Title: Distinct behavioral effects and neural mechanisms of reciprocal reputation on cooperative decision-making in gain and loss context

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Highlights:

Previous studies on human cooperative decisions are mostly in a sharing gain frame. However, cooperation in a loss context is vital both at the individual and societal level. For example, how the countries cooperate with other countries with a different reputation of reciprocity to deal with global issues (e.g., pandemic emergency, financial crisis). The present study revealed that partners' better reciprocal reputation enhanced cooperation, which was more salient in the gain than loss context. Our neural results suggested that individuals used a social heuristic mechanism (recruited the right anterior insula) in a gain context but involved more strategic concerns (recruited the superior parietal lobe) in the loss context when processing the partner's reputation before making a cooperative decision in the provision of a public good. Besides, the bilateral striatum plays as a neural modulator of this effect only in the gain context. The current findings contribute to a better understanding of human cooperation in a loss frame, one of the most important social interactions in human society.

Abstract:

Cooperation is essential for society's functioning, while reciprocity is one of the most critical factors for establishing and maintaining cooperative social relationships. Until now, however, the majority of studies exploring human social cooperation were in a sharing gain frame. The present study investigates the behavioral effects and neural correlates of other people's prior history of reciprocal reputation on cooperative decisions in both gain and loss contexts. 39 Chinese adult subjects participated in the study. Participants first played a Trust Game as Trustee to understand how we quantify the reciprocal reputation and then joined a modified Public Goods Game framed in gain and loss contexts with partners with various reciprocity levels. Behaviorally, individuals tended to be more cooperative with higher reciprocal reputation partners than lower ones, contributing a higher percentage of gain and a lower percentage of loss to the public pool. This effect was robust, especially in the gain context. Trial-wise mixed-effect regression results further demonstrated that the reciprocal reputation on cooperative decisions was more salient in the gain context than the loss context. Neurally, trial-wise parametric modulation analysis revealed two distinct neural systems that right anterior insula in the gain context and bilateral superior parietal lobule (SPL, including precuneus), left inferior parietal lobule (IPL), bilateral superior frontal gyrus (SFG), are positively correlated with partner's reciprocal reputation. Based on the behavioral and neural results, we propose that individuals use a social heuristic preference-based mechanism in the gain context while involving more strategic or reasoning concerns in the loss context in processing others' social reputation when making cooperative decisions in PGG. Furthermore, during the decision phase, cooperating with higher reputation individuals in the gain context increased the bilateral striatum activation, and the activation in the bilateral striatum function as a neural modulator of this effect only in the gain context. Finally, parametric modulation analysis using contribution as the modulator revealed the dorsal anterior cingulate cortex (dACC) in the gain context that suggested that the prefrontal cortex plays a vital role in computing the action values while making decisions in PGG. The current results contribute empirical evidence to our understanding of human cooperation from a new angle, through social interactions in a loss frame.

Keywords: reciprocity, reputation, cooperative decision-making, Public Goods Game, gain and loss context

Introduction

Cooperation between non-kin individuals is one of the critical features of human social life, which sets us apart from other species (Fehr & Fischbacher, 2004a; Rand & Nowak, 2013). Typically, mutual benefits are achieved through various types of social exchange between individuals during social interactions. However, receiving favors from others but not reciprocating in return can prevent setting up a stable and long-term cooperative partnership. For example, when you encounter a difficult task, your colleague works overtime to help you, but you say that you do not have time when he/she needs your help. Also, asking neighbors to help with receiving a mail delivery while telling them that you will not be available for moving in newly arrived furniture may very well lead to short-lived neighborhood relationships. Reciprocity plays a vital role in the establishment and maintenance of cooperative social relationships.

Previous studies have attempted to understand how reciprocity fosters cooperation through the investigation of the motivations and neural mechanisms underlying both individuals' reciprocal behaviors (Chang, Smith, Dufwenberg, & Sanfey, 2011; Delgado, Frank, & Phelps, 2005; King-Casas, Tomlin, Anen, & Camerer, 2005; McCabe, Houser, Ryan, Smith, & Trouard, 2001; Rilling, Gutman, Zeh, Pagnoni, & Berns, 2002), as well as non-reciprocal behaviors (Baumgartner, Fischbacher, Feierabend, Lutz, & Fehr, 2009; Sanfey, Rilling, Aronson, & Nystrom, 2003) during the social exchange. According to these studies, reciprocating cooperation is associated with the brain's reward processing system (Delgado et al., 2005; Rilling et al., 2002; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004), in which the ventral striatum (VS) and orbitofrontal cortex (OFC) are involved (Rilling et al., 2002). These findings suggest that reward processing when reciprocating another's favor might reinforce further cooperation. Besides, social emotions (Chang et al., 2011; Sanfey et al., 2003) and cognitive control of self-interest (Baumgartner, Fischbacher, Feierabend, & Lutz, 2009) are also related to reciprocal behaviors. For example, abuse of others' trust increased the activity in the ventromedial prefrontal cortex (vmPFC) (Chang et al., 2011), a brain region potentially related to affective processing (e.g., guilt) (Krajchich, Adolphs, Tranel, Denburg, & Camerer, 2009). Furthermore, fulfilling self-made promises increased the activation of control regions such as the anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (dlPFC). These regions, when disrupted, are related to a diminished capability to build a social reputation (Knoch, Schneider, Schunk, Hohmann, & Fehr, 2009). The aforementioned studies focused on neural processing when individuals are reciprocating or defecting in social interactions. However, none of these studies has examined how individuals interact (or more specifically cooperate) with others labeled with various reciprocity likelihood.

Research has shown that individuals are conditional cooperators (Fehr & Fischbacher, 2004b; Fischbacher, Gächter, & Fehr, 2001), indicating that most people cooperate on the condition that others cooperate too. Although the norm of conditional cooperation is supported by some evolutionary models (Axelrod & Hamilton, 1981; M. Nowak & Sigmund, 1993), these results are mostly based on mutual cooperation in a sharing gain context. However, it is just as likely for us to be faced with a loss situation with others, both at the individual and societal level. For example, imagine running a company with other partners, and the company encounters an enormous deficit this year. When the countries worldwide face a pandemic emergency (e.g., COVID-19), a financial crisis, or environmental issues (e.g., global warming, overfishing). Therefore, it is quite apparent that understanding cooperative decisions and the relevant neural mechanisms in a loss context in a public goods provision is entirely meaningful.

The present study aimed to bridge the gap between these previous findings and the effects (behavioral and neural) of partners' prior reciprocal reputation on individuals' cooperative decisions in both gain and loss contexts. To achieve this goal, we adopted a two-session game paradigm. Participants first played as Trustee in a Trust Game (TG), interacting with several investors, and then continued to a modified Public Goods Game (PGG). There are two advantages of this two-session paradigm: (1) Participants have the opportunity to reciprocate an investor's trust. Therefore, they will understand how we quantify partners' reciprocal reputation; (2) Participants were informed they would play the PGG with other players who previously participated in the TG. The players were assigned to different reciprocal reputation groups by their real probability of reciprocating behaviors. Notably, one novel aspect of the current paradigm is that we test cooperative decisions by designing a modified PGG with both gain and loss contexts. Participants encounter gain or loss situations together with other partners. Here, we also introduced an incentive threshold into PGG to measure how individuals cooperate to increase the positive gains versus cooperate to avoid negative losses.

By using the aforementioned game paradigm, our study provides the opportunity to answer the following research questions. Firstly, do individuals use a partner's prior reciprocal reputation to guide their subsequent cooperative decisions with these partners? If so, how does this information affect individuals' cooperative decisions in gain and loss situations, respectively? The previous theoretical research on the evolution of human social cooperation highlighted the importance of reputation on the subsequent social interactive decision-making (Fehr & Fischbacher, 2003; M. A. Nowak, 2006; Rand & Nowak, 2013). Moreover, studies have shown that social cooperation was affected by the knowledge of others' reputations in an integrated game (King-Casas et al., 2005; Rilling et al., 2002). The reputation might motivate cooperation through indirect reciprocity (M. A. Nowak & Sigmund, 2005). Therefore, we hypothesize that

individuals would show more cooperative behaviors in the PGG toward higher reciprocal reputation partners in the gain context. Considering individuals' generally greater sensitivity to losses and the typically exhibited loss aversion effect on financial decisions, especially when there is potential uncertainty about other players' behavior (Kahneman & Tversky, 1979; Tom, Fox, Trepel, & Poldrack, 2007; A. Tversky & Kahneman, 1991), we argue that individuals might have a more conservative attitude toward the prior reputation information in the loss context. Therefore, prior reciprocal reputation might be less influential on subsequent cooperative decisions here.

Second, we were also interested in how the brain processes a partner's reciprocal reputation information before making decisions. It is essential to know whether distinct brain circuits exist to support processing a partner's reputation in a gain and loss context. Previous research reported that risk decisions in gain and loss contexts were linked to overlapped sets of the brain; however, the potential loss was demonstrated by decreasing activity in several gain-sensitive areas (Tom, Fox, Trepel, & Poldrack, 2007). A recent study proposed two separate neural networks in gain and loss context, respectively, during intertemporal choices (Zhang et al., 2018). However, none of these studies examined the neural representations of social reputation on interpersonal choices under gain and loss contexts. Given that social reputation (e.g., social approval) is perceived to be a social reward (Izuma et al., 2008; Keise Izuma, Daisuke N. Saito, & Norihiro Sadato, 2010; K. Izuma, D. N. Saito, & N. Sadato, 2010b), reward circuitry might demonstrate increased activation when seeing higher reciprocal players. However, what if individuals know that they will make a decision that might be being taken advantage of by other players in the gain and loss context, respectively? Therefore we asked whether the brain would process seeing the higher reciprocity individuals as rewarding or representing a preparation state for the next step. Besides, there are two dominant theoretical accounts for human cooperative actions related to social reputations. One favored by the traditional social psychology proposes a person's social preference, particularly other-regarding preferences concerning the reciprocity, fairness, and well-being of others (Charness & Rabin, 2002; Fehr & Schmidt, 1999). These social preferences might internalize through the experience of promoted utility in the past and become like an approximate social heuristic to automatically influence an individual's behavior, such as prompt cooperative behaviors (Crockett, 2013; Rand et al., 2014). Another one is from evolutionary psychology that argues that cooperative behaviors are primarily driven by strategic concerns about maintaining a positive reputation in a specific community for further interactions (Yamagishi & Kiyonari, 2000). A previous fMRI study revealed cooperation occurring as social preference-based reciprocity recruited the anterior insula (AI), while reputation-based cooperation specifically recruited the precuneus (Watanabe et al., 2014). Besides, a study examined to what extent prosocial behaviors are driven by social preferences versus reputation concerns in both gain and loss contexts and revealed that people's strategic concerns were

more substantial in the loss context than the gain context (Everett, Faber, & Crockett, 2015). If this holds, we speculated that there might be distinct neural representations of reciprocal reputations in the gain and loss context, in which social preference-based neural circuitry (such as AI) might be more involved in the gain context, while the strategic concern-based brain network (e.g., precuneus) might be revealed in the loss context.

Finally, a fundamental question is whether reciprocal reputation reflects different neural processes' engagement when considering the cooperative decisions in the gain versus loss context. The research found that ratings of facial expressions of higher (trustworthy), as opposed to lower (selfish) social reputation, increased the brain activity of reward-related brain areas, notably the striatum (Izuma, Saito, & Sadato, 2008). Besides, processing of facial expressions labeled with better moral characteristics, which may be represented in the striatum, increased individuals' likeability ratings towards these individuals (Singer, Kiebel, Winston, Dolan, & Frith, 2004), and the perception of the moral character of others influenced the subsequent social interactions through modulation of reward processing in the striatum (Delgado et al., 2005). Furthermore, the striatum was also associated with learning a partner's social reputations through integrated social exchanges (King-Casas et al., 2005). Based on these findings, we hypothesize that individuals would prefer to cooperate with higher reciprocal reputation partners, and this cooperation itself would be a social reward compared to cooperation with lower reciprocity partners.

Summing up, cooperation is one of the fundamental components of human social interaction. It is crucial to examine the factors that could affect social cooperation, which helps to understand better cooperative decision-making's psychological and neural processes from different angles. The current novel paradigm provides the opportunity to examine the behavioral and neural influence of reciprocal reputation on cooperative decision-making in both gain and loss contexts. The evidence here will not only help to better understand underlying neural mechanisms of reciprocity on social cooperation but more broadly can provide new insights that may help improve the establishment of cooperative actions at both individual and societal levels.

Methods

Participants

39 Chinese adults (20 males, aged 19 to 29 years, mean age $\pm$ SD = 21.92 $\pm$ 2.45 years) participated in the experiment. They are all right-handed, with (corrected-to-) normal vision, and without neurological, psychiatric, cardiovascular disorders, head surgeries, or regular drug and alcohol use histories. Written informed consent was obtained from each participant before the experiment. We excluded two participants'

data from analyses because of the technical issue. The reported results were based on the statistics of 37 participants' data. They were compensated with 120 Chinese Yuan for participation. Participants were informed that they could receive an additional bonus (maximum of 60 Chinese Yuan), which depended on the monetary units (MUs) they achieved during the experiment. On average, they received 30 Chinese Yuan as a bonus payment. The study was conducted following the Declaration of Helsinki's principle and guideline and was approved by the Institutional Review Board at Beijing Normal University (BNU), Beijing, China.

Procedure

Participants completed a behavioral experiment (Trust Game, TG) before the fMRI experiment (a modified Public Goods Game, PGG).

Behavioral experiment

The TG is usually played by two players, Player1 (Investor) and Player2 (Trustee). In our experiment, participants played 30 rounds of TG in the role of Player2-Trustee (Chang et al., 2011) (**Supplementary, Figure S1a, b**). They were informed they would play with a different Player1 every round, and Player1s' offers and facial pictures were collected from our previous experiment. 30 Player1' offers were simulated based on an offer distribution from a large sample size (Chang et al., 2011)(**Figure S1c**). Thirty neutral facial expression pictures (of which 50% male) were selected from the Chinese Facial Affective Picture System (CFAPS) (Gong, 2011) to represent Players in the experiment. All facial pictures were balanced for background, brightness, age, and picture size. The game began with a facial picture of Player1 with his/her identity number in our database. After player1's transferred amount (quadrupled) had been revealed to the participants, they were asked to decide the amount of money (if any) they wanted to repay to Player1. The mean and the standard deviation of the percentage of repayment were calculated for each participant (**Supplementary**).

fMRI experiment

Modified Public Goods Game

After the behavioral experiment, participants continued a modified PGG in a 3T fMRI scanner. In a standard PGG (**Supplementary**), participants were paired with a group of anonymous partners from a data pool. Each player starts with an identical endowment at the beginning of each round and then has to decide on the amount of endowment he/she wants to contribute to a public-shared account. Whatever they decide not to share, they keep for themselves. Once all the players have made their decisions, the Total Contribution Amount (TCA, the sum of the contribution from all the group members) to the public-shared account is

multiplied by a factor of 1.6, and this final amount will be divided equally between all of the players (**Figure S2 a, b**).

In this experiment, participants paired with four anonymous players at the beginning of every round (**Figure 1 a, b**). A group of five players would encounter either a context of gain or loss, in which each player would initially receive an identical amount of monetary gain (e.g., 10 yuan) or loss (e.g., -10 yuan). Then, each player decided how much gain or loss they wanted to put into the public-shared account and how much they wanted to keep for themselves. We used the absolute value of the percentage of contribution to compare gains and losses. Once all the players made their decisions, the absolute value of TCA ($|TCA|$) to the public-shared account would be then increased or decreased (multiplied by a factor of 1.6 or 0.6, respectively) according to an incentive threshold and then divided equally among all the players (**Figure 1 a, b, c**).

Notably, in contrast to the standard PGG, an incentive threshold was defined here as the half amount of the sum of the initial total endowment from the five players. For example, each player had 10/-10 of initial monetary gain or loss, the absolute values of incentive threshold were 25 yuan ($50/2$ in gain and $(|-50/2|)$ in loss, respectively). This incentive threshold was an index of increasing or decreasing the $|TCA|$ in the public-shared account in the PGG (**Figure 1 a, b**). Specifically, in the gain context (**Figure 1a**), the $|TCA|$ would increase (multiplied by 1.6) only when the $|TCA|$ was larger than 25. Otherwise, the $|TCA|$ would decrease (multiplied by 0.6). To continue the previous example in the gain context, each player contributed 6; therefore, $|TCA|$ in the public-shared account was 30 (6 multiplied by 5). Here, $|TCA|$ was larger than incentive threshold 25; hence, the $|TCA|$ increased by multiplying a factor of 1.6 and becoming 48. The final monetary gain in the shared account was split equally among five players, and each player received 9.6. Therefore, each player obtained 13.6 (9.6 from a public-shared account and 4 kept for themselves at the beginning of the game). As can be seen, this was a cooperative example, in which $|TCA|$ larger than the incentive threshold in the gain context that each player received more monetary gain (9.6) as compared to their contribution (6) to the public-shared account initially. Correspondingly, in the loss context (**Figure 1b**), the $|TCA|$ would increase on the condition that the $|TCA|$ was larger than 25. Otherwise, the $|TCA|$ would decrease (multiplied by 0.6) (**Figure 1c**). To continue the example in the loss context, each player contributed -6; therefore, $|TCA|$ in the public-shared account was 30 (absolute value of -6 multiplied by 5). Here, $|TCA|$ larger than incentive threshold 25; therefore, the TCA increased by multiplying a factor of 1.6 and becoming -48. Reversely, each player received more monetary loss (-9.6 vs. -6). This example was noncooperative in the loss context, in which $|TCA|$ larger than incentive threshold in the loss context that

each player received more monetary loss (-9.6) as compared to their contribution (-6) to the public-shared account.

This key manipulation allowed us to examine how cooperative decisions were modulated by a partner's reciprocal reputation in both gain and loss contexts. Presumably, monetary gain increased in the public-shared account as a group reward while monetary loss increased as the group punishment. This novel paradigm with an incentive regulation encouraged participants to contribute more monetary gain and less monetary loss. Specifically, in the gain context, our paradigm encouraged each player to contribute at least 50% (e.g., 5 out of 10) to the public account as the necessary amount to increase the monetary gain (group reward). Similarly, in the loss context, the paradigm encouraged each player to contribute less than 50% (-5 out of -10) as the necessary required amount to avoid increasing the monetary loss (group punishment). If this incentive manipulation virtually affects participants' cooperative decisions in gain and loss context, we would speculate that a distinct distribution of frequencies of the percentage of contribution would show in gain and loss contexts, in which participants would demonstrate more frequencies of the percentage of contribution in the range [50%, 1] in the gain context, and more frequencies of the percentage of contribution in the range [0, 50%] in the loss context.

The advantages of behavioral testing TG before the scanning session are as follows: firstly, we wanted our participants to know how we quantified reciprocal reputation. By having participants experience the TG themselves, they understood how we defined different reciprocal reputation groups clearly. Secondly, we were particularly interested in how the partner's prior reciprocal reputation played a role in modifying participants' cooperative decisions in PGG. During the fMRI experiment, they were informed that their partners from our previous experiment were categorized into four groups based on their likelihood of reciprocal behaviors in the TG. Specifically, a high reciprocal group (H: average percent of repaying was ranged between 60%-40%), a middle reciprocal group (M: average percent of repaying was ranged between 40%-20%), a low reciprocal group (L: average percent of repaying was ranged between 20%-0%), and a no-information group (NI: the players in this group did not participate in the previous TG; therefore, we did not have any information about their reciprocal reputation).

Player 1's data were programmed and manipulated by the experimenter. Participants were also asked to use their data for our following participants to increase the plausibility. Participants randomly selected one trial of the task after the experiment to pay as a bonus. Before the experiment, participants were asked to answer a couple of questions to make sure they understood the task correctly. They practiced three rounds of TG and six rounds of PGG before the actual experiment, in which the practice data were not included in our

analyses. During scanning, participants were encouraged to relax and urged to try not to move too much in the scanner.

A 4×2 within-subject design was used, including the partner's reciprocal reputation (four levels: H, M, L, NI) and context (two levels: gain, loss) as independent variables. The percentage of contribution (the percentage of monetary gain or loss contribute to the public-shared account) and response time (RT), as well as the brain activity, were the dependent variables. Therefore, the experiment had 8 experimental conditions. Each condition had 14 trials; in total, the experiment consisted of 112 trials separated into two runs. Each run consisted of 56 trials and 420 scans. Endowment variations (10, 20) were introduced to avoid participant's fixed choices across the trials.

Data acquisition

Neuroimaging data were acquired with a 3.0 Tesla MRI scanner (Trio, Siemens, Erlangen, Germany) equipped with a 12 channel transmit/receive gradient head coil at Imaging Center of Beijing Normal University. Blood oxygen level dependent (BOLD) images were acquired using T₂*-weighted gradient-echo-planar imaging (EPI) sequences with parameters as follows: repetition time (TR) = 2000ms; echo time (TE) = 30ms; flip angle = 90°; matrix size = 64×64; field-of-view (FOV) = 224×224 mm; slice gap = 0.5 mm. 33 interleaved slices were acquired (slice thickness = 3.3 mm, voxel size = 3.5×3.5×3.5 mm) from the whole brain. Moreover, high-resolution anatomical T1-weighted images of the whole brain were collected using a Magnetisation-Prepared Rapid Gradient Echo (MP-RAGE) sequence with the following parameters: 192 slices, TR=2530ms; TE= 3.39ms; flip angle= 7°; number of slices =144; slices thickness = 1.33mm, matrix size = 256×256; field-of-view (FOV) = 256×256 mm.

Experiment stimulus presentation and behavioral data acquisition were conducted using PsychToolbox (<http://psychtoolbox.org/>) (Brainard, 1997; Pelli, 1997) integrated into Matlab (Matlab 2016a, The Mathworks, Inc., and Natick, MA, USA).

Data Analyses

Behavioral data Analyses

Behavioral data analyses were performed using R statistical packages (<https://www.r-project.org/>). Trial-wise percentage of contribution, which indicates the amount of money contributed to the public account relative to each trial's initial endowment, was used as the dependent variable. The absolute value of the percentage of contribution was used for the behavioral analysis if no other specification was mentioned. To

examine the robustness of the results, the p -values in the mixed effect model were reported by calculating using the Satterthwaite formula for degrees of freedom.

For general analyses, histogram and density plots were used to visualize the probability distribution of the percentage of contribution for all trials for all participants in gain and loss contexts (**Figure 2a**). To test all the potential factors that might contribute to predicting cooperative decision-making, a mixed effect regression was performed, including “the percentage of contribution” and “the duration of making a decision” as the dependent variables and “context” (two levels: gain, loss), “reputation” (four levels: H, M, L, NI), “endowment amount” (two levels: 10 and 20) and all the potential interactions between the three factors as the predictors. Participants were treated as a random effect, and by-subject random slopes for each fixed effect were also included in all the reported mixed-effect regression models. Our results showed that the endowment amount ($\beta=-0.0004\pm0.0005$, $t=-0.87$, $p=0.37$) and its interactions between other predictors did not significantly contribute to predicting the subsequent percentage of contribution in the PGG. Therefore, the “endowment amount” factor was not included as a predictor in the following analyses.

To avoid the multicollinearity problem in the regression analyses (Graham, 2003) and to test how the two predictors, “context” and “reputation,” contributed to affect participants’ cooperative decision-making in terms of their percentage of contribution in PGG, we compared five general linear mixed regression models (M0-M4) (**Table 1**). M0 was a null model only including the participants as a random effect. M1 contained context as a single predictor. M2 contained a reputation as a single predictor. M3 contained both context and reputation as predictors. M4 contained context, reputation, and interaction between these two as the predictors. Bayesian information criterion (BIC), which took both model fitness and complexity into account, was used to assess the model-fitting goodness. Parameters were estimated based on the best model (lowest BIC) (Farrell & Lewandowsky, 2010). Based on the best model, a mixed model ANOVA was implemented to illustrate two predictors’ e across-subject mean effects and their interaction on the percentage of contribution (**Figure 2b**). To further quantify the trial-wise change effect of reputation on trial-wise change of cooperative decisions in both contexts, two separate mixed-effect regressions were performed, including the trial-by-trial change of contribution (Δ contribution) as the dependent variable and the corresponding change of reciprocity (Δ reputation) as the predictor in gain and loss context (**Figure 2c, d**). These results would further illustrate how cooperative decisions were modified by the trial-wise increment/decrement of the partner’s reciprocal reputation.

Considering participants' reciprocal behavior tendency in TG might be associated with their general prosocial disposition (Aron, Behrens, Smith, & Frank, 2007); therefore, it might be an influential factor on

their cooperative behaviors in PGG. A control analysis was used to examine if a participant's reciprocal decisions in TG were predictive of cooperative decisions in PGG. Two mixed-effect regressions were performed using participants' average percentage of contribution in the PGG in gain and loss contexts as the independent variables and participants' average percentage of repayment in the TG as the predictors.

fMRI data analyses

Neuroimaging data analyses were performed with SPM12 (<http://www.fil.ion.ucl.ac.uk/spm/spm12/>). Image preprocessing procedures consisted of slice-timing correction, realignment through rigid-body registration to correct for head motion, co-registration of functional images to the anatomical images, segmentation of the anatomical image, normalization to the Montreal Neurological Institute (MNI) space, spatially smoothing (8-mm full-width/half-maximum kernel), and temporally filtering (a standard high-pass filter set a 128 s).

We started using a GLM (GLM1) to define multiple event-related regressors for each epoch of each participant's time course for the first level within-participant statistical analyses. The regressors modeled the blood oxygen level dependent (BOLD) response to each epoch of fixation, context, partner's reciprocal reputation, and decision to include all known sources of variance could account for the signal variance. Each event's regressors were time-locked to the epoch's onset with the onset's duration to the epoch's offset. Particularly, the regressor of the decision was subdivided into two regressors corresponding to gain and loss and modeled as a variable epoch, which time-locked to the onset of the decision screen until the final button press. Therefore, the orthogonalized response time was used as the duration of each decision event (Mumford, Davis, & Poldrack, 2014). Since our behavioral result of mean percentage of contribution in PGG revealed a significant main effect of reputation levels on contribution in PGG (H>M>NI>L), corresponding reputation levels were used as the indexes for parametric modulators for a trial-wise parametric modulation analysis for reputation and decision regressors. Besides, the trial-wise contributions in the PGG were added as a second modulator for the decision regressors. The six-movement parameters of the realignment were used as nuisance regressors in the model. All contrasts of interest were performed during the first level analyses for each participant and then submitted for second-level analyses.

The modeled BOLD signal from subject i , run j , and voxel k using the following equation:

$$y_{i,j,k} = \alpha_j + \beta_1 * \text{Fixation} + \beta_2 * \text{Context} + \beta_3 * \text{Reputation} + \beta_4 * \text{Reputation} * \text{Reputation}_{\text{pmod}} + \beta_5 * \text{Decision}_{\text{gain}} + \beta_6 * \text{Decision}_{\text{gain}} * \text{Reputation}_{\text{gain_pmod}} + \beta_7 * \text{Decision}_{\text{gain}} * \text{Contribution}_{\text{gain_pmod}} + \beta_8 * \text{Decision}_{\text{loss}} + \beta_9 * \text{Decision}_{\text{loss}} * \text{Reputation}_{\text{loss_pmod}} + \beta_{10} * \text{Decision}_{\text{loss}} * \text{Contribution}_{\text{loss_pmod}} + \beta_{11} * \text{FA} + \beta_{12} * \text{RW} + M_j + \varepsilon_i$$

In the GLM1, we included a regressor modeling the fixation window, a regressor of context window, and a regressor of partner's reciprocal reputation window of each trial. We used the partner's reciprocal reputation levels per trial as a parametric modulator for the reputation window. For the decision window, we further separated into two regressors, a decision in the gain context ($\text{Decision}_{\text{gain}}$), and a regressor of a decision in the loss context ($\text{Decision}_{\text{loss}}$). We used the partner's reciprocal reputation levels per trial as the first parametric modulator for the two decision regressors and the percentage of contribution per trial as the second parametric modulator for the two decision regressors. R is a 6-column matrix with realignment parameters, and W is the vector of coefficients that multiplies R .

Given that our behavioral results demonstrated the modulating effect of partner's reciprocal reputation on cooperative decision-making was more salient in the gain than the loss context, we speculated that there might be distinct brain circuits (or mechanisms) supporting the processing of reputation in the gain and loss context. Therefore, we performed a second GLM (GLM2) to examine the neural response of processing partners' reputation in gain and loss context separately (Mumford, Poline, & Poldrack, 2015). To reveal this, GLM2 modeled BOLD response to fixation, context, reputation, and decision, mainly focused on the neural correlates associated with partner's reciprocal reputation (time window of revealing reputation information). The reputation regressor was further split into two regressors, which corresponded to the two experimental conditions ($\text{Reputation}_{\text{gain}}$ and $\text{Reputation}_{\text{loss}}$). Partner's reciprocal reputation levels were used as the parametric modulator indexes for a trial-wise parametric modulation analysis in gain and loss context, respectively.

The modeled BOLD signal from subject i , run j , and voxel k using the following equation:

$$y_{i,j,k} = \alpha_j + \beta_1 * \text{Fixation} + \beta_2 * \text{Context} + \beta_3 * \text{Reputation}_{\text{gain}} + \beta_4 * \text{Reputation}_{\text{gain}} * \text{Reputation}_{\text{gain_pmod}} + \beta_5 * \text{Reputation}_{\text{loss}} + \beta_6 * \text{Reputation}_{\text{loss}} * \text{Reputation}_{\text{loss_pmod}} + \beta_7 * \text{Decision} + \beta_8 * \text{FA} + \beta_9 * \text{DW} + M_j + \varepsilon_i$$

In the GLM2, we were particularly interested if there were distinct neural systems in processing partner's reciprocal reputations in the gain and loss context, respectively. Therefore, we included a regressor modeling the fixation window, a regressor of context window, and a regressor for each trial's decision window. For the reputation window, we further separated into a regressor of reputation in the gain context ($\text{Reputation}_{\text{gain}}$) and a regressor of reputation in the loss context ($\text{Reputation}_{\text{loss}}$). We used the partner's reciprocal reputation levels per trial as the two reputation regressors' parametric modulators. D is a 6-column matrix with realignment parameters, and W is the vector of coefficients that multiplies R .

For all GLMs, the events in each regressor were convolved with the canonical hemodynamic response function. Second-level models were constructed as one sample t-tests using contrast images from the first-level models. The fMRI results were corrected for multiple comparisons using the threshold of $p < 0.001$ voxel-level combined with whole-brain family-wise correction $p < 0.05$ (FWE) cluster level if no specifications were indicated. Functional regions of interest (ROIs) were defined by group-level peak MNI coordinates of activation regions by whole-brain analyses. ROI analyses were performed with the MarsBar 0.44 SPM toolbox (<http://marsbar.sourceforge.net/>). Reported coordinates confirmed to the Montreal Neurological Institute space. Anatomic labeling of regions was conducted using the Anatomical toolbox in SPM12.

Results

On average across all trials, the mean percentage of contribution in the gain context ($M = 53.77\%$, $SD = 29.92\%$) was not significantly different as compared to the loss context ($M = 50.18\%$, $SD = 27.15\%$), $t = 0.628$, $p > 0.05$ (**Figure 2a**). However, as expected, the frequency distribution of the percentage of contribution was visually different in the two contexts (**Figure 2a**). At the range between 50%-1, the mean frequency of the contribution percentage was denser in the gain context ($M = 50.59\%$) compared to the loss context ($M = 36.59\%$). In contrast, at the range between 0, 50%, the mean frequency of percentage of contribution was less dense in the gain context ($M = 49.41\%$) than in the loss context ($M = 63.41\%$). In other words, participants demonstrated higher frequencies of contributing more than 50% of their endowment in the gain context while had lower frequencies of contributing less than 50% of their endowment in the loss context. This distinct distribution in gain and loss contexts indicated participants tended to make cooperative choices to increase group gains and to avoid group loss through complying with the incentive regulation in both contexts.

Our model comparison results showed that the model with two predictors (context and reputation) and their interactions was the best-predicted model (**Table 1**). Moreover, the main effect of reputation and the interaction between reputation and context were significant (reputation: $\beta = 0.19 \pm 0.038$, $t = 5.08$, $p < 0.001$; reputation $\times$ context: $\beta = -0.11 \pm 0.23$, $t = -4.74$, $p < 0.001$; the main effect of context did not reach the significance ($\beta = 0.13 \pm 0.08$, $t = 1.59$, $p = 0.11$). Based on the best-predicted model, a mixed model ANOVA further illustrated the main effects of the two factors and their interaction on cooperative decision-making (**Figure 2b**, **Table S1**). As we expected, the partner's reciprocal reputation affected cooperative decisions in the PGG, $F(3, 108) = 14.35$, $p < 0.001$. A linear trend effect indicated that participants tended to be more cooperative as their partner's reputation increased, $F(1, 36) = 17.11$, $p < 0.001$. The percentage of contribution in NI was lower than H, and no significant differences were found between NI and the M/L

($M_L < M_{NT} < M_M$, $p_s > 0.05$). Consistent with the mixed model regression results, the main effect of context was not significant, $F(1,36) = 0.44$, $p = 0.51$, with the mean percentage of contribution in the gain context ($M_{gain} = 0.54$, $CI = [0.47 \ 0.60]$) slightly higher than loss ($M_{loss} = 0.50$, $CI = [0.43 \ 0.57]$) context.

Interestingly, a significant interactive effect further illustrated the partner's reputation exerting discriminating influences on cooperative decision-making in gain and loss contexts, $F(3,108) = 15.56$, $p < 0.001$. In addition, two separate linear trend effect of reputation on cooperation in gain ($F(3,34) = 10.12$, $p < 0.001$) and loss ($F(3,24) = 3.65$, $p = 0.02$) were detected, which demonstrated that the absolute value of percentage of contribution increased in gain context but decreased in loss context as partner's reputation increased. These results suggested that cooperation enhanced as partners' reciprocal reputation improved in both contexts. Notably, however, this modulatory effect of partner's reputation on cooperation was more salient in gain ($p < 0.001$) versus loss context ($p = 0.02$) (**Figure 2b**). To further explore these subtle differences, two mixed-effect regressions were performed, including the trial-by-trial contribution (Δ contribution) as the dependent variable and the corresponding change of reciprocal reputation (Δ reputation) as the predictor in gain (**Figure 2c**) and loss (**Figure 2d**) contexts respectively. Consistent with our previous results, as the partner's trial-wise change of reputation improved, the corresponding trial-wise change of percentage of contribution increased in gain context ($\beta = 0.15 \pm 0.006$, $t = 23.4$, $p < 0.001$) and decreased in loss context ($\beta = -0.05 \pm 0.005$, $t = -9.73$, $p < 0.001$). Similarly, the increment and decrement of contribution modulated by the change of reputation were more extensive in the gain ($\beta = 0.15$) than in the loss context ($\beta = -0.05$). Again, our results demonstrated that partners' reciprocal reputation exert a more salient effect on cooperative decisions in PGG in gain compared to loss context.

Our control analyses result revealed that the mean percentage of contribution in PGG could not be predicted by participant's mean percentage of repayment in the TG, both in the gain and loss context ($p_s > 0.05$), which suggested that participant's reciprocal behavior in the previous TG was not a confounding factor for their cooperative decisions in the PGG in our experiment. To summarize the behavioral results, we found that better partners' reciprocal reputation enhanced cooperative decisions both in gain and loss contexts, but this moderating effect was more salient in the gain context than the loss context.

fMRI Results

Processing partner's reciprocal reputation

Trial-wise parametric modulation analyses revealed that the partner's reciprocal reputation was positively correlated with the activation of the right anterior insula (rAI) extending into the right inferior frontal gyrus (rIFG), left dorsal anterior cingulate cortex (dACC), and bilateral fusiform gyrus ($p_{FWE} < 0.05$) (**Figure 3**,

Table 2). The result also revealed a cluster of left insula (-41,14,0) ($p<0.001$, *unc.* 31 contiguous voxels, $t_{\text{peak}}=4.82$). Moreover, we did a contrast analysis between high reciprocal vs. low reciprocal reputation to confirm the results. Contrast analysis result further supported our findings, which revealed a cluster of left insula (-43,14, -1, 48 voxels, $t_{\text{peak}}= 5.18$, $p<0.001$, *unc.*), right insula (38,25,-1, 47 voxels, $t_{\text{peak}}= 4.19$, $p<0.001$, *unc.*), and left dACC (-8,39,24, 32 voxels, $t_{\text{peak}}= 4.06$, $p<0.001$, *unc.*). These results suggested increased activity in the AI (esp. right AI) and left dACC as the partner's reciprocal reputation improved.

To further illustrate how the two brain regions activated differently between the gain and loss context across the four reciprocal reputation conditions, parametric estimates were extracted from the cluster of rAI and left dACC (**Figure 3**). Two-way repeated ANOVAs, including the Context and Reputation as within-subject factors, were performed for the average parametric estimates from rAI and left dACC. In line with our expectation, increased activities were found in the rAI ($F(2,84)=6.7$, $p=0.001$) and left dACC ($F(2,87)=5.6$, $p=0.003$) as the partner's reciprocal reputation improved. Specifically, the activation of rAI was higher in the H as compared to the NI ($p=0.012$) and L ($p=0.04$), and no significant difference was found between H and M($p=0.12$) reputation conditions. Although significant effects of context and interaction between context and reputation were not detected, Wilcoxon tests between reputation levels in gain and loss context showed that effects of both rAI ($p=0.036$) and left dACC ($p=0.069$) were more salient in gain context as compared to loss context ($ps>0.05$).

Given the reputation effect of the activation pattern of rAI and left dACC was more salient in the gain context as compared to the loss context that was quite similar to our behavioral results, we hypothesized that they possibly are more involved in the processing of the partner's reciprocal reputation in the gain context than the loss context. Therefore, it is reasonable to infer that there might be a different (or an additional) brain mechanism underlying the processing of the partner's reciprocal reputation in the loss context. To confirm our hypothesis, we performed a trial-wise parametric modulation analysis using reciprocal reputation level as the modulator (GLM2) to examine the neural circuitry of the processing partner's reciprocal reputation in gain and loss context separately.

As we expected, our results showed distinct brain circuits that supported the processing of the partner's reciprocal reputation in the gain and loss, respectively. Specifically, in the gain context, the partner's reciprocal reputation was positively correlated with the activation of right anterior insular (rAI) extending into inferior frontal gyrus (rIFG) and bilateral fusiform gyrus ($p_{\text{FWE}}<0.05$). And this result also revealed a cluster of left insula (-41,14, -4, 26 voxels, $t_{\text{peak}}=4.25$), and left dACC (-10,31,30, 20 voxels, $t_{\text{peak}}=4.34$) although they were not survived through family-wise-error correction ($p<0.001$, *unc.*) (**Figure 4, Table3**).

It is worth noticing that these brain regions were consistent with the previous findings revealed by GLM1 while processing reputation in both contexts but illustrated a weaker effect due to the smaller effect size (reduced by half trials).

In contrast, trial-wise parametric modulation analysis results showed that the processing partner's reciprocal reputation in loss context was positively correlated with the activation of the bilateral superior parietal lobule (SPL), including left precuneus extending to the left angular gyrus (AG) and the intraparietal sulcus (IPS); left inferior parietal lobule (IPL); right precuneus extending to right IPS; bilateral superior frontal gyrus (SFG) extending to precentral gyrus (PG), and right fusiform gyrus ($p_{FWE} < 0.05$). We find a cluster of middle/inferior temporal gyrus (-55, -53, -11) which did not exceed the family-wise-error correction (34 voxels, $t_{peak} = 5.06$, $p < 0.001$, *unc.*) (**Figure 4, Table 4**). In line with our hypotheses, our results revealed that distinct brain circuits support the processing of a partner's reciprocal reputation in the gain and loss context before choosing PGG. Parametric estimates were extracted from rAI and rSPL for each participant in the gain and loss contexts. We further explored how the two distinct brain circuits could predict the subsequent cooperative decision-making in gain and loss context, respectively. Results showed a marginally significant correlation relationship between rAI and the average percentage of contribution in the loss context ($R = 0.31$, $p = 0.059$). Although there was a negative relationship between rAI and the average percentage of contribution in the gain context, the effect was not significant ($R = -0.24$, $p = 0.17$). Interestingly, a similar pattern of relationship between parametric estimates of rSPL and the average percentage of contribution was found, in which parametric estimates in the rSPL positively correlated with the average percentage of contribution in the loss context ($R = 0.33$, $p = 0.046$). However, this effect was not found in the gain context ($R = -0.23$, $p = 0.16$) (**Figure 4, c, d**). These results suggested that a distinct neural system might underlie the processing social reputation of other partners in the loss context as compared to the gain context before making cooperative decisions in a public goods provision.

Cooperative decision-making

Our next question of interest is how individuals react, in terms of brain activity, to the different types of partner's reciprocal reputation in gain and loss context after they have received (or brain has processed) this information. Behaviorally, individuals demonstrated more cooperative decisions while paired with partners from higher reciprocal reputation levels, which is more salient in the gain than the loss context. The partner's reciprocal reputation levels were used as the indexes for trial-wise parametric modulator for two decision regressors in gain (Decision_{gain_Rpmod}) and loss (Decision_{loss_Rpmod}) context. Results showed that in the gain context, reputation positively correlated with the brain activations in the bilateral striatum (**Table 2, Figure 5a**), which contained a cluster of left putamen extending to pallidum, a cluster of the right caudate

nucleus, and a cluster of calcarine gyrus ($p_{FWE} < 0.05$). However, no significant cluster was found in the loss context (**Table 2, Figure 5a**). To confirm these results, two contrasts were also compiled independently between higher reciprocal vs. lower reciprocal reputation ($H+M > L$) in the gain and loss context, respectively. Contrast analyses revealed a cluster of 112 voxels of right Caudate Nucleus (15,18,7) extending to right Putamen (19,11,-4), a cluster of 159 voxels of left Putamen (-20, 14,0), and a cluster of 240 voxels of right calcarine gyrus (12,-56,-14), particularly in the gain context, but not in the loss context (no significant cluster was found in loss context). These results consistently supported that making cooperative decisions with higher reciprocal partners as compared to the lower reciprocal partners was associated with the increased activity in the bilateral striatum in the gain context but not in the loss context.

To further understand how the brain regions of bilateral striatum were activated in gain and loss context across the four reciprocal reputation levels, parametric estimates in the cluster of left and right striatum were extracted. Two-way repeated ANOVAs corresponding to the behavioral analyses were performed, including the context and reputation as the two within-subject independent factors, and the parametric estimates from left and right striatum were the dependent variables (**Figure 5a, b, c**). The ANOVA analyses of the left striatum revealed a significant main effect of partner's reciprocal information, $F(2, 88) = 3.41$, $p = 0.029$. Contrast analysis further found that the left striatum increased activation in the H, M, and NI conditions compared to the L reciprocal reputation condition (**Figure 5b**). Interestingly, consistent with our behavioral results, a significant interaction effect between reputation and context was detected, $F(3,95) = 3.52$, $p = 0.023$. Pairwise comparisons demonstrated that the activation in the left striatum was increased in the H ($t = 4.01$, $p < 0.0005$), M ($t = 3.73$, $p = 0.0014$), NI ($t = 2.45$, $p = 0.07$) as compared to the L reputation condition. In contrast, however, no significant difference in parametric estimates between reputation levels was found in the loss context ($ps > 0.05$). We did not find a significant main effect of context ($p = 0.1$). Similarly, the ANOVA results in the right Striatum revealed a significant main effect of partner's reciprocal reputation (**Figure 5c**), $F(2,84) = 3.19$, $p = 0.034$, and a significant interaction between reputation and context, $F(3,92) = 5.79$, $p = 0.002$. Follow-up statistics revealed brain activation in the right striatum across the reputation levels were quite similar to the left striatum that the activations were increased in the H ($t = 3.49$, $p = 0.0012$), M ($t = 2.07$, $p < 0.05$), NI ($t = -1.78$, $p = 0.07$) as compared to L reputation condition. No significant effects were found in the loss context. Again, we did not find a significant main effect of context ($p = 0.25$). These neural results further supported that partner's reciprocal reputation exerted discriminating effects on bilateral striatum brain activities during decision phases in the gain context that cooperated with higher reciprocal partners increased the brain activation in the bilateral striatum in the gain context but not in the loss context.

Next, we averaged the beta values in the left and right striatum across the time course. (**Figure 5d**). The time courses were estimated with the finite impulse response model from the onset of the fixation in both contexts, for a length of 20s (10 scans). A significant difference between H and L reputation levels was detected in time bin 4 (the onset of partner's reciprocal reputation) in the gain context, but not in the loss context. These results further supported that bilateral striatum was mainly involved in cooperating with higher reciprocal reputation partners in the gain context rather than in the loss context.

Given that the parametric estimates activation pattern in the bilateral striatum across the four reciprocal reputations in the gain and loss context was similar to the behavioral results, we assumed that the striatum's activation might be particularly associated with cooperative decision-making in the PGG only in the gain context. Therefore, the average parametric estimates of the right striatum were extracted to predict the participant's percentage of contribution in the PGG in gain and loss context, respectively. As we expected, a significant positive correlation was found between the average parametric estimates from the right striatum and the percentage of contribution in the gain context ($R=0.33, p=0.043$) (**Figure 5e**). Moreover, a reversed weaker negative correlative tendency was detected in the loss context, but this correlation was not significant ($R=-0.24, p=0.15$).

Our results revealed that cooperating with higher reciprocal reputation partners in the gain context (rather than loss context) was associated with the increased bilateral striatum activation. Moreover, the parametric estimates from the right striatum positively predicted participants' average percentage of contribution in PGG in the gain context, but not in the loss context. It should be noted that trial-wise contribution was used as the second parametric modulator to understand further how reputation levels combined with trial-wise contribution link to brain processing during cooperative decision-making in gain and loss context. Our results revealed a cluster of the bilateral anterior cingulate cortex ($p_{FWE}<0.05$) (**Table 2**). Again, we did not find significant results in the loss context.

Individual differences in cooperative decision-making

As shown in the experiment design, our experimental paradigm introduced an incentive threshold, defined as the half amount of the sum of the initial total endowment from the five players in the PGG (e.g., 25 in the example), which was adopted to encourage cooperation (prompt collective gain and avoid collective loss) among all the players in both contexts. This manipulation encouraged participants to contribute at least half of their initial monetary gain (e.g., 5 in the example) to increase the TCA of the group and less than half of their initial monetary loss (e.g., -5 in the example) to avoid the decrease of the TCA of the whole group.

Corresponding to the game rule (**Figure 1c**), participants were subdivided into cooperative and noncooperative individuals according to their average percentage of contribution in gain and loss contexts (**Figure 6a**). Participants' average percentage of contributions higher than 50% were classified as cooperative in the gain context, while the average percentage of contribution equal to or lower than 50% was classified as non-cooperative. In the loss context, participants' average percentage contributions lower than 50% were classified as cooperative while the average percentage of contribution equal to or lower than 50% was classified as non-cooperative. We averaged the parametric estimates from the bilateral striatum. Increased striatum activities were observed in the cooperative individuals ($M=0.36$) compared to the noncooperative individuals ($M=0.18$), $t=2.69$, $p=0.009$. Moreover, the cooperative individuals increased brain activities compared to the non-cooperative individuals only in the striatum in the gain context ($p=0.019$), but no significant difference was detected in the loss context ($p=0.29$).

Discussion

The present study used a novel game paradigm in which participants played a Public Goods Game with other anonymous players labeled with a particular degree of previous reciprocity behavior, in both a gain and a loss context. This study aimed to identify the behavioral effects and neural representations of a partner's prior reciprocal reputation on cooperative decision-making when faced with monetary gain or loss contexts.

Our results showed a demonstrable effect of a partner's prior reciprocal reputation on an individual's cooperative decisions with these partners. This effect was in line with previous studies indicating that individuals prefer to cooperate with those who have higher reciprocity levels (Delgado et al., 2005; King-Casas et al., 2005; Milinski, Semmann, & Krambeck, 2002; M. A. Nowak & Sigmund, 2005). The current results indirectly support the theory of 'conditional cooperation,' which assumes that people cooperate on the condition of others' cooperation (Fischbacher et al., 2001). Notably, although the better prior reciprocal reputation of a partner enhanced cooperative decisions, the effects of prior reciprocal reputation on cooperation in the gain context loomed more massive than in the loss context, as demonstrated by the contribution being less influenced by the partner's prior reciprocity in the loss context. Individuals tended to show a more conservative attitude towards cooperation with social others in a loss frame, though this is relatively rarely studied in the cooperation literature. This result was in line with our expectations. Prospect theory, the most famous behavioral model, proposed a concept of loss aversion to explain human decision-making under risk and uncertainty in gain and loss frames. The model shows that individuals typically overweight potential losses compared to equivalent gains, and they tend to be more sensitive to monetary

loss than monetary gain (Kahneman & Tversky, 1979; Amos Tversky & Kahneman, 1974; A. Tversky & Kahneman, 1991). Consistent with this account, one interpretation of the current result is that individuals overweight potential losses compared to gain, making them more conservative to the influential social factors, such as social reputation, in a loss context, before making choices. Therefore, it can be inferred that the social utilities of others' reputations are less weighted in the utility function in the loss context than the corresponding gain context in PGG.

Our next question is, what are the relevant neural processes of reciprocal reputations that support the behavioral differences in gain and loss contexts in a cooperative situation? As can be seen (**Figure 1d**), partners' reciprocal reputation was uncovered after the monetary context (gain or loss) information has been delivered. Besides, our neuroimaging results did not reveal reward neural circuits while processing others' reciprocal reputation, which provided evidence that the brain processed the partner's reputation before making decisions as a preparation state for the next move. Parametric modulation analysis (GLM1) by using partner's reciprocal reputation levels as the modulator demonstrated that intensified brain activations in the rAI and left dACC while knowing paired with higher reciprocal reputation partners before playing the PGG in both gain and loss contexts. Besides, the average parametric estimates in the two brain regions were significantly modulated by the partner's reciprocal reputation only in the gain context, rather than the loss context. Given the similar effect patterns of reciprocal reputation on behaviors and neural responses, we, therefore, speculated that there might be distinct neural systems that support the processing of reciprocal reputation in the loss context compared to gain context before making decisions. Therefore, we did another parametric analysis using the partner's reciprocal reputation as the modulators in the gain and loss context separately (GLM2). Interestingly, our results demonstrated that the activation in rAI was particularly positively correlated with the gain context's reputation levels. The bilateral SPL (including precuneus), left IPL, bilateral SFG were revealed positively correlated with the reputation levels in the loss context. These results strengthened our hypothesis that two distinct neural mechanisms support reciprocal reputation processing in gain and loss context before making decisions in PGG.

According to our previous hypotheses, we argue that individuals used a social preference-based mechanism, recruiting AI, to process others' reputation in the gain context before making choices in PGG. On the one hand, the AI was reported to be highly associated with empathy for others' pain (Lamm, Decety, & Singer, 2011; Singer, Seymour, O'Doherty, Kaube, & Dolan, 2004). Empathy, the capacity to understand and share others' feelings, plays a central role in social preferences. On the other hand, the anterior insula was primarily reported in response to various social signals during interpersonal interactions. For example, the activation of AI has been reported sensitive to free-riding (Rilling, Goldsmith, Glenn, & Jairam, 2008),

social norm violations (Montague & Lohrenz, 2007; Sanfey et al., 2003), social exclusion by the peer group (Eisenberger, Lieberman, & Williams, 2003). Converging evidence suggested that AI functions to detect social signals changes if it is out of beliefs or violates the norms (Bellucci, Feng, Camilleri, Eickhoff, & Krueger, 2018). Hence, it can be inferred that AI plays a central role in perceiving the social salience that allows one to quickly detect social information that violates the subjective values of beliefs and norms in the environment. This viewpoint is in line with a resting-state large-scale brain network model, indicating that AI and dorsal ACC were involved in the salience network automatically detecting and orienting to salient external stimuli and internal events (Menon, 2011). In this study, the activations in AI while perceiving the partner's reputation, especially in the gain context, indexed the brain responses to social signals through the automatic social heuristic mechanism and further shaped the intuitive cooperation. Our results showed a similar behavioral effect and neural responses of reciprocal reputation on the percentage of contribution and AI activations in the gain context that consistently supported this interpretation. Moreover, it was also strengthened by the social heuristic hypothesis (SHH) that proposes social norms are internalized in the form of automatic behavioral dispositions and cooperation are intuitive behaviors with social heuristics processes more than deliberative processes (Rand et al., 2014; Zaki & Mitchell, 2013). Notably, the SHH was proposed only based on cooperative behaviors in the gain context.

Furthermore, a recent study using rTMS examined the causal relationships of the inferior frontal gyrus (IFG) and superior parietal lobule (SPL) in deductive reasoning (Tsujii, Sakatani, Masuda, Akiyama, & Watanabe, 2011). This study's results are consistent with the dual-process theory of reasoning that suggest the bilateral IFG, where AI is located, are associated with the belief-based heuristic system, and the bilateral SPL, where precuneus is located, may underlie the logical-based analytic system. Consistent with this, it is plausible that strategic or reasoning concerns, recruiting bilateral SPL (precuneus), and left IPL, were involved in processing others' social reputation when making cooperative decisions in the loss context PGG. This interpretation was also supported by a previous study that suggested the precuneus was explicit with the reputation-based cooperation while AI was contributed to pay-it-forward reciprocity cooperation (Watanabe et al., 2014). Besides, a meta-analysis about the contribution of the posterior parietal cortex to reasoning revealed the critical roles of left IPL in reasoning as well as mathematical cognition (Wendelken, 2015). Hence, it can be inferred that the intensified activations in bilateral SPL left IPL in the loss context might suggest enhanced strategic concerns while interacting with different reciprocal reputation partners before making decisions in the PGG. Our following correlation analysis results further supported this account that individuals' brain activation in rSPL positively predicted their absolute value of the loss context's average contribution but not in the gain context. Moreover, as suggested by previous research, bilateral superior prefrontal cortex (SFG) and IPL were positively correlated with behavioral loss aversion

(Tom et al., 2007). Different loss aversive behavior was strongly predicted by differences in neural responses in these regions. Our results were in line with these previous results that suggested the strategic concern might be the potential mechanism for loss aversion, especially in the social domain. It should be noted that rAI and left dACC was revealed in both gain and loss context in GLM1, which might indicate that the salience network functioned underlying both contexts; however, the brain recruited more strategic calculations in the loss context when interacting with social partners with different reputation levels. Taken together, these results supported our expectation that there might be two distinct neural systems in supporting processing social reputation in the monetary gain and loss contexts, respectively.

We further explored the neural processes when cooperating with various reciprocal players in both gain and loss contexts. Again, increased activation in the bilateral striatum was revealed when cooperating with higher reciprocal reputation partners in the gain context, rather than in the loss context. These results increased our understanding by providing new evidence that the bilateral striatum indexed the partner's reciprocity information, which played a role as a neural modulator and further reshaped the subsequent cooperative decision-making in the PGG, particularly in the gain context. Our neuroimaging findings support this argument in the following aspects. In animal literature, the striatum is a brain structure that is part of the reward center (Wolfram Schultz, 1997; W. Schultz, Dayan, & Montague, 1997; W. Schultz, Tremblay, & Hollerman, 2000). In the existing human neuroimaging studies, the activation of the striatum was also found in different types of reward processing, from basic physical reward, such as food reward (McClure, Berns, & Montague, 2003; Pagnoni, Zink, Montague, & Berns, 2002), sexual reward (Arnold et al., 2002), to a higher level of psychological reward, for example, monetary reward (Delgado, Stenger, & Fiez, 2004; Knutson, Adams, Fong, & Hommer, 2001) and social reward (Izuma et al., 2008; K. Izuma, D. N. Saito, & N. Sadato, 2010a) (e.g., social reputation, social approval). Our results illustrated that the bilateral striatum activation pattern across conditions mirrored our behavioral effects, which further indicated that cooperation with higher reciprocal reputation individuals might be 'rewarding' compared with the lower ones, especially in the gain context. This reward processing in the bilateral striatum might further foster the following cooperative decisions in the PGG with these players. Previous research supports this interpretation, suggesting that striatum is also a source of motivation for actions (Delgado et al., 2005; Harbaugh, Mayr, & Burghart, 2007; King-Casas et al., 2005; Rilling et al., 2002). For example, reward processing in the striatum prompts the subsequent risk-taking behaviors (Bault, Joffily, Rustichini, & Coricelli, 2011; Losecaat Vermeer, Boksem, & Sanfey, 2014). More importantly, we correlated individuals' average percentage of contribution and the neural activation of the right striatum in the gain and loss context, respectively. In line with this account, the striatum's activation positively predicted individuals' average percentage of contribution in the gain context. Although a negative relationship was observed between the

two in the loss context, the effect was not significant. According to this logic that striatum indexes reward processing with different levels of reciprocal reputation individuals, it can be inferred that cooperative individuals should demonstrate higher activation in the striatum as compared to the relatively non-cooperative individual. Therefore, we further classified participants into cooperative and non-cooperative individuals according to their average contribution to the public pool. Our results strengthened our speculation that increased striatum activities were detected in the cooperative individuals compared to the non-cooperative individuals. Cooperative individuals demonstrated higher brain activations in the striatum than the noncooperative individuals only in the gain context rather than loss context. Taken together, our results indicated that activation in the striatum acts as a modulator (or index) of the social reputation of others to shift the subsequent cooperative decisions, especially in the gain context PGG.

Trial-wise parametric modulation analyses using the percentage of contribution as the modulator selectively found a region, at the intersection of Brodmann 10/11/32, positively correlated with cooperative decisions in the gain context. This region is part of the ventral ACC, vmPFC, and mOFC, all involved in the brain's value system (Rangel & Hare, 2010). Specifically, mOFC was more associated with the stimulus value signals, for example, monetary prizes (Tom et al., 2007) and food repetitiveness (Plassmann, O'Doherty, & Rangel, 2010). The ACC was related to the cognitive part of processing values, specifically encoded and computed action values relative to stimulus values (Rudebeck et al., 2008; Rushworth & Behrens, 2008). The vmPFC, a region often described as an essential mediator of socio-emotional significance, has been in recent years found to perform a more cognitive role by reflecting the different types of values in social cognition (Hare, Camerer, Knoepfle, & Rangel, 2010; Hare, Camerer, & Rangel, 2009). Furthermore, recent views regarding stimulus and action value comparison emphasize the role of ACC-striatal loops. Therefore, our results' potential account is those cooperative decisions are made by integrating the reciprocity information reflected in the striatum and the action value computation reflected in the prefrontal cortex.

In summary, our behavioral data showed a demonstrable effect of a partner's perceived reciprocal reputation on cooperative decisions during social interactions. Partner's better reciprocal reputation enhances cooperation in the PGG both in gain and loss context, and this effect is extraordinarily salient in the gain context compared to the loss context. Our neuroimaging results further revealed distinct neural systems in gain and loss contexts that rAI was revealed in gain context and bilateral SPL(precuneus), left IPL, and bilateral SFG was found in the loss context while processing partner's reciprocal reputation before making choices in the PGG. These behavioral and neural results support that two distinct mechanisms, social preference-based in the gain context versus strategic concern-based in the loss context, potentially

support the effect of reciprocal reputation on a cooperative decision in the provision of a public good. Besides, the results point to reward processing in the bilateral striatum as a neural modulator of this effect, and the prefrontal cortex plays a vital role in computing the action values while making the relevant decision. Therefore, the current results contribute new empirical evidence to our understanding of social cooperation in a loss frame through social interactions.

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Credit authorship contribution statement

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Table 1 Models of the percentage of contribution in the PGG

Mode	Predictors	Df	BIC	logLi	Chis	Term	β	SE	t
1				k	q				
M1	Context	6	-715	382	1847	Reputation	0.028	0.006	4.18
M2	Reputation	15	1059	-467	0	Context	-0.036	0.056	-0.65
M3	Context + Reputation	21	-883	529	1991	Reputation	0.028	0.006	4.16
						Context	-0.036	0.056	-0.65
M4	Context + Reputation + Context× Reputation	45	- 2840	1607	2156	Reputation	0.19	0.038	5.08
						Context	0.13	0.08	1.59
						Reputation	-0.11	0.23	-4.74
						×Context			

Note: Df = degree of freedom; AIC = Akaike information criterion, BIC=Bayesian information criterion, logLik means log-likelihood, Chisq = Chi-square. The model with smaller AIC and BIC is better. The Bold font indicates the optimal model.

Table 2 Significant activation cluster associated with perceiving partner's reciprocal reputation and cooperative decision making (GLM1)

Anatomy	Hemisph ere	MNI			Cluster size voxels	T value
	L/R	x	y	z		
Reputation_pmod						
IFG/AI	R	33	18	-7	65	4.31
ACC	L	-10	39	25	64	4.46
Fusiform gyrus	R	36	-60	-	171	6.36
				14		
Fusiform gyrus	L	-34	-49	-	97	4.73
				18		
Decision_gainRpmod						
Putamen/Pallidum	L	-27	-14	-4	108	5.01
Caudate Nucleus	R	15	11	-4	109	5.23
Calcarine gyrus	R	19	-77	7	281	5.58
Decision_gain(R+C)pmod						
ACC	R/L	5	39	14	60	3.87
Calcarine gyrus	R	15	-77	11	441	

Note: Only clusters, significant at a height threshold of $p < 0.001$ at voxel level and an extent threshold of $p < 0.05$ with family-wise error corrections at group level for multiple comparisons were reported with local maxima Montreal Neurological Institute (MNI) space. T-value for each peak was given. Abbreviations: L, left; R, right; IFG, inferior frontal gyrus; AI, anterior insula; ACC, anterior cingulate cortex.

Table 3. Significant activation cluster associated with the processing of reputation in gain and loss context respectively (GLM2)

Anatomy	Hemisphere	MNI			Cluster size	T value
	L/R	x	y	z	voxels	
Reputation_gainpmo						
IFG/AI	R	40	32	4	69	4.60
Fusiform gyrus	R	33	-60	-14	190	5.17
Reputation_losspmo						
SPL	L	-27	-70	49	77	4.30
SPL	R	26	-60	53	53	4.79
IPL	L	-45	-42	42	44	3.89
SFG	R	29	-4	63	70	4.49
SFG/PG	L	-27	-7	53	58	4.19
Fusiform gyrus	R	36	-60	-14	127	5.03

Note: Only clusters, significant at a height threshold of $p < 0.001$ and an extent threshold of $p < 0.05$ with family-wise error corrections for multiple comparisons, were reported with local maxima in the Montreal Neurological Institute (MNI) space. T-value for each peak was given. Abbreviations: L, left; R, right; IFG, inferior frontal gyrus; AI, anterior insula; AG, angular gyrus; IPS, intraparietal sulcus; SPL, superior parietal lobule; IPL, inferior parietal lobule; SFG, superior frontal gyrus; PG, precentral gyrus.

Figure 1. fMRI experiment task (modified PGG) and timeline. (a). Illustration of an example of modified PGG in gain context; (b); Illustration of an example of modified PGG in loss context; (c) Game rule of incentive threshold and Total Contribution Amount (TCA); (d). Illustration of a single trial of the modified PGG. After a fixation cross presented for a jitter of 1 to 3 seconds in this trial, the context (gain or loss) was revealed on the screen for 3 seconds. Four players from one of the reciprocal groups (players in the current trial were from a low reciprocal reputation group that average repayment was range between 20%~0) were revealed for 3 seconds. Afterward, participants saw the amount of monetary gain or loss (10 or 20 Chinese yuan) and were asked to make their decision within 6 seconds. They were informed about, pressing KEY 1 using their index finger to decrease the number, KEY 2 using the middle figure to increase the number, and KEY 3 using the ring finger to input their final decision. Once the final decision button was pressed, the selected number on the screen would turn from blue to red, indicating that the choice was confirmed and could no longer be changed.

Figure 2 Behavioral results. (a) Histogram and density plots of the percentage of contribution in gain and loss context for all trials for all participants, the red-colored areas showed the density estimates of the percentage of contribution for all trials for all participants in gain context, respectively, and the green-colored areas showed the density estimates of the percentage of contribution for all trials for all participants in the loss context; (b) Illustration of the ANOVA result; (c) Mixed effect regression results in gain context; (d) Mixed effect regression in loss context.

Figure 3. Whole-brain analysis of parametric responses in the processing of partner's reciprocal reputation (GLM1). Brain activation in the rAI (a) and lACC(c), brain maps are corrected for multiple comparisons using the whole-brain family-wise correction ($p_{FWE} < 0.05$). Average parametric estimates from each participant in the rAI (b) and lACC (d) in four reciprocal reputations in gain and loss context, respectively. l=left, r=right.

Figure 4. Whole-brain analysis of parametric responses in the passing partners' reciprocal reputation in gain and loss context (GLM2). (a) Brain regions positively correlated with a reciprocal reputation in gain context, (b) Brain regions possibly correlated with a reciprocal reputation in the loss context. (c) Scatter plot of correlation between parametric estimates in the rAI from each participant and their absolute value of average percentage of contribution. (d) Scatter plot of correlation between parametric estimates in the rSPL from each participant and their absolute value of average percentage of contribution. All brain maps are corrected for multiple comparisons using the whole-brain family-wise correction ($p_{FWE} < 0.05$). l=left, r=right.

Figure 5. Neural results during the decision phase in gain and loss context. (a) Brain regions positively correlated with the partner's reciprocal reputation during the decision phase in the gain context, $p_{\text{FWE}} < 0.05$. (b, c) Parametric estimates extracted from the cluster of left Striatum (b) and right Striatum (c) across the four reputation levels in gain and loss context, in respectively. (d) The time courses were estimated with the finite impulse response model from the onset of the fixation in both contexts, for a length of 20s (10 scans). A significant difference between H and L reputation levels was detected in time bin 4 (the onset of partner's reciprocal reputation) in the gain context, but not in the loss context. (e) Correlations between the participants' average absolute value of the percentage of contributions in the PGG and their parametric estimates in the right striatum in gain and loss context.

Figure 6. Individual differences on cooperative behaviors.