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Neural responses to perceived pain in others predict real-life monetary donations in different socioeconomic contexts

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ABSTRACT

Empathy has been proposed to be a proximate mechanism underlying altruistic behavior. However, both empathy and altruistic behavior differ between human individuals with low and high socioeconomic status. Here we investigated whether subjective socioeconomic status (SSS) modulates the relationship between neural activity to perceived pain in others and human altruistic behaviors in a real-life situation. After being scanned using functional MRI while observing videos of others in pain, participants were invited to make an anonymous monetary donation to a charitable organization. Painful stimuli increased activity in the inferior frontal, insula and somatosensory cortices compared to non-painful stimuli. A hierarchical regression analysis revealed that neural responses to perceived pain predicted the amount of monetary donations with different patterns in high and low SSS individuals. Stronger neural responses to perceived pain were associated with greater monetary donations in high SSS individuals, whereas a reverse pattern was observed in low SSS individuals. Our results suggest that SSS moderates the functional role of empathy-related neural activity in predicting altruistic behavior. Empathy may follow different mechanisms involved in altruistic behaviors (e.g., donation) depending on the social environment.

Introduction

Human altruism – personal sacrifices on the behalf of others – is one of the most fundamental components of human society. Such human behaviors extend beyond reciprocal interactions and reputation-based cooperation (Fehr and Fischbacher, 2003; Nowak and Sigmund, 2005). Recent studies uncover different forms of human altruism (Fehr and Fischbacher, 2003) such as direct and indirect reciprocal altruism (Boyd et al., 2003; Nowak and Sigmund, 2005), altruistic punishment (Fehr and Gächter, 2002; de Quervain et al., 2004), and reputation-based altruism (Milinski et al., 2002). Among different examples of human altruism, anonymous donations to charities stand out in particular (Andreoni, 1990; Vogel, 2004) and the underlying neural mechanisms have obtained great interest recently (Moll et al., 2006; Harbaugh et al., 2007; Izuma et al., 2010; Hare et al., 2010). It has been shown that decisions to donate money to a charity activate the mesolimbic dopamine system (e.g., the ventral tegmental area and striatum) that engages in personal monetary rewards (Moll et al., 2006). Activity in the caudate nucleus and ventral striatum increases as a function of the amount of mandatory or voluntary charitable donations (Harbaugh et al., 2007). These findings showed empirical evidence for the involvement of reward-related neural circuit in charitable donations and support the evolutionary theory that intrinsic reward for oneself plays a motivational role in altruistic behaviors (Trivers, 1971; Axelrod and Hamilton, 1981).

However, human helping behaviors are not always and exclusively motivated by intrinsic rewards for oneself (Batson and Shaw, 1991; Wispé, 1991). It has been proposed that empathy, as a key contributor to altruism (Decety and Grèzes, 2006), may provide a proximate mechanism for altruistic behaviors such as comforting others in need, pain or distress (Preston and de Waal, 2002; de Waal, 2008). While previous behavioral studies suggested a close relationship between empathy and altruistic behaviors (Batson and Shaw, 1991; Kruger, 2003; Batson et al., 1997), recent functional magnetic resonance imaging (fMRI) studies showed that neural activity in brain regions associated with perceived action (e.g., the posterior superior temporal cortex, Tankersley et al., 2007) or perceived pain in others (e.g., the medial prefrontal cortex, Mathur et al., 2010) predicted self-reported altruistic tendencies, suggesting contributions of empathy-related neural mechanisms to human altruistic behaviors.

Interestingly, empathic capabilities and altruistic behaviors may vary across individuals with different socioeconomic status (SES). Objective SES has commonly been measured using relatively objective indices based on one's material resources (e.g., income) and access to social institutions such as education and healthcare (Lachman and Weaver, 1998; Oakes and Rossi, 2003). There has been increasing

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evidence that objective SES influences human traits, cognition, behaviors (Kraus et al., 2009; Snibbe and Markus, 2005; Stephens et al., 2007). Individuals' objective SES correlates with one's capability of empathy (Jolliffe and Farrington, 2006) and prosocial behaviors (Champion and Sear, 1969; Eisenberg et al., 2001; Piff et al., 2010). Moreover, objective SES modulates the relationship between empathy and altruism as such relationship was greatly weakened after controlling for objective SES (Jolliffe and Farrington, 2004). Recent studies have shown that objective SES not only influences human behaviors but also modulates the underlying neural mechanisms (Hackman et al., 2010). For example, an event-related brain potential study found that children from low objective SES families showed reduced effects of selective attention on neural processing compared to those from high SES families (Stevens et al., 2009). Amygdala responded more strongly to threatening facial expressions in low than in high objective SES adults (Gianaros et al., 2008). An early study suggested that objective SES may influence social behaviors by moderating the underlying neural mechanisms as a weaker testosterone-behavior relationship was reported in high than in low objective SES individuals (Dabbs and Morris, 1990).

Subjective socioeconomic status (SSS) refers to subjective assessments of one's relative socioeconomic status in society and can be measured using a typical SSS scale (e.g., a drawing of a ladder with 10 rungs, Kilpatrick and Cantril, 1960). It has been proposed that SSS represents a cognitive average of standard markers of SES, including elements representing an assessment of current and future prospects (Singh-Manoux et al., 2003). SSS is both a social and an economic phenomenon and may be a better measure of SES at the individual level than a single objective indicator of SES (Jackman, 1979; Singh-Manoux et al., 2005). Indeed, it has been shown that the association between health and SSS may be as strong as the association with traditional objective SES measures (Wilkinson, 1999) and that SSS may be more consistently and strongly related to health-related factors compared to objective indices of SES (Adler et al., 2000; Operario et al., 2004).

To our knowledge, there has been no research that directly assesses whether and how SSS influences the empathy–altruism relationship. The current work tested the hypothesis that SSS moderates the relationship between neural activity to perceived pain in others and real-life altruistic behavior. Individuals with high and low SSS were scanned using fMRI while they watched video clips of others receiving painful stimulation (needle penetration) or non-painful stimulation (cotton Q-tip touch). The neural activity to perceived pain was defined by contrasting painful versus non-painful stimulation. A real-life one-shot charitable donation was conducted after the scanning procedure. We first showed that perception of others in pain increased activity in the insula, inferior frontal (IF) and the secondary somatosensory cortices (SII), similar to previous findings (Han et al., 2009; Jackson et al., 2005; Saarela et al., 2007; Singer et al., 2004, 2006; Carr et al., 2003; Gu et al., 2010; Shamay-Tsoory et al., 2009). A hierarchical regression analysis was then conducted to evaluate whether neural responses to perceived pain in others predicted the amount of monetary donations in different ways in high and low SSS individuals.

Materials and methods

Participants

Thirty-three participants (16 females; age range: 19–27 years, mean age ± SD = 22.4 ± 2.0 years) were recruited in this study. All participants were right-handed, reported no history of neurological or psychiatric diagnoses, and had normal or corrected-to-normal vision. Informed consent, approved by a local ethics committee, was obtained prior to the study.

Stimuli and procedure

Stimuli consisted of 48 video clips showing faces or hands of six models (3 males). Each video clip subtended a visual angle of 21.4° × 17.1° (width × height) at a viewing distance of 80 cm and lasted for 3 s. Each clip depicted a neutral face or a hand receiving painful (needle penetration) or non-painful (Q-tip touch) stimulation, which was applied to the left or right cheek, or to the left or right hand. After each video clip, participants were instructed to judge whether the models in the video clips felt pain when their faces or hands were stimulated by a button press using the index or middle fingers. The correspondence between the stimulus type and responding fingers was counterbalanced across participants.

Each session consisted of painful or non-painful stimuli. Each participant finished a functional scan of 8 sessions, with 4 painful sessions and 4 non-painful sessions. An 8 s prompt screen with instructions was presented at the beginning of the functional scan. Each session lasted 36 s and consisted of 6 trials showing 6 video clips (3 face-video and 3 hand-video clips). Each trial consisted of a 3 s video clip and followed by a 3 s fixation. Two subsequent sessions were intervened by a 10 s fixation. Different sessions were presented in a random order across participants. The functional scan lasted 390 s. A high-resolution T1-weighted structural image was obtained after the functional scan. After the scanning procedure, participants were asked to complete questionnaires and behavioral measurements.

Data acquisition and analysis

Behavioral measurements

Participants were asked to complete the Interpersonal Reactivity Index (IRI) (Davis, 1996) to measure self-reported empathic abilities. A typical SSS scale (Kilpatrick and Cantril, 1960) was used to measure participants' SSS. Participants were given a drawing of a ladder with 10 rungs with the instruction: “Imagine that this ladder with 10 rungs represents where people stand in our society. At the top of this ladder are the people who are best off – those who have the most money, highest education, and best jobs. At the bottom are the people who are the worst off – those who have the least money, lowest education, and the worst jobs or no job. Please mark the rung that best represents where you think you stand in the society.”

To measure participants' real altruistic behaviors, rather than self-report of altruistic tendency, we asked participants to make a monetary donation to a real charitable organization. Participants were provided with a written description of the charity, which provides assistance for cataract patients in poverty-stricken areas, and an anonymous donation box. Participants stayed alone in a room to decide whether or not to donate and how much to donate. The amount of the monetary donations was used as a measurement of altruistic behavior. After participants made their donations, they were informed that the donation was a part of the experiment and their money was returned. One participant felt that the donation was an experimental manipulation, and thus his data was removed from the analysis.

fMRI imaging data acquisition

Imaging data were acquired using a 3-T Siemens Trio system using a standard head coil at Beijing MRI Center for Brain Research. Head motion was minimized using foam padding. Thirty-two transversal slices of functional images that covered the whole brain were acquired using a gradient-echo echoplanar pulse sequence (64 × 64 × 32 matrix with 3.75 × 3.75 × 4 mm^3 spatial resolution, repetition time (TR) = 2000 ms, echo time (TE) = 30 ms, flip angle = 90°, field of view (FOV) = 24 × 24 cm). Anatomical images were subsequently obtained using a standard 3D T1-weighted sequence ($256 \times 256 \times 144$ matrix with $1.0 \times 1.0 \times 1.3\ mm^3$ spatial resolution, TR = 2530 ms, TE = 3.37 ms, flip angle = 7°).

fMRI data analysis

The fMRI data were analyzed using Statistical Parametric Mapping (SPM2, the Wellcome Trust Centre for Neuroimaging, London, United Kingdom). The functional images were realigned to correct for head motion. Six movement parameters (translation; x, y, z and rotation; pitch, roll, yaw) were included in the statistical model. The anatomical image was co-registered with the mean functional image produced during the process of realignment. All images were normalized to a $2 \times 2 \times 2\ mm^3$ Montreal Neurological Institute (MNI) template. Functional images were spatially smoothed using a Gaussian filter with the full-width/half-maximum parameter (FWHM) set to 8 mm and temporally filtered using a cut-off of 256 s. The conditions (painful, non-painful and rest conditions) were modeled for participants at the single subject level, comparing activity while watching painful versus non-painful video clips. A random effects model was constructed, averaging over these single subject results at the group level. Brain areas associated with empathy for pain were defined using a threshold of $p < 0.05$ (false discovery rate correction).

Regions of interest (ROIs)

ROIs were functionally defined based on the random effects analysis that contrasted painful vs. non-painful sessions. The ROIs were defined as spheres with radii of 5 mm centered at the peak voxel of activated clusters that were engaged more strongly in the painful than non-painful condition.

Hierarchical regression analyses

To examine whether SSS affected the relationship between empathic neural responses (independent variable, IV) and the amount of the monetary donations (dependent variable, DV), we performed moderated hierarchical regression analyses separately for each ROI. To do this, we first normalized the IV (the parameter estimates of signal intensity in each ROI associated with empathy for pain) and the covariate variable (SSS). The interactions between empathic neural responses and SSS were calculated by multiplying the normalized variables together (Aiken and West, 1991). Normalized SSS (the moderator), empathic neural responses (IV), and their interactions were sequentially entered into the moderated hierarchical regression. The moderator effect was indicated by a significant interaction of individuals' SSS and empathic neural activity on the amount of monetary donations.

As a significant moderator effect of SSS on the empathy-donation relationship was observed, we divided participants into low and high SSS groups. The mean SSS across all participants was 5.92 ± 1.82. Participants with the top 40% of SSS constituted the high SSS group (13 individuals, mean ± SD = 7.73 ± 0.97) and the bottom 40% of SSS constituted the low SSS group (13 individuals, mean ± SD = 4.12 ± 0.89). *Post hoc* regression analyses were conducted for each SSS group.

To further examine to what extent the neural responses to perceived pain in others could predict the amount of monetary donations beyond self-report of empathy ability (indexed by IRI scores), a second moderated hierarchical regression analyses was conducted by including the IV (normalized IRI scores, normalized neural responses to perceived pain) and the moderator (normalized SSS) in the first step. The interaction between normalized SSS and IRI scores, and the interaction between normalized SSS and neural responses to perceived pain, were entered in the second and third steps of the hierarchical regression analysis.

Results

Behavioral results

During the scanning procedure, participants responded with high accuracy when judging whether the model was experiencing pain or not (>90%). Our participants donated 0~30 Chinese Yuan (RMB, equal to 0~4.5 US dollars, mean ± SD = 6.5 ± 7.68). The amount of monetary donations did not differ between the low and high SSS groups (8.08 ± 2.34 vs. 7.92 ± 8.85; $t(24) = 0.048$, $p = 0.962$). IRI scores did not differ between the low and high SSS groups (2.47 ± 0.19 vs. 2.58 ± 0.42; $t(24) = -0.819$, $p = 0.421$), suggesting comparable subjective ratings of empathy ability.

We conducted moderated hierarchical regression analyses to examine whether SSS affected the relationship between IRI scores and the amount of the monetary donations. Normalized SSS, IRI scores, and their interactions were sequentially entered into the moderated hierarchical regression. However, this model failed to show any significant effect, neither the IRI ($\beta = 0.078$, $p = 0.682$) nor its interaction with SSS ($\beta = -0.234$, $p = 0.320$) was able to predict the amount of monetary donations.

Localization of neural responses to perceived pain

Neural responses to perceived pain in others, defined by contrasting painful vs. non-painful stimuli, were localized in the left and right inferior frontal (IF) cortices (lIF: −58/12/28; rIF: 60/16/24, Z = 4.19 and 5.18) and the left and right SII (lSII: −64/−18/32, rSII: 66/−20/26, Z = 4.03 and 4.66; FDR correction, Fig. 1). Using a less stringent voxel-wise threshold of 0.005 (uncorrected), we also observed activation in the left insula (−42/−6/4, Z = 3.37, number of voxels = 113). The signal intensities of parameter estimates in these ROIs were then calculated respectively for low and high SSS groups. Two-sample t-tests failed to show any significant difference in neural responses to perceived pain in these brain regions between high and low SSS participants ($ps > 0.1$).

Hierarchical regression analyses

Hierarchical regression analyses were conducted to examine whether SSS affects the relationship between neural responses to perceived pain and the monetary amount participants decided to donate. The first model regressed the moderator (normalized SSS), IV (empathic neural responses), and their interaction. This analysis showed that the interactions of individuals' SSS and neural activity to perceived pain in the bilateral IF and SII (but not in the left insula) were predictive of the donated amount ($Fs = 3.287$ to 5.030, $ps = 0.035$ to 0.006; see Tables 1–4), suggesting that empathic neural responses in these brain regions predicted the amount of money donated differently between low and high SSS individuals. Importantly, we found that the interaction between neural responses to perceived pain and SSS explained more than a quarter of the variance in the amount of the monetary donations (lIF: 33.2%, rIF: 30.7%, lSII: 26%, and rSII: 29.8%).

Fig. 1 illustrates the relationship between the neural activity to perceived pain and the amount of monetary donations in high and low SSS individuals, respectively. *Post hoc* regression analyses showed a positive correlation between neural activity to perceived pain and the amount of the monetary donations in high SSS individuals (lIF: $\beta = 0.748$, $p = 0.003$; rIF: $\beta = 0.756$, $p = 0.003$; lSII: $\beta = 0.5768$, $p = 0.039$; rSII: $\beta = 0.666$, $p = 0.013$, see details in Table 5 of zero-order correlations). However, a negative correlation between neural activity to perceived pain and monetary donations was observed in low SSS individuals, though this was significant in the lIF ($\beta = -0.603$, $p = 0.029$) and rSII ($\beta = -0.571$, $p = 0.042$) but not in the rIF ($\beta = -0.252$, $p = 0.407$) and lSII ($\beta = -0.481$, $p = 0.096$).

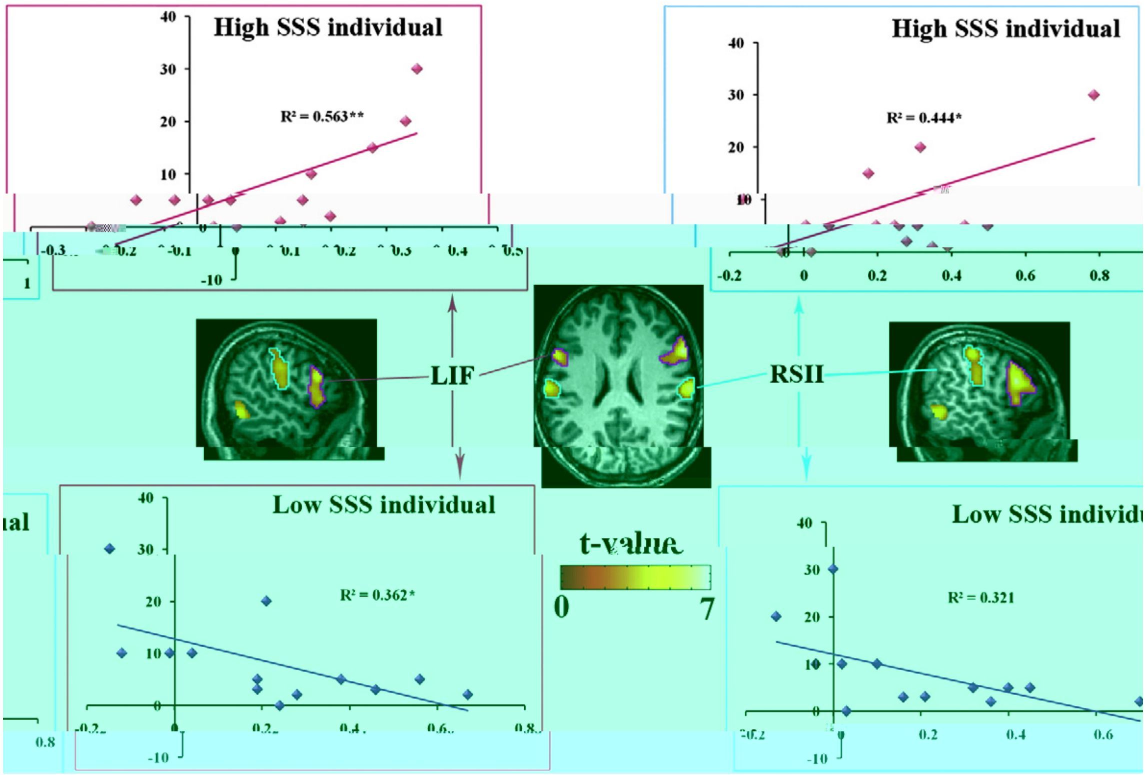

Fig. 1. Illustrations of empathy-related neural activity and the results of post hoc regression analyses. The contrast of painful versus non-painful stimuli identified neural activities in bilateral inferior frontal cortex and SII. The neural activity in these brain regions correlated with the amount of monetary donations positively in high SSS individuals but negatively in low SSS individuals. The y-axis denotes the amount of monetary donations. The x-axis denotes the contrast values of painful versus non-painful stimuli. LIF = left inferior frontal cortex; RSII = right somatosensory cortex; SSS = subjective socioeconomic status.

To further assess whether the interaction between SSS and neural responses to perceived pain could predict the amount of the monetary donations above and beyond self-reported empathy ability, the second model regressed the normalized IRI scores, SSS, and neural responses to perceived pain, the interaction between IRI scores and SSS, and the interaction between neural responses and SSS in a three-step hierarchical regression. We showed that, while neither self-reported empathic ability nor its interaction with SSS predicted the amount of monetary donations, the interaction between SSS and neural activity to perceived pain reliably predicted about an additional quarter of the variance of the amount of monetary donations beyond that predicted by self-reported empathic ability and its interaction with SSS (lIF: 27.5%, rIF: 24.8%, lSII: 22.2%, and rSII: 23.4% over subjective rating, see Tables 6–9).

Discussion

The current work provides the first evidence that SSS moderates the relationship between neural activity to perceived pain in others and real-life altruistic behaviors. We showed that self-reported empathic ability or its interaction with one's SSS could not predict the amount of real-life monetary donations. However, the interaction between neural activity to perceived pain and one's SSS was able to predict the amount of monetary donations, indicating that empathy-related brain activity are more efficient than self-reported empathy in predicting future altruistic behaviors. More interestingly, we showed that participants' SSS influenced the relationship between neural activity to perceived pain and monetary donations, with stronger neural activity in the inferior frontal cortex and SII predicting greater

Table 1
Hierarchical regression analysis on LIF activity with the amount of monetary donation as the dependent variable.

	Step1β	Step2β
lIF activity	−0.006	0.114
SSS	0.015	0.119
lIF×SSS		0.593***
⊿R^2	0.000	0.332
⊿F	0.004	13.931***
R^2	0.000	0.332
Adjusted R^2	−0.069	0.261
Overall F	0.004	4.648**
df	29	28

** $p<0.01$.
*** $p<0.001$.

Table 2
Hierarchical regression analysis on RSII activity with the amount of monetary donation as the dependent variable.

	Step1β	Step2β
rSII activity	0.115	0.040
SSS	0.011	0.072
rSII×SSS		0.554**
⊿R^2	0.013	0.298
⊿F	0.197	12.117**
R^2	0.013	0.311
Adjusted R^2	−0.055	0.238
Overall F	0.197	4.221*
df	29	28

* $p<0.05$.
** $p<0.01$.

Table 3
Hierarchical regression analysis on RIF activity with the amount of monetary donation as the dependent variable.

	Step1β	Step2β
rIF activity	0.208	0.367
SSS	0.038	0.058
rIF × SSS		0.576***
⊿R^2	0.043	0.307
⊿F	0.654	13.232***
R^2	0.043	0.350
Adjusted R^2	−0.023	0.281
Overall F	0.654	5.030**
df	29	28

** $p<0.01$.
*** $p<0.001$.

monetary donations in high SSS individuals. Such relationship between neural signals to perceived pain and monetary giving in high SSS individuals is consistent with the proposition that empathy as a motivation mechanism contributes to altruistic behaviors (Preston and de Waal, 2002; de Waal, 2008). However, such a functional role of empathy in altruistic behaviors may vary in different socioeconomic contexts as greater neural activity to perceived pain in others predicted less charitable donations in low SSS individuals.

Our findings contribute to the understanding of the mechanisms underlying human altruism in several aspects. First, while previous studies suggest that empathic neural activity can predict self-reported altruistic propensity (Tankersley et al., 2007) and self-reported willingness to donate (Mathur et al., 2010), it is still an open issue if empathy-related brain activity can predict real-life altruistic behavior given the numerous sources of bias that threaten the validity of introspective reports for predicting human social behaviors (Schwarz, 2007). Our fMRI results indicate that neural responses to perceived pain may predict the amount of monetary donations, providing brain imaging evidences for the functional role of empathy in real-life altruistic behaviors.

Second, while previous studies investigated the on-line neural processes involved in decisions about charitable donations (Moll et al., 2006; Harbaugh et al., 2007; Izuma et al., 2010; Hare et al., 2010), we took these findings a step further by showing that neural activity to perceived pain in others was predictive of future, rather than concurrent, real-life altruistic behaviors. Falk et al. (2010) recently showed that neural activity in the medial prefrontal cortex—a region often implicated in self-related processes (Kelley et al., 2002; Northoff and Bermpoh, 2004; Zhu et al., 2007; Ma and Han, 2011)—can predict changes of persuasion-induced self-related behavior (e.g., sunscreen use). Our results indicate that neural activity associated with understanding and sharing others' pain can predict social behaviors related to other individuals.

Table 4
Hierarchical regression analysis on LSII activity with the amount of monetary donation as the dependent variable.

	Step1β	Step2β
lSII activity	−0.005	0.086
SSS	0.016	−0.009
lSII × SSS		0.519**
⊿R^2	0.000	0.260
⊿F	0.004	9.849**
R^2	0.000	0.260
Adjusted R^2	−0.069	0.181
Overall F	0.004	3.287*
df	29	28

* $p<0.05$.
** $p<0.01$.

Table 5
Zero-order correlation of all measures.

	1	2	3	4	5	6	7	8
All participants:								
1. Donation	——							
2. SES	0.02	——						
3. IRI	0.08	0.27	——					
4. lIF	−0.01	−0.25	−0.19	——				
5. rIF	0.20	−0.10	−0.06	0.62***	——			
6. Left insula	−0.01	−0.11	−0.20	0.33	−0.05	——		
7. lSII	−0.00	0.04	−0.01	0.54**	0.39*	0.02	——	
8. rSII	0.12	0.04	−0.02	0.57***	0.340	0.33	0.60***	–
High SSS participants:								
1. Donation	——							
2. SES	−0.02	——						
3. IRI	−0.03	0.59*	——					
4. lIF	0.75**	−0.17	−0.04	——				
5. rIF	0.76**	0.01	−0.16	0.64*	——			
6. Left insula	0.06	0.05	−0.07	−0.16	−0.23	——		
7. lSII	0.58*	−0.33	−0.04	0.43	0.52	0.21	——	
8. rSII	0.67*	−0.25	0.07	0.56*	0.51	0.22	0.48	——
Low SSS participants:								
1. Donation	——							
2. SES	0.14	——						
3. IRI	0.46	−0.05	——					
4. lIF	−0.60*	−0.06	−0.48	——				
5. rIF	−0.25	−0.06	−0.26	0.72**	——			
6. Left insula	−0.25	0.48	−0.18	0.48	0.09	——		
7. lSII	−0.48	−0.35	−0.29	0.72**	0.44	0.07	——	
8. rSII	−0.57*	−0.17	−0.44	0.76**	0.42	0.55*	0.67*	——

* $p<0.05$.
** $p<0.01$.
*** $p<0.001$.

Third, and most importantly, our findings indicate that the relationship between neural activity to perceived pain in others and real-life altruistic behaviors is moderated by subjective assessments of one's own perceived SES. Behavioral studies suggest both empathy ability (Jolliffe and Farrington, 2006) and altruistic behavior (Eisenberg et al., 2001; Piff et al., 2010) differ between individuals with high and low objective SES. Participants in the current study were college students who had received similar education and did not have regular jobs. However, the participants reported different SSS. Unlike previous studies that showed influences of objective SES on self-reported empathic capability and altruistic behavior, we showed here that individuals' empathic capabilities and altruistic behaviors did not differ between individuals with high and low SSS. In addition, our fMRI results did not show any difference in empathy-related neural

Table 6
Hierarchical regression analysis on LIF activity with the amount of monetary donation as the dependent variable.

	Step1β	Step2β	Step3β
IRI	0.118	0.300	0.068
lIF activity	0.009	0.073	0.119
SSS	−0.014	0.064	0.085
IRI × SSS		−0.314	0.053
lIF × SSS			0.608**
⊿R^2	0.013	0.055	0.275
⊿F	0.123	1.582	10.872**
R^2	0.013	0.068	0.343
Adjusted R^2	−0.093	−0.070	0.216
Overall F	0.123	0.490	2.709*
df	29	28	27

* $p<0.05$.
** $p<0.01$.

activity between individuals with high and low SSS. However, these observations do not necessarily indicate that SSS has nothing to do with empathy and altruistic behavior. In contrast, our fMRI results uncover a complicated pattern of connections between neural activity to perceived pain in others and altruistic behaviors in high and low SSS individuals.

Specifically, we showed that, neural activity to perceived pain in the inferior frontal cortex and SII was positively correlated with the amount of monetary donations in high SSS individuals. According to the Perception–Action Model of Empathy, "attended perception of the object's state automatically activates the subject's representations of the state, situation, and object, and that activation of these representations automatically primes or generates the associated autonomic and somatic responses, unless inhibited" (Preston and de Waal, 2002, p. 3). This model suggests that empathy provides a proximate mechanism for costly helping behaviors (Preston and de Waal, 2002). Our findings of the positive correlation between empathy related neural activity and monetary donations are congruent with this model and suggest that empathy may immediately triggers helping behaviors such as monetary donations in individuals who recognize themselves high in SES. However, negative correlations were observed between neural activity to perceived pain and monetary donations in low SSS participants. It is likely that an intermediate mechanism may exist between empathic neural responses and monetary donations in low SSS individuals. One possibility is that consideration of one's own resources is of greater importance for low SSS participants, when deciding how much to donate, and thus modulates the immediate relation between empathy and altruistic behaviors. Alternatively, nerual responses to perceived pain in others in the SII and inferior frontal cortex might relate to empathy ability in different ways in high and low SSS individuals. To test this, we calculated the correlation between neural responses to perceived pain and subjective reports of empathy ability (i.e., IRI scores). We found that the neural responses in the left SII were positively correlated with the fantasy subscale of IRI measurements ($r = 0.551$, $p = 0.05$) in high SSS participants. In contrast, activities in the right SII and inferior frontal cortex were negatively correlated with the total IRI scores in low SSS participants ($r = -0.539$ and -0.611, $p = 0.057$ and 0.026). The different patterns of correlation results suggest that, for high SSS individuals, stronger neural responses to perceived pain in others were associated with greater subjective empathic ability. For low SSS participants, however, greater neural responses related to sensory (SII) and cognitive (inferior frontal) aspects of empathy may be associated with weaker self-reported empathy ability indexed by lower IRI scores, possibly due to that the inferior frontal activity regulates/inhibits the affective responses during social interactions (Eisenberger et al., 2003). This in turn results in fewer donations in low SSS individuals. The same mechanisms may also explain why low SSS participants with weaker neural responses to perceived pain donated more money—less SII and inferior frontal activity is associated with weaker regulation of affective responses (or with enhance affective responses) during empathy and thus results in more monetary donations. Future research may investigate the factors that regulate the relationship between empathic responses and altruistic behaviors in individuals with low SSS.

Interestingly, we found that the neural activity to perceived pain predicting the donated amount was localized in brain regions associated with sensory mapping and action perception rather than in those linked to affect aspects of empathy. The insular activity is involved in coding autonomic and affective dimensions of empathy for pain (Singer et al., 2004; Jackson et al., 2005; Han et al., 2009; Gu et al., 2010) but did not predict the amount of monetary donations given in our work. This is consistent with previous finding that empathy-relevant brain activation in the insula did not correlate with prosocial behavior (Singer et al., 2008). The SII activity, which is involved in somatosensory-motor representations (Blakemore et al., 2005) and reflects the sensory attributes of empathy for pain (Avenanti et al., 2005; Bufalari et al., 2007

One may notice that neural responses to perceived pain were limited to the inferior frontal cortex, insula and SII in the current work. Previous studies have shown that the pain matrix consisting of the ACC, insula, lateral inferior frontal cortices, and SII shows increased activity during empathy for pain in contrasts of painful vs. non-painful stimuli applied to body parts (Singer et al., 2004; Jackson et al., 2005; Gu and Han, 2007; Han et al., 2009; Bufalari et al., 2007), extreme vs. mild pain expression (Saarela et al., 2007), or painful vs. neutral scenes (Mathur et al., 2010). However, not all studies identified activations in every node of the pain matrix. Some studies found empathy related activity in the ACC and insula but not in the SII (Singer et al., 2004; Jackson et al., 2005). Other studies found empathy related activity in the inferior frontal cortex and insula but not in the ACC (Gu et al., 2010). Different brain regions of the pain matrix have distinct functional significances. The ACC and anterior/posterior insula mediate the affective component of empathy (Singer et al., 2004; Lamm et al., 2007) and the SII underlies the sensory component of empathy (Han et al., 2009). The pain judgment task used in our work emphasized pain intensity rather than subjective feeling of unpleasantness. This was possibly why the sensory component of the pain matrix was strongly engaged in the empathy. Moreover, our work used a block design. Repetition of painful stimuli in the same session might induce adaptation of neutral activity associated with affective responses to perceived pain and thus reduced the signals in brain areas such as ACC.

In summary, our results indicate that neural responses to perceived pain in others can predict the amount of monetary donations in a real-life situation. However, SSS strongly moderates the relationship between neural activity to perceived pain and charitable giving. Our brain imaging results implicate a direct link between neural activity to perceived pain and monetary giving in individuals with high SSS. Low SSS individuals, however, may adopt a regulatory mechanism between their neural activity to perceived pain and monetary giving behaviors. Our findings complement previous studies by showing that understanding the influence of SSS on the brain–behavior relationship can help to better predict human altruistic behaviors. Our findings have significant implications to social domain in that, besides improving objective SES, raising SSS via education may possibly manifold altruistic behaviors in human society. Finally, as the current work only recruited college students with similar and relatively high objective SES, future work may investigate whether the modulation effect of SSS observed in the current study can be applied to individuals with low objective SES.

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