



Neural basis of extraordinary empathy and altruistic motivation

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ABSTRACT

A central evolutionary challenge for social groups is uniting a heterogeneous set of individuals towards common goals. One means by which social groups form and endure is by endowing group members with extraordinary prosocial proclivities, such as ingroup love, towards other group members. Here we examined the neural basis of extraordinary empathy and altruistic motivation in African-American and Caucasian-American individuals using functional magnetic resonance imaging. Our results indicate that empathy for ingroup members is neurally distinct from empathy for humankind, more generally. People showed greater response within anterior cingulate cortex and bilateral insula when observing the suffering of others, but African-American individuals additionally recruit medial prefrontal cortex when observing the suffering of members of their own social group. Moreover, neural activity within medial prefrontal cortex in response to pain expressed by ingroup relative to outgroup members predicted greater empathy and altruistic motivation for one's ingroup, suggesting that neurocognitive processes associated with self identity underlie extraordinary empathy and altruistic motivation for members of one's own social group. Taken together, our findings reveal distinct neural mechanisms of empathy and altruistic motivation in an intergroup context and may serve as a foundation for future research investigating the neural bases of intergroup prosociality, more broadly construed.

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Introduction

Empathy is the capacity to share the emotional states of others (Batson et al., 1981; Preston and de Waal, 2002). The perception-action model of empathy indicates that empathy is a key motivator (Decety and Grèzes, 2006) and the proximate mechanism (de Waal, 2008) of altruistic behavior, whereby an individual perceives and shares in the distress of another person, and acts to reduce his or her suffering (Preston and de Waal, 2002). This perception-action cascade is seen even when altruistic behaviors are costly to the self and when escape from the situation would be easy (Preston and de Waal, 2002; Stocks et al., 2009). Prior research indicates that empathy is a multi-component process that includes affect sharing, cognitive perspective taking, and cognitive appraisal (Decety and Jackson, 2004; Hein and Singer, 2008; Lamm et al., 2007a; Olsson and Ochsner, 2008). Empathy for pain is supported by neuroanatomical circuits underlying both affective and cognitive processes (Decety and Jackson, 2004; Hein and Singer, 2008; Lamm et al., 2007a; Olsson and Ochsner, 2008). First, a distinct neural matrix, including bilateral anterior insula (AI) and anterior cingulate cortex (ACC) (Decety and Jackson, 2004; Hein and Singer, 2008; Olsson and Ochsner, 2008) is thought to

underlie the affective components of empathy. AI and ACC code the autonomic and affective dimension of pain and in particular, the subjective experience of empathy when perceiving pain or distress in others (Decety and Jackson, 2004; Hein and Singer, 2008; Olsson and Ochsner, 2008). Second, cognitive components of empathy, such as the capacity to take another person's perspective, are thought to rely on subregions of medial prefrontal cortex (MPFC) (Lamm et al., 2007a), which responds more when people are identifying with others who are more similar to themselves (Mitchell et al., 2006). Taken together, these findings suggest that the capacity to understand and share another's pain is supported by both affective (e.g., affect resonance) and cognitive (e.g., perspective-taking) mechanisms in the brain.

Empathy has been shown to vary depending on interindividual differences (Chiao et al., 2009; Singer et al., 2004), as well as on subjective judgments of targets made by perceivers (Singer et al., 2006). Under certain circumstances, people display extraordinary empathy and altruism. One route to enhanced empathy and altruism is through the increased inclusion of another person in the conception of the self (Aron et al., 2004). Love for one's social ingroup, resulting in ingroup loyalty or ingroup solidarity, may be an example of extraordinary empathy that is brought about by including other group members as part of one's self concept. Love for one's group members is common and has been demonstrated to increase resource sharing or helping behavior amongst diverse social groups, including

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race (Dovidio et al., *in press*), political affiliation (Rand et al., 2009), and even sports team allegiance (Levine et al., 2005). Furthermore, several models of empathy predict that increased similarity and identification with a target will lead to increased sharing of the experience, enhanced empathy, and increased altruistic motivation (Baron-Cohen and Wheelwright, 2004; Dovidio et al., *in press*; Preston and de Waal, 2002).

Belonging to a particular social group serves as a form of contingent or reciprocal altruism (Brewer, 1999; Hamilton, 1964; Trivers, 1971) whereby individuals expend resources (e.g., money and time) for another group member's benefit with the expectation that sharing of resources by ingroup members will later be reciprocated. For instance, a particularly ubiquitous example of group membership influencing reciprocal altruism is kin selection whereby people and animals expend greater resources and take more risks for their kin (e.g., family member) (Hamilton, 1964). By limiting resource sharing to mutually acknowledged ingroup members, individual costs and risks associated with nonreciprocated altruism may be contained. The human tendency to show extraordinary empathy towards, and respond to the suffering of ingroup more than outgroup members has been demonstrated (Brown et al., 2006), and may serve as a precursor (Preston and de Waal, 2002) to ingroup favoritism in prosocial behavior such as altruism (Bernhard et al., 2006). Notably, intergroup status can influence the extent to which people display ingroup favoritism (Dovidio et al., *in press*; Hewstone et al., 2002). Minority group members tend to display enhanced ingroup identification and favoritism when status differentials are perceived as illegitimate, whereas majority group members may display outgroup favoritism when the intergroup status gap is very wide (Dovidio et al., *in press*; Hewstone et al., 2002). By extension, in social contexts where intergroup status differences are accentuated, racial minority group members, such as African-Americans, may display stronger enhanced empathy favoring the ingroup relative to majority group members (e.g., Caucasian-Americans).

Social group identity, such as race, is a potent modulator of neural responses during social cognition (Chiao et al., 2008; Eberhardt, 2005; Golby et al., 2001; Ito and Bartholow, 2009; Krill and Platek, 2009; Lieberman et al., 2005; Van Bavel et al., 2008; Xu et al., 2009). Prior neuroimaging research has demonstrated that racial majority group members, such as Caucasian-Americans, show greater fusiform and parahippocampal response when perceiving own-race faces (Golby et al., 2001) and either heightened (Eberhardt, 2005; Krill and Platek, 2009; Lieberman et al., 2005) or attenuated (Chiao et al., 2008; Van Bavel et al., 2008) amygdala response to other-race faces, depending on social context. By contrast, members of racial minority groups, such as African-Americans, typically demonstrate greater fusiform (Golby et al., 2001) as well as amygdala activation to own-race faces (Lieberman et al., 2005), suggesting that intergroup status moderates the direction and magnitude of neural responses to ingroup and outgroup members (Chiao et al., 2008; Krill and Platek, 2009; Lieberman et al., 2005; Van Bavel et al., 2008). Additionally, recent neuroimaging studies show that evaluation of similar others is more likely to increase activity within medial prefrontal regions, including the ventral anterior cingulate cortex (Mitchell et al., 2006; Mobbs et al., 2009), suggesting that ingroup preferences resulting from similarity to others may modulate neural activity within this region. Finally, a recent study demonstrated that people have increased activity within the supplementary motor area, ACC, and lateral frontal cortices when viewing same- relative to other-race faces receiving a painful stimulus relative to another-race face (Xu et al., 2009). Notably, prior social neuroscience studies of intergroup relations to date have focused primarily on neural mechanisms associated with outgroup hate, rather than ingroup love (Amodio, 2008; Eberhardt, 2005; Ito and Bartholow, 2009). Additionally, despite a growing body of evidence demonstrating the influence of social identity, such as race, on social brain functioning, little is known about the neural

mechanisms underlying intergroup empathy and altruistic motivation in racial majority and minority group members.

Here we employed functional magnetic resonance imaging to examine neural activity underlying intergroup biases in empathy and altruistic motivation in both majority group (e.g., Caucasian-American) and minority group (e.g., African-American) members. First, we hypothesized that all participants would report empathy in response to the suffering of all targets, and that this would be associated with neural activity within the ACC and AI. Second, we hypothesized that individual variation in ingroup empathy bias, as well as extraordinary empathy and altruistic motivation toward ingroup members would be associated with neural mechanisms underlying cognitive empathy within MPFC.

Methods

Participants

Twenty-eight right-handed volunteers ($M = 23.7$ years, $SE = 0.80$), 14 African-American (10 female), and 14 Caucasian-American (13 female), with normal or corrected-to-normal vision participated in this study and were compensated \$25 for their time. This study was approved by the Northwestern University Institutional Review Board, and informed written consent was obtained from each participant prior to the experiment.

Stimuli

Stimuli consisted of naturalistic visual scenes (640 pixels \times 480 pixels) depicting either African-American (AA) or Caucasian-American (CA) individuals in a painful (e.g., in the midst of a natural disaster) or neutral (e.g., attending an outdoor picnic) situation (Fig. S1A). There were no significant differences in number of people, gender, or age between Pain and No Pain scenes as well as between CA and AA scenes (all $ps > 0.05$).

In a separate stimuli validation experiment, forty-five participants (22 AA, 26 female, $M = 18.8$ years, $SE = 0.14$) rated in how much pain people seemed in each scenario using an 8-point Likert scale (0 = not at all to 7 = very much). As predicted, results from this behavioral validation experiment confirmed that people in the pain scenes were perceived as in significantly more pain relative to people in the no pain scenes [*Pain*: $M = 5.43$, $SE = 0.14$; *No Pain*: $M = 0.62$, $SE = 0.07$; $t(44) = 38.54$, $p < 0.001$]. Furthermore, the AA and CA scenes were matched for pain intensity in the pain condition [*AA Pain*: $M = 5.45$, $SE = 0.14$; *CA Pain*: $M = 5.41$, $SE = 0.14$, $t(44) = 0.76$, $p = 0.453$]. Participants in the validation experiment rated the AA no pain scenes higher in pain intensity than the CA no pain scenes [*AA No Pain*: $M = 0.80$, $SE = 0.08$; *CA Pain*: $M = 0.45$, $SE = 0.07$, $t(44) = 6.93$, $p < 0.001$].

Additionally, AA and CA scenes were matched for valence and arousal in both the pain and no pain conditions. Seven independent coders (3 female, $M = 20.6$ years, $SE = 0.78$) completed valence and arousal ratings for all scenes. Participants rated valence ("How positive or negative does this picture seem?") on a 9-point scale ($-4 =$ very negative to $+4 =$ very positive), and arousal ("At this moment, I feel ____") on an 8-point scale (0 = very relaxed, 7 = very aroused/stressed). No differences in valence [*AA Pain*: $M = -2.52$, $SE = 0.24$; *CA Pain*: $M = -2.76$, $SE = 0.21$, $t(6) = 1.52$, $p = 0.18$; *AA No Pain*: $M = 1.87$, $SE = 0.16$; *CA No Pain*: $M = 1.83$, $SE = 0.23$, $t(6) = 0.89$, $p = 0.78$] or arousal [*AA Pain*: $M = 4.31$, $SE = 0.52$; *CA Pain*: $M = 4.14$, $SE = 0.46$, $t(6) = 1.01$, $p = 0.35$; *AA No Pain*: $M = 2.06$, $SE = 0.52$; *CA No Pain*: $M = 2.21$, $SE = 0.58$, $t(6) = -0.61$, $p = 0.57$] were found between AA and CA scenes. Inter-rater reliability was also high amongst these coders (Cronbach's alpha = 0.99).

Procedure

We employed a block design consisting of sixteen task blocks within a functional run. Each block consisted of six unique trials of that block type. There were four block types depicting either African-Americans or Caucasian-Americans in pain or no pain scenarios (Fig. S1B). There were 4 blocks for each condition (AA Pain, AA No Pain, CA Pain, and CA No Pain). For each trial, a complex visual scene was displayed for 2500 ms, followed by a centered fixation cross for 500 ms. Trials were displayed in a fixed random order. Additionally, there were control blocks which served as a baseline condition to subtract common primary processes (e.g. primary visual process, motor response) during which participants pressed a button with their right index finger when a simple gray square appeared.

During scanning, participants indicated the extent to which they felt empathy for the person in the target image (e.g., how badly do you feel for this person?) using a four point Likert scale (1 = not at all to 4 = very much) with a simple button press. Prior to entering the scanner, participants were shown examples of the task and given a practice trial in order to become familiar with the task.

Outside of the scanner, participants also rated how much money (0 = \$0; 7 = \$105+) and how much time (0 = 0 h; 7 = 105+ h) they would be willing to donate to help each target. Additionally, all participants were asked to complete the Interpersonal Reactivity Index (IRI) as a measure of trait empathy and perspective taking (Davis, 1980), the Social Dominance Orientation (SDO) scale to measure preference for social hierarchy or egalitarianism (Pratto et al., 1994), and the Multigroup Ethnic Identity Measure (MEIM) as a measure of identification with one's own ethnic group (Phinney, 1992). To assess implicit and explicit racial bias, Caucasian-American participants were also asked to complete the Implicit Association Task (IAT) as a measure of automatic race-based negative associations (Greenwald et al., 2003), and the Motivation to Control Prejudice Scale (MCP) (Dunton and Fazio, 1997). Ten of the 14 CA participants completed the IAT, and 11 completed the MCP (Table S2).

Imaging parameters

Functional whole-brain images were acquired using a 3 T Siemens Trio at the Center for Advanced Magnetic Resonance Imaging (CAMRI) facility located at the Northwestern University Medical School in Chicago, IL, USA. We acquired functional images by using T2*-weighted, gradient echo, echo planar imaging sequences [repetition time (TR) = 2000 ms; echo time (TE) = 25 ms; flip angle = 70°; FOV = 20 cm, 64 × 64 matrix; 34 slices; 4 mm slice thickness (no gap); in-plane resolution = 3.0 × 3.0 mm]. A high-resolution anatomical T1-weighted image was also acquired [TR = 2300 ms; TE = 2.91 ms; flip angle = 9°; FOV = 256 mm; 256 × 256 matrix; 160 slices; voxel size = 1.0 × 1.0 × 1.0 mm] for each participant. All stimuli were presented using Presentation software (Neurobehavioral Systems, Albany, CA) and projected onto a half-transparent viewing screen located behind the head coil.

Imaging processing

Functional images were analyzed using SPM2 software (Wellcome Department of Imaging Neuroscience, London, UK) implemented in Matlab (Mathworks, Chesham, MA, USA). The first 6 volumes were discarded due to unsteady magnetization, and all of the remaining volumes were realigned spatially to the first volume and a mean image was created. After a high-resolution image was coregistered onto the mean image, all volumes were normalized to the MNI (Montreal Neurological Institute) space using a transformation matrix obtained from the normalization process of the high-resolution image of each individual participant to the MNI template. The normalized images were then spatially smoothed with an 8 mm Gaussian kernel.

After preprocessing, statistical analysis for each individual participant was conducted using the general linear model (Friston et al., 1994). At the first level, each block of trials was modeled by convolving with a hemodynamic response function. For each participant, a linear regressor was applied to filter noise. In the subtraction analysis, 4 task conditions [Ingroup Pain, Ingroup No Pain, Outgroup Pain and Outgroup No Pain] were modeled separately, including fixation. Random effects analyses were conducted by averaging the contrast images for each effect of interest.

Independent regions of interest analyses were performed on regions-of-interest defined as a sphere (8 mm and 6 mm respectively) centered on a peak voxel defined by prior studies of pain and empathy [ACC: $X = -9, Y = 6, Z = 42$; RAI: $X = 39, Y = 12, Z = 3$; LAI: $X = -48, Y = 12, Z = -3$ (Singer et al., 2004)] and pain and perspective-taking [MPFC: $X = -9, Y = 57, Z = 33$ (Jackson et al., 2006)] using MarsBar toolbox in SPM2 (Brett et al., 2002). MNI coordinates were converted to Talairach using a non-linear transformation (<http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach>). Brodmann areas and brain regions were identified based on the Talairach Atlas (Talairach and Tournoux, 1988). Images for Figs. 2 and 3 were generated using Caret software (Van Essen, 2001), and the PALS human atlas (Van Essen, 2005).

Results

Behavioral results

All participants reported significantly greater empathy for people in the Pain ($M = 2.81, SE = 0.07$) than in the No Pain scenes ($M = 1.08, SE = 0.03$), $t(27) = 24.35, p < 0.001$. Additionally, all participants were willing to donate significantly more money and time to help people in the Pain [Money: $M = 4.78$ (approximately \$50), $SE = 0.27$; Time: $M = 5.25$ (approximately 60 h), $SE = 0.22$] than in the No Pain scenes [Money: $M = 0.68$ (approximately \$0.50), $SE = 0.19$, $t(27) = 15.25, p < 0.001$; Time: $M = 1.45$ (approximately 3 h), $SE = 0.32$, $t(27) = 14.16, p < 0.001$].

Empathy

Consistent with our predictions, there was a significant three-way [(participant race: AA, CA) × (target group: ingroup, outgroup) × (valence: Pain, No Pain)] interaction in empathy ratings, $F(1, 26) = 4.19, p = 0.05$. There was a significant interaction between target group and valence for AA participants, $F(1, 13) = 5.90, p = 0.03$, such that AA participants reported significantly more empathy for ingroup scenes ($M = 3.01, SE = 0.12$) than outgroup scenes ($M = 2.77, SE = 0.12$) in the Pain condition, $t(13) = 2.72, p = 0.02$ (Table S1). CA participants did not differ in their empathy ratings for ingroup or outgroup scenes. There was also a significant interaction between participant race and target group in empathy ratings, $F(1, 26) = 9.48, p = 0.005$ such that AA participants displayed enhanced empathy for ingroup members, but CA participants did not (Fig. 2A, Table S1). Importantly, this ingroup favoritism is not due to outgroup derogation, but rather extraordinary empathy for the ingroup above all other empathy reports across groups. Specifically, participant groups did not differ in their empathy for CA targets [AA: $M = 2.77, SE = 0.12$; CA: $M = 2.69, SE = 0.09$; $t(26) = 0.54, p = 0.59$], or respective outgroup targets [AA: $M = 2.77, SE = 0.12$; CA: $M = 2.75, SE = 0.09$; $t(26) = 0.14, p = 0.89$] (Fig. 2A). Finally, there was no difference between AA and CA participants in overall empathy response for the Pain [AA: $M = 2.89, SE = 0.12$; CA: $M = 2.72, SE = 0.08$; $t(26) = 1.17, p = 0.25$] or No Pain [AA: $M = 1.08, SE = 0.04$; CA: $M = 1.08, SE = 0.04$; $t(26) = 0.04, p = 0.97$] scenes, suggesting that the groups were similarly empathic or similarly likely to report empathy for target people in the stimuli scenes. No other interactions or main effects in empathy ratings were significant (all $p > 0.05$).

Altruistic motivation

There was a significant interaction between participant race and target group in amount of money participants were willing to donate, $F(1, 26) = 11.88$, $p = 0.002$ such that AA participants displayed ingroup favoritism, but CA participants did not. There was a similar two-way interaction between participant race and target group in amount of time participants were willing to donate, $F(1, 26) = 12.67$, $p = 0.001$. AA participants were willing to donate significantly more money and time to help an ingroup target (Money: $M = 5.40$, $SE = 0.35$; Time: $M = 5.77$, $SE = 0.33$) than an outgroup target (Money: $M = 4.80$, $SE = 0.41$; Time: $M = 5.18$, $SE = 0.34$) in the Pain condition, (Money: $t(13) = 2.38$, $p = 0.03$; Time: $t(13) = 2.91$, $p = 0.01$). CA participants did not differ significantly in their altruistic motivation toward ingroup or outgroup members. Moreover, there was no difference between AA and CA participants in overall willingness to donate help in either condition (all $ps > 0.20$).

Behavioral surveys

Two-sample t -tests conducted on behavioral exit surveys after scanning showed that AA ($M = 3.34$, $SE = 0.12$) participants reported greater identification with their own ethnic group (MEIM) than CA ($M = 2.24$, $SE = 0.15$) participants, $t(18) = 5.71$, $p < 0.001$. Additionally, degree of identification was positively and significantly correlated with ingroup empathy bias in behavior across all participants ($R = 0.45$, $p = 0.05$). The correlation between degree of identification and ingroup empathy bias was significant across AA ($R = 0.46$, $p = 0.04$) and marginally significant across CA ($R = 0.61$, $p = 0.06$) participants. There were no significant differences in scores for the SDO or IRI-subscales between AA and CA participants (all $ps > 0.05$, see Table S2).

Across individuals, simple regressions revealed significant relationships between degree of behavioral empathy bias in favor of one's ingroup and both perspective taking (as measured by the IRI subscale, $R = -0.41$, $p = 0.03$) and ethnic identification (as measured by the MEIM, $R = 0.46$, $p = 0.04$). No additional significant correlations were found between social attitude (i.e., IAT, MCP, SDO) scores and behavioral ingroup biases in reaction time or empathy ratings (all $ps > 0.05$).

fMRI results

To verify whether the pain stimuli were evoking empathic neural responses, a whole-brain voxel-wise analysis was performed on the simple contrast [Pain > No Pain] with a threshold of $p < 0.005$, extant threshold = 10 voxels (Fig. 1A, Table S3). A whole-brain regression was also performed on the simple contrast [Pain > No Pain] using online empathy ratings as a behavioral covariate with a threshold of $p < 0.005$, extant threshold = 10 voxels. Consistent with previous studies of empathic neural responses, the main effect of pain recruited areas of the pain matrix associated with the processing of pain and empathy. Across all participants, increased activation in bilateral AI and ACC was observed for the Pain scenes relative to the No Pain scenes (Fig. 1A, Table S2). Whole-brain regression analysis revealed a positive and significant correlation between degree of self-reported empathy for Pain scenes and neural response to pain targets within the ACC and right AI (ACC: $R = 0.62$, $p < 0.001$, Fig. 1B; AI: $R = 0.54$, $p = 0.003$, Fig. 1C). Altruistic motivation was not correlated with activity within these regions (all $ps > 0.05$).

To identify the main effect of group membership of the participant in relation to the group membership of the target stimuli on neural activity, a whole-brain voxel-wise analysis was performed on the simple contrast [Ingroup > Outgroup], and the reverse contrast [Outgroup > Ingroup], with a threshold of $p < 0.005$, extant threshold = 10 voxels (Tables S4 and S5), where the Ingroup condition included the neural response to both Ingroup Pain and Ingroup No Pain scenes and the Outgroup condition included the response to both Outgroup Pain

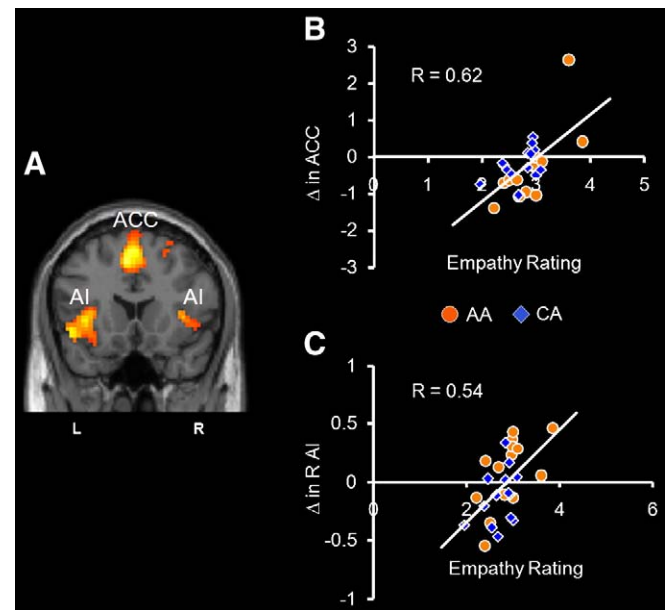


Fig. 1. (A.) Main effect of pain [Pain > No Pain], $y = 18$. (B., C.) Independent regression analyses [(B.) ACC regression performed on peak voxel: 3, -9, 45; (C.) right AI regression performed on 39, 12, 5] of [Pain > No Pain] with empathy rating as the covariate. ROIs defined by [Pain > No Pain] contrast.

and Outgroup No Pain scenes. More specifically, for AA participants, the contrast was modeled as [AA (Pain + No Pain) > CA (Pain + No Pain)], and for CA participants the contrast was [CA (Pain + No Pain) > AA (Pain + No Pain)]. Results from these analyses are reported in Tables S4 and S5, but are not further discussed here.

To identify neural responses underlying ingroup empathy biases in each participant group, whole-brain voxel-wise two-sample (AA and CA participants) analyses were performed on the contrast [Ingroup Pain > Outgroup Pain] with a threshold of $p < 0.005$, extant threshold = 10 voxels (Tables S6 and S7). Determination of what stimuli were ingroup or outgroup pain conditions was based on the race of the participant relative to the race of the stimuli target. African-American participants, who displayed ingroup favoritism in their behavioral empathy ratings, revealed increased activation within the MPFC in response to ingroup relative to outgroup pain scenes compared to CA participants (Table S6, Fig. 2B). By contrast, CA participants showed increased activation within bilateral parahippocampal gyrus and posterior cingulate cortex in response to ingroup relative to outgroup pain scenes compared to AA participants (Table S7, Fig. 2B), which is consistent with prior evidence of increased encoding-related neural activity for ingroup targets within medial temporal lobe among Caucasian-Americans (Golby et al., 2001).

Post-hoc region of interest analyses were performed on bilateral regions of the dorsolateral prefrontal cortex associated with regulation of racial bias. ROIs were defined as 8 mm spheres centered on peak voxels from a prior study [RDLPFC: $X = 39$, $Y = 48$, $Z = 27$; LDLPFC: $X = -39$, $Y = 48$, $Z = 27$ (Richeson et al., 2003)]. Importantly, analyses revealed that activity within the DLPFC was not greater in response to outgroup relative to ingroup across participants, and among CA participants only; nor was there greater response among CA relative to AA participants within these ROIs, suggesting differences in neural and behavioral responses between participant groups is not due to regulation of racial bias.

A 2 (participant race: AA, CA) \times 2 (target: ingroup, outgroup) \times 2 (valence: Pain, No Pain) repeated measures ANOVA was conducted on percent signal change within MPFC. There was a significant interaction between participant race and target group, $F(1, 26) = 8.70$, $p = 0.007$. Independent sample t -tests revealed significantly greater signal change among AA relative to CA participants in response to

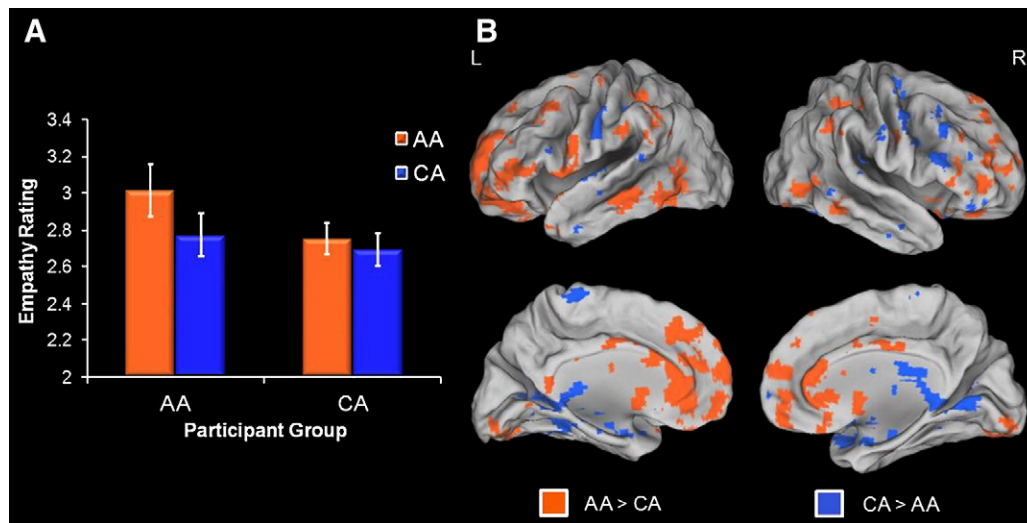


Fig. 2. (A.) Behavioral results for the empathy task. AA participants show enhanced empathy for ingroup targets relative to outgroup targets, and relative to CA participants. $*p < 0.05$ (B.). Results from whole-brain interaction analysis [Participant race (AA, CA) \times Target group (Ingroup > Outgroup)] revealing significantly greater activity within MPFC regions in AA relative to CA participants when judging empathy for ingroup relative to outgroup targets.

Ingroup Pain scenes [$t(26) = 2.41, p = 0.02$]. No other comparisons were significant (all $ps > 0.05$).

Additionally, whole-brain regression analyses were performed using the contrast image [Ingroup Pain > Outgroup Pain] with the relative ingroup biases in empathy and altruistic motivation calculated from behavioral reports [Ingroup – Outgroup] as the covariates of interest. To test hypotheses about regional specific covariate effects, the estimates were compared using a linear contrast with significance levels at $p < 0.005$, extent threshold = 10 voxels (Tables S8–S10, and Fig. 3B). Whole-brain regression analyses revealed that favorable ingroup biases (ingroup – outgroup) in empathy and altruistic motivation were correlated with activity within MPFC in response to ingroup relative to outgroup pain scenes (Fig. 3B, Tables S8–S10). Activity within this independently defined MPFC region was positively and significantly correlated with degree of behavioral ingroup bias of empathy and altruistic motivation (Fig. 3C).¹

Across individuals, simple regressions revealed a significant positive relationship between ingroup favoritism in activity within the MPFC and ingroup favoritism in behavioral empathy reports ($R = 0.77, p < 0.001$), willingness to donate money ($R = 0.70, p < 0.001$), and willingness to donate time ($R = 0.65, p < 0.001$). Ingroup favoritism in activity within the MPFC was also negatively associated with perspective taking ($R = -0.50, p = 0.007$). These results suggest that increased perspective taking is associated with decreased activity within the MPFC in response to ingroup relative to outgroup pain. No additional significant correlations were found between IRI-subcales, IAT, MCP, or SDO scores and neural ingroup biases (all $ps > 0.05$).

Furthermore, simultaneous multiple regression analyses suggest the best model for predicting ingroup favoritism in empathy was the model including the independently significant predictors ethnic identification and MPFC activity, $R^2 = 0.75, F(2,17) = 24.88, p < 0.001$. Additionally, even after controlling for individual differences in perspective taking, ethnic identification ($\beta = 0.34, t(16) = 2.65, p = 0.02$) and MPFC activity in response to ingroup relative to outgroup pain scenes ($\beta = 0.72, t(16) = 4.57, p < 0.001$) remain significant independent predictors of behavioral ingroup favoritism in empathy. Ethnic identification was not significantly correlated with

MPFC response to ingroup or outgroup scenes independently (all $ps > 0.05$).

Discussion

Here we demonstrate that extraordinary empathy and altruistic motivation for ingroup members is associated with neural regions underlying cognitive, but not affective, components of empathy. Consistent with prior social neuroscience studies of empathy, we found that empathy was associated with affective neural response with the ACC and bilateral insula, irrespective of social group membership (i.e., race). Importantly, our findings indicate for the first time that African-Americans who experienced greater empathy for ingroup members relative to Caucasian-Americans in pain also showed greater response within the MPFC for ingroup relative to outgroup members in pain. Additionally, across individuals, activity within the MPFC when perceiving pain expressed by ingroup relative to outgroup members predicted the degree to which people demonstrated an ingroup bias in empathy and altruistic motivation at a behavioral level. Whereas empathy for humankind is associated with affective empathic processing, the current findings demonstrate that extraordinary empathy and altruistic motivation for members of one's own social group is associated with cognitive empathic processing.

There are several possible explanations for why people display extraordinary empathy and altruistic motivation for members of one's own group. One likely explanation is reciprocal altruism (Trivers, 1971) whereby people tend to help family members (Hamilton, 1964), or those who they expect to return the favor (Rand et al., 2009). That is, people may demonstrate greater empathy and altruism towards ingroup members because they believe that ingroup members are more likely to share resources with them in the future. Although reciprocal altruism theory is a compelling explanation for ingroup love broadly construed, we suggest that reciprocal altruism is an incomplete explanation for the current findings, as reciprocal altruism cannot account why African-Americans, but not Caucasian-Americans, showed extraordinary empathy and altruistic motivation for group members.

A second possible explanation is that both African-Americans and Caucasian-Americans demonstrate reciprocal altruism, however, Caucasian-Americans, as a racial majority group, also exhibit self-regulation of their reciprocal altruistic motivation in order to maintain

¹ One AA participant was a significant outlier in all regression analyses. When this participant was excluded from the analyses, all correlations either remained significant or became trends (all $ps \leq 0.08$).

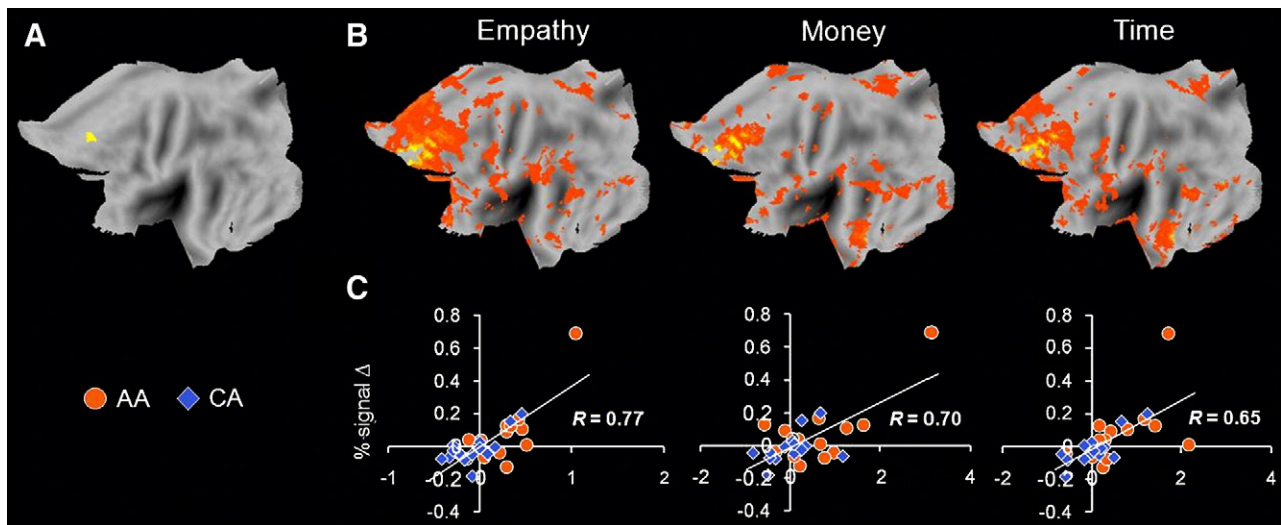


Fig. 3. (A.) Independently defined region of interest within the MPFC region based on a prior neuroimaging study on perspective-taking during empathy [$X = -9, Y = 57, Z = 25$]; (B.) Results from whole-brain regression analyses using [Ingroup Pain > Outgroup Pain] contrast image and behavioral ratings for empathy felt for the target, money willing to donate to help the target, and time willing to donate to help the target respectively [Ingroup Pain – Outgroup Pain.]; (C.) Correlation analysis performed using activity within the independently defined ROI and ingroup bias behavioral ratings for empathy for, money willing to donate to, and time willing to donate to help the target, respectively. The x-axis for all three scatterplots depicts the relative magnitude of ingroup bias [Ingroup Pain – Outgroup Pain] across all participants (all $p \leq 0.001$). Note: Upper range outlier is the same participant in all cases. When this participant is excluded from analyses, all correlations either remain significant or become trends (all $p \leq 0.08$).

an a more egalitarian appearance. Consistent with this view, prior neuroimaging research has shown that Caucasian-Americans exhibit greater dorsolateral prefrontal cortex (DLPFC) response to African-American faces when regulating their racial bias (Richeson et al., 2003). However, the present results show that neural response to outgroup faces within brain regions associated with regulation of racial bias (DLPFC) did not differ between CA and AA participants. Hence, it is unlikely that the lack of ingroup favoritism in empathy and altruistic motivation in Caucasian-Americans observed in the current study is due to self-regulation of racial bias.

A third possible explanation is that interindividual and intergroup variation in social and political attitudes, such as implicit racial bias or preferences for egalitarianism, leads to interindividual and intergroup variation empathy and altruistic motivation. For instance, people who exhibit greater implicit racial prejudice or lower preference for egalitarianism may be more likely to display greater empathy and altruistic motivation towards ingroup members as well as less prosocial proclivities towards outgroup members. However, Caucasian-Americans and African-Americans in the current study did not differ in their degree of preference for egalitarianism. Moreover, the current findings revealed no relationship between implicit racial bias or social dominance orientation and behavioral or neural empathic response and altruistic motivation across individuals. Hence, we suggest that social and political attitudes are not a plausible explanation for extraordinary prosocial proclivities towards members of one's own group observed in the current study.

A fourth possible explanation is that people are more likely to take the perspective of members of their own group. Prior research has shown that individual variation in empathy modulates neural activity during on-line empathy tasks (Singer et al., 2004), and perspective taking, specifically, relies on activity within the MPFC (Vogel and Fink, 2003). Moreover, interindividual differences in perspective-taking have been shown to correlate with individual differences in MPFC during empathic responding (Lamm et al., 2007b). This prior work suggests that the greater MPFC activity for ingroup members in pain observed in the current study may reflect greater ability to take the perspective of ingroup members in painful scenarios. However, perspective taking has also previously been shown to decrease ingroup favoritism (Galinsky and Ku, 2004).

Consistent with this prior work, we observed in the current study that interindividual variation in perspective taking was negatively associated with ingroup favoritism in empathy in both behavioral and neural response. However, the current results further reveal that although African-Americans demonstrate greater ingroup empathy and altruistic motivation, they did not show greater perspective taking ability relative to Caucasian-Americans. Additionally, results from multiple regression analyses further revealed that when accounting for MPFC activity, perspective taking was not a unique predictor of ingroup favoritism in empathy. When controlling for perspective taking, racial identification emerges as a significant predictor, along with MPFC activity, of ingroup favoritism in empathy, suggesting that individual differences in perspective taking do not sufficiently explain interindividual differences in empathy observed in the current study.

A more plausible explanation for the current findings is that inclusion of other group members in one's self concept underlies intergroup and interindividual differences in extraordinary empathy and altruistic motivation. Prior social psychological research has shown that inclusion of another person in the self leads to enhanced empathy (Aron et al., 2004) and altruistic motivation (Cialdini et al., 1997). Supporting this view, African-Americans in the current study reported greater identification with their social group relative to Caucasian-Americans, a finding that is consistent with prior studies showing that racial minority members often exhibit greater ease in identifying with their social group relative to racial majority members (Knowles and Peng, 2005; Phinney, 1996). Moreover, individual differences amongst African-Americans in degree of ingroup identification were positively associated with ingroup empathy in the current study. Finally, across all individuals, increased MPFC activity was correlated with intergroup and interindividual differences in ingroup empathy and altruistic motivation. Although degree of racial identification was not significantly correlated with ingroup favoritism in altruistic motivation, identification and MPFC activity predicted ingroup favoritism in empathy, and both ingroup favoritism in empathy and in MPFC activity predicted the like in altruistic motivation. Consistent with the perception-action model (Preston and de Waal, 2002), this suggests a proximate mechanism by which identification leads to ingroup favoritism in empathy, and a distal

mechanism by which this modulation of empathy results in ingroup favoritism in altruistic motivation. Consistent with prior social neuroscience studies of MPFC and the self (Amodio and Frith, 2006; Northoff et al., 2006), we suggest that MPFC response in the current study reflects greater self evaluative processing when viewing ingroup relative to outgroup members in pain, likely due to greater perceived similarity between ingroup relative to outgroup members (Krill and Platek, 2009; Mobbs et al., 2009; Platek and Kemp, 2009). Notably, it remains unknown what aspects of similarity may be associated with increases in MPFC response. For instance, Hamiltonian kin selection theory posits that reciprocal altruism is driven by genetic similarity, whereas recent empirical evidence has demonstrated an association between perceived similarity as indexed by self-report and greater response within the MPFC region. An important direction for future research will be to disentangle the relative contributions of genetic and perceived similarity on neural response when evaluating ingroup and outgroup members. Nevertheless, taken together, our findings suggest that greater group identification or inclusion of other group members in one's self concept can lead to extraordinary empathy and altruistic motivation for members of one's own group. Future research may also examine a broader range of ways in which inclusion of other group members in one's self concept may be expressed or measured and how collective identification more broadly construed predicts extraordinary empathy and altruistic motivation at neural and behavioral levels of analysis.

As a social species, humans have evolved for cooperative living in social groups and possess potent psychological and neural mechanisms that foster adaptive sociality. In particular, empathy serves as a powerful means by which individuals share and respond to the emotional states of others. Importantly, effective cooperative living sometimes entails belonging to smaller social groups and limiting resource sharing to members of that group so that individual costs and risks associated with nonreciprocated altruism are reduced. Here we show that empathy for ingroup members is neurally distinct from empathy for humankind, more generally. People recruit affective neural circuitry when observing the suffering of others, but additionally recruit cognitive neural processes when observing the suffering of members of their own social group. Our findings further indicate that cognitive, but not affective, empathic neural processing is associated with subsequent altruistic motivation. The current work reveals distinct neural mechanisms of empathy and altruistic motivation in an intergroup context and may serve as a foundation for future research investigating the neural bases of intergroup prosociality, more broadly construed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2010.03.025.

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