



The ties that bind: Group membership shapes the neural correlates of in-group favoritism



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ABSTRACT

Across species, including non-human primates, rodents, and humans, prosocial behavior, the act of helping others, is preferentially provided to members of one's own group. Whereas a particularly ubiquitous example of this is kinship, whereby humans and animals expend greater resources and take more risks for their own kin, in-group prosocial behavior has been demonstrated among diverse shared social groups, including race and culture. In the current study, we made group membership salient by recruiting Chinese and American participants to engage in a prosocial decision-making task during fMRI with an American and Chinese confederate. We found across all participants that donations to the in-group relative to out-group was associated with increased activation in the ventral striatum. Moreover, participants with a greater sense of group identity and Chinese participants relative to American participants, showed heightened activation in self-control (VLPFC, ACC) and mentalizing (TPJ, DMPFC) regions when contributing to the out-group relative to in-group. Our findings provide novel evidence about the neural mechanisms involved in intergroup prosocial behavior.

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Across species, including non-human primates, rodents, and humans, preferential treatment is provided to members of one's own group (Bartal et al., 2014; Levine et al., 2005; Flippen et al., 1996). Such in-group biases develop early, with infants and young children demonstrating strong preferences that favor their own group over the out-group (Patterson and Bigler, 2006; Mahajan and Wynn, 2012). While a particularly ubiquitous example of group membership is kinship, whereby humans and animals expend greater resources and take more risks for their own kin (Hamilton, 1964), in-group biases have also been demonstrated among diverse social groups, including race, culture, religion, political affiliation, residential community, university affiliation, and sports team allegiance (Mathur et al., 2010; Stürmer et al., 2006; Rand et al., 2009; Hornstein, 1972; Levine et al., 2005; Platos et al., 1999; van Vugt and Hart, 2004). In-group preference is even found within minimal groups, that is, individuals who are assigned to belong to the same group based on an arbitrary trait (e.g., eye color), shared preference (e.g., artwork), or even random assignment (Tajfel et al., 1971), suggesting a basic need to affiliate and prefer in-group members. Indeed, strong in-group identification fulfills many basic human needs, from promoting a group's chances for survival and reproduction to increasing a sense of belonging and self-esteem (Brewer, 1991; Tajfel and Turner, 1979; Hogg, 2003). By limiting prosocial behavior to in-group members,

risk of nonreciprocation is limited, and mutual trust, loyalty, and cooperation are developed among the in-group (Brewer, 1999).

According to social identity theory, individuals attach positive utility to the welfare of their own group members but no utility, or even negative utility, to the welfare of out-group members (Tajfel, 1974). Individuals will therefore feel the benefits (i.e., feel good) when their own group is doing well but derive no benefit or even feel worse when members of the out-group are experiencing improvements in their welfare. Such in-group positivity biases have been shown to affect prosocial behaviors. For example, people are more likely to help an in-group member than an out-group member in similar need and distribute more resources to in-group than out-group members (Levine et al., 2005; Flippen et al., 1996), especially when individuals are highly committed to their group (Ellemers et al., 1999, 2002). Indeed, one's overall sense of connection to and identification with a social group results in greater in-group loyalty. Thus, when a social identity is particularly salient, a greater sense of collective identity among in-group members will result in greater feelings of closeness and an increased sense of responsibility for in-group members (Brewer and Kramer, 1986; Levine et al., 2005; Stürmer et al., 2005; Zaleski, 1992). In contrast, individuals whose identification is weak or absent are more likely to view themselves as unique individuals rather than as members of a collective group and will therefore be less likely to place weight on collective gains over individual gains (Stürmer et al., 2005). Therefore, prosocial behavior to in- and out-group members will depend on how much individuals regard themselves as sharing

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membership in and identification with their larger social group (Brewer and Kramer, 1986).

While biases favoring one's own group may be somewhat universal, as seen across species and diverse social groups, cultural values and norms may shape the extent to which one engages in preferential treatment to the in-group. For example, in interdependent societies like China, prosocial behaviors to in-group members are highly valued and encouraged because they are seen as essential to the functioning of the collective group by promoting in-group solidarity (Chen et al., 2002; Kimmelman et al., 2006). Individuals from China often see their role as an individual in relation to family or society, and their primary obligations are to support in-group members (Stevenson, 1991; Markus and Kitayama, 1991). Moreover, ingroup-outgroup boundaries are more rigid, and so individuals from interdependent societies are less likely to help out-group members (Eckstein, 2001; Kimmelman et al., 2006). In contrast, individuals from Western societies, like the United States, are more likely to focus on personal need, and prosocial behavior is seen as a matter of individual agency (Kimmelman et al., 2006). Their focus on individuals rather than group solidarity guides prosocial decisions based on those who are valued and deserving apart from their group membership (Kimmelman et al., 2006). Although in-group biases are still highly salient, American individuals are less in-group focused compared to East Asian individuals.

Theories of helping suggest that the psychological processes and motivations differ when helping in-group and out-group members (Dovidio et al., 1997). Yet, the neural mechanisms supporting in- and out-group prosocial behaviors have not been empirically tested. By incorporating a social cognitive neuroscience perspective, we can begin to untangle the underlying mechanisms that lead an individual to orient more towards in-group prosocial behavior. Although no study to date has examined the neural correlates of helping members of ones in-versus out-group, significant work has examined the neural correlates of prosocial behavior more generally (e.g., Moll et al., 2006) as well as the neural correlates of empathy for in- and out-group members' suffering (Hein et al., 2010). Building upon this previous research, we hypothesize that three primary neural networks will be involved in in-group relative to out-group prosocial decision-making, including the reward, self control, and mentalizing networks.

Recent neuroimaging research has shown that prosocial behaviors may be guided by feelings of reward. For instance, financial sacrifices for charities, strangers, and family members engage the mesolimbic reward network, including the ventral striatum and medial orbitofrontal cortex (mOFC) (Harbaugh et al., 2007; Izuma et al., 2010; Moll et al., 2006; Telzer et al., 2010). Given that individuals feel good when their own-group is doing well and that it is rewarding to belong to a social group (Tajfel, 1974), we hypothesized that prosocial decisions to help in-group members relative to out-group members would be associated with heightened reward-related activation. Indeed, prior work has shown that rewarding in-group members leads to increased activation in the ventral striatum and mOFC compared to rewarding out-group members (Molenberghs et al., 2014).

In addition, prosocial decisions may be guided by self-control and mentalizing. Individuals who are particularly oriented to their in-group feel more in-group loyalty, greater self-other overlap with in-group members, and greater self-other dissimilarities with out-group members (Brewer and Kramer, 1986; Stürmer et al., 2005, 2006; Zaleski, 1992). Thus, individuals who more strongly identify with their social group will likely identify more with unfamiliar in-group members and feel less social distance among group members, making it less likely that they will make strong distinctions between their own and an in-group member's welfare (Brewer and Kramer, 1986). Prior neuroimaging research has found that prosocial decisions engage both the self control (e.g., ventrolateral prefrontal cortex (VLPFC); anterior cingulate cortex ACC)) and mentalizing networks (e.g., dorsomedial prefrontal cortex (DMPFC), temporal parietal junction (TPJ)), suggesting that prosocial decisions are

guided, in part, by the ability to both regulate and control one's automatic feelings and behaviors as well as focus attention on the needs and values of others (Telzer et al., 2011). While these brain networks may be involved in prosocial decisions more broadly, they may be differentially recruited depending on whether one is helping the in-group or out-group. Helping in-group members may be a more automatic decision whereas helping out-group members may be more effortful and systematic. For example, decisions to help out-group members may involve carefully contemplating the costs and benefits resulting from helping the out-group (Stürmer et al., 2006). Therefore, prosocial behavior towards out-group members may engage brain regions involved in cognitive control and mentalizing to a greater extent due to the social distance and effort involved in such decisions. Particularly in competitive instances, prosocial decisions to out-group members may elicit more activation in mentalizing regions (see Cikara and van Bavel, 2014). Alternatively, it is also possible that in-group relative to out-group prosocial donations elicit greater activation in these neural networks. For example, prior research has shown that individuals engage in less spontaneous mentalizing for out-group members and show greater activation in brain regions involved in mental state attribution and empathy when decoding the mental states of in-group members (Adams et al., 2010; Mathur et al., 2010; see Cikara and van Bavel, 2014). Other research has also shown greater activation in the DMPFC when allocating points to an in-group versus out-group member (Volz et al., 2009).

In the current study, we examined the behavioral and neural mechanisms involved in in- and out-group prosocial behavior among individuals from China and the United States. In order to make group membership salient, American (all White, European American) and Chinese (all born in China and living in the United States for less than one year) participants were introduced to an American and Chinese confederate. During an fMRI scan, participants had the option to make costly financial contributions to both the in-group and out-group confederates. We examined whether there are both common (i.e., neural patterns that are similar between American and Chinese individuals) as well as culture-specific processes (i.e., differential neural patterns between American and Chinese individuals) involved in intergroup prosocial behaviors. We examined this by testing three primary research questions: (1) Across participants, are there common neural patterns that differentiate decisions to provide support to in-group relative to out-group members? (2) Does a stronger sense of group identity enhance in-group biases? and (3) Are there culture-specific neural processes involved in providing support to in-group relative to out-group members? Providing initial evidence for cultural differences in neural processing to prosocial behavior, we recently found that youth from Latin-American backgrounds (a culture that emphasizes in-group solidarity) show greater reward-related neural activation when contributing to their kin (i.e., in-group) than do European-American youth (Telzer et al., 2010). In the current study, we extend this work by examining culture-specific neural processing of intergroup behavior to both in-group and out-group members.

Methods

Participants

Twenty-nine first-year undergraduate students participated in the current study. Three participants did not provide enough donations during the prosocial task for analyses. Our final sample therefore included 26 participants, 13 American (6 male, $M = 19.02$ years) and 13 Chinese (7 male, $M = 19.38$ years). All American participants were born in the United States, and all Chinese participants were born in China and had moved to the United States less than one year prior to their scan. Participants provided written consent in accordance with the University of Illinois' Institutional Review Board.

Pre-scan procedure

Prior to the scan, all participants were trained on the prosocial task. Chinese participants were trained in Chinese by a native Chinese speaking experimenter and American participants were trained in English by an American experimenter. In order to bolster the validity of the task as well as the salience of cultural identity, following the training, each participant interacted with one American confederate and one Chinese confederate (both gender- and age-matched). An experimenter told each participant that he or she would meet two other participants (confederates) who were completing a different decision-making experiment, and that it would be important for each of them to get to know each other so that they could make informed decisions during their respective tasks. The experimenter brought the participant into a room where the confederates were waiting with another experimenter. One experimenter explained to the participant and the confederates that they would complete an “ice-breaker” session in which they would each respond to a series of questions about themselves (e.g. what is your favorite food?; who is your favorite actor?; what is your favorite band?). In order to encourage participants to attend to the confederates’ responses, the experimenter informed the participants that they would be quizzed on each other’s responses. The

participant and confederates were given a few minutes to write their responses and were then asked to read their responses aloud to the group. The confederates provided answers that emphasized their cultural identity (e.g. favorite food: American = hamburger, Chinese = lo mein; favorite actor: American = Johnny Depp, Chinese = Bruce Lee). Once the participant and confederates had finished reading their responses, the experimenter quizzed the group on the responses asking participants and confederates to take turns answering which of them had provided a given response to each question. The participant and confederates then posed for a picture to be used during the prosocial task.

Prosocial task

During the fMRI scan, participants completed a modified dictator game (Zaki and Mitchell, 2011), in which they were presented with a series of financial offers to keep one sum of money or donate a different sum of money to one of the other confederates. During each trial, participants were presented with a picture of themselves and a picture of one of the confederates. Above each picture was a dollar amount separated by the word “or” for American participants or the semantically equivalent character “或” for Chinese participants. Each trial included the participant’s picture and one of the confederates (Fig. 1). The participants’

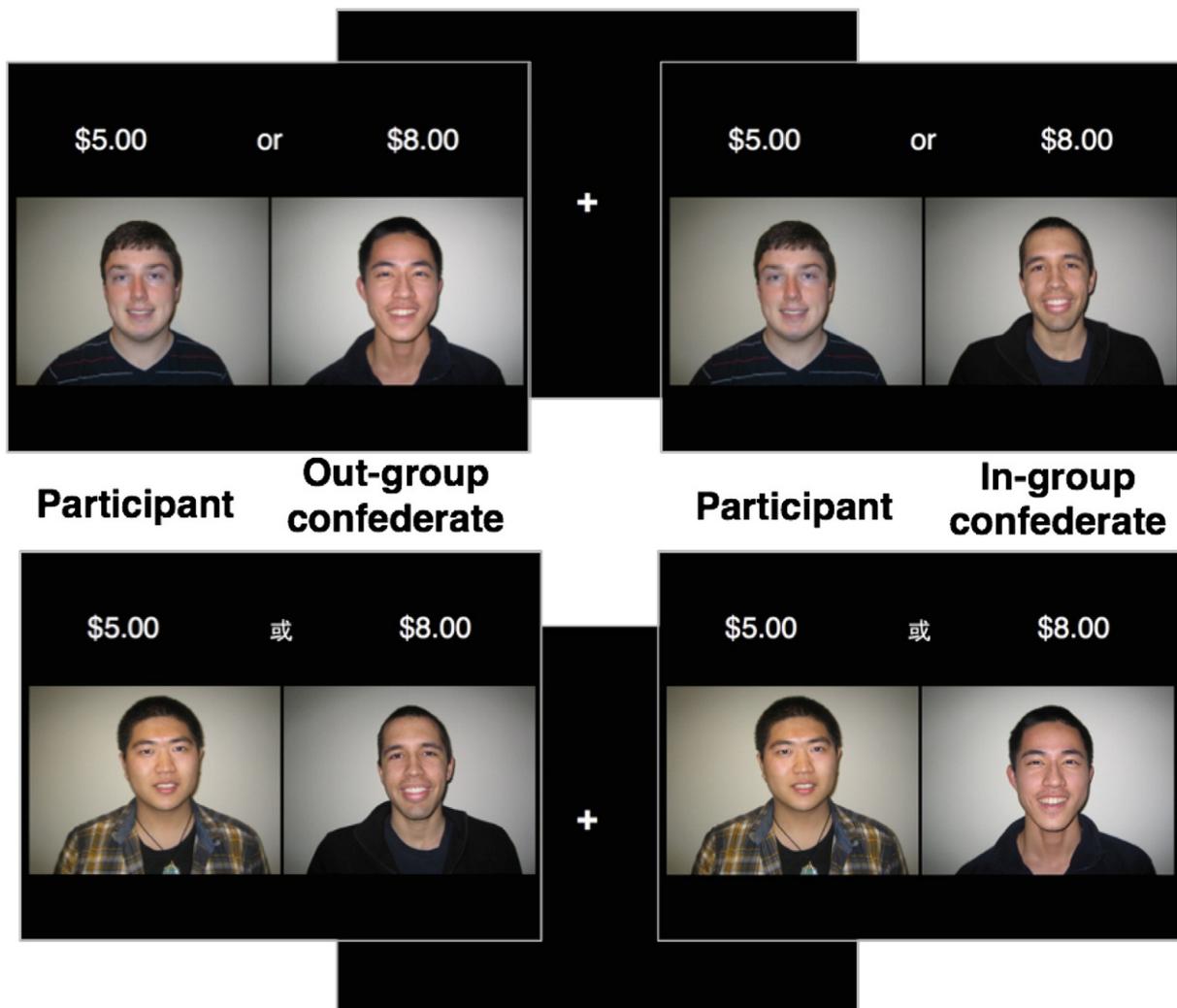


Fig. 1. Example trials of the prosocial task. Images along the top panel are for an American participant, and images along the bottom panel are for a Chinese participant.

picture appeared on the right on half of the trials and on the left on the other half. Participants selected which financial offer they would accept by pressing a button under either their left or right index fingers (i.e. left button presses accepted the offer for the person on the left, and right button presses accepted the offer for the person on the right).

Participants completed a total of 148 trials, divided across two functional runs. Three types of trials were presented. In-group donations (64 trials), during which participants could choose to sacrifice earning money in order to donate to the in-group confederate; out-group donations (64 trials), during which participants could choose to sacrifice earning money in order to donate to the out-group confederate; pure rewards (20 trials), during which the participant could earn money at no cost to the confederates. Because of low acceptance rates for prosocial decisions, three participants were excluded from analyses as they had too few trials for analysis (2 participants accepted 0 trials for in- and out-group donations, and 1 participant accepted 4 and 8 trials respectively). All other participants had at least 12 trials with an average of 28 trials per condition.

Each trial was presented for 2 seconds and was separated by an inter-trial interval, which displayed a fixation cross for an average of 2.5 seconds (range = 1.5–5 seconds). The value of each financial offer ranged from \$1 to \$9, and the ratio between the participant and the confederates' earnings varied. Participants saw 74 unique payments, which were presented twice, once per confederate. Trials were presented in a pseudorandom order.

Prior to completing the task, an experimenter told participants that 5 trials would be randomly selected from their responses on the task, and that participants' decisions would be honored for those 5 trials (i.e. if participants chose to keep money for themselves during any of those 5 trials, they would receive the corresponding amount of money in addition to \$50 for completing the study, and if participants chose to give money to either of the confederates during any of those 5 trials, the confederates would receive the corresponding amount of money). The experimenter also explained to participants that if confederates received any money because of the participants' decisions during this task, no one would inform the confederates of the participants' responsibility in determining that extra payment. Explaining this was important in minimizing participants' motivation to respond to the task in a way that would bolster his or her reputation.

fMRI data acquisition and analysis

fMRI data acquisition

Imaging data were collected using a 3 Tesla Siemens Trio MRI scanner. The Prosocial task included T2*-weighted echoplanar images (EPI) [slice thickness = 3 mm; 38 slices; TR = 2 sec; TE = 25 msec; matrix = 92x92; FOV = 230 mm; voxel size 2.5x2.5x3mm³]. Structural scans consisted of a T2*-weighted, matched-bandwidth (MBW), high-resolution, anatomical scan (TR = 4 sec; TE = 64 msec; FOV = 230; matrix = 192x192; slice thickness = 3 mm; 38 slices) and a T1* magnetization-prepared rapid-acquisition gradient echo (MPRAGE; TR = 1.9 sec; TE = 2.3 msec; FOV = 230; matrix = 256x256; sagittal plane; slice thickness = 1 mm; 192 slices). The orientation for the MBW and EPI scans was oblique axial to maximize brain coverage.

fMRI data preprocessing and analysis

Neuroimaging data were preprocessed and analyzed using Statistical Parametric Mapping (SPM8; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Preprocessing for each participant's images included spatial realignment to correct for head motion (no participant exceeded 2 mm of maximum image-to-image motion in any direction). The realigned functional data were coregistered to the high resolution MPRAGE, which was then segmented into cerebrospinal fluid, grey matter, and white matter. The

normalization transformation matrix from the segmentation step was then applied to the functional and T2 structural images, thus transforming them into standard stereotactic space as defined by the Montreal Neurological Institute (MNI) and the International Consortium for Brain Mapping. The normalized functional data were smoothed using an 8 mm Gaussian kernel, full-width-at-half maximum, to increase the signal-to-noise ratio. Statistical analyses were performed using the general linear model in SPM8. Each trial was convolved with the canonical hemodynamic response function. High-pass temporal filtering with a cutoff of 128 seconds was applied to remove low-frequency drift in the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model order of 1.

In each participant's fixed-effects analysis, a general linear model (GLM) was created with the regressors of interest, which included (1) decisions to donate to the in-group, (2) decisions to keep the reward over the in-group, (3) decisions to donate to the out-group, (4) decisions to keep the reward over the out-group, and (5) pure reward trials. The task was modeled as an event-related design, with the duration of each trial lasting 2 seconds. Null events, consisting of the jittered inter-trial intervals were not explicitly modeled and therefore constituted an implicit baseline. The parameter estimates resulting from the GLM were used to create linear contrast images comparing each of the conditions of interest. The individual subject contrasts were then submitted to random-effects, group-level analyses. As done in prior research, our primary analyses focused on the trials in which participants chose to make donations (i.e., costly, prosocial decisions; Moll et al., 2006; Telzer et al., 2010, 2011, 2013). We conducted the following analyses at the group-level: (1) one-sample t-tests examining neural regions involved in donating to in-group > out-group members across the whole sample (controlling for cultural group), (2) regression analyses correlating group identity with neural activation during donations to in-group > out-group, and (3) two-sample t-tests to compare American and Chinese participants' neural activation when donating to in-group > out-group. All group-level analyses included covariates for the percentage of decisions donated to the in-group and the out-group in order to control for differences in the number of trials across participants. By controlling for the number of trials, all significant clusters of activation are likely due to the contrast of interest rather than to individual differences in the number of trials available in the analysis.

Thresholds for reporting neural activity were determined using 3dClustSim in the software package AFNI (Ward, 2000), which estimates combinations of voxel-wise *p*-values and cluster extents (in voxels) that together control the false discovery rate. We investigated activity within a mask of *a priori* brain regions. Using ROIs adds specificity to our analyses relative to a whole-brain search and helps to minimize the Type I error rate. We created a mask which included reward regions (ventral striatum, mOFC), mentalizing regions (DMPFC, TPJ, pSTS), and self-control regions (DLPFC, VLPFC, ACC). These ROIs were created structurally based on prior studies using similar tasks and the same structural ROIs (see Telzer et al., 2011, 2014) or ROIs based on structures within the Automated Anatomical Labeling atlas (AAL; Tzourio-Mazoyer et al., 2002). The mask included 4,512 voxels. For a full description of the ROI see Supplementary methods and Supplementary Fig. 1. Results of the 3dClustSim indicated a voxel-wise threshold of $p < .005$ combined with a minimum cluster size of 42 voxels, corresponding to $p < .05$, False Wise Error (FWE) corrected. Based on a second Monte Carlo simulation, regions outside of the mask were set at a threshold of $p < .005$ combined with a minimum cluster size of 42 voxels, corresponding to a corrected $p < .05$ for the whole brain. All coordinates reported in Tables and Figures are in MNI space. For descriptive purposes, parameter estimates of signal intensity were extracted from the significant clusters using MarsBar. Parameter estimates were extracted from the entire cluster of activation.

Questionnaire measures

The measures were completed in Chinese by all Chinese participants and in English by all American participants. A bilingual speaker translated the original measures, and a second bilingual speaker back-translated the measures to ensure the translation was accurate.

Group identity

In order to test how the strength of one's group identity was associated with intergroup prosocial behavior, we measured participants' cultural identity. Participants were first presented with an alphabetical list of 45 cultural labels that has been used successfully in prior research examining the type of labels that individuals from different cultural and generational backgrounds use to describe themselves (e.g., "American" "Asian," "Asian-American," "Chinese," "Chinese-American," "European-American," "Latino/a," "Latin-American," "White;" Fuligni et al., 2008). Participants checked all the labels that they felt described them and to add any labels that applied to them that were not on the list. In the current study, all 13 American participants selected the label "White," 1 selected "European-American," and 6 selected "American." Eleven Chinese participants selected the label "Asian," and 11 selected "Chinese." Importantly, no Chinese participant selected "American," "Asian-American," or "Chinese-American."

Participants then completed the Multigroup Ethnic Identity Scale (MEIM, Phinney, 1992). The MEIM has been widely used across cultural groups and taps aspects of cultural belonging and exploration (e.g., "I feel good about my cultural or ethnic background," "I have spent time trying to find out more about my ethnic group, such as its history, traditions, and customs"). Participants completed 12 items using a 5-point scale (1 = strongly disagree, 5 = strongly agree). A cultural identity score was computed by taking the mean of the 12 items. The scale had good internal consistency for both American ($\alpha = .86$) and Chinese ($\alpha = .88$) participants. Two-sample t-tests revealed that Chinese participants ($M = 3.1$, $SD = .48$) reported a significantly higher sense of cultural identity than American participants ($M = 2.5$, $SD = .47$; $t(24) = 3.2$, $p < .005$).

Intergroup feelings

Following the scan, participants used a 7-point scale (1 = not at all, 7 = very much) to indicate how much they liked each confederate (e.g., "how much did you like participant A?"). This measure was used to examine behavioral biases in liking the in-group relative to out-group confederate. A bias score was calculated by subtracting the in-group score from the out-group score (i.e., out-group feelings - in-group feelings). Thus, higher positive scores indicate a greater bias to liking the out-group relative to in-group member whereas negative scores indicate a greater bias to liking the in-group relative to out-group member.

Results

Behavioral results

Prosocial donations

We first examined differences in the percent of trials donated and the total money donated to the in-group and out-group. We computed a repeated measures analysis of variance with group membership (in-group, out-group) as the within person variable and culture (Chinese, American) as the between person variable. We found a marginally significant culture by group membership interaction for percent of donations, $F(1,24) = 4.1$, $p = .055$. To explore this interaction, we computed *post hoc* t-tests within each cultural group. Because we had *a priori* hypotheses, such that individuals would donate more to their in-group than out-group, we computed one-tailed t-tests. Whereas Chinese participants donated significantly more trials to their in-group

($M = 42\%$, $SE = 4\%$) than out-group ($M = 39\%$, $SE = 4\%$, $t(12) = 1.9$, $p = .04$), American participants did not significantly differ in their donations to in-group ($M = 49\%$, $SE = 4\%$) and out-group members ($M = 50\%$, $SE = 4\%$, $t(12) = .94$, $p = .37$). For total money donated, we found a significant culture by group membership interaction, $F(1,24) = 4.5$, $p = .04$. To explore this interaction, we computed *post hoc* t-tests within each cultural group. Whereas Chinese participants tended to donate more money to the in-group ($M = \$137$, $SE = \$13$) than the out-group ($M = \128, $SE = \$14$, $t(12) = 1.6$, $p = .06$), American participants did not differ in their donations to the in-group ($M = \$169$, $SE = \$13$) and out-group ($M = \177, $SE = \$14$, $t(12) = 1.4$, $p = .19$). In a multiple regression controlling for cultural group, group identity was not associated with donations to the in-group or out-group. We did not find any significant effects for mean response times when making decisions to donate to in-group and out-group members.

Intergroup feelings

As a manipulation check to ensure that one confederate was not more likeable than the other, we computed paired samples t-tests examining how much participants liked the Chinese confederates relative to the American confederates. There was not a significant difference in likeability ($t(25) = .22$, ns). We found a trend, such that participants reported liking the in-group confederate ($M = .84$, $SE = .18$) more than the out-group confederate ($M = .57$, $SE = .14$), $t(25) = 1.6$, $p = .06$, one tailed. This did not differ by cultural group. In a multiple regression analysis controlling for cultural group, participants with a higher sense of group identity reported a greater bias for liking the in-group compared to the out-group confederate ($\beta = -.59$, $p = .02$). In other words, participants whose cultural identity was more salient reported liking the in-group confederate more than the out-group confederate. Intergroup feelings were not associated with donations to the in-group or out-group confederate during the task, and this did not vary by cultural group.

fMRI results

Neural correlates of donating to the out-group and in-group

Our first analyses collapsed across cultural groups to examine more universal neural mechanisms that are involved in prosocial decisions. We first examined neural activation when making costly, prosocial donations compared to gaining a pure reward for the self. In this contrast, we collapsed across in- and out-group donations (prosocial donations > pure reward). We controlled for cultural group membership. As shown in Table 1, when making prosocial donations to others, participants showed heightened activation in the ventral striatum, ACC, DLPFC, VLPFC, insula, putamen, cuneus, and TPJ.

Next, we examined neural regions involved in making prosocial decisions to in-group > out-group members. We controlled for cultural group membership as well as the percent of donations to the in-group and the out-group. Participants demonstrated heightened ventral striatum activation when donating to the in-group relative to the out-group (Table 1). For descriptive purposes, we extracted parameter estimates of signal intensity for in-group and out-group donations separately from the ventral striatum cluster (see Fig. 2). *Post hoc* t-tests within each cultural group confirmed that both Chinese and American participants demonstrated greater ventral striatum activation to in-group relative to out-group donations (Chinese: $t(12) = 2.6$, $p < .05$; American: $t(12) = 3.9$, $p < .005$). No brain regions were more activated during out-group > in-group decisions. Finally, we examined whether decisions to donate to the in-group and out-group recruited different neural regions than decisions to accept pure monetary rewards. In separate analyses, we examined neural activation during in-group donations > pure reward trials and out-group donations > pure reward trials. The ventral striatum was significantly more activated during decisions to donate to the in-group relative to gaining a

Table 1
Neural activation during prosocial donations.

| Anatomical Region | BA | x | y | z | t | k |
|---|------|-----|-----|-----|------|-------------------|
| <i>Donations > Pure Reward</i> | | | | | | |
| Ventral Striatum | | 6 | 17 | 5 | 3.60 | 45 |
| Left TPJ | | 45 | −43 | 46 | 3.85 | 54 |
| Right TPJ | | −40 | −46 | 46 | 3.95 | 67 |
| ACC | 6/32 | 9 | 23 | 37 | 5.82 | 2351 ^a |
| Left VLPFC | 10 | −32 | 58 | 1 | 4.32 | 60 |
| Left DLPFC | 10/9 | −24 | 41 | 28 | 3.87 | 111 |
| Right Insula | | 33 | 17 | 10 | 4.05 | ^a |
| Right DLPFC | 10/9 | 33 | 53 | 28 | 4.69 | ^a |
| Right Putamen | | 30 | 5 | 1 | 3.88 | ^a |
| Left Putamen | | −30 | 5 | −2 | 4.45 | 150 ^b |
| Left Insula | | −27 | 26 | 7 | 3.18 | ^b |
| Left Postcentral gyrus | | −42 | −22 | 40 | 3.65 | 49 |
| Cuneus | | 2 | −81 | 16 | 5.99 | 3210 |
| <i>In-group Donations > Outgroup Donations</i> | | | | | | |
| Ventral Striatum | | 18 | 20 | −8 | 3.50 | 19 |
| <i>In-group Donations > Pure Reward</i> | | | | | | |
| Ventral Striatum | | 12 | 22 | −2 | 3.63 | 65 |
| Left DLPFC | 10 | −33 | 56 | 19 | 5.49 | 200 |
| Right DLPFC | 10/9 | 33 | 44 | 34 | 4.54 | 446 |
| ACC | 6/32 | 3 | 17 | 46 | 5.77 | 726 |
| Right Precentral gyrus | | 45 | −22 | 61 | 4.53 | 160 |
| Left Precuneus | | −12 | −55 | 49 | 3.41 | 75 |
| Right Cuneus | | 12 | −97 | 7 | 4.93 | 1955 |
| <i>Out-group Donations > Pure Reward</i> | | | | | | |
| Right Amygdala | | 28 | −1 | −14 | 4.61 | 367 |
| Left Insula | | −38 | 8 | −2 | 4.71 | 287 |
| ACC | 6/32 | −6 | 5 | 58 | 6.91 | 907 |
| Left DLPFC | 10 | −33 | 53 | 22 | 5.13 | 235 |
| Right DLPFC | 10/9 | 30 | 53 | 25 | 3.76 | 73 |
| Left Postcentral gyrus | | −42 | −22 | 37 | 3.82 | 108 |
| Left Postcentral gyrus | | −27 | −34 | 49 | 3.96 | 54 |
| Right Precentral gyrus | | 42 | −10 | 40 | 4.48 | 290 |
| Left Precentral gyrus | | −18 | −28 | 58 | 3.89 | 47 |
| Right Cuneus | | 8 | −85 | 20 | 5.54 | 2550 |

Note. x, y, and z refer to MNI coordinates; t refers to the t-score at those coordinates (local maxima); BA refers to putative Brodman's area. ACC refers to anterior cingulate cortex; DLPFC refers to dorsolateral prefrontal cortex; VLPFC refers to ventrolateral prefrontal cortex; TPJ refers to temporal parietal junction. Regions denoted with the same superscript are part of the same cluster of activation.

pure reward, whereas the ventral striatum was not differentially activated for decisions to donate to the out-group relative to gaining a pure reward (Fig. 3; Table 1).

Group identity and the neural correlates of donating to the out-group and in-group

Next, we tested how group identity was associated with neural processing to out-group > in-group donations. In whole-brain regression

analyses, we entered group identity as a regressor, and controlled for cultural group and percentage of donations to the in-group and out-group. A higher sense of group identity was associated with greater activation in the bilateral DMPFC, ACC, and left TPJ during decisions to donate to the out-group versus the in-group (Table 2, Fig. 4). For descriptive purposes, we extracted parameter estimates of signal intensity from each cluster of activation and plotted them for Chinese and American participants. As shown in the scatterplots of Fig. 4, the associations between cultural identity and neural response to out-group > in-group donations are nearly identical for American and Chinese participants. Indeed, *post hoc* analyses indicate similar effects for American and Chinese participants in all regions (right DMPFC: American: $B = .70$, $SE = .19$, $p < .005$; Chinese: $B = .71$, $SE = .25$, $p < .05$; left DMPFC: American: $B = .87$, $SE = .26$, $p = .007$; Chinese: $B = .88$, $SE = .36$, $p < .05$; left TPJ: American: $B = .52$, $SE = .26$, $p < .05$; Chinese: $B = .92$, $SE = .32$, $p < .05$; ACC: American: $B = .54$, $SE = .14$, $p < .005$; Chinese: $B = .71$, $SE = .36$, $p < .05$). Group identity was not associated with neural activation to in-group > out-group donations.

Cultural group differences in neural activation to donations to the out-group and in-group

In whole brain, two-sample t-test analyses, we examined cultural group differences (Chinese > American) during decisions to donate to out-group versus in-group members (Out-group > In-group). Chinese participants demonstrated significantly more activation than American participants during out-group > in-group donations in the bilateral VLPFC, bilateral TPJ, and right pSTS (Table 2, Fig. 5). To decompose this interaction for descriptive purposes, we conducted *post hoc* analyses by extracting parameter estimates of signal intensity from the significant clusters for in-group and out-group donations and plotted the mean estimates for American and Chinese participants. As shown in Fig. 5, American and Chinese participants did not differ in VLPFC or TPJ activation for in-group donations. However, for out-group donations, Chinese participants demonstrated greater activation in the VLPFC ($t(24) = 3.97$, $p = .001$) and TPJ ($t(24) = 2.88$, $p = .008$) than American participants. We did not find any cultural differences in brain regions during in-group > out-group donations.

Mediating cultural group differences in neural activation with group identity

Given that cultural group and group identity were both significantly related to activation in the left TPJ to out-group > in-group donations, we conducted mediation analyses to examine whether group identity explains cultural group differences in TPJ activation. We calculated the magnitude and the significance of the indirect effects of cultural group on TPJ activation, through group

In-group>Out-group Donations

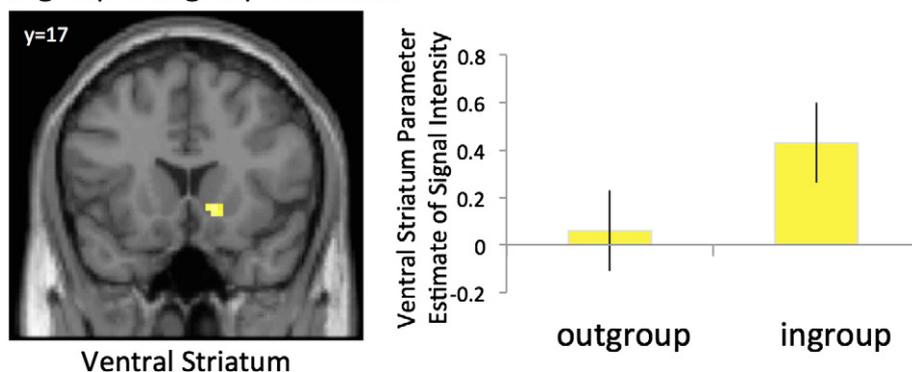


Fig. 2. Decisions to donate to the in-group relative to out-group was associated with heightened activation in the ventral striatum. Error bars represent the S.E.M.

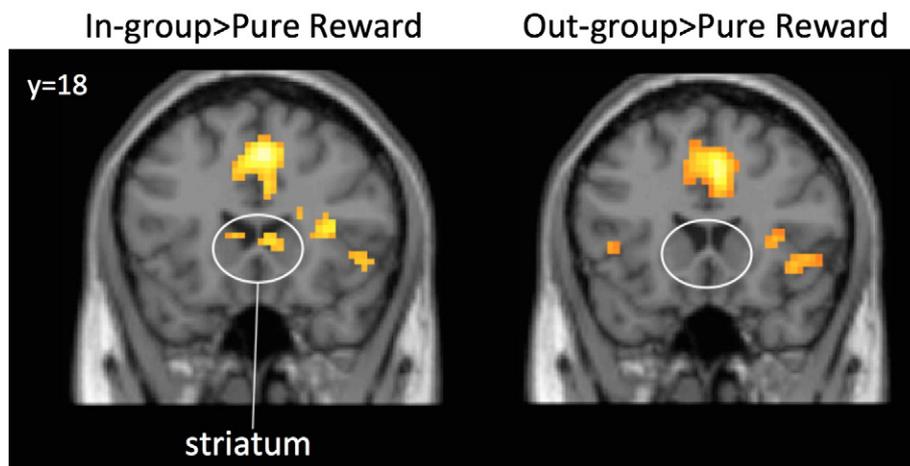


Fig. 3. Decisions to donate to the in-group but not the out-group relative to pure reward trials engaged the ventral striatum.

identity using the methods outlined by MacKinnon and colleagues, in which the asymmetric confidence limits were computed based on the distribution of products (MacKinnon et al., 2007). The product of coefficients test uses the path weights for each indirect pathway and the corresponding standard errors to compute the test statistic, which calculates the asymmetric confidence interval based on the distribution of the products. Parameter estimates of signal intensity from the TPJ cluster were extracted, and the path coefficients were computed in SPSS and used in MacKinnon and colleagues' RMediation program (Tofghi and MacKinnon, 2011). The original direct effect of cultural group on TPJ activation ($B = -.75$, $SE = .26$, $p < .005$) is reduced and becomes nonsignificant when group identity is entered into the model ($B = -.33$, $SE = .27$, ns). Group identity continues to predict TPJ activation ($B = -.72$, $SE = .25$, $p < .005$). The confidence interval for the indirect effect $[-.89 \text{ } -.09]$ does not include zero, consistent with statistically significant mediation. Group identity did not mediate any other brain regions.

Discussion

The conditions under which people engage in prosocial behavior have been at the heart of theoretical and scientific exploration within the fields of psychology, philosophy, political science, and economics.

Table 2

Neural activation during out-group > in-group donations as a function of group identity and cultural group.

| Anatomical Region | BA | x | y | z | t | k |
|-------------------------------|-------|-----|-----|-----|------|-----|
| <i>Group Identity</i> | | | | | | |
| Left TPJ | | -48 | -67 | 31 | 4.29 | 106 |
| Left DMPFC | 8 | -15 | 41 | 46 | 4.95 | 194 |
| Right DMPFC | 8 | 15 | 41 | 49 | 5.33 | 76 |
| Right ACC | 32 | 9 | 41 | 13 | 4.21 | 53 |
| Right Inferior Temporal gyrus | | 57 | -19 | -26 | 4.50 | 60 |
| <i>Chinese > American</i> | | | | | | |
| Right VLPFC | 10/47 | 45 | 50 | -5 | 4.68 | 70 |
| Left VLPFC | 11 | -39 | 53 | -12 | 3.21 | 35 |
| Left TPJ/pSTS | | -48 | -58 | 21 | 4.93 | 441 |
| Right TPJ | | 50 | -67 | 37 | 4.48 | 160 |
| Right TPJ | | 60 | -52 | 25 | 3.94 | 66 |
| Right pSTS | 21 | 63 | -28 | -5 | 4.28 | 59 |
| Left MPPC | 7/31 | -12 | -70 | 40 | 3.64 | 108 |

Note. x, y, and z refer to MNI coordinates; t refers to the t-score at those coordinates (local maxima); BA refers to putative Brodman's area. VLPFC refers to ventrolateral prefrontal cortex; TPJ refers to temporal parietal junction; DMPFC refers to dorsomedial prefrontal cortex; pSTS refers to posterior superior temporal sulcus; MPPC refers to medial posterior parietal cortex.

Decades of research across multiple social contexts and species have described the social conditions under which individuals preferentially assist members of their own group (e.g., Mahajan and Wynn, 2012; Bartal et al., 2014; Levine et al., 2005; Flippen et al., 1996; Rand et al., 2009; Hornstein, 1972, 1976; Platow et al., 1999). Yet, the neural mechanisms differentiating these processes remain relatively unknown. The current study provides novel evidence that decisions to help in-group and out-group members recruit unique neural processes. Our findings support a “universalism without the uniformity” (Shweder and Sullivan, 1993) perspective on the neural correlates of prosocial behavior. We found both universal effects (i.e., similarities between American and Chinese groups), and culture-specific effects (i.e., differences in American and Chinese groups).

Among both Chinese and American participants, we found that decisions to donate to in-group relative to out-group members recruited the ventral striatum. Prior work has consistently found that decisions to donate to others, including charities, strangers, and family members, recruits the ventral striatum (Harbaugh et al., 2007; Izuma et al., 2010; Moll et al., 2006; Telzer et al., 2010; Molenberghs et al., 2014). We build upon this work and show that striatal response when donating to unfamiliar others is modulated by group membership. Only when participants were providing donations to an in-group member did they evidence heightened striatum activation. Notably, all prosocial decisions were costly, such that individuals chose to give up a monetary reward in order to contribute to the confederates. Therefore, even when the outcome of their decision is a loss to the self, the striatum is recruited when donating to the in-group. Importantly, the ventral striatum was even more active when contributing to the in-group relative to gaining a personal non-costly reward, which is consistent with prior work on charitable donations, highlighting the joy of giving or “warm glow” involved in being charitable (e.g., Moll et al., 2006). These findings are further supported by social identity theory, which posits that individuals' attitudes towards their own group are more positive, such that they attach positive utility to the welfare of their own group and therefore feel good when their group is doing well (Tajfel, 1974). Finally, we find the same effect in Chinese and American participants, suggesting that across two cultural groups with diverse values, individuals show heightened ventral striatum activation when donating to in-group members, suggesting that the rewarding nature of helping in-group members is perhaps a universal phenomenon.

These findings have important implications for our understanding of intergroup behavior. While in-group positivity does not necessarily entail out-group derogation, a dampened sense of reward during out-group prosocial behavior may lead an individual to be less likely to help an out-group member in need. Thus, a sense of reward may govern whom one helps and consequently whom one does not help, resulting

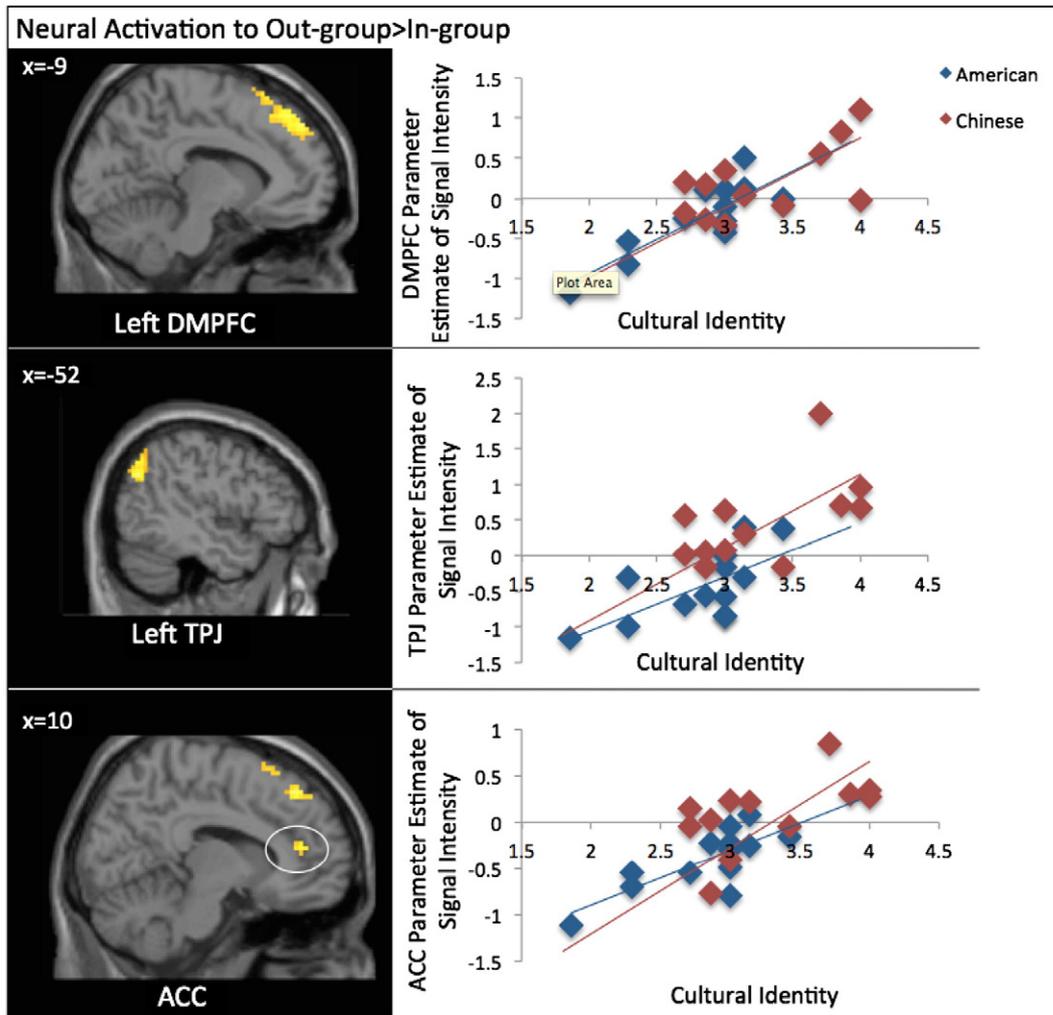


Fig. 4. A higher sense of group identity is associated with heightened activation in the DMPFC, TPJ, and ACC during decisions to donate to the out-group relative to the in-group.

in differential distribution of resources. These preferential attitudes towards in-group members could result in the relative neglect of prosocial behavior towards out-group members, and lead to the subsequent reinforcement of group boundaries as individuals orient more towards in-group members (Brewer, 1999).

In addition, we also found that individuals who more strongly identified with their group (controlling for cultural group membership) reported a greater bias to liking the in-group relative to out-group confederate. At the neural level, a greater sense of group identity was associated with greater activation in brain regions involved in conflict monitoring (ACC) and mentalizing (TPJ, DMPFC) when making out-group relative to in-group donations. These findings extend prior work showing that prosocial decisions engage neural regions involved in self control and mentalizing (Telzer et al., 2011) and show that these same neural networks are differentially recruited depending upon the social group to whom one is donating and the strength of one's own sense of group identity. Our findings suggest that prosocial decisions to in-group members may be a more automatic process for those with a strong group identity, whereas donating to out-group members may be more effortful, requiring the recruitment of the ACC. Because a stronger sense of group identity may result in greater self-other overlap with in-group members (Brewer and Kramer, 1986; Zaleski, 1992), collective gains may be more valued, and so prosocial decisions to in-group members are an easier, more automatic decision. In contrast, decisions to donate to out-group members may require the individual to step outside of their own shoes and take the perspective of the other, a process requiring greater recruitment of brain regions

involved in self-control and mentalizing. These findings suggest that if one has to regulate the prepotent tendency to reject out-group prosociality and take the perspective of the other, prosocial behavior to the out-group may be less frequent.

We also found interesting culture-specific differences in the ways that individuals processed decisions to help in-group versus out-group members. Chinese participants made more costly donations to their in-group than out-group. This behavioral finding is consistent with research showing that individuals from interdependent societies are group focused with more rigid intergroup boundaries that promote in-group solidarity (Stevenson, 1991; Markus and Kitayama, 1991; Eckstein, 2001; Kimmelmeier et al., 2006). At the neural level, this preferential bias towards in-group members among Chinese participants was associated with heightened activation in regions involved in self-control (VLPFC) and mentalizing (TPJ) when donating to out-group members. Together, these findings suggest that intergroup biases and behaviors are shaped and reinforced by one's culture. Despite the ubiquitous nature of biases favoring the in-group, one's social context can increase these biases.

Finally, mediation analyses indicated that group identity explained, in part, cultural group differences in TPJ activation during decisions to contribute to the out-group relative to in-group. In other words, Chinese individuals had a higher sense of belonging to their cultural group, and this sense of belonging was associated with greater activation in the TPJ when making prosocial decisions to the out-group. This finding suggests that one reason why Chinese individuals may be more in-group focused is their higher sense of cultural group identity. Having a more central

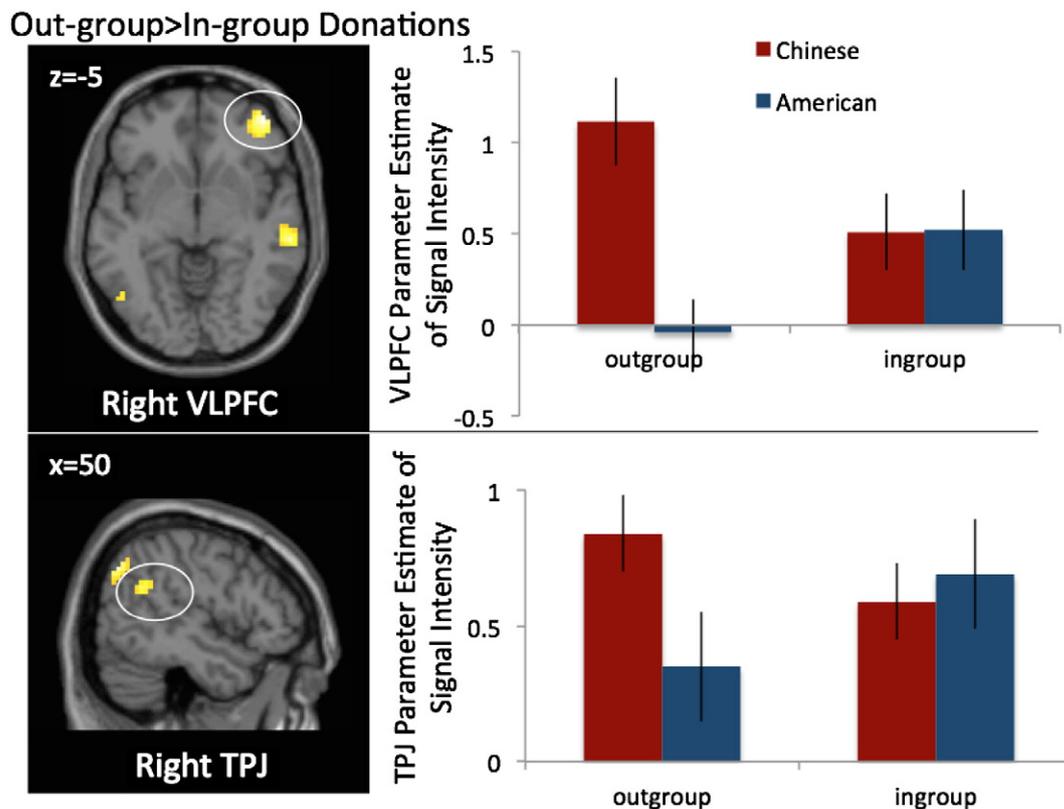


Fig. 5. Chinese participants showed greater activation than American participants in the VLPFC and TPJ during decisions to donate to the out-group relative to the in-group. Error bars represent the S.E.M.

cultural identity may increase in-group and out-group boundaries, and make group membership more salient.

While our cultural group differences support theory and research showing greater in-group loyalty among individuals from more interdependent societies like China, these results could also suggest different social experiences based on cultural minority status. As immigrants who have been in the United States for less than one year, our Chinese participants may feel more threatened or marginalized by the broader U.S. society, and their minority status may be especially salient. This may result in the greater in-group orientation that we found. Indeed, the extent of one's social identity is largely determined by the social context. For instance, certain social identities may become more inclusive as the context makes one's identity more salient (e.g., being among the minority group). Thus, the social context may increase self-other overlap with individuals, who, in another context, may not be a part of the in-group (Cikara and van Bavel, 2014). Future research should replicate this study with Chinese participants in China as well as Chinese-American participants in the United States in order to fully understand how much our effects are due to culture versus minority status. In addition, future research should examine whether in-group favoritism is engrained through a history of cultural transmission or whether in-group loyalty can be manipulated within individuals. Finally, we are unable to differentiate between in-group positivity and out-group derogation in the current study. Our task design only had conditions that could reward the self and other. While this design is important for examining the conditions under which individuals are prosocial, we cannot test the conditions under which individuals will act in more negative ways to exclude or punish the out-group. Lastly, our sample size is relatively small, and so future research should replicate this study with a larger sample.

In conclusion, psychological theories suggest that the underlying mechanisms involved in helping in-group relative to out-group members differs (Dovidio et al., 1997), yet, prior research has not empirically

uncovered these processes. Although biases favoring one's own group may be somewhat ubiquitous across species and diverse social groups, we show that there are both universal and culture-specific processes involved in prosocial behavior to in-group versus out-group members. Our findings provide novel evidence that decisions to help in-group and out-group members recruit differential brain regions, and these neural processes are modulated by culture. These differential neural processes likely promote a group's chances for survival by limiting prosocial behavior to in-group members, thereby increasing mutual trust, loyalty, and cooperation, and diminishing prosocial behavior to out-group members.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2015.04.035>.

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