Love flows downstream: mothers' and children's neural representation similarity in perceiving distress of self and family

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Abstract

The current study aimed to capture empathy processing in an interpersonal context. Mother–adolescent dyads ($N = 22$) each completed an empathy task during fMRI, in which they imagined the target person in distressing scenes as either themselves or their family (i.e. child for the mother, mother for the child). Using multi-voxel pattern approach, we compared neural pattern similarity for the self and family conditions and found that mothers showed greater perceptual similarity between self and child in the fusiform face area (FFA), representing high self–child overlap, whereas adolescents showed significantly less self–mother overlap. Adolescents' pattern similarity was dependent upon family relationship quality, such that they showed greater self–mother overlap with higher relationship quality, whereas mothers' pattern similarity was independent of relationship quality. Furthermore, adolescents' perceptual similarity in the FFA was associated with increased social brain activation (e.g. temporal parietal junction). Mediation analyses indicated that high relationship quality was associated with greater social brain activation, which was mediated by greater self–mother overlap in the FFA. Our findings suggest that adolescents show more distinct neural patterns in perceiving their own *vs* their mother's distress, and such distinction is sensitive to mother–child relationship quality. In contrast, mothers' perception for their own and child's distress is highly similar and unconditional.

Key words: representational similarity analysis (RSA); mother–child dyads; empathy; maternal empathy; adolescent; self–other overlap

Introduction

Emotional experiences often occur in an interpersonal context. For example, parents may experience more negative feelings themselves when their child is upset. Experiencing empathy with regard to others' pain or distress is found across species including rodents, non-human primates and humans, in infants as young as a few months of age, as well as across many forms of social relationships (e.g. for strangers, loved ones, etc.; Preston and De Waal, 2002; Decety, 2011b; Batson, 2009). At its most basic core, empathy facilitates parental care of their offspring and paves the way for successful social and emotional development in youth (Mikulincer *et al.*, 2001; De Waal, 2008; Decety, 2011b). A parents' ability to perceive and respond to emotional cues of their offspring, such as hunger, pain or distress, is essential for survival and has been hardwired at the neural level to promote parental care in mammalian species as an innate protective system for their offspring (Decety, 2011b). Indeed, studies have shown that parental empathic experiences

and neural engagement of the empathy network are more intensified when parents see their own child's pain compared with an unknown child's pain (Leibenluft *et al.*, 2004; Goubert *et al.*, 2008). Similarly, when mothers make caregiving decisions for their child, neural activation in the empathy network, including the prefrontal cortex (PFC), limbic and sensory regions, increases to meet the needs of their child (Ho *et al.*, 2014). Although emerging evidence supports maternal empathy for their own child's emotions, it is unclear whether children's empathy is equivalent to their parents' emotional perception of their offspring. Thus, the current study aimed to capture empathy processes in an interpersonal context within parent–child dyads.

One important aspect of empathy is the phenomenon by which one blurs the line between self and other (Davis *et al.*, 1996; Hodges and Klein, 2001; Decety and Sommerville, 2003; Galinsky *et al.*, 2005; Decety and Lamm, 2006; Batson, 2009). Theories suggest that understanding others' emotions and actions begin by perceptually representing or mirroring others' feelings and actions onto one's own states (Rizzolatti *et al.*, 2001; Preston and De Waal, 2002; Gallese, 2007; Keysers and Gazzola, 2009). According to Preston and de Waal's (2002) perception–action model, the initial perception of others' states can lead perceivers to have high self–other mental representation in feelings and actions, thereby eliciting emotional contagion and empathic responses as behavioral outcomes. Perceiving others' emotion (i.e. perceptual encoding) enables individuals to simulate others' states as one's own states, and thereby forms self–other overlap (Rizzolatti *et al.*, 2001; Gallese, 2007; Keysers and Gazzola, 2009). That is, how we perceive others' emotions could be an important gateway to how we share mental representations with others for empathic actions. An important consideration for the emergence of empathy is thus whether individuals show a similar representation of the self and other during perceptual encoding and whether such perceptual similarity facilitates further empathic responding.

Perceptual representation for self–other overlap can be characterized as a bottom-up process because it requires one to detect and encode others' states first (Singer, 2006; Decety, 2011a). Indeed, studies have shown that empathic responses during the observation of others' pain are associated with increased activation in early perception-sensory regions such as extrastriate body area, fusiform gyrus and sensory-motor area (e.g. Jackson *et al.*, 2005; Lamm *et al.*, 2007; Lamm and Decety, 2008). This bottom-up process may influence social cognitive top-down modulation, in which the perceptual representation for others is evaluated to make subsequent inferences for others' situation (Decety and Sommerville, 2003; Jackson and Decety, 2004; Singer, 2006; Decety, 2011a). For example, social cognitive regions, such as the temporal parietal junction (TPJ), medial PFC (MPFC) and posterior cingulate cortex (PCC), show increased activity for in-group member's pain (Amodio and Frith, 2006; Adams et al., 2010; Cheon *et al.*, 2010; Mathur *et al.*, 2010; Morrison *et al.*, 2012), along with increased neural activation of sensory-perception regions (Azevedo *et al.*, 2013; Zuo and Han, 2013). In this vein, researchers highlight the importance of both affective and cognitive components of empathy that influence the extent of empathic concern and potential prosocial behavior (Decety, 2005; Eisenberg and Eggum, 2009; Goubert *et al.*, 2009). In this model, the bottom-up affective component helps perceivers to increase personal distress and attention for understanding other's affective states, and the top-down cognitive component regulates perceiver's emotional arousal and leads to prosocial behavior by recruiting cognitive control

resources. However, too much personal distress, induced by emotional arousal and contagion, can impede the perceiver's empathic behaviors as it depletes cognitive resources to regulate their own affective arousal, thereby failing to attend to others' needs (Eisenberg and Eggum, 2009).

Previous work has focused on the neural involvement of either early sensory-perception processes (e.g. Singer *et al.*, 2004; Jackson *et al.*, 2005) or higher-order social cognitive processes (e.g. Saxe *et al.*, 2004) independently, instead of conceptualizing empathy as a continuum from the initial representation at the perception level to later social cognitive processes. Thus, empirical research which integrates how the self and others are represented during the initial perception and how this perceptual representation is associated with mentalizing processes will shed light on our understanding of how empathy arises in the brain. In the current study, we scanned both mothers and their adolescent child as they engaged in a task that measures empathic responses when perceiving their own and each other's distress. We sought to examine how empathic experiences are modulated by perceptual representation based on the perception-action perspective (Preston and De Waal, 2002; Preston, 2007). In particular, we examined perceptual encoding of self–other overlap in the fusiform face area (FFA), and whether higher perceptual similarity is associated with empathic responses in social–cognitive brain regions. Our perceptual similarity analysis of self–other overlap focused on neural patterns in the FFA because evidence indicates that the FFA is involved in the initial encoding of faces as an early visual perception process (Ghuman *et al.*, 2014). Importantly, the mental imagination of faces and encoding emotionality and social information from faces significantly increases neural activation in the FFA (O'Craven and Kanwisher, 2000; Adolphs, 2009; Sabatinelli *et al.*, 2011). To quantify the representation similarity, we adopted the representational similarity analysis (RSA; Kriegeskorte *et al.*, 2008) as a form of multi-voxel pattern approach. This pattern-focused approach allows us to test how neural representations when perceiving self and other are similar by focusing on signal variations of neural response across voxels (i.e. multi-voxel pattern), rather than simply changes in the overall fMRI magnitude between parent and adolescent groups (i.e. univariate neural activation).

We tested three key hypotheses. First, mothers' perceptual representation of distress for self and child would be highly similar, as evidenced by greater neural pattern similarity in the FFA regardless of the quality of their relationship. In contrast, adolescents would show less similar perceptual representation of distress for self and mother, and such representational similarity would depend upon their relationship quality. Previous studies have indicated that parental concerns for their offspring are stable and unconditional regardless of social environmental factors (Acock and Bengtson, 1980; Leibenluft *et al.*, 2004; Goubert *et al.*, 2008; Proulx and Helms, 2008; Driscoll and Pianta, 2011). For instance, parents' perception of closeness to their child is stable as parents focus on deemphasizing conflicts and increasing support in their roles as parents for their child's well-being (Acock and Bengtson, 1980; Proulx and Helms, 2008; Driscoll and Pianta, 2011). Indeed, following pregnancy, mothers' socioemotional neural system shifts to support empathy and care of their child (Hoekzema *et al.*, 2016). In contrast, the adolescent period is marked by a social reorientation away from parents and towards peers (Nelson *et al.*, 2005). Adolescents report decreased closeness in parent–child relationship quality (Tsai *et al.*, 2013), combined with exaggeration of conflicts to diminish closeness with parents as a means of establishing

autonomy (Fuligni and Eccles, 1993; Larson *et al.*, 1996; Collins and Steinberg, 2006). Thus, adolescents' perceptual representation of distress for self and mother would be more conditional, such that adolescents will only show high neural pattern similarity in the FFA when they report stronger relationship quality.

Second, we tested whether perceptual encoding (i.e. representational pattern similarity in the FFA) is associated with higher social cognitive processing. Perceptual representation similarity in the FFA, an index of self–family overlap, was used as a regressor in a univariate general linear model (GLM) analysis to link initial perception to subsequent empathic processes in social brain regions, which include the TPJ, MPFC and PCC (Saxe *et al.*, 2004). In other words, the level of neural engagement in the social brain when processing family and self will depend on the perceptual similarity in the FFA. As suggested by theories of empathy (e.g. Preston and de Waal's, 2002), the initial perceptual representation process for others' states subsequently elicits emotional contagion and empathic response. Although the sluggish nature of the fMRI signal does not allow us to test direct temporal influences between processes, we hypothesized that higher perceptual similarity in the FFA, a neural index of self–family perceptual overlap, would be associated with greater neural recruitment of mentalizing processes in social brain regions.

Finally, we performed mediation analyses to test an integrated model linking mother–child relationship quality, the perceptual similarity in self—family overlap and neural engagement of social brain regions. We hypothesized that greater relationship quality in adolescents would be associated with the recruitment of social brain regions during empathic responses, and this path would be mediated by greater encoding of perceptual similarity in the FFA. Whereas relationship quality would be a key predictor of perceptional similarity and social brain responding in adolescents, we predicted that relationship quality would not influence empathic responses in mothers because mothers' socioemotional system is more stable and invariable for their offspring (Acock and Bengtson, 1980; Proulx and Helms, 2008; Driscoll and Pianta, 2011; Hoekzema *et al.*, 2016).

Materials and methods

Participants

Twenty-two healthy mother–adolescent dyads were recruited to participate in this study (adolescents: $M_{age} = 13.90$ years, s.d. = 0.11, 21% female; mothers: $M_{age} = 44.26$ years, s.d. = 1.57, 100% female). Mothers and their adolescent child each underwent an fMRI scan on the same day. Participants were compensated $50 each for their participation. All participants provided written informed consent and assent approved by the Institutional Review Board.

Task design and procedure

The task was modified from prior work on neural processing of empathy, a task which has reliably recruited neural regions involved in mentalizing (Rameson *et al.*, 2012; Morelli *et al.*, 2014). During the task, adolescents and mothers each saw individuals expressing emotional distress in negative contexts (e.g. at a funeral or being bullied), with instructions to perceive the target face as either their family member (family-condition; mother for the child's scan or child for the mother's scan) or themselves (self-condition). Participants were instructed to

imagine the person in the picture as themselves and to take the perspective of the person in the picture during the self-condition. For the family-condition, participants were instructed to imagine the person in the picture as their parent/child, and to take the perspective of the person in the picture as if it were their family member. When the target individuals appeared in the social scenes with many other people, a white arrow was inserted to guide participants to the target face (see Figure 1A). The stimulus conditions were balanced by gender of target face. The gender of faces was not matched to the subject, and participants were instructed to imagine the person in each image as themselves (self-condition) or their family member (family-condition) regardless of the gender of the person. The age of the target face for each group (e.g. family and self) was matched. Each trial lasted between 8 and 9.2 s and was followed by 2 s rating phase consisting of a 10-point Likert scale to indicate how they felt from −5 (very negative) to 5 (very positive).[1] Two independent blocks for self- and family conditions consisted of 12 event-related trials each (i.e. mixed-design). Each block was separated by a 5-s blank screen, and inter-trial intervals were inserted between trials to separate the BOLD signal jittered between 2.0 and 3.2 s (mean = 2.4 s).

fMRI data acquisition and analysis

Image acquisition, preprocessing and registration. Imaging data were collected using a 3T-Siemens Trio MRI scanner with a 32-channel matrix coil. High-resolution structural images (T1-MPRAGE) were acquired first (repetition time or TR = 1.9 s; echo time or TE = 2.3 ms; matrix size = 256 × 256; field of view or FOV = 230 mm; flip angle or FA = 90°; 1 mm isotropic voxel). T2*-weighted echoplanar images were acquired during the emotion perception task (38 slices with 0.3 mm inter-slice gap; TR = 2 s; TE = 25 ms; matrix = 92 × 92; FOV = 230 mm; FA = 90°; voxel size 2.5 × 2.5 mm; slice thickness = 3 mm).

Preprocessing was carried out using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library; Smith *et al.*, 2004). The following pre-statistics processing was applied: motion correction using MCFLIRT (Jenkinson *et al.*, 2002); non-brain removal using BET (Smith, 2002); grand-mean intensity normalization of the entire 4D data set by a single multiplicative factor; spatial smoothing applied only for univariate whole-brain analysis with Gaussian kernel of full width at half maximum 6 mm. For univariate analysis, registration matrix was estimated additionally between functional images, high-resolution structural images and standard Montreal Neurological Institute (MNI) 2-mm brain using FLIRT (Jenkinson and Smith, 2001; Jenkinson *et al.*, 2002).

RSA (multi-voxel pattern analysis). For the RSA, we first estimated single-trial activation patterns for each trial using least squares single methods (Mumford *et al.*, 2012) where each single-level GLM included regressors for a current trial and all other remaining trials with temporal derivate regressor. We included the

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1 A repeated measure of ANOVA (condition: self and family X group: mother and adolescent) found that there was no main effect of condition or interaction (all $ps > 0.29$), but a significant main effect of group ($p = 0.001$), indicating mothers rated painful scenes as more negative than adolescents regardless of stimulus types (children: -0.84 vs. mothers: -2.19). Subsequent t-tests indicated that all ratings for both self and family conditions of mothers and adolescents were significantly different from 0 (0 = rating as non-arousing, all $ps < 0.001$), indicating that both mothers and children perceived painful scenes as negative across all stimulus types.
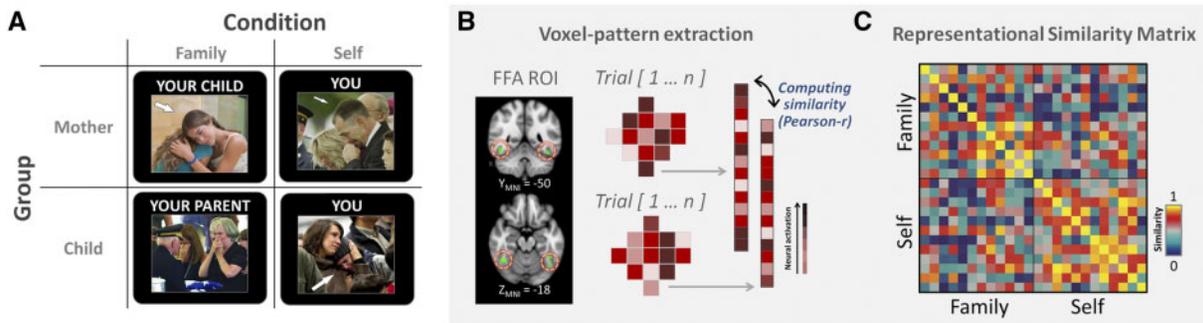
Fig. 1. (A) Experimental condition for mothers and adolescent children, (B) schematic procedure of computing similarity values within the region of interest between trials and (C) example of the representational similarity matrix.

rating phase in the model as a regressor of non-interest (i.e. nuisance regressor) as well as motion regressors (six motion parameters and motion-outlier points). For each participant, the standardized voxel-wise pattern activity (i.e. z-transformed parameter estimates) was extracted and vectorized within the FFA region of interest (ROI) (see ROI selection for more details). The extracted patterns were then analyzed by calculating pairwise *Pearson* coefficient (i.e. similarity value) between each trial with every possible pair of other trials (Figure 1B), and then applied Fisher's *r*-to-*z* transformation, producing a symmetric 24×24 similarity matrix for each dyad and the ROI (Figure 1C). Finally, the average of self–family similarity values was used for subsequent analyses (e.g. Visser *et al.*, 2011).

Univariate group-level analysis with RSA as a covariate. To assess how perceptual encoding (i.e. representational pattern similarity in FFA) is associated with higher-level social cognitive processing, an additional standard two-stage mixed-effects analysis was performed. The GLM of the BOLD signal for each perception type (family and self) was estimated with temporal derivate regressors at the first level using a double-gamma hemodynamic response function. We added the rating phase in the model as a regressor of non-interest (i.e. nuisance regressor) to the design matrix as well as motion regressors (six motion parameters and motion-outlier points). The individuals' data were then inputted into a random-effects model using cluster detection statistics with outlier-deweighting at a threshold of $Z > 2.3$ and a cluster probability of $P < 0.05$ (one-tailed), corrected for whole-brain multiple comparisons using Gaussian Random Field Theory. In particular, we entered each individual's FFA similarity values (demeaned for each group) as covariates in the group-level analysis to examine how perceptual similarity in the FFA to self and other is associated with neural encoding of self and other in social–cognitive regions.

ROI selection. In this study, we indexed neural representation at the encoding stage by examining neural pattern similarity within the FFA, a key region in visual face encoding (Kanwisher *et al.*, 1997). We constructed the ROI mask of a priori voxels associated with 'FFA', 'emotional face', 'faces' and 'face perception' from the reversed inference map ($q < 0.1$ FDR-corrected) in the NeuroSynth database (http://www.neurosynth.org; downloaded on 24 November 2015). The final FFA voxels were then selected along with the ventral temporal cortex at $Z = 3.71$ (Figure 1B; a total 321 voxels).

Family relationship quality

To capture a comprehensive measure of relationship quality between mothers and adolescent children, three measures were assessed from both mothers and adolescent children: family cohesion (Family Adaptation and Cohesion Evaluation Scales II inventory, FACE II; Olson *et al.*, 1979), family conflict (Ruiz *et al.*, 1998; Telzer *et al.*, 2014) and family identity (Tyler and Degoey, 1995). We created a composite score of positive family relationship quality by taking the score of family cohesion, reverse-scored family conflict and family identity, with higher scores indicating more positive parent–child relationships. This composite score provides us with a comprehensive measure of relationship quality using these three dimensions (Qu *et al.*, 2015). Details for each scale are as follows:

Family cohesion. Participants completed the Cohesion subscale of the FACE II (Olson *et al.*, 1979). They responded to 10 items that assessed how close they feel and how much time they spend with their mother [child] on a 5-point Likert scale from 1 (almost never) to 5 (almost always). Sample items included 'My mother [child] and I do things together', 'My mother [child] and I are supportive of each other during difficult times', and 'My mother [child] and I feel close to one another' (internal consistency $\alpha = 0.81$ for mother; $\alpha = 0.88$ for child). The 10 items were averaged, and higher scores indicate greater relationship closeness.

Family conflict. Parent–child conflict was assessed by 10 items (Ruiz *et al.*, 1998; Telzer *et al.*, 2014) (e.g. 'You and your parents [child] had a serious argument or fight' and 'You and your parents [child] yelled or raised your voices at each other'). Participants reported how true each item was for them in the past month on a 5-point scale ranging from 'almost never' to 'almost always' ($\alpha = 0.88$ and 0.92 for mother and child, respectively). The 10 items were averaged, such that higher scores indicate greater conflicts with family members.

Family identity. Participants completed an eight-item scale that assessed the extent to which their family is an important aspect of their identity (Tyler and Degoey, 1995). Using a 5-point scale from 1 (strongly disagree) to 5 (strongly agree), participants indicated how much their sense of self was internalized to their family value (e.g. 'I feel like a valued member of my family' and 'My family is important to the way I think of myself as a person'; $\alpha = 0.83$ and 0.87 for mother and child, respectively). The eight items were averaged, and higher scores indicate greater internalized family values.

Results

RSA: perceptual similarity for self and family

To examine how mothers and adolescent children perceive the emotional distress of their family and self at the perceptual level, we compared the similarity value in FFA of mothers when perceiving their own and their child's emotional distress and of adolescents when perceiving their own and their mother's emotional distress. As shown in Figure 2A, mothers showed greater neural similarity in perceptual representation in the FFA when perceiving emotional distress in self vs child ($M = 0.24$, s.d. $= 0.06$), whereas their adolescent children showed significantly less neural pattern similarity between the conditions ($M = 0.17$, s.d. $= 0.07$), paired-$t(20) = -4.11$, $P < 0.05$, 95% confidence interval (CI) $^{50\ 000\ bootstrap\ resampling} = -0.09$ to -0.03. That is, mothers' perception of their child's emotional distress within each dyad is more similar to their own emotional distress compared with their own adolescent child's perception of self and mother.

As hypothesized, children's perceptual similarity was dependent upon their family relationship quality, such that they showed greater perceptual similarity when they reported higher relationship quality, $r(22) = 0.45$, $P < 0.05$, 95% CI $^{50\ 000\ bootstrap\ resampling} = 0.09-0.72$, whereas mothers' neural pattern similarity was high and independent of relationship quality, $r(21) = 0.07$, $P > 0.05$, 95% CI $^{50\ 000\ bootstrap\ resampling} = -0.42$ to 0.52 (Figure 2B). To rule out the possibility of ceiling effects relating to the finding that there was no association between mother's perceptual similarity and relationship quality compared to adolescents, we compared the relationship quality in dyads and found no significant difference between mother and child, paired-$t(21) = -0.14$, $P > 0.05$, 95% CI $^{50\ 000\ bootstrap\ resampling} = -0.38$ to 0.32. This result indicates that the null finding for mothers was not due to ceiling effects for relationship quality. In sum, mothers show high self–child overlap in perceptual similarity in the FFA regardless of their relationship quality with their child. In contrast, adolescent children only showed high perceptual similarity in the FFA when they also reported high relationship quality with their family, suggesting that adolescent children's self–family overlap is dependent upon their relationship quality.

Group-level univariate analysis with FFA similarity predicting social brain activation for self and family

To test the prediction that higher neural similarity for self and family at the perceptual level is associated with neural processing in higher-level, social–cognitive regions, we examined which brain regions covaried with perceptual similarity in the FFA. To this end, we used FFA similarity from the self and family conditions and regressed this similarity value onto neural activation when perceiving self vs family's emotional distress (self $>$ family). Note that greater activation for this contrast represents greater differences in neural responses to self and family. We found that greater perceptual similarity between self and family in adolescents was negatively associated with neural activation in several social brain regions including bilateral TPJ, PCC and mPFC (Figure 3A and Table 1), suggesting that greater similarly in the FFA at the encoding stage was associated with lower differentiation of self and family in the social brain processing for empathy.

Next, we regressed family relationship quality onto neural activation when perceiving self vs family's emotional distress and found negative correlations in several social brain regions as a function of adolescents' family relationship quality (Figure 3B and Table 2). That is, adolescents who reported greater relationship quality showed lower differentiation of self and family in the social brain during empathic responding. Social brain regions of mothers were not modulated by the perceptual similarity for self and child (see Table 1 for local maxima regions in the clusters).

Mediation analysis

To integrate the results of perceptual similarity in the FFA, neural engagement in the social brain and family relationship quality, we performed a mediation analysis. We tested whether relationship quality (i.e. independent variable) is associated with less differentiation of self and family in social–cognitive regions (i.e. outcome) through increased perceptual similarity in the FFA (i.e. mediator). To this end, we extracted and averaged activation from the social brain regions which were identified in the analyses above, and performed mediation analyses using the mediation toolbox in Matlab (Wager $et\ al.$, 2008). As shown
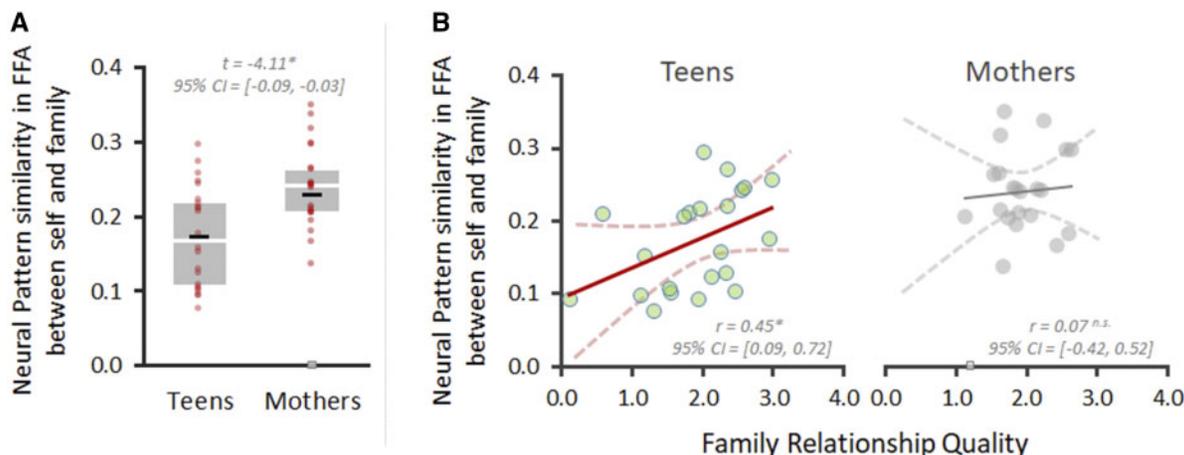
Fig. 2. (A) Whisker plot for the neural pattern similarity between self and family condition calculated within FFA ROI. Black and white bar within indicate mean and median, respectively. Red-colored dots indicate individual's similarity point; one mother had extremely low similarity value (0.002; gray-colored square) that was far less than 2.5 s.d. under the mean. We excluded this mother for the final analyses. (B) Scatter plots of the similarity values and relationship quality for adolescents and mothers. Dotted lines indicate 95% CI of the regression line. Note that all statistical results remained same when the outlier mother was included; 95% CI $= -0.09$ to -0.03 for panel A and 95% CI $= -0.29$ to 0.68 for panel B.

Fig. 3. Negatively covaried social brain regions (circled area) with (A) the increased family–self perceptual similarity of FFA (B) the degree of family relationship quality in family–self contrast of adolescent children. See also Table 1 and 2 for other clusters.

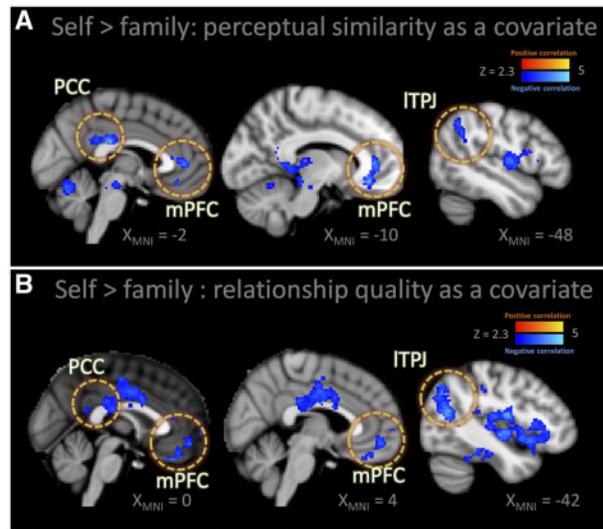in Figure 4, the path between family relationship quality and perceptual similarity in the FFA for self and mother (path a; $a = 0.05$, $P < 0.05$, 95% CI $^{50\,000\ \text{bootstrap resampling}} = 0.01–0.09$) and the path between perceptual similarity and social brain regions identified in the univariate analysis (path b; $b = -2.50$, $P < 0.05$, 95% CI $^{50\,000\ \text{bootstrap resampling}} = -4.07$ to -1.20) were statistically significant. Importantly, the mediation effect was significant ($ab = -0.11$, $P < 0.05$, 95% CI $^{50\,000\ \text{bootstrap resampling}} = -0.25$ to -0.01), indicating that greater perceptual similarity for self and family explains the link between strong family relationship quality and less differentiation in the social brain for self *vs* family. Only adolescents showed this significant mediating effect, whereas mothers did not ($ab = 0.01$, $P > 0.05$, 95% CI $^{50\,000\ \text{bootstrap resampling}} = -0.07$ to 0.09). In sum, these results suggest that not only is the quality of the relationship important for high perceptual similarity for both the self and their family but also that high self–other overlap at the perceptual level explains the link between family relationship quality and empathic responding in higher-level social–cognitive regions.

Discussion

In this study, we examined mothers and their child's empathic neural representations for the self and family. Using representation similarity analysis, we found that mothers' perceptual similarity in the FFA for self and their child's emotional distress was significantly higher compared to their child's self–mother perceptual similarity, indicating that mothers show high self–child overlap compared to their adolescent child. In contrast, adolescents' perceptual similarity was dependent upon their relationship quality, such that they showed high self–other overlap for their mother's emotional distress and their own only when they reported high relationship quality with their family. It is worth noting that these similarity results were based on within-family comparisons, indicating that each mother shows higher perceptual similarity than her own child. Moreover, this initial perceptual representation in the fusiform in adolescents was associated with neural activation in social

brain regions required to put oneself in another's shoes (Saxe *et al.*, 2006), whereas no such modulatory effects of perceptual similarity on the social brain were found in mothers. Consistent with previous evidence showing that parents' perspective to their child is more stable and robust, whereas adolescent children begin to reduce closeness with their parents as a means of establishing autonomy (Acock and Bengtson, 1980; Proulx and Helms, 2008; Driscoll and Pianta, 2011), these results suggest that mothers' empathy to their child is more unconditional compared to that of their adolescent child. Finally, the mediation model confirmed that family relationship quality is associated with adolescent's mental representation for both the self and their family at the perceptual (i.e. fusiform perceptual representation similarity) and higher-level social cognitive processing level.

Mothers' attention is unconditionally directed toward their offspring to understand, make sense of and respond to their child's feelings and behaviors across the lifespan. This maternal empathic bias has deep evolutionary underpinnings at the neural level to be selective and protective of her own offspring (De Waal, 2008; Decety, 2011b) such that mothers' empathy promotes positive developmental outcomes, such as mood stability and regulated stress reactivity in developing youth (Abraham *et al.*, 2017). Our findings support this perspective for maternal empathy by showing that maternal empathic processes for their child are more robust compared to children. In our mediation model, we found that mothers' mentalizing process for their child's emotional distress was modulated by neither the relationship quality nor the degree of self–child overlap in the FFA. It is possible that mothers were at ceiling with less variability in perceptual similarity in the FFA as well as social brain activation. Importantly, a recent neuroimaging study revealed that brain regions associated with empathy are dramatically reconfigured after pregnancy in a mother's brain (Hoekzema *et al.*, 2016), which enables mothers to be more selective and sensitive to their own offspring. In other words, the neural connections in mothers' brains become fine-tuned and strengthened to utilize neural resources optimally for their own offspring. This neural reconfiguration is enduring for mothers after pregnancy and into adolescence, highlighting mothers' strong self–child overlap. In contrast, adolescents are establishing a sense of identity by expanding their social network, spending more time and sharing their affection with others outside of the family (Larson *et al.*, 1996). Unlike mothers, adolescents' brains are more likely to be sensitive to their social environment (Blakemore and Mills, 2014), particularly their peers (Nelson *et al.*, 2005). Therefore, adolescents' mental representations are more flexible depending on social contexts (Crone and Dahl, 2012). Thus, this study suggests that adolescents' empathy is more conditional whereas mothers show empathy for their child that is stable and unconditional.

The current findings elaborate upon previous theories (Rizzolatti *et al.*, 2001; Preston and De Waal, 2002; Gallese, 2007; Keysers and Gazzola, 2009) by showing how empathic experiences arise based on the interaction of two different processes, the bottom-up perceptual encoding process and the top-down social cognition process. Theories of empathy propose that empathy to others includes various mental and behavioral phenomena, such as shared and vicarious emotional experiences associated with prosocial (helping) reactions as a result of perceiving others' emotional states (Preston and De Waal, 2002; Singer, 2006; Preston, 2007; Decety, 2011a). Therefore, an approach to integrate these two

Table 1. Brain regions which correlated with perceptual similarity on family-self condition in adolescents

Adolescent

Self > Family	H	BA	Z-score	k	MNI x	y	z
Perceptual similarity: negative covariation							
Temporal parietal junction (TPJ)	L	39	4.21	279	−34	−68	44
	R	39	4.17	468	42	−64	48
Medial PFC (mPFC)	L	11	3.64	28	−4	36	−12
Posterior cingulate gyrus (PCC)	–	–	4.12	209	−2	−28	28
Angular gyrus/inferior parietal lobe (IPL)	R	40	3.55	63	46	−52	54
Anterior cingulate gyrus (ACC)	–	32	3.78	194	−6	42	4
Brain stem	–	–	2.98	43	−10	−30	−10
Insula	L	4	4.02	186	−42	−8	16
	L	13	3.41	85	−40	−8	0
	R	1	2.75	28	44	−18	16
Dorsal lateral PFC (DLPFC)	L	46	3.17	53	−40	44	6
	R	9	2.86	22	42	40	34
Inferior temporal gyrus (ITG)	R	37	3.59	47	56	−52	−16
DLPFC	R	8	4.07	137	42	16	52
Auditory cortex	R	41	2.93	20	62	−24	12
Primary somatosensory cortex	R	1	3.13	60	62	−16	36
Secondary somatosensory cortex	R	40	3.11	20	42	−26	18
Primary motor cortex	R	6	3.37	151	42	−10	64
Superior parietal lobule (SPL)	R	7	3.11	22	30	−54	62
Superior temporal gyrus (STG)	R	41	3.27	49	68	−26	10
TPJ	R	40	3.95	181	64	−24	42
	R	40	3.38	45	56	−36	52
Fusiform gyrus	R	37	3.65	67	40	−56	−16
Thalamus	L	50	3.33	151	−14	−30	8
Perceptual similarity: positive covariation				No significant activations			
Mothers							
Perceptual similarity: negative covariation							
Auditory Cortex	L	41	3.32	58	−40	−22	10
	L	41	3.08	29	−42	−34	10
Insula	L	6	3.35	88	−52	−2	2
	L	13	2.9	20	−42	−10	0
	R	6	2.74	20	54	−4	8
Primary somatosensory cortex	L	4	4.2	88	−64	−12	18
Secondary somatosensory cortex	L	40	3.01	29	−54	−26	16
Primary motor cortex	R	6	3.41	39	64	4	16
STG	R	22	4.44	30	68	−12	0
	L	6	3.74	31	−54	−2	0
Perceptual similarity: positive covariation				No significant activations			

Notes: Reported regions and their 'local maxima' were at 50% probability locations on the Harvard–Oxford atlas with more than 20 voxels. H, hemisphere; BA, Brodmann area; k, the number of voxels.

empathy components ('perception and action' or 'bottom-up and top-down processing') with a continuum perspective is critical for understanding empathic experiences. The current study demonstrates that perceptual representation similarity in the fusiform, representing an initial mental representation of self–other emotional distress, is an important gateway to neural activation involved in higher social cognitive processing. Interestingly, this two-component model was only valid for adolescents.

In our study, the quality of perceptual representation at the encoding level in the FFA was quantified using RSA as a form of multi-voxel pattern approach. Employing neural pattern approach allows us to examine neural representational patterns in the perceptual region (i.e. FFA for facial expression) rather than simply examining whether this region shows differential neural activation to self *vs* others' emotional distress (i.e.

univariate analysis). To our knowledge, this is the first study to examine how perceptual representation at the encoding level is related to the degree of empathy processing at the social–cognitive level. However, it should be noted that our model implying the temporal aspects of empathic experience from the initial encoding to later social cognition could not be tested directly. Although we built this model based on previous theories and empirical evidence in empathy (Rizzolatti *et al.*, 2001; Preston and De Waal, 2002; Jackson *et al.*, 2005; Singer, 2006; Gallese, 2007; Lamm *et al.*, 2007; Lamm and Decety, 2008; Keysers and Gazzola, 2009; Decety, 2011a), the sluggish nature of the BOLD signal precludes our ability to test the model in a temporal manner, and thus the current results cannot confirm causality explicitly between these two distinct processes. Experimental designs that can disentangle these two processes in a causal manner would help us to probe the temporal influences

Table 2. Brain regions which correlated with mother-child relationship quality on family-self condition in adolescents

Adolescent

Self > Family	H	BA	Z-score	k	MNI x	y	z
Relationship quality: negative covariation\							
Medial PFC (mPFC)	L	10	3.97	125	−2	50	−12
	R	10	3.55	79	2	50	−10
	L	10	3.45	74	−6	54	4
	R	10	3.14	23	4	48	−8
Posterior cingulate cortex (PCC)		31	3.22	212	−4	−30	46
Temporal parietal junction (TPJ)	L	19	3.82	394	−44	−66	20
Anterior cingulate gyrus (ACC)		32	3.5	371	6	6	36
Amygdala	L	34	3.95	230	−26	2	−20
	R	49	3.52	123	26	2	−10
Angular gyrus/inferior parietal lobe (IPL)	L	39	3.5	21	−56	−54	24
	R	39	2.76	48	60	−50	36
Insula	L	13	4.4	255	−40	−14	−2
	R	44	4.26	266	42	6	6
	R	13	4.21	250	38	−8	6
	L	4	4.17	216	−42	−8	16
Orbitofrontal cortex (OFC)	L	47	4.3	197	−28	34	−14
	R		3.37	176	22	12	−16
mPFC	L	10	3.84	240	−2	62	2
	R		2.86	22	2	62	2
Auditory cortex	R	41	3.85	59	46	−28	12
	R	41	3.37	31	44	−22	12
	L	41	3.14	30	−40	−22	10
Hippocampus	L	54	3.76	219	−28	−16	−18
	R	54	3.09	121	28	−32	−6
Inferior frontal gyrus (IFG)	L	45	3.62	29	−52	16	0
	L	45	3.35	54	−40	22	6
	R	9	2.65	20	56	28	16
Inferior temporal gyrus (ITG)	L	37	3.49	108	−36	−38	−28
	R	20	3.06	24	58	−30	−26
Lateral occipital cortex—inferior division	R	37	3.45	67	54	−64	−12
	L	19	3.09	32	−50	−70	12
Lingual gyrus	L	19	3.18	70	−8	−60	−2
Middle temporal gyrus (extended to posterior superior temporal sulcus pSTS)	R	21	3.98	38	62	−2	−18
	R	37	3.63	106	60	−54	10
	L	39	3.24	32	−56	−58	6
	R	21	3.06	115	66	−24	−20
	L	21	2.99	54	−56	−26	−8
Basal ganglia: pallidum	R	51	3.65	87	22	−6	2
	L		3.41	34	−26	−16	0
Putamen	R	49	3.88	258	24	8	−10
	L	49	3.75	273	−30	−14	0
Parahippocampal gyrus	L	37	3.46	31	−28	−30	−22
Primary somatosensory cortex	L	1	3.72	138	−56	−18	30
	R	40	3.69	112	66	−16	20
Secondary somatosensory cortex	R	40	4.59	85	58	−24	18
	L	40	3.24	119	−48	−34	20
Superior temporal gyrus (STG)	R	22	3.92	27	56	2	−2
	R	22	3.72	58	68	−14	−2
	L	22	3.53	23	−42	−16	−4
	R	22	3.02	26	56	2	−14
Primary motor cortex	R	6	4.17	101	42	−10	56
Supplementary motor area	R	6	2.86	21	6	−4	52
Precuneous	L	18	2.96	31	−14	−58	16
Supramarginal gyrus	L	21	4.05	99	−62	−26	38
	R	40	3.9	164	62	−22	36
	R	40	3.15	80	56	−36	52
Fusiform gyrus	R	37	4.06	66	38	−32	−20

(continued)

Table 2. (continued)

Adolescent

Self > Family	H	BA	Z-score	k	MNI x	y	z
	R	37	3.49	101	50	−44	−22
	R	37	2.99	25	32	−68	−14
Temporal pole	R	38	3.94	281	56	8	−16
	L	38	3.83	105	−54	14	−8
Thalamus	L	50	3.24	128	−10	−16	4
	R		3.09	71	22	−24	12
Relationship quality: positive covariation			No significant activations				
Mothers							
Relationship quality: negative covariation			No significant activations				
Relationship quality: positive covariation			No significant activations				
ACC		24	3.53	50	0	28	16

Notes: Reported regions and their 'local maxima' were at 50% probability locations on the Harvard–Oxford atlas with more than 20 voxels. H, hemisphere; BA, Brodmann area; k, the number of voxels.
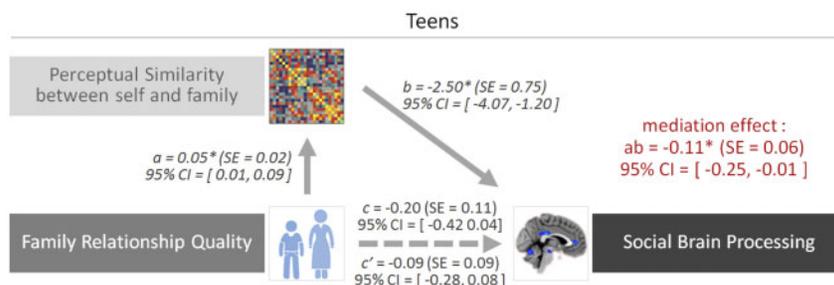

Fig. 4. Perceptual similarity in the FFA mediates the link between perceived family connectedness and social brain activation in adolescents. Note that asterisk indicates statistical significance at $P = 0.05$ (95% CI) based on 50 000 bootstrapping resampling.

between the bottom-up and top-down processes in empathic experiences.

Nonetheless, some evidence highlights the importance of early sensory-perception processing for later social–cognitive processing. For example, emotion perception studies have demonstrated that emotional information is pre-evaluated during the early encoding in perception-sensory regions, such as somatosensory and early visual cortex (e.g. Stolarova *et al.*, 2005; Greening *et al.*, 2016;). Importantly, early sensory-perception bottom-up processing shifts the quality of later cognitive top-down processing, such that impairment of somatosensory processing can impair recognition of face emotions at the later top-down stage (Adolphs *et al.*, 2000). Similarly, event-related potential (ERP) research has shown that late top-down processing in face emotion recognition reflected by late the cognitive component (400–800 ms) is significantly modulated depending on how face stimuli are encoded at the early bottom-up stage represented at the early sensory-perception component (200–300 ms; Lee *et al.*, 2010). Thus, it is plausible that social brain region changes observed in the current study are influenced by perceptual representation at the encoding level first. Our regression model using mediation also supports this pathway, such that perceptual similarity in the FFA significantly mediated the association between relationship quality and social brain activation to self and family.

In the current study, we recruited mothers and adolescents using dyadic recruitment (i.e. mothers and adolescents from the same family), which is a strength of the sample. However, the sample size is relatively small, precluding our ability to examine sex differences among adolescents or between mothers and fathers. Furthermore, our adolescent-only sample does not allow us to probe why adolescents show less self–other overlap compared to adults (i.e. mothers). For example, it is possible that there may be linear increases in self–family overlap across development, as social cognitive abilities increase across this age range. Thus, recruitment of pre-adolescent children would further enable us to probe whether the effects we found change linearly with age. Moreover, examining other targets in the task (e.g. peers) would help us tease apart whether the source of low self–mother overlap is due to adolescents beginning to show greater self–other overlap with their peers as they transition into adolescence (Nelson *et al.*, 2005). Longitudinal research and studies recruiting larger and different samples including children, adolescents, peers and other family members (e.g. sibling and father) will help to unpack developmental trajectories in empathic responding for self and other.

This study shows that relationship quality may set the stage for social–cognitive processing and may positively affect brain development in social–cognitive regions. Such development may have broader implications for empathy development and adolescents' ability to mentalize and take the perspective of others' emotions. Our results can inform future interventions for increasing empathy and related prosocial behavior by elucidating the role of relationship quality in promoting social–

cognitive processing. Thus, interventions designed to enhance relationship quality with others may promote greater self–other overlap, thereby enhancing empathy and prosocial relationships in youth.

To our knowledge, this is the first study to directly examine empathy processes with a continuum perspective from the initial perceptual representation to the later mentalizing stage at the neural level by employing both multivariate (i.e. representational neural pattern analysis) and univariate approaches (i.e. general linear model). Moreover, by scanning both mothers and their children, we compared how adolescents' and their mothers' empathy for their family and the self are similar. Our results suggest that mothers have unconditional empathic responses to their child's emotional distress based on higher self–child overlap in their mental representation, whereas adolescents' empathy is more conditional. This study contributes to our knowledge about empathy processes with the critical importance of perceptual representation in mentalizing others' emotional distress.

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