Neural Reactivity to Emotional Faces May Mediate the Relationship between Childhood Empathy and Adolescent Prosocial Behavior

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Abstract

Reactivity to others' emotions can result in empathic concern (EC), an important motivator of prosocial behavior, but can also result in personal distress (PD), which may hinder prosocial behavior. Examining neural substrates of emotional reactivity may elucidate how EC and PD differentially influence prosocial behavior. Participants (N=57) provided measures of EC, PD, prosocial behavior, and neural responses to emotional expressions at age 10 and 13. Initial EC predicted subsequent prosocial behavior. Initial EC and PD predicted subsequent reactivity to emotions in the inferior frontal gyrus (IFG) and inferior parietal lobule, respectively. Activity in the IFG, a region linked to mirror neuron processes, as well as cognitive control and language, mediated the relation between initial EC and subsequent prosocial behavior.

Empathy is frequently defined as an affective response that is similar to what the other is feeling (Batson et al., 1987; Batson, 1998; Eisenberg, 2000). This shared experience of emotion, sometimes called affective resonance, can produce sympathy or feelings of empathic concern (Davis, 1983), widely considered to be important motivators of prosocial behavior (Eisenberg & Miller, 1987; Eisenberg & Fabes, 1998). Yet it can also result in personal distress, a predominantly self-focused negative reaction (Eisenberg & Fabes, 1990). As children transition through adolescence, levels of empathic concern, personal distress, and prosocial behavior all change (Davis & Franzoi, 1991; Eisenberg, Miller, Shell, McNalley, & Shea, 1991; Eisenberg, Shell, Pasternack, Lennon, et al., 1987; Eisenberg, Cumberland, Guthrie, Murphy, & Shepard, 2005; Hawk, Keijsers, Branje, Van der Graaff, Wied, & Meeus, 2013), as do the neurobiological systems implicated in affective resonance (Pfeifer & Blakemore, 2012). Such a convergence of changes makes it a critical period of development in which to examine these phenomena. The current study investigates whether and how empathic concern and personal distress interact to influence prosocial behavior during the transition to early adolescence, and uses neuroimaging to assess how affective resonance (in terms of neural reactivity to emotional faces) may explain some of this influence.

Associations between Empathic Concern, Personal Distress, and Prosocial Behavior in the Transition to Early Adolescence

In general, empathy and sympathy have been consistently positively associated with prosocial behavior throughout development (Barr & Higgins-D’Alessandro, 2007; Brownell et al., 2013; Eisenberg, 2003; Eisenberg et al., 1991; Eisenberg et al., 1987; Farrant et al., 2012; Litvack-Miller et al., 1997). Associations between personal distress and prosocial behavior are somewhat less clear, but in general there is some evidence for a negative association, particularly when also accounting for trait levels of empathic concern or sympathy (Barr & Higgins-D'Alessandro, 2007; Eisenberg et al., 1989; Eisenberg et al., 1991; Hulle et al., 2013; Trommsdorff, Friedlmeier, & Mayer, 2007). Despite theoretical and empirical expectations of negative relationships between the two (Batson, 1987; Eisenberg, Fabes, Miller, Fultz, Shell, Mathy, & Reno, 1989), personal distress and empathic concern as measured by self-report (e.g., on the Interpersonal Reactivity Index; Davis, 1983) are often either positively correlated or unrelated in childhood and adolescence (Barr & Higgins-D'Alessandro, 2007; Davis & Franzoi, 1991; Hawk et al., 2013; Litvack-Miller et al., 1997). Finally, cross-sectional and longitudinal data converge in reporting decreases in personal distress during adolescent development, compared with tendencies towards stability or increases in empathic concern (Hawk et al., 2013; Davis & Franzoi, 1991; Eisenberg et al., 2005; Van der Graaff, Branje, Wied, Hawk, Lier, & Meeus, 2014). Given the mixed literature, we therefore modeled both main effects and the interaction between empathic concern and personal distress.

The Potential Role of Neural Reactivity to Emotional Expressions, as an index of Affective Resonance, in Empathic Concern and Personal Distress

While there is research on neural correlates of prosocial behavior in adults (Greening et al., 2013; Masten, Morelli, & Eisenberger, 2011; Morelli, Rameson, & Lieberman, 2012; Utevsky & Huettel, 2015) as well as during adolescence (Güroğlu, van den Bos, & Crone, 2014; Telzer, Fuligni, Lieberman, & Galván, 2013; Telzer, Masten, Berkman, Lieberman, & Fuligni, 2010), and on neural mechanisms of empathic concern (or personal distress) during adolescence (Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008; Decety, Michalska, & Akitsuki, 2008; Marsh et al., 2013; Masten, Eisenberger, Pfeifer, Colich, & Dapretto, 2013; Masten, Eisenberger, Pfeifer, & Dapretto, 2010; Masten, Eisenberger, Pfeifer, & Dapretto, 2013; Mella, Studer, Gilet, &

Labouvie-Vief, 2012), the authors are unaware of research investigating neural correlates of the link between empathy and prosocial behavior during the period of rapid change from childhood to adolescence. Although there are many processes and associated neural mechanisms implicated in such complex phenomena, examining neural responses to emotional expressions may provide insight into how even rudimentary and sometimes implicit processes may connect empathic concern and personal distress with different tendencies towards prosocial behavior.

There are multiple candidate regions and systems that may be of interest when focusing on this basic level of neural reactivity to emotions. For example, as noted above, both empathic concern and personal distress may involve a shared experience of emotion, also called affective resonance; and concerned or distressed tendencies might also shape future proclivities to experience affective resonance. Affective resonance is proposed to be supported by the putative human mirror neuron system (MNS; Decety, 2010; Iacoboni, 2009), a network of brain regions that respond both to the execution and observation of goal directed actions including affective facial displays (emotional expressions). This network includes the bilateral inferior frontal gyrus (IFG), and rostral inferior parietal lobule (IPL) which receives higher order visual input from the posterior superior temporal sulcus (pSTS; Iacoboni & Dapretto, 2006). While we use this network as a guide, it is important to note that these regions are involved in many processes, a point that will be expanded on in the discussion. In addition to these MNS regions, in both adults and children, empathy-related activity is seen in the amygdala and anterior insula, regions widely implicated in affective processing (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Pfeifer et al., 2008). Together, these regions of interest (IFG, IPL, amygdala, and anterior insula) represent a logical starting point for investigating how a rudimentary construct like affective resonance indexed at the neural level may contribute to relationships between empathic concern, personal distress, and prosocial behavior.

In the current study, we expected that prosocial behavior would be associated with individual differences in empathic concern (EC), particularly by early adolescence. It is also possible that EC at an earlier age could predict future prosocial tendencies. For example, a child high in EC at age 10 may be motivated to maintain or increase her level of prosocial behavior over time, especially as more independent opportunities arise to do so. Furthermore, we expected that neural responses to emotional expressions in MNS regions (IFG, IPL) and/or in affective processing regions (amygdala, anterior insula) would account for some of (i.e., statistically mediate) the association between EC and prosocial behavior. Finally, as explained above, because personal distress (PD) may modify the effect of EC on prosocial behavior, we tested PD as a possible moderator of any relation between EC and prosocial behavior, as well as any mediation by neural responses to emotional expressions (see Figure 1 for diagrammatic representation of our theoretical model).

Method

Data analyzed are part of an existing longitudinal neuroimaging study. Typically-developing children, recruited from the broader Los Angeles metropolitan area, provided both fMRI and self-report data at two time points (N=90 and 57 at waves 1 and 2, respectively). Participants that did not return for the second wave (due to acquiring orthodontic work, moving out of the area, or lack of interest) and one participant that did not provide a response for our outcome of interest were excluded from the analysis, and thus all results arise from 56 participants (26 boys; mean age = 10.1 and 13.1 years, SD = 0.31 and 0.31, at waves 1 and 2, respectively). Assent/consent was obtained from participants and their parents according to IRB guidelines. The sample was ethnically diverse, with 47% of parents identifying their child as white, 30% multiracial/multiethnic, 12% Hispanic or Latino/a, 4% black or African-American, 2% American Indian/Native American Hispanic or Latino/a, 2% Asian or Pacific Islander, and 4% other. Household income ranged from less than $15k, to more than $400k (median=$80-100k).

Self Report Measures

Empathy. Participants filled out the Interpersonal Reactivity Index (IRI; Davis, 1983; Litvak-Miller, 1997), which provided measures of empathic concern (EC) and personal distress (PD), and has been previously used with this age group (Eisenberg et al., 1991; Eisenberg et al., 1987). Scores were linearly transformed from the original scale to a percent of the maximum score possible (Cohen, Cohen, Aiken, & West, 1999) to aid in interpretation. Means, standard deviations, and reliability coefficients are reported in Table 1. Note that although EC has a small alpha coefficient at Wave 1, significant correlations with several closely related measures provide evidence of convergent validity (Supplementary Table S3).

Prosocial Behavior. Participants also completed measures from the 4-H Study of Positive Youth Development survey (PYD; Lerner et al., 2005), which provides two items relevant to prosocial *behavior* (as opposed to prosocial values). The first item assesses the number of hours per week children spend volunteering: “During an average week, how many hours do you spend helping other people without getting paid (such as helping out at a hospital, daycare center, food shelf, youth program, community service agency, or doing other things) to make your city a better place for people to live?” Response options were “0, 1, 2, 3-5, 6-10, 11 or more.” These responses were recoded to reflect the number of hours reported, or the average of the range given (e.g., 4 for the “3-5” response). The high end was coded as 11 hours. The second item asked participants if they are often kind to other children, with responses ranging from 1 to

4. The prosocial behavior outcome was formed by first log-transforming the volunteering item, transforming both items to a percent of their respective maximum possible scores, and then taking the mean of both items (Wave 1 M = 49.1, SD = 16.2; Wave 2 M = 48.0, SD = 18.2). The 2-item index provides better conceptual coverage of the prosocial behavior construct than either item by itself. Although the kindness and volunteerism items were not significantly correlated at Wave 1 ($r = -.11$) or Wave 2 ($r = .14$), the aggregate score was significantly correlated with many self-report measures of prosocial attitudes and values (e.g., helping, equality and justice, and social responsibility; see Supplementary Table S3) at both waves, providing evidence for its convergent validity.

All measures except for the IRI were part of the PYD, which is a collection of measurements related to the "Cs of PYD" (competence, confidence, connection, character, caring, and compassion; Lerner et al., 2005). Also included in the PYD are measures of activities, individual and ecological assets, developmental regulation, pubertal status, problem behaviors, and demographics (not all of which are pertinent to this analysis). References for relevant measures within the PYD may be found in Supplementary Table S2.

fMRI Paradigm

During fMRI, participants were instructed to "look at the expression on each face" while passively observing facial expressions of emotion (angry, fearful, sad, happy, and neutral) from the NimStim set (Tottenham et al., 2009). Each face was displayed for 2 seconds with an inter-trial interval that varied between 0.5–1.5s (M=1s). The order of emotion presentation was counterbalanced to optimize the detection of contrast between emotions (Wager & Nichols, 2003). A total of 96 whole-brain volumes were collected comprising 80 emotional face events (16 per emotion) and 16 null (fixation cross) events.

This paradigm was utilized because of its ability to elicit neural reactivity to emotional expressions in the regions of interest supporting affective resonance listed in the introduction (IFG, IPL, amygdala, anterior insula). Observation of emotional expressions minimizes contamination of neural activity by motion inherent during execution of actions, and can be mapped directly onto the experience of sharing someone else's emotions, which is frequently implicated in both empathic concern and personal distress (Davis, 1983). In other words, when encountering someone else looking sad (for example), an individual predisposed toward more or less empathic concern and/or personal distress may show stronger or weaker responses in these regions of interest. This might inform our understanding of prosocial behavior because an automatic neural response that favors a certain type of empathic engagement with emotional stimuli may provide a strong foundation for motivating effortful prosocial behavior in part because that engagement is not effortful. This task is not meant to directly evoke sympathy or empathic concern itself (unlike e.g., Bernhardt, Klimecki, Leiberg, & Singer, 2013; Decety, Chen, Harenski, & Kiehl, 2013; see Bernhardt & Singer, 2012 and Decety, 2011 for overviews), emotion regulation (e.g., McRae, Misra, Prasad, Pereira, & Gross, 2012; Zaki, Ochsner, Hanelin, Wager, & Mackey, 2007), or any number of more proximal constructs, and is thus arguably more conservative. Prior publications of subsets of participants from this dataset reveal that at the group level, observation of emotional expressions indeed engages these regions (see Pfeifer et al., 2008; Pfeifer et al., 2011). Finally, a large-scale, automated meta-analysis of studies of the neural response to emotional faces also indicates that this task would be expected to elicit activity in the systems we wish to investigate (see Supplementary Figure S2).

fMRI Acquisition and Analysis

fMRI data were acquired using a Siemens Allegra 3.0T scanner. Functional images were collected in a 4m, 54s session of blood oxygen level dependent echo-planar imaging (BOLD-EPI; TR = 3000ms, TE = 25ms, flip angle = 90, matrix size 64 by 64, FOV = 20cm, 36 slices, 3.125mm in-plane resolution, 3mm thick). Co-planar high-resolution structural images were also obtained for each participant (T2-weighted echo-planar imaging volume, spin-echo, TR = 5000ms, TE = 33ms, matrix size 128 by 128, FOV = 20cm, 36 slices, 1.56mm in-plane resolution, 3mm thick). Stimuli were presented to participants through high-resolution magnet-compatible goggles (Resonance Technology, Inc.).

DICOM images were converted to NIfTI format using MRIConvert (http://lcni.uoregon.edu/jolinda/MRIConvert/), and all non-brain voxels were removed using FSL's Brain Extraction Tool (Smith, 2002). Preprocessing, first, and second level models were conducted in SPM12b (Wellcome Department of Cognitive Neurology, London, UK; http://www.fil.ion.ucl.ac.uk/spm/). Functional images were realigned to the mean image of each run, coregistered to the anatomical image, and warped to MNI space using the EPI template included with SPM12b. Finally, functional images were smoothed using a 9mm full-width at half maximum Gaussian kernel.

Neural responses to each emotion were modeled with a fixed effects GLM using the canonical hemodynamic response function with time and dispersion derivatives, 128s high pass filter, correction for serial autocorrelation (AR1), and optimally thresholded explicit mask (Ridgway et al., 2009). Position parameters from the realignment step above were entered as regressors of no interest to ameliorate the influence of motion. Only one participant had a transverse displacement > 3mm, and only one subject had a rotation > 3deg. Only two participants had > 10% of volumes displaced more than 1mm, and one participant had >8% of volumes displaced more than 1mm. Running the analyses without these three subjects does not change the significance of any results. Estimates of amplitude, width, time to peak, and area under the curve were recalculated from the fitted responses of each trial type (emotion) in order to create summary statistic images that more robustly describe the hemodynamic response (Lindquist & Wager, 2007; http://wagerlab.colorado.edu/tools). Random effects models at the group level included the contrasts for all emotional expressions versus rest regressed on empathic concern, personal distress, and their interaction as described below.

Analytic Plan

The relation between empathic concern, prosocial behavior, and neural response to emotional expressions was examined within and across waves (fMRI and questionnaires were collected at both waves). Neural activity significantly associated with empathic concern was then tested as a mediator of any relation between empathic concern and prosocial behavior.

Based on the literature reviewed above, we tested whether empathic concern (EC) accounted for variance in prosocial behavior within each wave, as well as whether EC at wave 1 accounted for variance in prosocial behavior at wave 2. We included personal distress (PD) and the interaction of empathic concern and personal distress (ECxPD) to account for possible moderation. For the cross-wave autoregressive model (Twisk, 2003; Zapf, Dormann, & Frese, 1996), prosocial behavior at wave 1 was entered as a predictor of prosocial behavior at wave 2.

We then tested whether neural responses to emotional expressions explained some or part of the relation between prosocial behavior and empathic concern or personal distress. As in prior studies (Pfeifer et al., 2008; Pfeifer et al., 2011; Moore et al., 2012), emotion reactivity was indexed by averaging across responses to all expressions (angry, fearful, sad, happy, and neutral), relative to fixation. “Neutral” expressions were included in the average because they are not an effective control, as they elicit significant activity in affective processing regions like the amygdala (Van der Gaag, Mindera, & Keysers, 2007) and are often perceived as mildly negative (Lee, Kang, Park, Kim, & An, 2008; Kesler-West et al., 2001; Russel & Fehr, 1987). First, EC, PD, and EC×PD were entered in whole brain regressions within each wave, as well as across waves (i.e., self-report data from wave 1 predicting neural data from wave 2). Thresholds for reporting neural activity were determined using 3dClustSim, part of AFNI (Cox & Hyde, 1997), which estimates combinations of voxel-wise *p*-values and cluster extents (in voxels) that together control the false discovery rate (set at $p<.05$ in this case). We also investigated activity within a mask of *a priori* brain regions, all defined by the Harvard Oxford Cortical and Subcortical Structural Atlases bundled with FSL (Desikan et al., 2006; Goldstein et al., 2007), comprising the inferior frontal gyrus (pars opercularis and pars triangularis), rostral inferior parietal lobule (anterior and posterior divisions of supramarginal gyrus), anterior insula, and amygdala. Summaries of activity (specifically, the first eigenvariate) in significant clusters were extracted from each participant using the REX toolbox (Whitfield-Gabrieli, 2009), and were used in tests of mediation.

Statistical tests of mediation were conducted using the mediation package in R (Tingley, Yamamoto, Hirose, Keele, & Imai, 2013), which corrects some problems with the typical path-tracing approach to estimating the mediated effect, and which allows mediation to be tested in a wide variety of model types (Imai, Keele, Tingley, & Yamamoto, 2011). Unlike the more common methods popularized by Baron and Kenny (1986) and Preacher and Hayes (2004), this method does not estimate mediated effects by multiplying estimated coefficients, and instead relies on counterfactual reasoning that extends Rubin's causal model (1974). The algorithm estimates the average direct effect (ADE) from the predictor variable (in this case, EC), to the outcome (prosocial behavior), as well as the average causal mediation effect (ACME) from predictor to outcome via the mediator (neural activity). Covariates can be included and moderation of both the ADE and ACME can be tested. We tested whether neural activity associated with EC mediated any effect of EC on prosocial behavior. We included PD as a moderating variable, and any brain activity associated with PD or EC×PD as covariates. When testing mediation of effects across waves, prosocial behavior at wave 1 was also included as a covariate to account for stability of prosocial behavior over time.

Results

Associations between Empathic Concern, Personal Distress, and Prosocial Behavior

Within wave 1, empathic concern (EC) did not account for a significant amount of variance in prosocial behavior. Within wave 2, EC was significantly associated with prosocial behavior (b=0.66, SE=0.17, p<.001). In the cross-lagged model, wave 1 EC significantly positively predicted prosocial behavior at wave 2, controlling for prosocial behavior at wave 1 (Table 2). Including socioeconomic status in the above analyses did not substantively change the results. The estimate of the temporally reversed association between prosocial behavior at wave 1 and EC at wave 2 was positive, but not significantly different from zero (b=0.18, SE=0.10, p=.07). Finally, while parental levels of helping significantly predict children's prosocial behavior both in the within-wave model at wave 2 (b=7.29, SE=2.32, p<.01), and the cross-lagged model (b=7.66, SE=2.55, p<.01), controlling for this variable does not substantively change the above results. Correlations among all variables of interest can be found in Supplementary Table S1.

Associations between Empathic Concern, Personal Distress, and Neural Response to Emotional Expressions

To confirm that our stimuli elicited the expected neural response, a t-test statistic map for the estimate of average per-voxel activity was analyzed using the Neurosynth Image Decoder (Yarkoni et al, 2011), which yielded high correlations with statistical maps associated with expected meta-analytic features (e.g., the highest correlation was with the 'faces' feature, r=.452; see Supplementary Table S9 for more information).

Regressing neural activity at wave 2 on EC, PD and their interaction at wave 1 revealed four significant clusters. For this analysis, the voxel-wise threshold was p<.005 with cluster extent k>41 for the search within our *a priori* mask; and voxel-wise p<.005 with cluster extent k>74 voxels for the whole brain search (Table 3). First, in the *a priori* region of interest search, greater EC at age 10 was associated with more activity in the inferior frontal gyrus (IFG) in response to emotional expressions at age 13, while greater PD at age 10 was associated with less activity in the inferior parietal lobule (IPL) at age 13 (Figure 2). In the whole-brain search, the interaction between PD and EC at age 10 was also associated with less activity in the perigenual anterior cingulate cortex (pACC) and cuneus at age 13 (Figure 2). All associations were estimated to be in the same direction across emotions, with some variation in the significance of those estimates (see Supplementary Figures S5 and S6). Correlations among significant clusters can be found in Supplementary Table S4. Within wave 1, no significant brain-behavior correlations were detected. Results for whole brain and *a priori* region of interest regressions within wave 2 can be found in Supplementary Table S13 and Figure S8.

Mediation of Behavioral Associations by Neural Response to Emotional Expressions

EC at age 10 predicted prosocial behavior at age 13, as well as neural activity in the left IFG at age 13, and so we tested whether activity in the left IFG mediates the relationship between EC and prosocial behavior (see Figure 1 for an illustrative diagram of this model). As described in the analytic plan, we included wave 1 prosocial behavior, PD and its interaction with EC, and summaries of activity in clusters detected in the whole-brain regression: IPL, pACC, and cuneus at wave 2. There was a positive, significant effect of EC on prosocial behavior mediated by IFG, a non-significant positive direct effect, and a significant positive total effect (Table 4). In short, the significant total effect of EC on prosocial behavior is accounted for largely by activity in IFG in response to emotional stimuli. This mediated effect was not moderated by PD, as evidenced by no significant difference (p=.49) between the estimated average causal mediation effect (ACME) in models conditional on high levels of PD (mean + 1 SD) versus low levels of PD (mean – 1 SD). Mediation was robust to the exclusion of all covariates, including PD and ECxPD, except for neural activity in the IPL (see Supplementary Table S4b for correlations of prosocial behavior at wave 1 and 2 with all significant clusters).

Discussion

We find that empathy at age 10 prospectively predicts prosocial behavior at age 13 and that this association is partly mediated by neural response to emotional expressions in the left IFG at age 13. The association of empathic concern and personal distress with activity in regions often identified as part of the human MNS, including the left IFG, is consistent with the notion that this system supports a shared experience of emotion (Pfeifer et al., 2008). This longitudinal relationship suggests that reactivity to emotions in this system may be shaped by prior levels of empathic concern, which then supports translation of trait-level concern into prosocial action. Our finding that empathic concern is related to concurrent prosocial behavior at age 13 is consistent with prior research (Eisenberg et al., 1987; Eisenberg et al., 1991).

Activity in the IFG has been strongly linked to action imitation and mental simulation, though it has also been linked to linguistic processing, as well as cognitive control. With regard to MNS-like processes, the IFG may decode the goals of an observed action (Grèzes & Decety, 2001; Iacoboni & Dapretto, 2006; Molenberghs, Cunnington, & Mattingley, 2012), especially when there is a conflict between the perspective of the self and the other (van der Meer, Groenewold, Nolen, Pijnenborg, & Aleman, 2011). The left IFG has also been long associated with verbal fluency (Broca, 1861), and modern neuroimaging supports this link (Costafreda et al., 2006). Activity in this region linked to empathy may therefore reflect semantic and conceptual engagement with emotional content. Many studies have also found that the left IFG is important for cognitive control (Bahlmann et al., 2012; Dwyer et al., 2014; Herwig et al., 2007), which in the context of prosocial behavior may be important to aid planning and execution of effortful action. A quantitative meta-analysis found four distinct clusters of peak activity reported within IFG, which corresponded to semantic processing, working memory, motor control, and empathy tasks (Liakakis et al., 2011). Interestingly, the IFG peak reported in this paper is closest to the working memory and semantic processing regions, suggesting that linguistic engagement with emotional stimuli, or perhaps general levels of executive function, may help link concern with prosocial action. Future work could examine tasks that manipulate behavior in these four domains within the same participants to better characterize the nature of the contribution by the left IFG.

The IPL is also part of the MNS (Iacoboni & Dapretto, 2006; Molenberghs et al., 2012), and thus the negative association with previous levels of personal distress suggests that tendencies to experience distress in the presence of emotion may lead to lower levels of engaging affective resonance processes. Buhle and colleagues (2013) note that this region is also implicated in processing observed actions, decoding intentions, and processing semantic information (Rapp, Mutschler, & Erb, 2012; Van Overwalle & Baetens, 2009; Vigneau et al., 2006), and that all of these processes may be utilized during emotional reappraisal. In short, lower levels of neural activity related to processing negative emotional stimuli, and perhaps action processing or inhibition, are predicted by earlier levels of personal distress, possibly as a result of developmental downregulation.

Mediation of the link between empathic concern and prosocial behavior by neural reactivity in the left IFG suggests that empathic concern leads to future prosocial behavior in part through shaping engagement of this region in response to emotional stimuli. Heightened processing in this region implicated in simulation, shared experiencing, language, and cognitive control may lead to greater salience of the need of a conspecific, or a more nuanced and personal understanding of that need, and thus lead to increased motivation to act prosocially. This is consistent with the literature showing that automatic mimicry is a learned, unconscious process, and that it may increase prosocial behavior (Baaren, Holland, Kawakami, & Knippenberg, 2004; Heyes, 2011). As noted above, linguistic and/or cognitive control processes are also likely explanations of activity we find associated with EC, and offer a complementary explanation for the mediated effects. For example, linguistic processing of affect has been shown to attenuate negative emotion behaviorally and neurally (Brownell et al., 2013; Lieberman et al., 2007; Warner et al., 2006; Wilson & Schooler, 1991). Perhaps children higher in EC at an earlier age learn to engage more symbolically with emotional experience, which facilitates committed prosocial behavior. Thus, empathic concern may motivate engagement in prosocial behavior in part by encouraging the automatic processing of socioemotional content by psychological processes supported by the left IFG.

Limitations and Future Directions

The observed brain activity during passive viewing of emotional expressions likely represents participants' default patterns of functioning during engagement with emotional expressions, rather than any kind of intentional processing of these stimuli (or overt empathy). As such, we interpret the longitudinal associations with empathic concern and personal distress, and the mediation of the longitudinal association between empathic concern and prosocial behavior, as reflecting individual differences in tendencies to engage certain neural systems when confronted with facial expressions, and socioemotional stimuli more broadly.

However, these specific neural systems could be explored more thoroughly using neuroimaging paradigms that can evaluate theoretically driven process models and/or isolate specific processes (e.g., a task requiring linguistic engagement with emotive stimuli, or a prosocial decision making task). In addition, while our results are suggestive, to begin to establish causality future work should attempt to directly manipulate the independent variable (empathic concern) as well as the mediator (affective resonance) when feasible (see Bullock, Green, & Ha, 2010 for an in depth discussion of this and other challenges for causal mediation analyses).

It is also important to note that many cognitive processes other than those discussed in this article are presumably involved in both sustained long-term prosocial behavior and more momentary types. For example, there is evidence that perspective-taking, which continues to develop until late adolescence, mediates age related differences in sharing (Güroğlu, van den Bos, & Crone, 2014). There are also developmental changes in the degree to which the relational identity of one's interaction partner predicts sharing behavior, another important factor to consider in exploring motivations of helping behavior as well, especially given peer influences on prosocial behavior during adolescence (van Goethem, van Hoof, van Aken, Orobio de Castro, & Raaijmakers, 2014; van Hoorn, van Dijk, Meuwese, Rieffe, & Crone, 2014).

Concluding Comments

In conclusion, these results describe a possible set of associations that developmentally links empathic concern to prosocial behavior via a brain region implicated in affective mirroring processes, language, and cognitive control. The automatic neural responses to socioemotional stimuli that gave rise to activity in this region may not be accessible to self-report or behavioral measures, highlighting the value of this approach. Future work may build on these results to characterize the way empathic concern shapes these automatic processes over this developmental period.

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Table 1. Descriptive Statistics for Empathic Concern, Personal Distress, and Prosocial Behavior

IRI Subscale	**Mean**	**SD**	**α**	$\boldsymbol{r_{12}\ (\rho_{12})}$
EC_1	59.0	13.3	0.45	
PD_1	45.1	13.1	0.45	
EC_2	63.8	12.9	0.73	*.38* (*.28*)
PD_2	39.7	14.8	0.74	.19 (*.31*)

Note: Subscripts denote study wave (1 or 2). EC: empathic concern; PD: personal distress. α is Cronbach's alpha. r_{12} is the Pearson correlation, and ρ_{12} is the Spearman rank order correlation between the variable at wave 1 and wave 2 (significant values italicized).

Table 2. Association between Empathic Concern at Wave 1 and Prosocial Behavior at Wave 2

Parameter	***B***	**SE(*B*)**	***t*(51)**	***p***
Intercept	43.94	7.68	5.72	<.01
PSB_1	0.08	0.15	0.55	.58
EC_1	0.44	0.18	2.42	.02
PD_1	-0.16	0.18	0.89	.38
$EC_1 \times PD_1$	0.00	0.01	-0.14	.89

Note: Subscripts denote study wave (1). EC: empathic concern; PD: personal distress; PSB: prosocial behavior.

Table 3. Peak Voxel Statistics for Significant Clusters

Region Label	**t**	**k (mm^3)**	**x**	**y**	**z**
EC_1					
Inferior Frontal Gyrus (L)	3.50	52 (1404)	-51	20	25
PD_1					
Inferior Parietal Lobule (L)	-3.87	77 (2079)	-60	-46	40
$EC_1 \times PD_1$					
Cuneus	-3.75	163 (4401)	-3	-88	40
Perigenual Anterior Cingulate Cortex	-3.56	89 (2403)	3	29	13

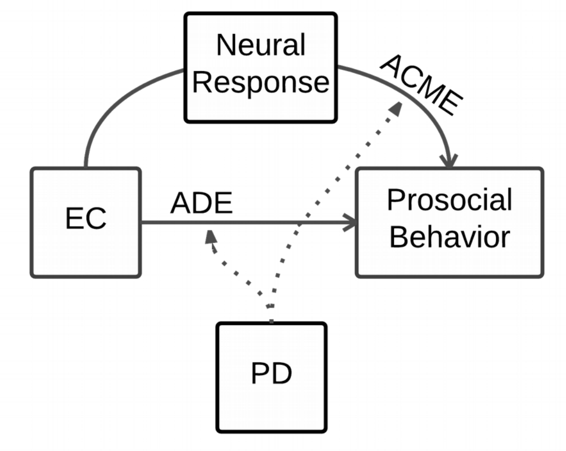
Note: Subscripts denote study wave (1). EC: empathic concern; PD: personal distress; L: left hemisphere. x, y, and z refer to the MNI coordinates corresponding to the left-right, anterior-posterior, and superior-inferior axes, respectively.

Table 4. Estimates of Mediated, Direct and Total Effects of Empathic Concern on Prosocial Behavior

	Estimate	**95% CI Lower**	**95% CI Upper**	***p***
ACME	3.608	0.930	7.267	0.00
ADE	3.304	-2.057	8.389	0.22
Total Effect	6.912	1.790	11.966	0.01
Prop. Mediated	0.511	0.128	1.709	0.01

Note: Estimates of the average direct effect (ADE), average causal mediated effect (ACME), and total effect on the prosocial behavior outcome for a 1 SD change in empathic concern. Prop. Mediated is an estimate of the ratio between the ACME and total effect.

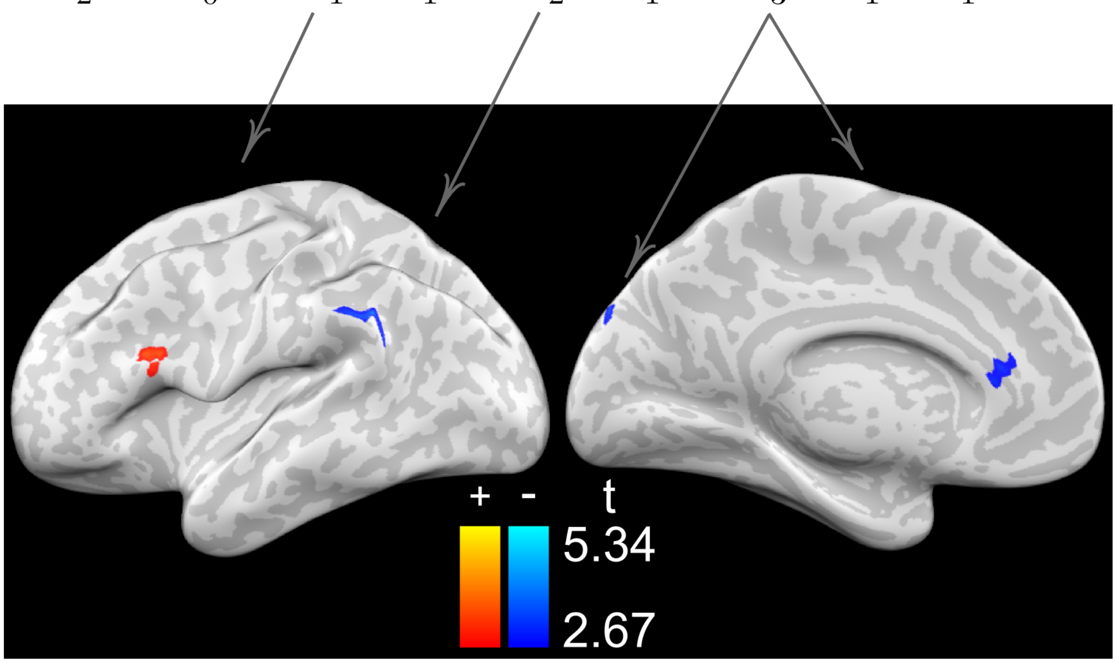
Figure 1. Diagram of theoretical model.



Note: Solid lines indicate theoretically positive relations, and broken lines indicate theoretically negative, moderating relations. EC: empathic concern; PD: personal distress; ADE: average direct effect; ACME: average causal mediation effect. Neural response refers to brain activity during passive viewing of emotional expressions.

Figure 2. Neural response to emotional expressions at wave 2 associated with wave 1 empathic concern and personal distress

$$N_2 = b_0 + b_1 EC_1 + b_2 PD_1 + b_3 EC_1 PD_1 + e$$



Note: Subscripts denote study wave (1 or 2). EC: empathic concern; PD: personal distress; N_2 is the estimate of neural response to emotional faces. Arrows from the regression equation indicate clusters where the relevant parameter estimate exceeds the statistical significance threshold. N_2 was positively associated with EC_1 in the left inferior frontal gyrus (IFG; warm colors, left-lateral view; $p<.005$, k>41), negatively associated with PD_1 in the left inferior parietal lobule (IPL; cool colors, left-lateral view), and negatively associated with EC_1PD_1 in the cuneus (midline view; $p<.005$, k>74), and in the perigenual anterior cingulate cortex (ACC, on figure right; midline view; $p<.005$, k>74).