and empathic ability—relate to emotional and cognitive neural responses while witnessing peer rejection. Our findings show positive links between pubertal development and empathic ability across the adolescent transition and provide preliminary evidence that neural responses to witnessed peer exclusion are associated with both concurrent levels of, and longitudinal changes in, these two developmental indices. Next, we discuss the significance of these findings and their potential implications for understanding adolescents' responses to peer interactions that they witness in their daily lives.

First, correlations among self-report variables indicated both concurrent and longitudinal associations between pubertal development and empathic ability. Specifically, puberty was positively related to empathic concern and personal distress at age 13. Additionally, there were positive relations between changes in pubertal development and changes in both empathic concern and personal distress from ages 10 to 13, which were not evident for perspective taking. These longitudinal findings provide some initial evidence that increases in affective aspects of empathic ability may be most likely to accompany pubertal changes in early adolescence. This is consistent with prior work that has linked pubertal development and social emotion processing (Burnett et al., 2010), social evaluative stress (Gunnar et al., 2009; Sumter et al., 2010), and other types of emotional reactivity (e.g., Silk et al., 2009; Spear, 2009). Of course, it would be premature to dismiss a potential link between pubertal development and perspective taking based on these data, but these findings nevertheless highlight the importance of examining related changes in pubertal development and emotional functioning during the adolescent transition.

In terms of links with neural functioning, we separately examined how pubertal development and empathic ability each related to neural responses to observed peer exclusion. First, we found that adolescents who reported higher levels of physical maturation at age 13 displayed more evidence of cognitive empathy-related processes at the neural level (i.e., more activity in regions involved in mentalizing). This is consistent with the notion that puberty onset is accompanied by a greater sensitivity toward peers, as well as with the common assertion that pubertal development may trigger a host of social cognitive advances during adolescence—evident in both behavior and neural function (see Blakemore et al., 2010; Forbes & Dahl, 2010; Nelson et al., 2005; Steinberg, 2004, 2007). Furthermore, this finding builds on the small body of prior empirical work linking pubertal development, neural activity, and social cognitive processing in adolescence (Forbes et al., 2010; Keulers et al., 2010; Martin et al., 2002; Moore et al., 2012; Silk et al., 2009; Spear, 2009).

Next, using a whole brain analysis we also found that increases in pubertal development from ages 10 to 13 related to heightened activity in the DMPFC and temporal pole when observing a peer being rejected during adolescence. This suggests that not only the concurrent level of pubertal development, but also the degree of change in pubertal development that occurs across the adolescent transition, is positively associated with differential processing in regions linked with mentalizing, when observing a peer being excluded. Perhaps, as adolescents experience pubertal change as a significant life stressor (see Ge et al., 2003), individuals who endure more rapid change may become particularly sensitive to others' responses to stress, based on insights from their own experiences. Of course, conclusive interpretations are not possible at this early stage; however, this finding builds on prior work indicating that the velocity of pubertal change across adolescence is an important predictor of psychosocial outcomes (e.g., Ge et al., 2003; Mendle et al., 2010) and highlights the importance of examining the rate of pubertal change as an unique predictor of adolescent outcomes. We did not find that concurrent, or longitudinal changes in, pubertal development related to activity in affective pain-related regions while observing peer rejection. As this is somewhat inconsistent with our finding that pubertal development is positively related to self-reported empathic concern and personal distress, additional research will be useful for disentangling how pubertal change is associated with particular cognitive and affective aspects of empathic processing.

Next, consistent with our hypotheses regarding empathic ability, we found that adolescents who reported more affective aspects of empathy—specifically, greater empathic concern or personal distress at age 13—displayed more neural evidence of both mentalizing and affective pain processing when observing a peer being excluded. This supports the idea that individuals with a greater tendency to feel concern for others and experience their emotions vicariously may better understand the plight of others and feel more distress when they see them being rejected. In fact, it is possible that the heightened activity in affective pain-related regions among these highly empathic individuals reflects some sharing of the victim's pain or efforts to imagine the victim's distress. In terms of perspective-taking ability, adolescents who reported higher perspective-taking ability at age 13 also displayed more neural evidence of mentalizing, but not affective pain processing. This is consistent with our hypothesis and suggests that individuals who are better at perspective taking may be more likely to spontaneously think about the thoughts and feelings of others that they see engaged in social interactions.

It is worth noting that adolescents' reports on these three dimensions of empathy related to neural activity in different ways. In other words, the more affective dimensions—empathic concern and personal distress—were associated with neural activity in regions linked to both mentalizing and affective pain processing, whereas perspective taking was only associated with activity in regions linked with mentalizing. Thus, these findings build on our previous work, in which we focused on a unidimensional measure of empathy and only found associations with activity in the mentalizing network and not the network of regions involved in affective pain processing (Masten et al., 2010). Of course, these patterns warrant further examination in future research; however, these findings highlight the utility of using multidimensional measures of empathy when examining empathy for social interactions—particularly at the neural level. Additionally, these findings raise another intriguing possibility—that perspective taking might be more strictly cognitive in nature without necessarily having an emotional element, whereas emotional aspects of empathy might require some mentalizing (as evidenced by the presence of activation in regions linked to both mentalizing and affective pain processing) in order to understand a peer's plight enough to display an appropriate emotional response. In fact, the cognitive ability to understand others' emotions might be particularly important early in the empathic process and help facilitate more emotional aspects of empathy (i.e., concern, sharing of others' emotions) among those who show heightened affective empathic tendencies (see Masten et al., 2011, for a discussion of this possibility).

In terms of longitudinal changes in empathic ability across the adolescent transition, increases in all three dimensions of empathic ability from ages 10 to 13 were related to greater activity in neural regions linked to both mentalizing and affective pain activity. Thus, although some research shows that different aspects of empathic ability develop via different trajectories (i.e., perspective taking typically increases, while personal distress decreases; Eisenberg, Cumberland, Guthrie, Murphy, & Shepard, 2005), these data suggest that increases on any of these dimensions at the individual level is linked with greater empathy-related neural activity in both mentalizing and affective pain-related regions. One possibility is that the social changes that occur during the transition to adolescence—such as increases in peer interactions—necessitate improvements in overall empathic ability. In other words, there may be an increased need for empathy and mentalizing in order for adolescents to successfully navigate their changing social climate (see Eisenberg & Morris, 2004; Eisenberg et al., 2009). In this case, greater neural sensitivity during observed peer rejection might characterize those individuals who have been most successful in terms of improving their empathic ability. Another way of conceptualizing this possibility is that more rapid increases in empathic ability and greater neural sensitivity to observed peer rejection are both characteristics of individuals who are more socially sensitive and responsive to others at a trait level. In other words, upon entering adolescence, these individuals may be more sensitive to their changing surroundings and adjust their empathic tendencies accordingly, and also be more impacted by peer interactions that they witness. Finally, it is worth noting that the correlations between adolescents' neural responses to observed peer rejection and their longitudinal changes in empathic ability were somewhat distinct from the correlations found with concurrent levels of empathic ability. This highlights the utility of measuring developmental variables of interest at multiple time points, particularly when examining brain–behavior relations within developing populations.

Finally, to gain preliminary insights into the possible direction and causality of our effects, we performed exploratory tests of possible mediation pathways via which pubertal development, empathic ability, and neural responses to observed peer exclusion might be interrelated. We found initial evidence that increases in empathic concern that accompany pubertal change from ages 10 to 13 may help explain the heightened neural sensitivity that adolescents display toward their peers. Notably, tests for mediation among these variables measured concurrently at age 13 did not yield significant results, suggesting that examining interrelated patterns of longitudinal change as youth transition to adolescence may be important for understanding the salience of observed peer interactions later in the adolescent years. Along with prior work showing the importance of physical maturation and increasing empathic ability for promoting interest in peers and social acceptance (Eisenberg & Morris, 2004; Eisenberg et al., 2009; Forbes & Dahl, 2010), these findings highlight the need for additional longitudinal investigations of potential contributors to peer salience in adolescence.

Future Directions

Future studies with larger samples will be able to more thoroughly interrogate these relations and determine the order and timing of these effects. For example, it would be interesting to conclusively test whether pubertal maturation leads to improvements in empathic ability, which in turn influence neural function, as our initial findings suggest. Or, will future work uncover evidence in favor of the alternate possibility that changes in neural function precipitated by pubertal onset enable adolescents to better understand others' emotions? Multimethod research with large samples will facilitate continued exploration of these questions. Eventually, uncovering the directionality and temporal order of these interrelated processes will broaden understanding of how social, cognitive, and physical changes unfold in adolescence.

In addition to pursuing these questions, future work will also be useful in addressing the limitations of this study. First, as mentioned previously, our sample size was relatively small and did not permit meaningful exploration of gender or other individual differences (e.g., related to race or ethnicity, socioeconomic status, etc.). Males' and females' social cognitive processing in adolescence may differ in meaningful ways due to their differential trajectories of pubertal onset and development (e.g., girls typically mature earlier than boys). Thus, it will be useful to examine gender and other individual differences, in future studies with larger samples.

Next, it would also be useful for future research to examine other measures of longitudinal biological change and physical maturation, for example, additional indices of puberty such as Tanner Staging or hormonal assays, or changes in brain structure at this age. These additional measures would provide more precise, multidimensional indices of the participants' level of physical and brain maturation, which could reveal additional interesting relations among various measures of physical, social, cognitive, and neural development that were not detectable in this study. Additionally, controlling for potential behavioral correlates of puberty (e.g., risk taking, sensation seeking, changes in self-image) or social contextual factors that are salient at this age (e.g., transitioning to middle school, time spent with peers vs. parents, frequency of firsthand and witnessed peer rejection) would also be useful, because we cannot be sure that pubertal maturation, rather than a related change in behavior or context, lead to our reported findings. Finally, this study used a single task to simulate the experience of observing peer exclusion. Using additional tasks (e.g., proxies for peer rejection such as rejection film clips or "mean" social networking pages, as well as other types of social interaction tasks) in future studies could help determine if the patterns observed here are specific to observing peer exclusion, or if they characterize other social cognitive processes as well.

Conclusion

Overall, these findings provide initial insights into adolescents' responses when they witness peer rejection and suggest that physical and cognitive emotional development across the transition to adolescence relate to these responses at the neural level. This study builds on the limited prior research that has examined adolescents' neural functioning in the context of pubertal development, and in relation to longitudinal indices of development (Pfeifer & Blakemore, 2012). We hope these findings pave the way for new longitudinal research examining the complex interplay of peer relationships and brain function in adolescence.

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher's website:

Figure S1. Activity During Observed Exclusion Versus Inclusion in the DMPFC, Found Through Whole Brain Regression Analyses to Be Positively Related to Longitudinal Changes in: (a) Pubertal Development, (b) Empathic Concern, and (c) Personal Distress, Across the Transition to Adolescence.