Social status modulates the neural response to unfairness

Jie Hu,[1] Philip R. Blue,[1] Hongbo Yu,[1] Xiaoliang Gong,[2] Yang Xiang,[2] Changjun Jiang,[2] and Xiaolin Zhou[1,3,4,5]

[1]Center for Brain and Cognitive Sciences and Department of Psychology, Peking University, Beijing 100871, China, [2]Key Laboratory of Embedded System and Service Computing (Ministry of Education), Tongji University, Shanghai 201804, China, [3]Key Laboratory of Machine Perception (Ministry of Education), [4]Beijing Key Laboratory of Behavioral and Mental Health, Beijing 100871, China, and [5]PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China

Correspondence should be addressed to Xiaolin Zhou, Department of Psychology, Peking University, Beijing 100871, China. E-mail: xz104@pku.edu.cn

Jie Hu and Philip Blue contributed equally to this study.

Abstract

In human society, which is organized by social hierarchies, resources are usually allocated unequally and based on social status. In this study, we analyze how being endowed with different social statuses in a math competition affects the perception of fairness during asset allocation in a subsequent Ultimatum Game (UG). Behavioral data showed that when participants were in high status, they were more likely to reject unfair UG offers than in low status. This effect of social status correlated with activity in the right anterior insula (rAI) and with the functional connectivity between the rAI and a region in the anterior middle cingulate cortex, indicating that these two brain regions are crucial for integrating contextual factors and social norms during fairness perception. Additionally, there was an interaction between social status and UG offer fairness in the amygdala and thalamus, implicating the role of these regions in the modulation of social status on fairness perception. These results demonstrate the effect of social status on fairness perception and the potential neural underpinnings for this effect.

Key words: social status; fairness perception; insula; aMCC; amygdala; fMRI

Introduction

Fairness is a crucial norm in human and animal social behavior. The past couple of decades have provided an abundance of findings that people tend to maintain fairness norms by punishing individuals who behave unfairly, even at personal costs to themselves. Economic games, like the Ultimatum Game (UG), have been the primary experimental tools used to find the mechanisms that drive human fairness (Güth, 1982). UG involves two players, one of whom (the proposer) divides a sum of money between the two players and the other (the responder) who decides whether or not to reject the allocation of the money, which results in both parties coming away with nothing. The responder's rejection of an unfair UG offer is often

associated with inequity aversion elicited by unfairness and seen as punishment of norm-violating behaviors, which makes UG especially useful in testing for fairness considerations. A desire for fairness in UG holds even when the asset distribution has no effect on the participant (Loewenstein *et al.*, 1989) and is affected by certain variables such as social comparison (Wu *et al.*, 2011a), intention (Radke *et al.*, 2012), loss-gain domain (Zhou and Wu, 2011) and the social distance between the two parties (Wu *et al.*, 2011b).

Among these social factors, the social status of the individuals involved in asset distribution has a clear effect on fairness consideration (Albrecht *et al.*, 2013; Hu *et al.*, 2014). Albrecht *et al.* (2013) found that individuals with higher status (as determined by scores on a quiz) were less satisfied with disadvantageous

unequal offers than their lower status counterparts, supporting the perspective that high-status individuals feel entitled to more than low-status individuals in bargaining situations (Ball *et al.*, 2001). Consistent with these studies, in one of our previous studies (Hu *et al.*, 2014), we dynamically manipulated individuals' social status through a simple task and found that individuals reject more unfair offers when endowed with high status than when endowed with low status. Although it is common knowledge that endowment of low status induces negative emotions (Kraus *et al.*, 2011), which make an individual more likely to reject offers in UG (Harlé and Sanfey, 2007), research has shown that deference in low status and entitlement in high status increase the high-status individuals' rejection rate for unfair offers during asset distribution (Albrecht *et al.*, 2013, Hu *et al.*, 2014), which reinforces the importance of a social hierarchy in fairness interactions. In this study, combining our previous paradigm with functional magnetic resonance imaging (fMRI), we aimed to investigate the neural effects of social status on fairness consideration by recording the brain hemodynamic response while participants, as responders in the UG, were offered a range of fair and unfair asset distributions after being endowed with both high and low social status.

Previous neuroimaging studies have shown that several brain regions are involved in fairness consideration, such as the anterior insula (AI), anterior cingulate cortex/anterior middle cingulate cortex (ACC/aMCC), amygdala, and dorsolateral prefrontal cortex (DLPFC) (van den Bos *et al.*, 2010; Wu *et al.*, 2014). It is suggested that activations of the AI and ACC/aMCC are associated with negative affect elicited by unfair asset distribution (Sanfey *et al.*, 2003; Güroğlu *et al.*, 2010) and with reaction to norm-violating behaviors (King-Casas *et al.*, 2008; Xiang *et al.*, 2013). Moreover, the involvement of the DLPFC in UG is associated with the top-down inhibition of self-interested impulses to accept unfair offers (Knoch *et al.*, 2006, 2008; Güroğlu *et al.*, 2010). Recent studies have also shown that amygdala activity is related to inequity aversion (Haruno and Frith, 2010; Gospic *et al.*, 2011). Another line of research on social status has shown that social status processing involves the amygdala and hippocampus (Kumaran *et al.*, 2012) and the medial prefrontal cortex (Zink *et al.*, 2008; Wang *et al.*, 2014). For instance, Kumaran *et al.* (2012) found that the amygdala/anterior hippocampus not only tracked knowledge about social rank, but also expressed signals coding for social rank which influenced the effect of social rank on behavior. Taken together, these findings suggest that the amygdala may encode both social status and fairness considerations.

In this study, we were interested in how responders' own social status affects the behavioral responses (i.e. rejection) to UG offers and the underlying neural mechanisms of this effect. At the behavioral level, in line with previous studies, we predicted that rejection rates for unfair offers would increase with the responders' social status (Hu *et al.*, 2014). At the neural level, we expected that the activations of brain regions involved in fairness consideration, such as the AI, ACC/aMCC, amygdala, and DLPFC, may be modulated by the level of social status. In addition, we were also interested in identifying which brain regions' activations and/or functional connectivity could predict the effect of social status on individuals' responses to unfair offers.

Materials and methods

Participants

Thirty-three right-handed undergraduate and graduate students participated in the experiment. Ten participants were excluded from the data analysis: four were excluded because they were suspicious of the cover story or accepted all UG offers regardless of the fairness level, four participants were excluded due to excessive head movement and two were excluded due to equipment malfunction. The remaining 23 participants were aged between 19 and 25 years (mean = 21.22, s.d. = 1.73; 13 female). No participants reported any history of psychiatric, neurological or cognitive disorders. Informed, written consent was obtained from each participant before scanning. The study was carried out in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Department of Psychology, Peking University.

Design and procedure

The experiment had a 2×2 within-participant factorial design, with the first factor referring to social status (low *vs* high) and the second factor referring to offer fairness (unfair *vs* fair). Similar to past fMRI research (Zink *et al.*, 2008), social status was assigned using a star system, with one star indicating low status, two stars indicating middle status (filler condition), and three stars indicating high status. UG offers were considered unfair if they were ≤3 out of 10 yuan and fair if ≥4 out of 10 yuan. We also included sub-fair offers ranging between 3 and 4 out of 10 yuan as filler trials. No offer was >5 yuan.

On arriving at the laboratory, participants were informed that the experiment involved two roles: one role entailed acting as the proposer in UG, and the other as the recipient. Participants were also informed that six proposers were not being scanned and would be seated in a separate computer laboratory with computers that were connected to the fMRI laboratory via internet. Proposers were six same-sex confederates and only their pictures were used. To increase the perceived connection with other players but also to control for the potential effects of attractiveness on UG offer responses, pictures were only used during the status-inducing task and were not used in UG. During UG, the participants were notified that only their status and not any personal information (e.g. photo) or decision information (UG accept or reject responses) would be seen by the proposer.

The experiment was composed of two alternating tasks, both of which were performed in the scanner. Each task was performed in each of the six sessions. The first was a math competition (i.e. 'rank-inducing session'; Zink *et al.*, 2008; Boksem *et al.*, 2012) between the participant and the 6 same-sex confederates who would later act as proposers in UG (Figure 1A and Supplementary Method). After each rank-inducing session which included six trials, the participant was shown his/her rank in comparison with the six confederates (2 assigned to each ranking, with rankings randomly changed after each rank-inducing session; Figure 1B). The participant was endowed with each of the two critical levels of rank—high and low—each for two sessions, with another two sessions of middle rank as filler. The sequence of the participant's rank was Latin-squared across participants.

The second task was UG (Figure 1C). Participants acted as recipients in all rounds of UG. At the start of each UG trial, participants were shown their own star ranking derived from the preceding rank-inducing session (which remained the same throughout the entire session) beneath a self-photo (facial portrait, subtended $1.5° \times 1.6°$) and were informed that they had been successfully matched to a proposer for that trial, which lasted between 1000 and 2000 ms. The participant was then informed that the proposer was deciding on an offer, which lasted
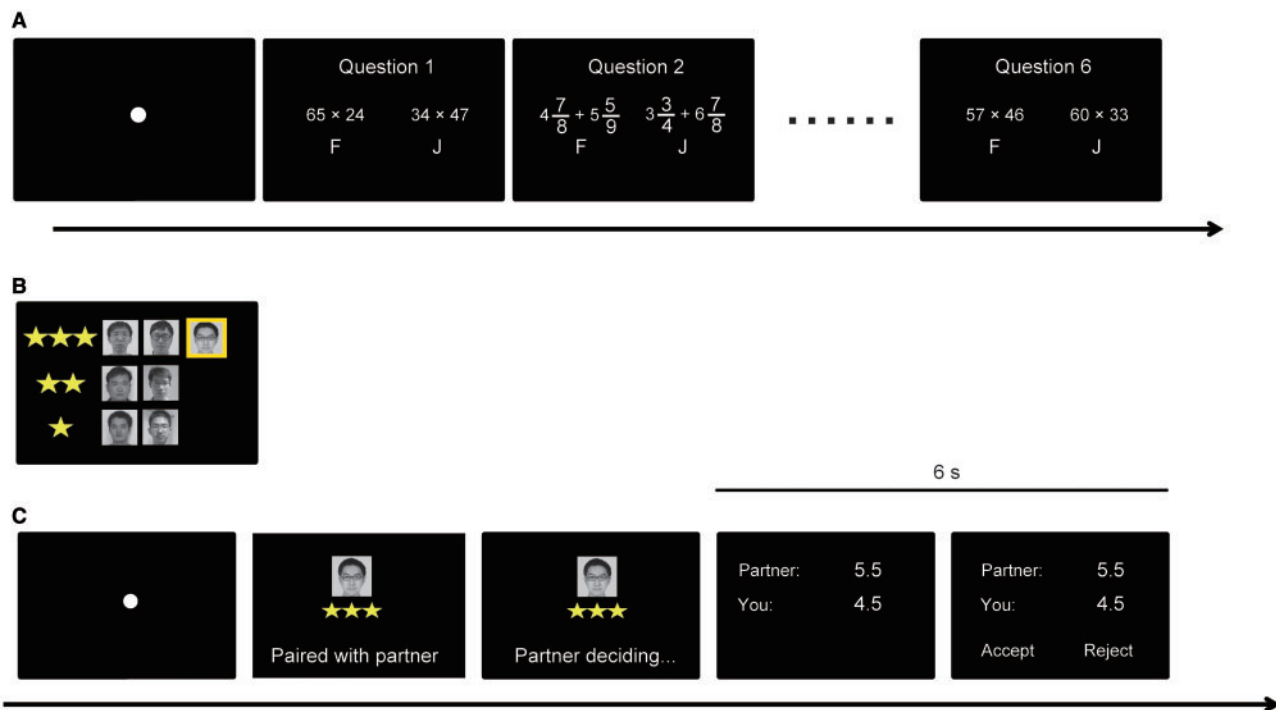
Fig. 1. Task, timing and design. The experiment was composed of two alternating tasks, both of which were performed in the scanner: the first was a math competition (i.e. rank-inducing session); the second was UG. Each session of the math competition was composed of six arithmetic expressions (A). Participants were given 10 s for each question to indicate, by pressing the left or right button corresponding to the "F" or "J" expression, which expression had a greater value. After each session, participants were given a ranking in relation to six same-sex confederates who would later act as proposers in UG (B). After ranks were given, the participant entered UG as the recipient (C). Each session of UG was composed of 24 UG offers with randomly paired and anonymous proposers. Each trial of UG began with a fixation, which was followed by the participant's self-portrait, self-ranking, and a notification that the computer was randomly pairing the participant with a proposer (1–2 s). After the proposer was paired, the participant waited for 1–2 s while the proposer made the offer decision (ranging from 1 to 5 yuan out of 10 yuan). The participant then viewed the offer for 3 s and was given 3 s to accept or reject the offer (fMRI data analysis was conducted during this 6 s time frame).

between 1000 and 2000 ms. Then the proposer's offer was shown to the participant. After 3000 ms of viewing the offer, the participant was asked to make a decision (accept or reject) within 3000 ms. As confirmation of the decision, a box was placed around the decision selection. After 3000 ms, the next trial began. Each offer type (unfair and fair) appeared 20 times for each status level (low, middle, high), resulting in 4 trials for each specific offer level (unfair: 1/9, 1.5/8.5, 2/8, 2.5/7.5, 3/7; fair: 4/6, 4.2/5.8, 4.5/5.5, 4.8/5.2, 5/5) for each social status level. The sub-fair offers (3.2/6.8, 3.8/6.2) appeared 8 times for each status level. The number before the slash denoted the amount offered to the recipient and the number after the slash denoted the amount given to the proposer. Participants were endowed with each rank for 2 sessions; each session consisted of 24 UG offers (10 unfair, 10 fair and 4 sub-fair offers). Unknown to the participant, all the offers were predetermined by a computer program and pseudo-randomized with the restriction that no more than three consecutive trials were of the same offer fairness. After 24 rounds of UG, the participant performed the next session of the rank-inducing task during which he or she would obtain a new rank before entering the next 24 rounds of UG. Although the participants were aware that their decisions in each trial would not be sent to the proposers immediately, they were explicitly instructed that their decisions in UG (i.e. acceptance or rejection of the offers) would determine the proposers' and their own final payments.

Before scanning, participants practiced at least 6 arithmetic expressions and 10 trials of UG until they felt comfortable with the buttons and presentation layout. After the experiment, participants reported on a 7-point Likert scale to what extent they felt superior or inferior (1 = very inferior; 7 = very superior) to the other players in the experiment while occupying each of the social status levels. Participants also indicated to what extent they were influenced by their social status during the UG (1 = influenced very little; 7 = influenced very much). To measure for perceived entitlement, two post-experimental measures were recorded for both low and high social status: participants indicated their minimal acceptable amount (out of 10 yuan) during UG and how much they would allocate to a recipient if they were proposer in UG. Finally, participants reported their socioeconomic status (i.e. parents' highest level of education and annual income) and completed the MacArthur Subjective Social Status Scale (Adler, 2000), which asks participants to indicate their subjective status in Chinese society on a ladder, with the lowest rungs indicating individuals with the lowest level of money, education and vocation and the highest rungs indicating individuals with the highest level of money, education and vocation. Finally, we randomly selected 10 rounds of UG and averaged the participant's payoff according to his/her decisions as a bonus in addition to his/her basic payment.

MRI data acquisition

Imaging data were collected using a GE-MR750 3.0 Tesla scanner with a standard head coil at Tongji University, Shanghai, China. $T2^*$-weighted echo-planar images with blood oxygenation level-dependent (BOLD) contrast were acquired in 40 axial slices parallel to the AC–PC line with an interslice gap of 3.1 mm, allowing for full-brain coverage. Images were acquired in an interleaved order, with a repetition time of 2000 ms, an echo time of 30 ms,

a flip angle of 90° and a field of view of 200 mm × 200 mm, and 3.1 mm × 3.1 mm × 3.1 mm voxels.

fMRI preprocessing

Preprocessing of the fMRI images was done using Statistical Parametric mapping software SPM8 (Wellcome Trust Department of Cognitive Neurology, London, UK), which was run through MATLAB (Mathworks). For each run, the first five volumes were discarded to allow for stabilization of magnetization. Then, the remaining images were slice-time corrected, motion-corrected, re-sampled to $3 \times 3 \times 3$ isotropic voxel, normalized to Montreal Neurological Institute (MNI) space and spatially smoothed using an 8 mm FWHM Gaussian filter. Data were filtered using a high-pass filter with 1/128 Hz cutoff frequency.

General linear model analyses

To analyze how social status influenced the entire decision-making processes, we estimated a general linear model (GLM) of blood-oxygen-level-dependent (BOLD) responses, which combined BOLD responses during the viewing of the UG offer and during the implementation of each UG decision (accept or reject). For the first-level analysis, nine regressors of interest were included in the model for each participant: low status unfair offer, low status sub-fair offer, low status fair offer, middle status unfair offer, middle status sub-fair offer, middle status fair offer, high status unfair offer, high status sub-fair offer and high status fair offer. In addition, we included the onsets of the partner pairing screen and the proposer deciding screen as regressors of no interest in the model. Six head motion parameters were included as regressors of no interest in all models. All regressors of interest were convolved with a canonical hemodynamics response function (HRF). For the second-level group analysis, four beta images of interest (low status unfair offer, low status fair offer, high status unfair offer and high status fair offer) were fed into a flexible factorial model. We defined four contrasts corresponding to the main effects of fairness and status ('Unfair > Fair', 'Fair > Unfair', 'High status > Low status' and 'Low status > High status'). We tested the interaction contrast values '(Low status unfair − Low status fair) − (High status unfair − High status fair)'. We also conducted a one-sample *t*-test for the correlation between the contrast of interest (High status unfair − Low status unfair) and the measure of social status effect (i.e. the increased rejection rate for unfair offers in the high-status condition relative to the low-status condition).

Psycho-physiological interaction analysis

The GLM analysis showed that activity in the right anterior insula (rAI) during the contrast of interest (High status unfair offer − Low status unfair offer) was associated with individual differences in rejection rates during UG. We were interested in the functional connectivity between rAI and a network of brain regions during the UG offer fairness processing. In order to test for how functional connectivity between brain regions during unfairness processing varied with social status, we estimated a psycho-physiological interaction (PPI) model (Friston *et al.*, 1997) for the contrast of interest (High status unfair offer − Low status unfair offer). We defined a 3 mm radius volume of interest around the peak coordinates of rAI. This rAI seed region was extracted from the whole-brain correlation analysis mentioned above. As we were most interested in the regions for which the change in the functional connectivity with the rAI varied with the differences in rejection rates of unfair offers between high and low status, we
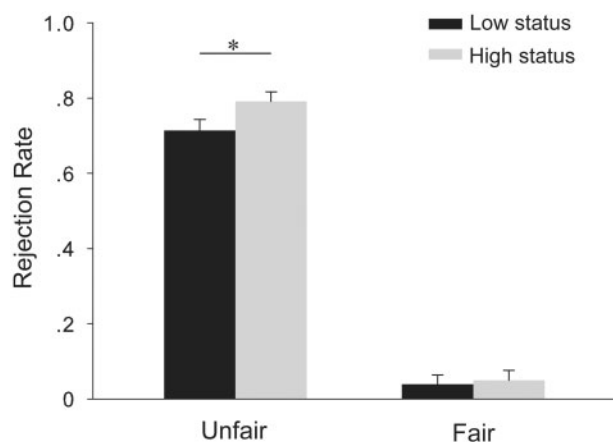

Fig. 2. Mean and standard error of the means for rejection rates of unfair and fair offers while occupying low and high social status.

correlated this social status measure (High status unfair rejection rate − Low status unfair rejection rate) with the contrast of interest (High status unfair offer − Low status unfair offer) in the PPI model. More specifically, the PPI regressor was the element-by-element product of the physiological activity in rAI and the vector coding for the effect of social status on unfair offers. The model included this product convolved by the canonical HRF as the effect of interest, and the main effect of social status convolved by the HRF, neural time course for rAI and the six head-movement regressors as effects of no interest. We ran the PPI model and generated contrast images for the effect of interest. At the second level, we entered the contrast images and the difference in rejection rate (High status unfair − Low status unfair) into the regression model to check for regions for which the changes in connectivity with the rAI correlated with the rejection rate difference (High status unfair − Low status unfair) (Passamonti *et al.*, 2008; Yu *et al.*, 2014).

Throughout the GLM and PPI analysis, we used the AFNI program AlphaSim to determine our significance criterion. Areas of activation were identified as significant only if they passed the threshold of a corrected $P < 0.05$ with a minimum of 23 contiguous voxels each significant at $P < 0.001$, uncorrected.

Results

Behavioral results

The behavioral variable of interest was the rejection rate of UG offers. A repeated-measures analysis of variance (ANOVA) showed that rejection rates varied as a function of both social status [$F(1, 22) = 9.52$, $P = 0.005$, $\eta^2_{partial} = 0.30$] and UG offer fairness [$F(1, 22) = 222.49$, $P < 0.001$, $\eta^2_{partial} = 0.91$], with a marginally significant interaction between social status and offer fairness [$F(1, 22) = 3.65$, $P = 0.07$, $\eta^2_{partial} = 0.14$]. Pairwise comparisons showed that rejection rates for participants in high social status (mean ± standard error, 0.42 ± 0.01) were greater than when in low status (0.38 ± 0.01). As expected, participants rejected unfair offers (0.75 ± 0.02) more than fair offers (0.05 ± 0.02). Tests for simple effects showed that unfair offers were rejected more by participants in high status (0.79 ± 0.03) than in low status (0.72 ± 0.03), $P = 0.011$; this difference did not exist for fair offers, $P = 0.50$. Figure 2 displays the rejection rates of UG offers in low and high social status.

A one-factor (star ranking: one star *vs* three star ranking) repeated-measures ANOVA confirmed that the manipulation of
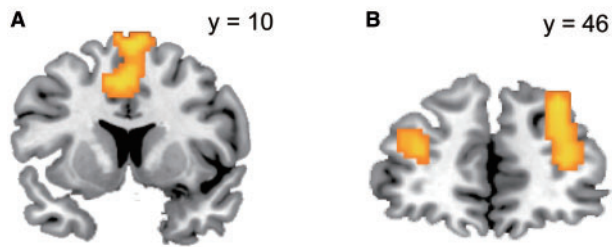
Fig. 3. Whole-brain unfair > fair contrast revealed activity in the ACC, SMA (**A**) and bilateral DLPFC (**B**). Activations were thresholded at corrected $P < 0.05$ (voxel-wise $P < 0.001$ uncorrected with a minimum cluster extent of 23 voxels).

Table 1. Brain areas of significant activation for the main effect (unfair > fair) and for the interaction effect between social status and fairness, corrected $P < 0.05$ (voxel-wise $P < 0.001$, minimum cluster extent = 23 voxels)

Regions	Laterality	Peak MNI coordinates			Max T-value	Voxel size (k)
		x	y	z		
Main effect: unfair > Fair						
ACC/SMA	L, R	6	23	37	5.20	479
DLPFC	R	36	50	16	4.75	182
	L	−36	50	22	4.12	45
Interaction effect: (Low status unfair > Low status fair) > (High status unfair > High status fair)						
AMY	L	−21	−4	−11	4.76	41
Thalamus	L	−15	−19	4	4.16	47
Precentral Gyrus	L	−36	−22	64	3.66	54

Note. MNI coordinates are reported for peak activation.
R = right; L = left; AMY = amygdala, HPC = hippocampus.

social status was successful in changing feelings of superiority/inferiority [$F(1, 22) = 97.59$, $P < 0.001$, $\eta^2_{partial} = 0.81$, with participants perceiving themselves as higher in status after attaining three stars (5.26 ± 0.15) than after attaining one star (2.35 ± 0.15). As expected, when compared with low status, participants in high status felt entitled to higher offer amounts as the recipient [$F(1,22) = 12.58$, $P = 0.002$, $\eta^2_{partial} = 0.36$] and to higher allocations to the self while acting as the proposer [$F(1,22) = 10.07$, $P = 0.004$, $\eta^2_{partial} = 0.31$]. In particular, participants evidenced higher minimum acceptable amounts in high status (3.4 ± 0.06) than in low status (3.0 ± 0.06), and indicated that they would allocate to themselves a greater amount while in high status (5.73 ± 0.12) than in low status (4.94 ± 0.12).

The primary behavioral measure was the difference in rejection rates between high and low status. This measure proved to be an effective representation of the behavioral data as it positively correlated with how superior participants reported feeling in the high status condition ($r = 0.46$, $P = 0.028$, $d.f. = 21$) and with participants' self-reports of being influenced by their social status during the UG ($r = 0.82$, $P < 0.001$, $d.f. = 21$). Additionally, it is unlikely that this measure was confounded by participant social status outside the experiment, as it was not correlated with either objective (i.e. socioeconomic status) or subjective social status (parent highest level education, $P = 0.6$; annual family income, $P = 0.35$; subjective social status, $P = 0.74$).

fMRI results

Main effects of social status and fairness. To confirm our results with past findings on UG, we estimated a GLM of the BOLD responses during the UG offer encoding process. We first identified voxels that were more activated for unfair UG offers than for fair UG offers. Consistent with past research (Sanfey *et al.*, 2003, van den Bos *et al.*, 2010), there was a main effect of unfairness, with greater activation for unfair offers than for fair offers in the ACC, which extended to the supplementary motor area/middle cingulate cortex (SMA/MCC; Figure 3A and Table 1), and in the DLPFC (Figure 3B). It is surprising that we found no insula activation during the unfair > fair contrast; however, if we relax our threshold ($P < 0.005$, minimum cluster extent = 46 voxels, a threshold of corrected $P < 0.05$ according to AlphaSim), we did find significant activity in the left AI ($x = −39$, $y = 11$, $z = −8$, Mas T-value = 3.10, $k = 75$). There was no significant activation for the reversed contrast (fair > unfair) or for the main effect of social status.

Interaction between social status and fairness. In addition to the main effect of unfairness, the analysis also revealed an interaction between fairness and social status [(Low status unfair − Low status fair) − (High status unfair − High status fair)]

in the left amygdala ($x = −21$, $y = −4$, $z = −11$; Figure 4A), left thalamus ($x = −15$, $y = −19$, $z = 4$; Figure 4C) and left precentral gyrus ($x = −36$, $y = −22$, $z = 64$; Supplementary Figure). The left amygdala beta values were greater in low status unfair (0.14 ± 0.02) than low status fair (0.07 ± 0.02, $P = 0.015$), and showed no difference between high status unfair (0.08 ± 0.02) and high status fair (0.12 ± 0.02, $P = 0.140$) (Figure 4B). The left thalamus beta values were also greater in low status unfair (0.04 ± 0.02) than low status fair ($−0.04 \pm 0.02$, $P = 0.001$), and showed no difference between high status unfair ($−0.005 \pm 0.02$) and high status fair ($−0.02 \pm 0.02$, $P = 0.469$) (Figure 4D).

Correlation analyses. At the group level, we performed a whole-brain analysis to identify brain regions that correlated with the increased rejection rate for unfair offers in the high-status condition relative to unfair offers in the low-status condition. For the contrast of interest (High status unfair – Low status unfair), activations of the rAI (Table 2) correlated positively with increases in rejection rate in the high status unfair condition relative to the low status unfair condition (Figure 5).

Functional connectivity analysis. Given that activity in the right AI during the contrast of interest (High status unfair offer – Low status unfair offer) was positively associated with the increased likelihood to reject unfair offers in high status (Figure 5), we were interested in finding a network of brain areas that were functionally connected during status-related fairness processing. A PPI comparing the high status unfair condition and low status unfair condition showed that the amount of increased rejection rates significantly correlated with the change in connectivity between the rAI and the aMCC (Craig, 2009) (Figure 6 and Table 2). A whole-brain analysis revealed no significant changes in connectivity between the right AI and other voxels of the brain.

Discussion

It is important to understand the effects of social status on fairness perception for many reasons. Humans, and many social animals (Rabb *et al.*, 1967; Sapolsky, 2005; Grosenick *et al.*, 2007), have evolved social hierarchies, and within these hierarchies resources are allocated unequally and based on social status.
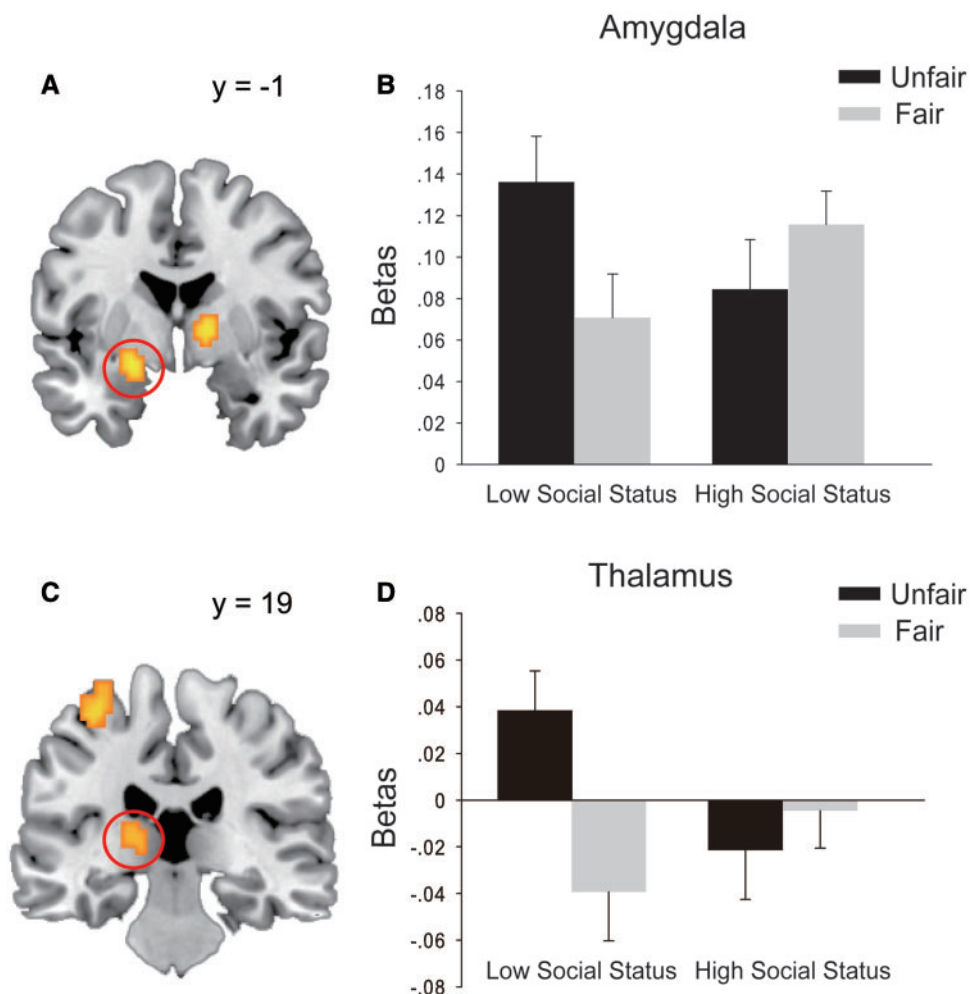
Fig. 4. Interaction between fairness and social status [(Low status unfair − Low status fair) − (High status unfair − High status fair)] revealed significant activity in the left amygdala (A). Activity in this region was greater for unfair offers during low status; no difference is evident between unfair and fair offers in the high-status condition (B). Interaction between fairness and social status [(Low status unfair − Low status fair) − (High status unfair − High status fair)] also revealed significant activity in the left thalamus (C). Activity in this region was greater for unfair offers than for fair offers in low status; no difference is evident between unfair and fair offers in the high-status condition (D).The beta values were the averaged beta values across the voxels in a spherical region with 3 mm radius and centered at the peak coordinate of the activation region. Activations were thresholded at corrected $P < 0.05$ (voxel-wise $P < 0.001$ uncorrected with a minimum cluster extent of 23 voxels).

Here we used a paradigm in which the social status of participants was manipulated through math competitions before acting as recipients in UG. Importantly, the paradigm allowed us to test the neural tracking of social status influences on fairness perception using a within-subject design, thereby avoiding many potentially confounding factors. At the behavioral level, participants were more likely to reject unfair offers when they were in high status than when they were in low status. At the neural level, we found that the left AI, ACC/SMA and bilateral DLPFC were activated in the unfairness *vs* fairness contrast. Interestingly, an interaction between social status and UG offer fairness was found in the thalamus and amygdala. Furthermore, individual difference analyses revealed that individuals who rejected more unfair offers in the high-status relative to in the low-status condition had increased right AI activation and stronger functional connectivity between the right AI and the ACC/aMCC when they were exposed to unfair offers in the high-status than in the low-status condition. These findings further reinforced the importance of an AI connection to the ACC/aMCC during the perception of asset distribution between individuals within a hierarchy.

The increased likelihood of rejecting unfair offers while in high status than in low status is in line with past research showing an entitlement effect during asset distribution (Ball *et al.*, 2001; Albrecht *et al.*, 2013; Hu *et al.*, 2014). In support of this entitlement effect, post-experiment questionnaire data showed that, when compared with low status, participants in high status had a higher bottom line and indicated that they would allocate more to themselves if given the opportunity to act as proposer in UG. This entitlement effect may have arisen from differences in orientations toward others while occupying different levels of social status. In comparison with high status, low-status individuals tend to give more to strangers (Piff *et al.*, 2010), which is true even for children as young as 4 and 5 years of age (Guinote *et al.*, 2015), and individuals in low status are less likely to break laws or social norms (Piff *et al.*, 2012). This increased tendency for prosocial behavior in low-status individuals may be used to increase status (Flynn *et al.*, 2006), as decreased rejection rates would lead to a happier partner and, in this study, would lead to an increase in money earned during UG, suggesting that the entitlement effect may be an adaptive mindset for low-status individuals in social hierarchies.
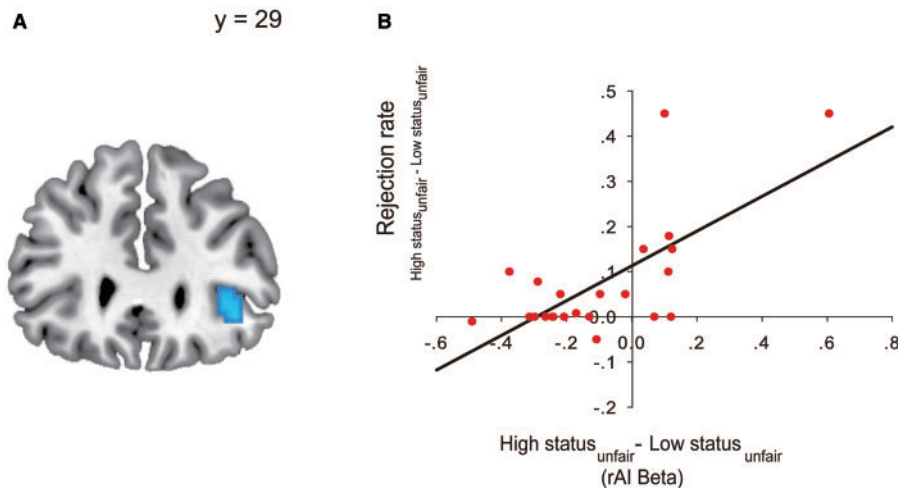
Fig. 5. Group level whole-brain analysis revealed a significant positive correlation between activity in the right AI and the increased tendency to reject unfair UG offers in high status for the contrast of interest (High status unfair – Low status unfair) (A). Scatter plot displaying the significant relationship between the rAI and the increased tendency to reject unfair UG offers in high status (B), as reported in (A). The finding remained significant after removal of the two participants whose rejection rate differences were greater than 2 s.d. above the group mean. The beta values were the averaged beta values across the voxels in a spherical region with 3 mm radius and centered at the peak coordinate of the activation region. Activations were thresholded at corrected $P < 0.05$ (voxel-wise $P < 0.001$ uncorrected with a minimum cluster extent of 23 voxels). Note, the scatter plot is for the illustration of the correlation reported in (A) and was not subject to additional statistical analyses.

Table 2. Brain areas showing a positive correlation with the difference in rejection rates for unfair offers between high and low status in the contrast of interest (High status unfair > Low status unfair) and in the PPI analysis, corrected $P < 0.05$ (voxel-wise $P < 0.001$, minimum cluster extent = 23 voxels)

Regions	Laterality	Peak MNI coordinates			Max T-value	Voxel size (k)
		x	y	z		
Correlation: High status unfair > Low status unfair						
AI	R	39	29	−2	3.70	24
MTG	R	42	−49	16	3.74	40
Correlation: functional connectivity with right AI for the contrast 'High status unfair > Low status unfair'						
aMCC	L	−12	5	46	3.45	74

MNI coordinates are reported for peak activation.
R = right; L = left; MTG = middle temporal gyrus.

Consistent with previous studies, we found that unfair offers evoked stronger activations in the left AI, ACC/SMA and bilateral DLPFC than fair offers (Sanfey *et al.*, 2003; Dulebohn *et al.*, 2009; Gabay *et al.*, 2014). A likely explanation for the AI activity is that it represents and responds to violations of fairness norms (Civai *et al.*, 2012; Corradi-Dell'Acqua *et al.*, 2013; Gabay *et al.*, 2014). In this study, stronger AI activity in the high status unfair condition was associated with a higher rejection rate for unfair offers in high status. Given that when individuals are endowed with high status, they feel entitled to more in bargaining situations (Ball *et al.*, 2001; Albrecht *et al.*, 2013) and have stronger motivation to preserve their social standing (Blader and Chen, 2012; Hu *et al.*, 2014), the association between higher AI activity and higher rejection rates for unfair offers in the high-status condition suggests that AI is engaged in the integration of motivation (e.g. inequity aversion) and contextual factors (e.g. social status level) to promote punishing norm violations (Sanfey *et al.*, 2003; Seymour *et al.*, 2007; White *et al.*, 2014). This interpretation is in line with a recent study which showed that the AI is associated with rejections of unfair offers regardless of whether the recipient of the offer is a stranger or the participant him/herself (Corradi-Dell'Acqua *et al.*, 2013) and with research showing that the AI integrates cognitive, emotional and motivational information (Singer *et al.*, 2009; Lamm and Singer, 2010).

It is surprising that we did not find a main effect of brain activation for social status, especially since research has shown that viewing differently ranked others increases activity in a wide array of brain regions related to cognition and affect in social settings (i.e. dorsomedial prefrontal cortex and amygdala; Zink *et al.*, 2008). One reason for the lack of a main effect, however, may be because in past studies on social status, participants focused solely on the processing of social status information itself (Zink *et al.*, 2008; Kumaran *et al.*, 2012), whereas in this study, the participants processed fairness in the context of social status. In line with this reasoning, we did find an interaction between social status and UG offer fairness in the thalamus and amygdala, which both have been implicated in the representation of social hierarchy information (Zink *et al.*, 2008; Kumaran *et al.*, 2012) and in processing inequity (Haruno and Frith, 2009; Gospic *et al.*, 2011; Lamichane *et al.*, 2014), suggesting that these brain regions may be crucial for the modulation of social status on fairness processing.

Past research on social status processing showed that the thalamus was most activated when viewing superior others in unstable social hierarchies (Zink *et al.*, 2008). However, this study showed that thalamus activity is related to the effect of one's own status on fairness processing. In particular, the interaction between social status and fairness appears to be driven by a large difference in neural response to UG offer fairness in low but not in high social status (Figure 4D), which may suggest that the thalamus activation reflects motivational concerns related to social status and its effects on fairness processing (Haber and Calzavara, 2009).

In this study, while the amygdala showed stronger activation to unfair offers than fair offers in the low-status condition, this pattern was absent in the high-status condition. It is possible that the neural effect of social status on the amygdala
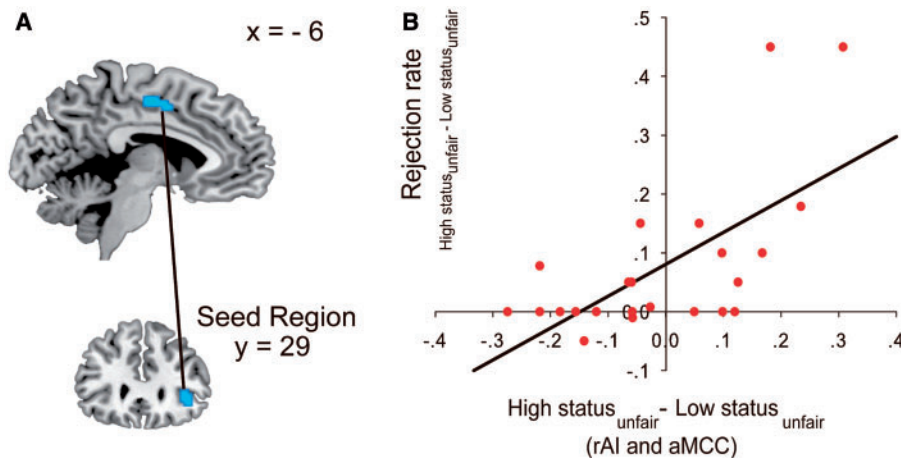
Fig. 6. PPI analysis comparing the high status unfair condition with the low status unfair condition showed that increases in rejection rates were positively correlated with increases in functional connectivity between the rAI and ACC/aMCC (A). Scatter plot displaying the significant relationship between the rAI and ACC/aMCC (B). This finding remained significant after removal of the two participants whose rejection rate differences were greater than 2 s.d. above the group mean. The beta values were the averaged beta values across the voxels in a spherical region with 3 mm radius and centered at the peak coordinate of the activation region. Activations were thresholded at corrected $P < 0.05$ (voxel-wise $P < 0.001$ uncorrected with a minimum cluster extent of 23 voxels). Note, the scatter plot is for the illustration of the correlation reported in (A) and was not subject to additional statistical analyses.

resulted from changes in hormone and neurotransmitter levels while occupying different social statuses. Changes in social status have been shown to influence the neuroendocrine system (Chiao, 2010; Knight and Mehta, 2014; Zilioli *et al.*, 2014). For example, changes in social status affect testosterone levels of individuals in a hierarchy (Zilioli *et al.*, 2014). Moreover, manipulation of hormone and neurotransmitter levels can change amygdala responses to positive and negative stimuli. In a recent study, Aupperle *et al.* (2011) showed that the amygdala exhibits a stronger activation during the anticipation of positive stimuli than during the anticipation of negative stimuli; additionally, Pregabalin, an anxiolytic which decreases the levels of certain neurotransmitters, can reverse this amygdala activation pattern. Given these findings, we speculate that the difference in amygdala activity between participants in high and low status may be due to changes in hormone or neurotransmitter levels, which influence downstream fairness processing of UG offers in the amygdala. Nevertheless, the neurobiological basis of this effect still needs to be clarified in future studies.

At the group level, individual difference analysis showed that activity in the right AI positively correlated with the difference between the rejection rates for unfair offers in the high- and low-status conditions, suggesting that the insula may act to integrate fairness preferences and social status information to modulate punishments of unfair behaviors. In support of this postulate, the PPI comparing the high status unfair and low status unfair conditions showed that the change in functional connectivity between the right AI and aMCC was positively associated with the difference between the participants' rejection rates in these two conditions. It is possible that in the high-status condition, relative to the low-status condition, the stronger connectivity between the AI and aMCC is associated with a greater motivation to punish unfair behaviors, as the aMCC is involved in conflict resolution and may act to initiate altruistic punishment by overriding the self-interested motivations to accept unfair offers and gain more money. In support of this explanation for the relationship between the AI and aMCC, there is an abundance of research confirming both the structural and functional connectivity between these two brain regions (Watson *et al.*, 2006; Sridharan *et al.*, 2008; Craig, 2009;

Taylor *et al.*, 2009). In a recent study, Klumpp *et al.* (2012) revealed that compared with patients with generalized social anxiety disorder, healthy controls evidenced stronger AI-dorsal anterior cingulate (dACC) connectivity when processing fearful faces, suggesting an important role of the AI-dACC network in cognitive control and emotion regulation. In addition, the aMCC and AI are often co-activated in the unfairness *vs* fairness contrast (Sanfey *et al.*, 2003; Civai *et al.*, 2012; Corradi-Dell'Acqua *et al.*, 2013; Craig, 2009; for a review, see Feng *et al.*, 2015). Our results extended previous neuroimaging studies by showing that the connectivity between the AI and aMCC is associated with fairness-related behavior.

Conclusion

By manipulating the social status of participants in the UG, we found that participants endowed with high status were more likely to reject unfair offers than when they were endowed with low status. In addition, this effect was tracked by activity in the rAI and by its functional connectivity with aMCC, further implicating these two brain regions in being responsible for punishing violators of social norms. Finally, the fairness-related amygdala and thalamus activity was modulated by social status, suggesting that, in line with past research, these regions may be responsible for encoding both social status and fairness-related stimuli. These findings demonstrate that social status affects the behavioral and neural responses to asset distributions.

Acknowledgements

We would like to thank Yiyuan Wang for her help in data collection and two anonymous reviewers for their constructive comments on an earlier version of the manuscript.

Funding

grants from the Natural Science Foundation of China (91232708, 31170972).

Supplementary data

Supplementary data are available at *SCAN* online.

Conflict of interest. None declared.

References

Adler, N.E., Epel, E.S., Castellazzo, G., Ickovics, J.R. (2000). Relationship of subjective and objective social status with psychological and physiological functioning: preliminary data in healthy white women. *Health Psychology,* **19**, 586–92.

Albrecht, K., von Essen, E., Fliessbach, K., Falk, A. (2013). The influence of status on satisfaction with relative rewards. *Frontiers in Psychology,* **4**, 804.

Aupperle, R.L., Lakshmi, R., Tankersley, D., *et al.* (2011). Pregabalin influences insula and amygdala activation during anticipation of emotional images. *Neuropsychopharmacology,* **36**(7), 1466–77.

Ball, S., Eckel, C., Grossman, J., Zame, W. (2001). Status in markets. *Quarterly Journal of Economics,* **116**, 161–88.

Blader, L., Chen, Y. (2012). Differentiating the effects of status and power: a justice perspective. *Journal of Personality and Social Psychology,* **102**, 994–1014.

Boksem, A., Kostermans, E., Milivojevic, B., De Cremer, D. (2012). Social status determines how we monitor and evaluate our performance. *Social Cognitive and Affective Neuroscience,* **7**, 304–13.

Chiao, J. (2010). Neural basis of social status hierarchy across species. *Current Opinion in Neurobiology,* **20**(6), 803–9.

Civai, C., Crescentini, C., Rustichini, A., Rumiati, R.I. (2012). Equality versus self-interest in the brain: differential roles of anterior insula and medial prefrontal cortex. *Neuroimage,* **62**, 102–12.

Corradi-Dell'Acqua, C., Civai, C., Rumiati, R.I., Fink, G.R. (2013). Disentangling self- and fairness-related neural mechanisms involved in the ultimatum game: an fMRI study. *Social Cognitive and Affective Neuroscience,* **8**(4), 424–31.

Craig, A.D. (2009). How do you feel now? The anterior insula and human awareness. *Nature Reviews Neuroscience,* **10**(1), 59–70.

Dulebohn, J.H., Conlon, D.E., Sarinopoulos, I., Davison, R.B., McNamara, G. (2009). The biological bases of unfairness: neuroimaging evidence for the distinctiveness of procedural and distributive justice. *Organizational Behavior and Human Decision Processes,* **110**(2), 140–51.

Feng, C., Luo, Y., Krueger, F. (2015). Neural signatures of fairness-related normative decision making in the ultimate game: a co-ordinate-based meta-analysis. *Human Brain Mapping*, **36**(2), 591–602.

Flynn, F.J., Reagans, R.E., Amanatullah, E.T., Ames, D.R. (2006). Helping one's way to the top: self-monitors achieve status by helping others and knowing who helps whom. *Journal of Personality and Social Psychology,* **91**(6), 1123–37.

Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., Dolan, R.J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *Neuroimage,* **6**(3), 218–29.

Gabay, A.S., Radua, J., Kempton, M.J., Mehta, M.A. (2014). The Ultimatum Game and the brain: A meta-analysis of neuroimaging studies. *Neuroscience and Biobehavioral Reviews,* **47**, 549–58.

Gospic, K., Mohlin, E., Fransson, P., Petrovic, P., Johannesson, M., Ingvar, M. (2011). Limbic justice—amygdala involvement in immediate rejection in the Ultimatum Game. *PLoS Biology,* **9**(5), e1001054.

Grosenick, L., Clement, T.S., Fernald, R.D. (2007). Fish can infer social rank by observation alone. *Nature,* **445**(7126), 429–32.

Guinote, A., Cotzia, I., Sandhu, S., Siwa, P. (2015). Social status modulates prosocial behavior and egalitarianism in preschool children and adults. *Proceedings of the National Academy of Sciences,* **112**(3), 731–6.

Güroğlu, B., van den Bos, W., Rombouts, S.A.R.B., Crone, E.A. (2010). Unfair? It depends: neural correlates of fairness in social context. *Social Cognitive and Affective Neuroscience,* **5**, 414–23.

Güth, W., Schmittberger, R., Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior and Organization,* **3**, 367–88.

Haber, S.N., Calzavara, R. (2009). The cortico-basal ganglia integrative network: the role of the thalamus. *Brain Research Bulletin,* **78**, 69–74.

Harlé, M., Sanfey, G. (2007). Incidental sadness biases social economic decisions in the ultimatum game. *Emotion,* **7**, 876–81.

Haruno, M., Frith, C.D. (2010). Activity in the amygdala elicited by unfair divisions predicts social value orientation. *Nature Neuroscience,* **13**(2), 160–1.

Hu, J., Cao, Y., Blue, P.R., Zhou, X. (2014). Low social status decreases the neural salience of unfairness. *Frontiers in Behavioral Neuroscience,* **8**, 402.

King-Casas, B., Sharp, C., Lomax-Bream, L., Lohrenz, T., Fonagy, P., Montague, P.R. (2008). The rupture and repair of cooperation in borderline personality disorder. *Science,* **321**(5890), 806–10.

Klumpp, H., Angstadt, M., Phan, K.L. (2012). Insula reactivity and connectivity to anterior cingulate cortex when processing threat in generalized social anxiety disorder. *Biological Psychology,* **89**(1), 273–6.

Knight, E.L., Mehta, P.H. (2014). Hormones and hierarchies. In: Cheng, J.T., Tracy, J.L., Anderson, C., editors. *The Psychology of Social Status.* New York: Springer, pp. 269–301.

Knoch, D., Nitsche, M.A., Fischbacher, U., Eisenegger, C., Pascual-Leone, A., Fehr, E. (2008). Studying the neurobiology of social interaction with transcranial direct current stimulation—the example of punishing unfairness. *Cerebral Cortex,* **18**(9), 1987–90.

Knoch, D., Pascual-Leone, A., Meyer, K., Treyer, V., Fehr, E. (2006). Diminishing reciprocal fairness by disrupting the right prefrontal cortex. *Science,* **314**(5800), 829–32.

Kraus, W., Horberg, J., Goetz, L., Keltner, D. (2011). Social class rank, threat vigilance, and hostile reactivity. *Personality and Social Psychology Bulletin,* **37**, 1376–88.

Kumaran, D., Melo, H.L., Duzel, E. (2012). The emergence and representation of knowledge about social and nonsocial hierarchies. *Neuron,* **76**(3), 653–66.

Lamichane, B., Adhikari, B.M., Brosnan, S.F., Dhamala, M. (2014). The neural basis of perceived unfairness in economic exchanges. *Brain Connectivity,* **4**(8), 619–30.

Lamm, C., Singer, T. (2010). The role of anterior insular cortex in social emotions. *Brain Structure and Function,* **214**(5–6), 579–91.

Loewenstein, G.E., Thompson, L., Bazerman, M.H. (1989). Social utility and decision making in interpersonal contexts. *Interpersonal Relations and Group Processes,* **57**(3), 426–41.

Passamonti, L., Rowe, J.B., Ewbank, M., Hampshire, A., Keane, J., Calder, A.J. (2008). Connectivity from the ventral anterior cingulate to the amygdala is modulated by appetitive motivation in response to facial signals of aggression. *Neuroimage,* **43**(3), 562–70.

Piff, K., Kraus, W., Côté, S., Cheng, H., Keltner, D. (2010). Having less, giving more: the influence of social class on prosocial behavior. *Journal of Personality and Social Psychology,* **99**, 771–84.

Piff, K., Stancato, M., Côté, S., Mendoza-Denton, R., Keltner, D. (2012). Higher social class predicts increased unethical behavior. *Proceedings of the National Academy of Sciences,* **109**, 4086–91.

Rabb, G.B., Woolpy, J.H., Ginsburg, B.E. (1967). Social relationships in a group of captive wolves. *American Zoologist,* **7**(2), 305–11.

Radke, S., Güroğlu, B., de Bruijn, E.R.A. (2012). There's something about a fair split: intentionality moderates context-based fairness considerations in social decision-making. *PLoS One,* **7**(2), 1–6.

Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E., Cohen, J.D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science,* **300**(5626), 1755–8.

Sapolsky, M. (2005). The influence of social hierarchy on primate health. *Science,* **308**, 648–52.

Seymour, B., Singer, T., Dolan, R. (2007). The neurobiology of punishment. *Nature Reviews Neuroscience,* **8**(4), 300–11.

Singer T., Critchley HD, Preuschoff K. (2009). A common role of insula in feelings, empathy and uncertainty. *Trends in Cognitive Science,* **13**, 334–40.

Sridharan, D., Levitin, D.J., Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proceedings of the National Academy of Sciences,* **105**(34), 12569–74.

Taylor, K.S., Seminowicz, D.A, Davis, K.D. (2009). Two systems of resting state connectivity between the insula and cingulate cortex. *Human Brain Mapping,* **30**(9), 2731–45.

van Den Bos, W., Rombouts, S.A.R.B., Crone, E.A. (2010). Unfair? It depends: neural correlates of fairness in social context. *Social Cognitive and Affective Neuroscience,* **5**, 414–23.

Wang, F., Kessels, H.W., Hu, H. (2014). The mouse that roared: neural mechanisms of social hierarchy. *Trends in Neuroscience,* **37**(11), 674–82.

Watson, K.K., Jones, T.K., Allman, J.M. (2006). Dendritic architecture of the von Economo neurons. *Neuroscience,* **141**(3), 1107–12.

White, S.F., Brislin, S.J., Sinclair, S., Blair, J.R. (2014). Punishing unfairness: rewarding or the organization of a reactively aggressive response? *Human Brain Mapping,* **35**(5), 2137–47.

Wu, Y., Leliveld, C., Zhou, X. (2011b). Social distance modulates recipient's fairness consideration in the dictator game: an ERP study. *Biological Psychology,* **88**, 253–62.

Wu, Y., Yu, H., Shen, B., *et al.* (2014). Neural basis of increased costly norm enforcement under adversity. *Social Cognitive and Affective Neuroscience,* **9**(12), 1862–71.

Wu, Y., Zhou, Y., van Dijk, E., Leliveld, C., Zhou, X. (2011a). Social comparison affects brain responses to fairness in asset division: an ERP study with the ultimatum game. *Frontiers in Human Neuroscience,* **5**, 131.

Xiang, T., Lohrenz, T., Montague, P.R. (2013). Computational substrates of norms and their violations during social exchange. *Journal of Neuroscience,* **33**(3), 1099–108.

Yu, R., Calder, A.J., Mobbs, D. (2014). Overlapping and distinct representations of advantageous and disadvantageous inequality. *Human Brain Mapping,* **35**(7), 3290–301.

Zhou, X., Wu, Y. (2011). Sharing losses and sharing gains: Increased demand for fairness under adversity. *Journal of Experimental Social Psychology,* **47**, 582–8.

Zilioli, S., Mehta, P.H., Watson, N.V. (2014). Losing the battle but winning the war: uncertain outcomes reverse the usual effect of winning on testosterone. *Biological Psychology,* **103**, 54–62.

Zink, C.F., Tong, Y., Chen, Q., Bassett, D.S., Stein, J.L., Meyer-Lindenberg, A. (2008). Know your place: neural processing of social hierarchy in humans. *Neuron,* **58**(2), 273–83.