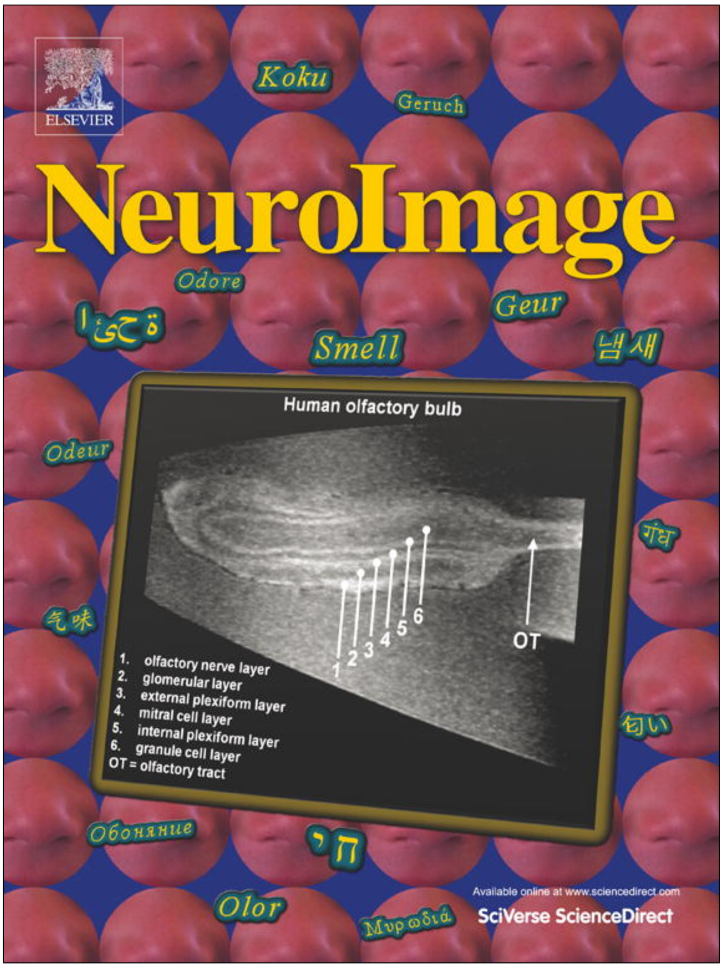
ELSEVIER
NeuroImage
Koku
Geruch
Odore
Geur
Smell
냄새
Odeur
Human olfactory bulb
1. olfactory nerve layer
2. glomerular layer
3. external plexiform layer
4. mitral cell layer
5. internal plexiform layer
6. granule cell layer
OT = olfactory tract
OT
匂い
Обоняние
Olor
Available online at www.sciencedirect.com
SciVerse ScienceDirect

NeuroImage 77 (2013) 246–253

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Increased neural responses to unfairness in a loss context

Xiuyan Guo [a], Li Zheng [b], Lei Zhu [c,*], Jianqi Li [d], Qianfeng Wang [d], Zoltan Dienes [e], Zhiliang Yang [b]

[a] Shanghai Key Laboratory of Magnetic Resonance and School of Psychology and Cognitive Science, East China Normal University, North Zhongshan Road 3663, Shanghai, SH 200062, China
[b] School of Psychology and Cognitive Science, East China Normal University, North Zhongshan Road 3663, Shanghai, SH 200062, China
[c] Department of Psychology, Fudan University, Handan Road 220, Shanghai, SH 200433, China
[d] Shanghai Key Laboratory of Magnetic Resonance and Department of Physics, East China Normal University, North Zhongshan Road 3663, Shanghai, SH 200062, China
[e] School of Psychology, University of Sussex, Sussex House, Brighton BN1 9RH, United Kingdom

ARTICLE INFO

Article history:
Accepted 14 March 2013
Available online 3 April 2013

Keywords:
Unfairness
Loss
Gain
fMRI

ABSTRACT

Unfairness plays an important role in economic decision making. This fMRI study sought to investigate how the loss and the gain contexts could modulate behavioral and brain responses to unfairness by focusing on participants' rejection behaviors during an Ultimatum Game paradigm. Participants were scanned while they were playing the Ultimatum Game as responders in both loss and gain contexts, i.e. receiving ¥50 as gains and paying for ¥50 as losses. At the behavioral level, lower fairness ratings and higher rejection rates were revealed for unfair losses than unfair gains. At the neural level, left dorsolateral prefrontal cortex, bilateral anterior insula, anterior cingulate cortex/anterior middle cingulate cortex and bilateral dorsal striatum were associated with rejection (vs. acceptance) in the loss context, but not in the gain context. Together, our data indicated that participants may experience more unfairness in UG and stronger desire to sanction social norm violations in the loss context than in the gain context, inducing more fairness-related neutral activities when rejecting (vs. accepting) unfair losses than unfair gains. These findings shed light on the significance of context (i.e. loss or gain) in fairness-related social decision-making processes.

Introduction

Standard economic theories of human decision-making idealize individuals as perfectly rational cognitive machines aiming to maximize their personal benefits. However, recently, abundant empirical evidence in the field of behavioral economics showed that additional psychological and emotional factors could drive one's decision-making process to deviate from the goal of personal benefit maximization and finally lead to irrational behaviors (Kahneman and Tversky, 1979). A good example is the Ultimatum Game (UG), which has been used widely to illustrate the influence of unfairness on decision-making in behavioral and neuroimaging studies. In this game, two players work together to split a sum of money. One player proposes how to split it and the other one responds (i.e. the proposer and the responder). The responder can accept or reject the offer. Her/his acceptance leads to the suggested division of money, whereas the rejection results in both players receiving nothing. According to standard economic models, in order to maximize personal benefits, responder should accept all the offers. However, an increasing number of UG studies have revealed that responders were likely to reject unfair offers, especially for offers below 20% of the total (e.g., Camerer and Thaler, 1995; Güth et al., 1982), indicating that unfairness had a great impact on human decision-making process.

Irrational rejection behaviors in studies using UG paradigm have been investigated widely in the gain context, i.e. players split a sum of money as their gains (e.g., Corradi-Dell'Acqua et al., in press; Güroğlu et al., 2010, 2011; Sanfey et al., 2003). However, many studies in the field of economics showed that people weighed loss greater than equivalent gain when making a decision and thus human decision-making in the loss context and the gain context diverged in dramatic ways (De Martino et al., 2006; Kahneman and Tversky, 1979; Novemsky and Kahneman, 2005; Tom et al., 2005; Tversky and Kahneman, 1981). A recent behavioral study has tried to explore the potential impact of loss and gain contexts on players' responses in UG (Zhou and Wu, 2011). The set of gain context was the same as typical UG, whereas in the loss context, proposer and responder needed to pay for a sum of money. Responder's acceptance led to the suggested division of payment, and the rejection resulted in both players incurring the whole loss. It was revealed that responders reported lower fairness ratings and rejected more often in the loss context than those in the gain context. Furthermore, Zhou (2010) suggested that the loss vs. gain and unfair vs. fair contrasts showed similar activations in their earlier unpublished fMRI study. However, the neural mechanism underlying rejection of unfair losses and unfair gains in UG was still to be determined.

Neuroimaging studies have identified several fairness-related brain regions involved in UG in the gain context, including anterior insula (AI), anterior cingulate cortex (ACC) extending to anterior middle cingulate cortex (aMCC), striatum, and dorsolateral prefrontal

* Corresponding author. Fax: +86 21 64674201.
E-mail address: judy1981_81@hotmail.com (L. Zhu).

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.03.048

cortex (DLPFC) (Corradi-Dell'Acqua et al., in press; Dulebohn et al., 2009; Güroğlu et al., 2010, 2011; Sanfey et al., 2003). Empirical evidence recently suggested that AI and/or ACC were engaged in detecting and responding to norm violations (Güroğlu et al., 2010, 2011; King-Casas et al., 2008; Montague and Lohrenz, 2007; Spitzer et al., 2007; Strobel et al., 2011). Unfair offers in UG have been considered as violations of social norms, i.e. fairness and cooperation norms (de Quervain et al., 2004; Güroğlu et al., 2010, 2011; King-Casas et al., 2008; Spitzer et al., 2007). AI and ACC/aMCC activities in rejection in UG might be associated with the desire to sanction behaviors violating fairness norm. Another region of interest was striatum which also showed greater activation when comparing unfair offers with fixation (Dulebohn et al., 2009). Striatum activity has been associated with altruistic punishment, i.e. punishing others' behaviors violating social norms at a cost to themselves (de Quervain et al., 2004; Strobel et al., 2011). The involvement of striatum in UG may also reflect the wish to sanction proposers' unfair divisions violating fairness norm. Finally, DLPFC activity has been also observed in decision-making during the UG paradigm. The engagement of DLPFC in UG was interpreted in terms of top–down executive control of impulses to accept unfair offers, supported by greater activation during rejection relative to acceptance (Güroğlu et al., 2010, 2011).

In the present event-related fMRI study, we adopted a variant of the UG developed by Zhou and Wu (2011) in which loss context with different levels of unfairness was firstly employed. Participants were scanned while they were playing UG as responders in both loss and gain contexts (Fig. 1A), i.e. receiving ¥50 as gains and paying for ¥50 as losses. Proposer could propose fair offers or unfair offers. Participants were asked to give responses (rejection or acceptance) to the offers. Within unfair offers, participants' responses could be divided into two kinds: rejection and acceptance (participants never reject fair offers; see behavioral results). Buchan et al. (2005) have initially showed that loss and gain contexts have different impacts on human fairness preference. Zhou and Wu (2011) further found that unfair losses would be perceived as more unfair than unfair gains in subjective rating, leading to higher rejection rates in the loss context than the gain context. Based on Zhou and Wu (2011), we aimed to investigate the brain mechanism underlying the modulation of rejection in UG by context (loss vs. gain). We expected greater activations in brain regions involved in UG (i.e. DLPFC, AI, ACC/aMCC and striatum) for rejection of unfair losses than unfair gains.

Methods

Participants

Twenty-seven right-handed volunteers from the university community with normal or corrected-to-normal vision [10 men and 17 women, mean age = 22.44 ± 3.49 (SD) years] participated in this experiment. Six participants were excluded from further statistic analysis because of lack of rejected trials or accepted trials in at least one condition. Three of them did not reject at all. Two of them did not give rejection responses in the gain context and the last one did not give acceptance responses to unfair offers in the loss context.

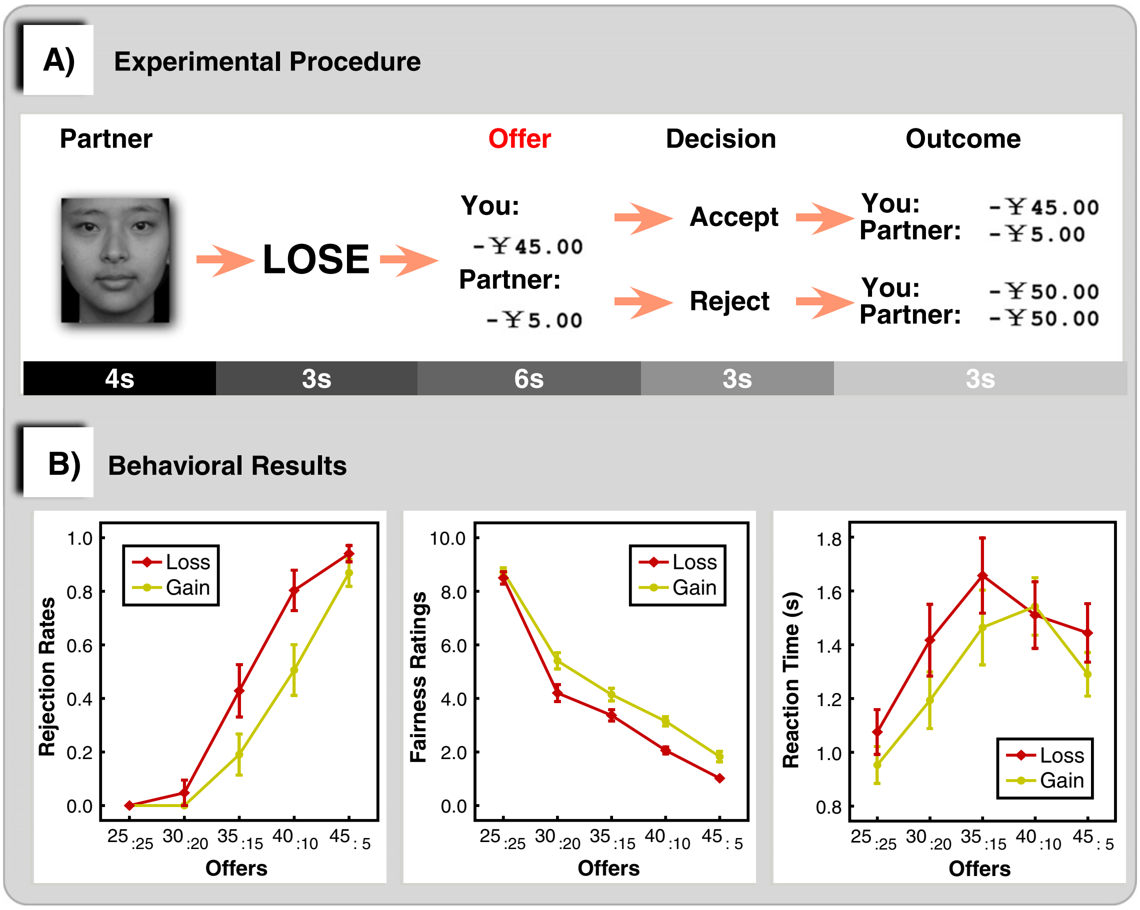

Fig. 1. (A) Experimental procedure. Participants were scanned while playing the game for 64 trials, 32 in each context. Each trial involved splitting a gain or loss of ¥50. Fair offers (25:25) were given in 8 trials of each context, with the remaining 24 unfair trials (4 trials of 30:20, 4 trials of 35:15, 8 trials of 40:10 and 8 trials of 45:5). (B) Behavioral results. Rejection rates, fairness ratings and RTs (s) are plotted as a function of unfairness level in both loss (red rhombuses) and gain (yellow circles) contexts. Error bars indicate s.e.m.

None of the participants reported a significant abnormal neurological history. All the participants gave informed consent before scanning and were paid according to outcomes from a random selection of 10% trials plus a 200RMB (approximately equal to 32 dollars) bonus.

Materials

Sixty-four face pictures, half of which depict female faces, were selected from the Chinese Facial Affective Picture System (Gong et al., 2011), and randomly allocated to 2 context (loss vs. gain) $*$ 2 unfairness (fair vs. unfair) conditions. There were, respectively, 8, 8, 24 and 24 pictures in loss–fair, gain–fair, loss–unfair and gain–unfair conditions. The emotional valence, arousal and attractiveness of pictures were counterbalanced across different conditions.

Procedure

Before scanning, participants were told the rules of the game and that they would play with 64 different partners (students from another university in Shanghai) whose offers about splitting the money were collected before the experiment. They were also informed that their decision in each trial would not affect other partners' offers, nor would other partners be informed of their decisions. In addition, they were told that both she/he and the proposer in each trial would be paid according to her/his decision (after some kind of transformation to reduce the amount of money involved). They would be given a basic payment for their participation (200RMB) plus or minus the amount of money obtained or lost from a random selection of 10% trials in the game.

The participants then completed 64 trials (Fig. 1A), 32 in each context in the scanner. Functional images were acquired simultaneously. All the trials were presented randomly, and involved splitting a gain or loss of ¥50. Fair offers (25:25) were given in 8 trials of each context. Offers were unfair in the other 24 trials of each context, including 4 trials of 30:20, 4 trials of 35:15, 8 trials of 40:10 and 8 trials of 45:5. In the gain context, 30, 35, 40 and 45 were for proposer, whereas in the loss context, 20, 15, 10 and 5 were for proposer. The participants were required to make the “acceptance” or “rejection” decision to each trial by pressing the corresponding buttons of a magnet-compatible button box below their right hands. In the gain context, accepting the offer led to the suggested division of the gain, whereas rejection resulted in both players receiving nothing. In the loss context, accepting the offer led to the suggested division of the loss, whereas rejection resulted in both players incurring the whole loss, i.e. both of them lose ¥50. Each trial began with a 4 s presentation of the partner's face, followed by a 3 s presentation of “win” or “lose”. Then, the partner's offer was presented for 6 s. After that, a 4 s decision cue appeared and participants were required to decide within 4 s. In the end, the final outcome was viewed for 3 s. Each trial was jittered with inter-stimulus intervals (ISI) from 5–8 s, during which a black fixation cross was presented against a gray background.

After scanning, the participants were presented with the same stimuli as inside the scanner and asked to rate how fair they felt each offer was by using a 9-point Likert-type scale (1 indicated extremely unfair and 9 indicated extremely fair).

fMRI image acquisition and analysis

Scanning was carried out on a 3 T Siemens scanner at the Functional MRI Lab (East China Normal University, Shanghai). Functional images were acquired using a gradient echo echo-planar imaging (EPI) sequence (TR = 2200 ms, TE = 30 ms, FOV = 220 mm, matrix size = 64 $*$ 64). Thirty five slices paralleled to the AC–PC line (slice thickness = 3 mm, gap = 0.3 mm) were acquired and covered the whole brain. The first five TRs acquired were discarded to allow for T1 equilibration. Before the functional run, a high-resolution structural image was acquired using a T1-weighted, multiplanar reconstruction sequence (MPR) (TR = 1900 ms, TE = 3.42 ms, 192 slices, slice thickness = 1 mm, FOV = 256 mm, matrix size = 256 $*$ 256).

Data preprocessing and statistical analyses were performed with Statistical Parametric Mapping (SPM5, Wellcome Department of Cognitive Neurology, London). During data preprocessing, all volumes were corrected for differences in slice acquisition timing and realigned spatially to the first volume of the first time series. Then, the resulting images which were re-sampled to 2 $*$ 2 $*$ 2 mm voxel size were spatially normalized to a standard echo-planar imaging template based on the Montreal Neurological Institute (MNI) reference brain and smoothed with an 8 mm full-width, half-maximum (FWHM) isotropic Gaussian kernel.

Statistical analyses were performed using the general linear model (GLM) implemented in SPM5. At the first-level analysis, six types of events (LF, fair offers in the loss context; LUA, accepted unfair offers in the loss context; LUR, rejected unfair offers in the loss context; GF, fair offers in the gain context; GUA, accepted unfair offers in the gain context; GUR, rejected unfair offers in the gain context) were defined. There were, respectively, 8.14 ± 5.12, 15.86 ± 5.12, 12.24 ± 5.47, 11.76 ± 5.47 trials in the LUA, LUR, GUA, GUR conditions. Events were convolved with a canonical hemodynamic response function (HRF) and its time derivatives. All the encoding trials were modeled from the onset time of the offers (with zero duration). Additional regressors of no interest were created for partner presentation, win or loss, decision and final outcome. Six regressors modeling movement-related variance and one modeling the overall mean during the whole phase were also employed in the design matrix. High pass temporal filtering with a cutoff of 180 s was also applied in the models. For each subject at the first-level analysis, simple main effects for each type of event were computed by applying the ‘1 0’contrasts. The six first-level individual contrast images (LF, LUA, LUR, GF, GUA, and GUR) were then analyzed at the second group level employing a random effects model (flexible factorial design in SPM5).

Brain activities related to unfairness were defined by contrasting fair trials with unfair trials and the reverse contrast. Brain activations corresponding to gain relative to loss trials were identified by the (Gain–Loss) and reverse contrasts. The $(\text{Reject–Accept})_{\text{Unfair}}$ and reverse contrasts were tested to compute brain activations related to participant's responses (rejecting and accepting unfair offers). Then, the context $*$ unfairness interactions defined by $(\text{Unfair–Fair})_{\text{Loss}}$–$(\text{Unfair–Fair})_{\text{Gain}}$ and $(\text{Accepted Unfair–Fair})_{\text{Loss}}$–$(\text{Accepted Unfair–Fair})_{\text{Gain}}$ contrasts (and their reverse contrasts) were computed to explore how contexts affect unfairness in all trials and accepted trials respectively. The response $*$ context interaction defined by $(\text{Reject–Accept})_{\text{Unfair Loss}}$–$(\text{Reject–Accept})_{\text{Unfair Gain}}$ and reverse contrasts were also tested to extract specific regions showing modulation of responders' responses to unfair offers by different contexts. To further test how context affects brain activations associated with unfairness and related rejection behaviors, specific activations in fairness-related brain regions identified in the interactions were used to compute regions of interest (ROIs). All the significant voxels in the activated clusters within 6-mm spherical regions centered on the peak or local maximum coordinates were included in each ROI. ROIs were defined in the same way throughout the paper. A voxel-level threshold of $p < .001$ (uncorrected) and a spatial extent threshold of $k > 40$ were used.

In addition, a parametric analysis, which is an efficient statistical procedure to reveal voxels that show a particular pattern of activation throughout several conditions (Buchel et al., 1998), was conducted at the first-level to assess how brain activity was modulated by the levels of unfairness. Specifically, a parametric regressor was created to represent the different weights for unfair trials in four different conditions (30:20 = 1, 35:15 = 2, 40:10 = 3, 45:5 = 4). The resulting subject-specific estimates of the parametric regressor at each voxel were then entered into a second-level one sample *t*-test, treating participants as a random variable. Regions showing increased responses to unfair offers with the increase of unfairness levels were identified by parametric analysis.

Results

Behavioral results

The rejection rates, fairness ratings and mean RTs (restricted to responded trials whose RTs are within means ± 2 standard deviations) for each subject in each condition were calculated. A 2 (context: loss vs. gain) ∗ 5 (unfairness level: 25:25 vs. 30:20 vs. 35:15 vs. 40:10 vs. 45:5) repeated measures ANOVA on rejection rates revealed significant main effects of context and unfairness level, indicating higher rejection rates in the loss than in the gain contexts, and increased rejection rates with the levels of unfairness ($Fs > 30.66$, $ps < .01$). A significant interaction was also found ($F(4, 80) = 4.81$, $p < .01$). Further paired t-tests showed that rejection rates for trials of 35:15, 40:10 and 45:5 in the loss context were significantly higher than those in the gain context ($ts > 2.67$, $ps < .05$ with sequential Bonferroni correction, Fig. 1B).

For fairness ratings, similar ANOVA indicated lower ratings in the loss than in the gain contexts and decreased ratings with increasing unfairness level ($Fs > 33.86$, $ps < .01$). The interaction was also significant ($F(4, 80) = 6.52$, $p < .01$). Paired t-tests revealed lower ratings in the loss context relative to the gain context for trials of 30:20, 35:15, 40:10 and 45:5 ($ts > 4.22$, $ps < .01$) with sequential Bonferroni correction (Fig. 1B). We also calculated the correlation coefficient between fairness ratings and responses (rejection or acceptance) for each participant. One-sample t-test showed that correlation coefficients were significantly higher than zero (mean $r = .69$, $t(20) = 22.15$, $p < .01$), indicating that lower fairness ratings were associated with rejection.

Similar ANOVA on RTs was also carried out. Results showed the main effects of context and unfairness level ($Fs > 12.66$, $ps < .01$), indicating longer RTs in the loss context than the gain context and longer RTs for medium unfairness levels (35:15 and 40:10) than for low unfairness levels (25:25 and 30:20) ($ps < .05$) (Fig. 1B).

fMRI results

Main effects

Main effects of unfairness

Experiencing unfair offers (Unfair–Fair) activated bilateral DLPFC (MNI −36 40 38 and 42 28 40), AI (MNI −30 24 6 and 32 28 4), dorsal striatum (DS, MNI −10 14 6 and 16 18 10), ACC (MNI 6 12 28) and aMCC (MNI 10 22 34) (Table S1). Additional activations in posterior cingulate cortex (MNI −6 −44 18) and precuneus (MNI 18 −68 42) were also found. The reverse contrast did not show suprathreshold activation.

In order to examine the possibility that the null result in the reverse contrast was due to an unbalanced distribution of trials for fair and unfair offers (i.e. 8 vs. 24), the loss context and the gain context were collapsed and the unfair trials of 30:20 and 35:15 were also collapsed, yielding a new model containing four events with the same numbers of trials, i.e. 16 trials of 25:25, 16 trials of 30:20 and 35:15, 16 trials of 40:10, and 16 trials of 45:5. Results showed that, when compared with fair trials respectively, unfair trials with different levels of unfairness (30:20 and 35:15, 40:10, 45:5) activated DLPFC, AI, ACC and aMCC. Trials of 40:10 and 45:5 additionally activated bilateral DS. No suprathreshold activation was found in the reverse contrasts. Parametric analysis revealed that activations in left DLPFC (MNI −42 44 30), bilateral AI (MNI −32 10 6 and 32 14 14), ACC (MNI 6 28 22), aMCC (MNI 4 18 30) and bilateral DS (MNI −24 10 10 and 16 16 8) increased with unfairness levels, indicating stronger fairness-related activities were associated with higher level of unfairness. Thus, the unbalanced distribution of trials for fair and unfair offers could not explain the lack of activation in the (Fair–Unfair) contrast.

Main effects of context

Data analyses revealed that precuneus (MNI 16 −54 24) survived by contrasting loss trials with gain trials, whereas no region of interest was activated in the reverse contrast (Table S2). Further, the $(\text{Loss–Gain})_{\text{Fair}}$, $(\text{Loss–Gain})_{\text{Unfair}}$, $(\text{Loss–Gain})_{\text{Unfair Accepted}}$ and $(\text{Loss–Gain})_{\text{Unfair Rejected}}$ contrasts and the reverse contrasts were computed to identify brain regions showing simple effects of context. The $(\text{Loss–Gain})_{\text{Unfair}}$ contrast revealed activations in precuneus (MNI 16 −54 24) and posterior cingulate gyrus (MNI 12 −44 20). The $(\text{Loss–Gain})_{\text{Unfair Rejected}}$ contrast revealed activations in left DS (MNI −16 −6 22), aMCC (MNI -6 8 40), precuneus (MNI −4 −54 60), posterior middle cingulate gyrus (MNI 18 −26 44) and posterior cingulate gyrus (MNI 12 −44 20) (Table S2). The other contrasts showed no activated region of interest.

Main effects of response during unfair trials

We observed increased fairness-related activities in left DLPFC (MNI −32 28 46), bilateral AI (MNI −36 16 14 and 32 16 12), aMCC (MNI −6 4 44) and bilateral DS (MNI −24 14 4 and 18 14 12) during unfair offers that were rejected relative to those that were accepted (Fig. 2, Table S3). Precuneus (MNI −12 −50 48), posterior middle cingulate gyrus (MNI −10 −34 48) and bilateral temporo-parietal junction (MNI −42 −60 26 and 58 −40 24) activations were additionally found. The reverse contrast showed no activated region of interest.

Interactions

Interaction between unfairness and context computed by the $(\text{Unfair–Fair})_{\text{Loss}}$–$(\text{Unfair–Fair})_{\text{Gain}}$ contrast and reverse contrasts showed no activated region of interest. When restricted to accepted trials, the $(\text{Accepted Unfair–Fair})_{\text{Loss}}$–$(\text{Accepted Unfair–Fair})_{\text{Gain}}$ and reverse contrasts also revealed no suprathreshold activation, indicating that the context did not influence acceptance responses to unfair offers in UG.

Then, the brain regions associated with the modulation of rejection of unfair offers by context were explored by computing the $(\text{Reject–Accept})_{\text{Unfair Loss}}$–$(\text{Reject–Accept})_{\text{Unfair Gain}}$ and reverse contrasts. Results showed that left DLPFC (MNI −30 38 26), ACC/aMCC (MNI −2 18 26) and bilateral DS (MNI −20 2 20 and 28 16 4) were activated (Fig. 3, Table 1). Precuneus (MNI 16 −42 46) and posterior middle cingulate gyrus (MNI −10 −32 44) were also found. No regions survived from the reverse contrast. Further ROI analyses based on activations identified in the $(\text{Reject–Accept})_{\text{Unfair Loss}}$–$(\text{Reject–Accept})_{\text{Unfair Gain}}$ contrast revealed that greater brain activities in left DLPFC, ACC/aMCC and bilateral DS for rejection vs. acceptance in the loss context ($ts > 2.19$, $ps < .05$), but not in the gain context ($ts < 1.01$, $ps > .32$, ns) (Fig. 3).

To further clarify the impact of context on rejection of unfair offers, we searched for regions showing rejection-specific activation (relative to acceptance) selective to unfair losses, but not unfair gains by two steps. Two contrasts $(\text{Reject–Accept})_{\text{Unfair Loss}}$ and $(\text{Reject–Accept})_{\text{Unfair Gain}}$ were carried out and exclusively masked by each other at a threshold of $p < 0.05$, uncorrected. Rejection-specific activations (relative to acceptance) in left DLPFC (MNI −30 38 42), bilateral AI (MNI −34 18 14 and 34 12 12), ACC (MNI −4 18 24), aMCC (MNI −4 6 42) and bilateral DS (MNI −20 2 20 and 26 8 4) were exclusively found for unfair losses (Table 2). In addition, precuneus (MNI −6 −50 48), posterior middle cingulate gyrus (MNI −10 −34 46) and bilateral temporo-parietal junction (MNI −54 −40 32 and 60 −44 28) activations were also observed. No

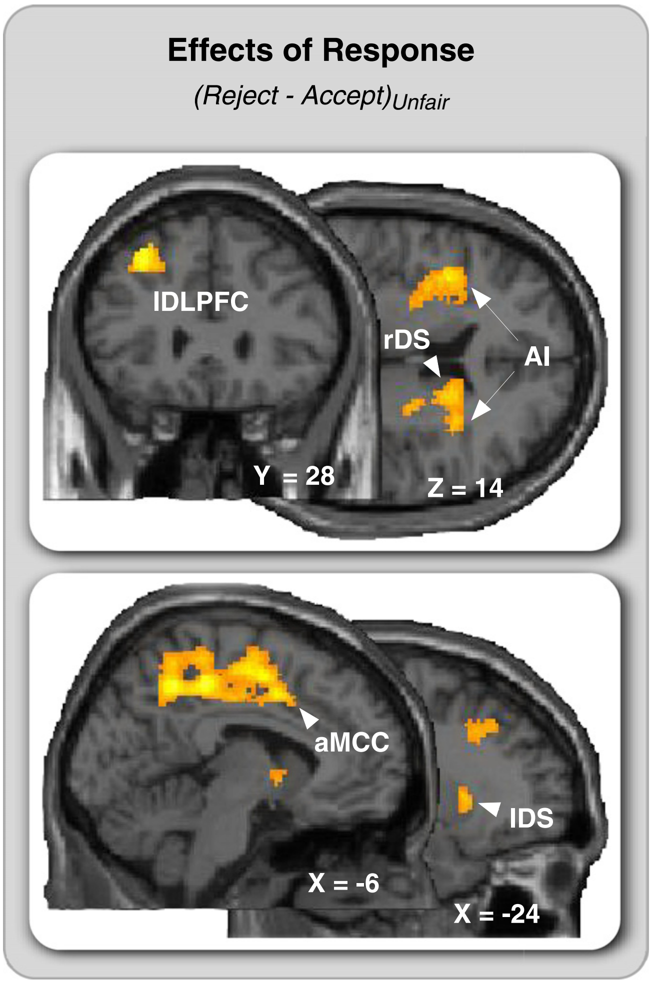

Fig. 2. Left DLPFC, bilateral AI, aMCC and bilateral DS showed increased neural responses to rejection of unfair offers compared with acceptance of unfair offers. l = left hemisphere; r = right hemisphere.

brain region exhibited rejection-specific activation (relative to acceptance) selective to unfair gains.

Finally, in order to clarify whether the main effect was driven by the interaction, we overlapped the response main effect (Reject–Accept)$_{\text{Unfair}}$ with the response ∗ context interaction. The clusters located in right DS and aMCC overlapped between two contrasts (Fig. 4).

Correlation analyses

Correlation analysis was performed to determine fairness-related regions whose BOLD signal change detected from the (Reject–Accept)$_{\text{Unfair Loss}}$ contrast varied with the corresponding fairness rating difference between rejected and accepted unfair losses. Significant positive correlation was found in right DLPFC (MNI 38 16 46, $r = .88$, $p < .01$). A similar correlation analysis was also performed between the (Reject–Accept)$_{\text{Unfair Gain}}$ contrast and the corresponding fairness rating difference. No significant correlation result was found.

Discussion

We employed a modified version of the UG (Zhou and Wu, 2011) to investigate how loss vs. gain context modulates brain responses to unfairness through identifying neural activities associated with participants' fairness-related rejection (relative to acceptance) in different contexts. Consistent with previous findings (Zhou and Wu, 2011), rejection rates increased and fairness ratings decreased with increasing unfairness levels. Lower fairness ratings and higher rejection rates were observed for unfair losses than unfair gains. At the neural level, bilateral DLPFC, AI, DS and ACC/aMCC were engaged during unfair relative to fair offers. Further analyses based on participants' responses revealed that greater left DLPFC, bilateral AI, aMCC and bilateral DS activations were found during rejected relative to accepted unfair offers. When focusing on participants' behavioral responses (rejection or acceptance) in different contexts, left DLPFC, bilateral AI, ACC/aMCC and bilateral DS showed rejection-specific activations (relative to acceptance) in the loss context, but not in the gain context.

Fairness-related neural networks

Along with prior studies (Corradi-Dell'Acqua et al., in press; Dulebohn et al., 2009; Güroğlu et al., 2010, 2011; Sanfey et al., 2003), DLPFC, AI, ACC/aMCC and DS were involved in perception of unfairness. When compared with fair offers respectively, unfair offers with different unfairness levels activated DLPFC, AI, ACC/aMCC and DS. Combined with the results of parametric analysis showing activations in these brain regions increased with unfairness levels, DLPFC, AI, ACC/aMCC and DS were confirmed to be a neural network engaged in emotional, cognitive and motivational processes associated with (un)fairness. Based on participants' responses, we further compared rejection with acceptance during unfair offers. Greater activations in left DLPFC, bilateral AI, aMCC and bilateral DS were found, indicating that these regions in the fairness-related neural network were further involved in sanctioning the proposers' behaviors violating fairness norm.

Modulation of rejection responses in UG by context

We further studied the impact of context on participants' behavioral and neural responses to unfair offers. It was revealed that participants reported lower fairness ratings and rejected more often in the loss context than the gain context, consistent with Zhou and Wu's findings (2011). Accordingly, rejection-specific activations (relative to acceptance) in left DLPFC, bilateral AI, ACC/aMCC and bilateral DS were found in the loss context, but not in the gain context at the neural level. Taken together, these results suggested that participants experienced more unfairness in UG and stronger desire to sanction social norm violations in the loss context than in the gain context, inducing more fairness-related neutral activities when rejecting (vs. accepting) unfair losses than unfair gains.

In the present study, left DLPFC was involved in rejection of unfair offers, providing support for the engagement of fairness-related DLPFC activity in top–down executive control over impulses to maximize personal benefits (Güroğlu et al., 2010, 2011). We also found that DLPFC activities during rejected vs. accepted unfair offers was modulated by context, i.e. rejection-specific activations (relative to acceptance) were found in the loss context, but not in the gain context. It is widely acknowledged that a loss has a higher subjective value than the equivalent gain (Novemsky and Kahneman, 2005; Tom et al., 2005; Tversky and Kahneman, 1981). Even though monetary losses caused by rejection relative to acceptance in the loss context and the gain context are the same amount, unfair losses would be perceived as more unfair than unfair gains. Thus, rejecting unfair losses may require more executive control over impulses to maximize personal benefits than rejecting unfair gains. The involvement of DLPFC in rejecting (vs. accepting) unfair losses rather than unfair gains in the present study provided support for this argument.

AI activity was found during unfair offers and their rejection. When focusing on the impact of context on participants' behaviors, AI was only activated when rejecting vs. accepted unfair offers in the loss context, but not in the gain context. AI has been associated with detecting social norm violations (Güroğlu et al., 2010, 2011)

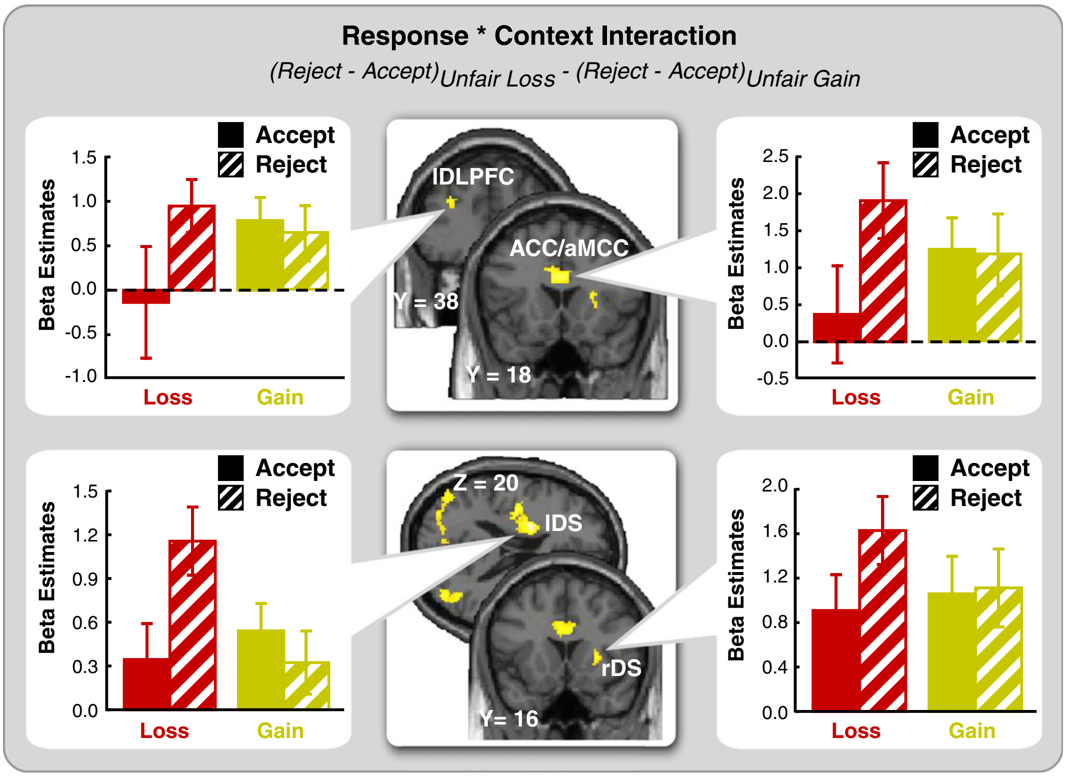

Fig. 3. Left DLPFC, ACC/aMCC and bilateral DS showed increased activities during rejection vs. acceptance in the loss context relative to the gain context. Error bars indicate s.e.m. l = left hemisphere; r = right hemisphere.

and sanctioning the proposers' behaviors violating fairness norm through rejection of unfair offers (Corradi-Dell'Acqua et al., in press). Our data further indicated that the need to abide by social norms seems to be more urgent and induce more desire to sanction social norm violations in the loss context than the gain context, because norm violations in aversive situations may threaten the survival of the species (Zhou and Wu, 2011). AI activity during unfair offers and their rejections in the loss context rather than the gain context was accompanied by ACC/aMCC activity. On the other hand, ACC/aMCC also survived when overlapping the context simple effect $(\text{Loss–Gain})_{\text{Unfair Rejected}}$ with the response * context interaction. The engagement of ACC/aMCC in UG may relate to monitoring conflicts

Table 1
Regions showing response * context interactions during Unfair Trials.

Region	Side	Peak activation			*t* value	Voxels
		X	Y	Z		
(Reject–Accept)$_{\textit{Unfair Loss}}$–*(Reject–Accept)*$_{\textit{Unfair Gain}}$						
Dorsal striatum	L	−20	2	20	5.20	1475
Anterior middle cingulate cortex	R	10	10	36	5.32	841
Anterior cingulate cortex	L	−2	18	26	4.22	
Precuneus	R	16	−42	46	4.69	322
Posterior middle cingulate cortex	L	−10	−32	44	4.36	
Hippocampus	R	20	−4	−12	4.61	434
Dorsal striatum	R	28	16	4	4.10	
Linual gyrus	R	10	−42	4	4.38	413
	L	−24	−52	−6	3.84	121
Precentral gyrus	L	−32	−14	46	4.33	164
Middle occipital gyrus	R	42	−76	16	4.32	222
Middle temporal gyrus	L	−48	−72	14	4.26	974
	R	48	−38	2	3.74	42
Calcarine gyrus	R	18	−76	16	4.24	59
Parahippocampal gyrus	R	36	−32	−16	4.23	62
Superior temporal gyrus	L	−66	−36	12	4.14	69
Dorsal lateral prefrontal cortex	L	−30	38	26	3.94	47
Supramarginal gyrus	R	64	−26	30	3.94	129
	L	−64	−30	38	3.75	69
Cuneus	R	14	−84	30	3.63	62
(Reject–Accept)$_{\textit{Unfair Gain}}$–*(Reject–Accept)*$_{\textit{Unfair Loss}}$						
No regions						

Coordinates (mm) are in MNI space. L = left hemisphere; R = right hemisphere. $p < .001$, uncorrected. $k > 40$.

Table 2
Regions showing rejection-specific activation (relative to acceptance) selective to Unfair Losses and Unfair Gains.

Region	Side	Peak activation			*t* value	Voxels
		X	Y	Z		
(Reject–Accept)$_{\textit{Unfair Loss}}$ *exclusively masked by (Reject–Accept)*$_{\textit{Unfair Gain}}$						
Posterior middle cingulate cortex	L	−10	−34	46	6.54	9679
Precuneus	L	−6	−50	48	6.01	
Anterior middle cingulate cortex	L	−4	6	42	5.64	
Anterior cingulate cortex	L	−4	18	24	5.17	
Dorsal striatum	L	−20	2	20	5.06	
Anterior insula	L	−34	18	14	3.87	
Middle temporal gyrus	R	48	−36	2	6.31	3742
Dorsal striatum	R	26	8	4	4.93	
Anterior insula	R	34	12	12	4.10	
Temporo-parietal junction	R	60	−44	28	3.81	
Precentral gyrus	L	−24	−26	58	5.14	253
Temporo-parietal junction	L	−54	−40	32	5.00	2622
Superior occipital gyrus	R	22	−82	30	4.75	952
Thalamus	R	14	−22	12	4.18	75
Dorsal lateral prefrontal cortex	L	−30	38	42	4.11	71
Fusiform gyrus	L	−30	−72	−12	4.00	62
Inferior temporal gyrus	L	−58	−54	−8	3.93	103
(Reject–Accept)$_{\textit{Unfair Gain}}$ *exclusively masked by (Reject–Accept)*$_{\textit{Unfair Loss}}$						
No regions						

Coordinates (mm) are in MNI space. L = left hemisphere; R = right hemisphere. $p < .001$, uncorrected. $k > 40$.

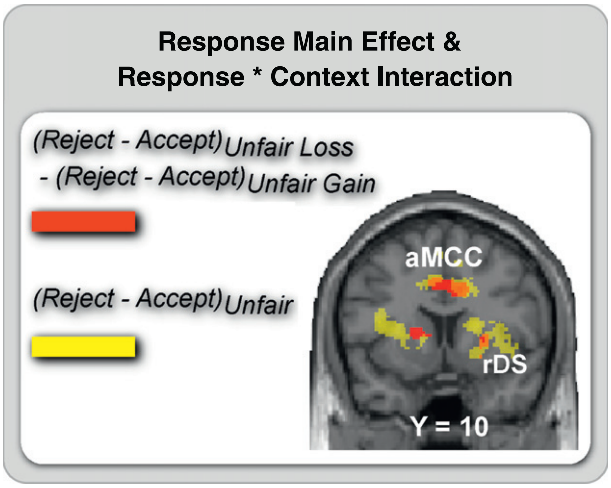

Fig. 4. Clusters in right DS and aMCC overlapped between the response main effect and the response ∗ context interaction. r = right hemisphere.

associated with norm violations (Güroğlu et al., 2010, 2011), based on prior findings of the involvement of ACC/aMCC in conflict monitoring (Kerns et al., 2004; van Veen et al., 2001). More engagement of ACC/aMCC in rejections of unfair losses than unfair gains may suggest more conflicts between cognitive and emotional motivations when people faced with loss than gain.

In addition, DS was also activated during the rejection vs. acceptance contrast. DS activity has been related to altruistic punishment, i.e. punishing behaviors violating social norms. de Quervain et al. (2004) revealed that DS activated when participants carried out altruistic punishment, and individuals who invested higher amount of punishment had higher DS activations during altruistic punishment. Thus, rejection behaviors in UG, leading to nothing (vs. the suggested division of money when accepting unfair offers) or a whole loss (vs. a lesser amount of loss when accepting unfair offers), could be reckoned as altruistic punishment. Rejection-specific activation in DS (relative to acceptance) in our data set provided evidence for the role of DS in altruistic punishment. On the other hand, DS activity was also associated with rejection vs. acceptance in the loss context relative to the gain context. And this region also survived when overlapping the context simple effect $(\text{Loss–Gain})_{\text{Unfair Rejected}}$ with the response ∗ context interaction. We argue that greater DS activation during rejections of unfair losses than unfair gains might indicate stronger desire to sanction proposers' behaviors violating fairness norms in the loss context relative to the gain context.

Precuneus, posterior cingulate gyrus/posterior middle cingulate gyrus and temporo-parietal junction activities were also found when identifying activations associated with unfairness or rejection of unfair offers (especially in the loss context). Studies on theory of mind repeatedly revealed that posterior cingulate gyrus/posterior middle cingulate gyrus, precuneus and temporo-parietal junction engaged in mentalization, i.e. the capacity to interpret and predict others' behaviors based on an understanding of their internal mental states (Gobbini et al., 2007; Lombardo et al., 2010; Saxe and Kanwisher, 2003; Saxe et al., 2006). Thus, it is plausible that precuneus, posterior cingulate gyrus/posterior middle cingulate gyrus and temporo-parietal junction activities in the present study might be related to responders' mentalization associated with detecting and responding to fairness norm violations.

Conclusion

A loss has been considered to have a higher subjective value than the equivalent gain (Novemsky and Kahneman, 2005; Tom et al., 2005; Tversky and Kahneman, 1981). The present study further revealed that the loss and the gain contexts modulate responders' behavioral and neural responses to unfair offers in UG. Results showed that, at the behavioral level, participants reported lower fairness ratings and rejected more often in the loss context than the gain context. At the neural level, rejection-specific activations (relative to acceptance) in left DLPFC, bilateral AI, ACC/aMCC and bilateral DS involved in the fairness-related neural network were found in the loss context, but not in the gain context. Together, our data indicated that participants experienced more unfairness in UG and stronger desire to sanction social norm violations in the loss context than in the gain context, inducing more fairness-related neutral activities when rejecting (vs. accepting) unfair losses than unfair gains. These findings shed light on the significance of context (i.e. loss or gain) in fairness-related social decision-making processes.

Acknowledgments

Xiuyan Guo and Li Zheng contributed equally to this work. This research was supported by National Natural Science Foundation of China (31271090, 31100728 & 90924013), Projects Planning in Shanghai Philosophy and Social Sciences Research (2012JJY001), Innovation Program of Shanghai Municipal Education Commission (12ZS046), 985 Project of Fudan University (2011SHKXZD008).

Conflict of interest

There is no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.03.048.

References

Buchan, N.R., Croson, R.T.A., Johnson, E.J., Wu, G., 2005. Gain and loss ultimatums. In: Morgan, John (Ed.), Advances in Applied Microeconomics. JAI Press, Greenwich, CT.
Buchel, C., Holmes, A.P., Rees, G., Friston, K.J., 1998. Characterizing stimulus–response functions using nonlinear regressors in parametric fMRI experiments. Neuroimage 8, 140–148.
Camerer, C., Thaler, R.H., 1995. Anomalies: ultimatums, dictators and manners. J. Econ. Perspect. 9, 209–219.
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. Soc. Cogn. Affect. Neurosci. (in press).
De Martino, B., Kumaran, D., Seymour, B., Dolan, R.J., 2006. Frames, biases, and rational decision-making in the human brain. Science 313, 684–687.
de Quervain, D.J.-F., Fischbacher, U., Treyer, V., Schellhammer, M., Schnyder, U., Buck, A., Fehr, E., 2004. The neural basis of altruistic punishment. Science 305, 1254–1258.
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. Organ. Behav. Hum. Decis. Process. 110, 140–151.
Gobbini, M.I., Koralek, A.C., Bryan, R.E., Montgomery, K.J., Haxby, J.V., 2007. Two takes on the social brain: a comparison of theory of mind tasks. J. Cogn. Neurosci. 19, 1803–1814.
Gong, X., Huang, Y., Wang, Y., Luo, Y., 2011. Revision of the Chinese facial affective picture system. Chin. Mental Health J. 25, 40–46 (Chinese).
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. Soc. Cogn. Affect. Neurosci. 5, 414–423.
Güroğlu, B., van den Bos, W., van Dijk, E., Rombouts, S.A.R.B., Crone, E.A., 2011. Dissociable brain networks involved in development of fairness considerations: understanding intentionality behind unfairness. Neuroimage 57, 634–641.
Güth, W., Schmittberger, R., Schwarze, B., 1982. An experimental analysis of ultimatum bargaining. J. Econ. Behav. Organ. 3, 367–388.
Kahneman, D., Tversky, A., 1979. Prospect theory: an analysis of decision under risk. Econometrica 47, 263–292.
Kerns, J.G., Cohen, J.D., MacDonald, A.W., Cho, R.Y., Stenger, V.A., Carter, C.S., 2004. Anterior cingulate conflict monitoring and adjustments in control. Science 303, 1023–1026.
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, 806–810.
Lombardo, M.V., Chakrabarti, B., Bullmore, E.T., Wheelright, S.J., Sadek, S.A., Suckling, J., MRC AIMS Consortium, Baron-Cohen, S., 2010. Shared neural ciruits for mentalizing about the self and others. J. Cogn. Neurosci. 22, 1623–1635.

Montague, P.R., Lohrenz, T., 2007. To detect and correct: norm violations and their enforcement. Neuron 56, 14–18.
Novemsky, N., Kahneman, D., 2005. The boundaries of loss aversion. J. Mark. Res. 42, 119–128.
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, 1755–1758.
Saxe, R., Kanwisher, N., 2003. People thinking about thinking people: the role of the temporo-parietal junction in "theory of mind". Neuroimage 19, 1835–1842.
Saxe, R., Moran, J.M., Scholz, J., Gabrieli, J., 2006. Overlapping and non-overlapping brain regions for theory of mind and self reflection in individual subjects. Soc. Cogn. Affect. Neurosci. 1, 229–234.
Spitzer, M., Fischbacher, U., Herrnberger, B., Gron, G., Fehr, E., 2007. The neural signature of social norm compliance. Neuron 56, 185–196.
Strobel, A., Zimmermann, J., Schmitz, A., Reuter, M., Lis, S., Windmann, S., Kirsch, P., 2011. Beyond revenge: neural and genetic bases of altruistic punishment. Neuroimage 54, 671–680.
Tom, S.M., Fox, C.R., Trepel, C., Poldrack, R.A., 2005. The neural basis of loss aversion in decision-making under risk. Science 315, 515–518.
Tversky, A., Kahneman, D., 1981. The framing of decisions and the psychology of choice. Science 211, 453–458.
van Veen, V., Cohen, J.D., Botvinick, M.M., Stenger, V.A., Carter, C.S., 2001. Anterior cingulate cortex, conflict monitoring, and levels of processing. Neuroimage 14, 1302–1308.
Zhou, X., 2010. Increased Demand for Fairness under Adversity. An International Symposium on Neuroeconomics and Social Neuroscience. Beijing, China.
Zhou, X., Wu, Y., 2011. Sharing losses and sharing gains: Increased demand for fairness under adversity. J. Exp. Soc. Psychol. 47, 582–588.