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Fear or greed? Oxytocin regulates inter-individual conflict by enhancing fear in men

Huimin Zheng [a], Keith M. Kendrick [b], Rongjun Yu [a,c,d,e,*]

[a] School of Psychology, Center for Studies of Psychological Application and Key Laboratory of Mental Health and Cognitive Science of Guangdong Province, South China Normal University, Guangzhou, China
[b] Key Laboratory for Neuroinformation, Center for Information in Medicine, University of Electronic Science and Technology of China, Chengdu, China
[c] Department of Psychology, National University of Singapore, Singapore
[d] Neurobiology/Ageing Programme, Center for Life Sciences, National University of Singapore, Singapore
[e] Institute for Neurotechnology (SINAPSE), Center for Life Sciences, National University of Singapore, Singapore

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ABSTRACT

People may choose non-cooperation in social dilemmas either out of fear (if others choose to defect) or out of greed (when others choose to cooperate). Previous studies have shown that exogenous oxytocin motivates a "tend and defend" pattern in inter-group conflict in which oxytocin stimulates in-group cooperation and out-group defense. Using a double-blind placebo-controlled design combined with a modified Prisoner's dilemma game (PDG), we examined the effect of oxytocin on social motivations in inter-individual conflict in men. Results showed that compared with the placebo group, oxytocin-exposed participants were less cooperative in general. Specifically, oxytocin amplified the effect of fear on defection but did not influence the effect of greed. Another non-social control study confirmed participants' decisions were sensitive to social factors. Our findings suggest that even when social group conflict is removed, oxytocin promotes distrust of strangers in "me and you" inter-individual conflict by elevating social fear in men.

The strongest emotions in the marketplace are greed and fear ——— Adam Smith.

1. Introduction

Competition prevails in human societies, but nevertheless humans also cooperate on a larger scale than most other mammals. The neurobiological mechanisms regulating competition and cooperation remain elusive. The neuromodulator oxytocin is a nine amino acid peptide produced in the hypothalamus and is well known for its key role in facilitation of social bonds and cooperation (De Dreu, 2012). A number of studies have proposed that oxytocin biases in-group cooperation against out-groups. Intranasal oxytocin treatment promotes trust and conformity toward in-groups (Baumgartner et al., 2008; Stallen et al., 2012); improves in-group favoritism and parochial protectionism (De Dreu et al., 2010; De Dreu et al., 2012) and can also increase non-cooperation with potentially threatening out-groups (De Dreu et al., 2010). Thus overall, oxytocin may play an inter-group "tend and defend" role. In a social context, oxytocin increases trusting behavior and generosity in the trust game (Kirsch et al., 2005). However, if the trustee is depicted as untrustworthy, lacks sufficient social information or is a member of an out-group (De Dreu et al., 2010; De Dreu et al., 2012; Declerck et al., 2014), oxytocin may not foster trust-related behaviors. Similarly, situational differences can influence effects of oxytocin on cooperation. In an iterated Prisoner's Dilemma Game (PDG), oxytocin increased brain activation in response to reciprocated cooperation and even improved cooperation following unreciprocated cooperation (Rilling et al., 2012). However, Declerck et al. (2010) demonstrated that oxytocin strengthened cooperation only with strong incentives to cooperate (a Coordination Gamer versus a PDG and social information). Additionally, in another between-group PDG which involves self-interest and in/out-group member's interest, oxytocin increased protective competition only when personal vulnerability was guaranteed (De Dreu et al., 2012). The positive effect of oxytocin on cooperation is thus rather conditional.

Mutual cooperation calls for cooperative willingness and trusting others to cooperate as well (Pruitt and Kimmel, 1977). In contrast, two intrinsic motivations partially elucidate non-cooperation. The first motivation is greed, which is to take advantage of other's cooperative choices and maximize one's own self-interest. Free-riding on others' cooperation (choosing to defect), compared with cooperating, guarantees more gain and power (Simpson, 2006). Individual self-interest often leads to a breakdown of social cooperation (Piff et al., 2012; Steinel and De Dreu, 2004). However, it has also been shown that a moderate amount of greediness can be cooperation-enforcing (Roca and

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Helbing, 2011). Non-cooperation might reflect a willingness to exploit others for personal gain. The second motivation is fear of being taken advantage of by others, i.e., the concern of the opponent choosing non-cooperation while he/she chooses cooperation and ends up being "suckered". Choosing non-cooperation can prevent exploitation from non-cooperators and reflect a defensive desire to protect oneself. It has been proposed that the human mind is specialized for detecting cheaters in reciprocal social exchange (Cosmides and Tooby, 2000) and being betrayed during social interactions activates brain regions associated with aversive emotions (Sanfey et al., 2003). Together, these two intrinsic emotional states strongly affect human cooperation and societal cohesion. One might argue that choosing not to be the "sucker" may not be because of fear motivation but loss aversion. Here we used two experiments to test social fear and social greed. Experiment 1 involved not only fear of loss but also fear of being exploited (others may choose non-cooperation). Moreover, we also used a non-social context in Experiment 2 which only included a win or loss component without any social factor. Thus, the inherent differences between Experiment 1 and Experiment 2 could allow us to determine whether fear as opposed to loss aversion was of most importance. In the same way with greed one might also argue that if defection is the operational choice in PDG then it is not greed but just the nature of the task. However, if the other player chooses cooperation but the subject chooses noncooperation in order to gain more interest at the expense of others, and defection means sacrificing others' interests, then it is more appropriate to be defined as greed. It needs to be stressed that fear and greed in our experiment are not the same as other tasks, such as seeing fearful faces.

Previous evidence has indicted that oxytocin dampens activation in the amygdala evoked by fear stimuli, and it may therefore regulate fear and multifarious aggression (Kirsch et al., 2005; Wu et al., 2005). This is referred to as the fear-dampening hypothesis (De Dreu et al., 2014). Specifically, participants receiving oxytocin showed reduced activation in response to fearful faces (Kirsch et al., 2005; Petrovic et al., 2008) and were less worried about being exploited (Baumgartner et al., 2008). Moreover, in cooperative tasks, oxytocin also promoted defense-motivated aggression out of fear (De Dreu et al., 2010). On the other hand, oxytocin has also been found to drive pro-social exploration and even temper deliberate greed (De Dreu et al., 2014; Rilling et al., 2014). These studies have demonstrated that oxytocin is essential in regulating fear and greed motivation, although most have focused on inter-group interaction. However, it is also equally important to consider how interpersonal conflicts can take place at the individual level as we interact with other people individually almost on a daily basis and not necessarily as a group. Only a limited number of studies have directly investigated how oxytocin modulates inter-individual conflict (De Dreu et al., 2014; Rilling et al., 2014; Rilling et al., 2012). The aim of the present study was therefore to directly investigate the effect of oxytocin on fear and greed motivation in interpersonal conflict.

2. Experiment 1: the PDG in inter-individual conflict

2.1. Participants

In line with most previous studies on oxytocin effects on trust (MacDonald et al., 2011), only healthy male participants were recruited. We calculated that the sample size in each treatment group should be about 40 at an alpha of 0.05 and a power of 0.80. The 84 healthy male-students (mean age ± SD, 23.74 ± 1.34 years) were recruited from South China Normal University and received monetary compensation. Seven participants (4 in the oxytocin condition and 3 in the placebo condition) were excluded due to their failure to meet the three post-experiment criteria stated below. All participants were right-handed and had no history of significant cognitive or psychiatric disorder. Exclusion criteria included smoking more than five cigarettes a day, abusing drugs or alcohol, and having a fever or common cold on test days. The study was approved by the Academic Committee of the School of Psychology at South China Normal University. All participants gave informed consent and were informed of their right to discontinue participation at any time.

2.2. Substance administration

We followed the recommended guidelines for the standardization of oxytocin nasal administration (Guastella et al., 2013). Participants self-administrated an intranasal dose of 24 international units (IU) oxytocin (Oxytocin-Spray, Sichuan Meike Pharmacy Co. Ltd., China; 3 puffs per nostril, with 30 s interval, each with 4 IU) or placebo (also 3 puffs per nostril) under the experimenter supervision. The placebo treatment contained all of the same ingredients except for the neuropeptide (sodium chloride and glycerine), and was manufactured in the same bottle by the pharmaceutical company supplying the oxytocin nasal spray. Participants and experimenter were blind to the drug condition. To maximize effectiveness of the intranasal treatment in in increasing cerebrospinal fluid concentrations of oxytocin, participants were given a 45-min break before performing the formal experimental task.

2.3. Experimental paradigm

The study was conducted in a double-blind, placebo-controlled, mixed design. We used a modified PDG to disentangle the effects of fear and greed motives on non-cooperation by directly manipulating payoff parameters to simulate these motivations (Ahn et al., 2001; De Dreu et al., 2010). PDG describes the basic problem of cooperation. Classical PDG is usually a two-person social dilemma in which Player 1 and Player 2 are confronted with the same situation: to cooperate or to non-cooperate. All possible combinations of their choices are listed in the payoff matrix (Fig. 1a). If both of them choose cooperation, they receive the "reward" (R). If both of them choose non-cooperation, they receive the "punishment" (P) instead. If one of them chooses non-cooperation while the other one chooses cooperation, the one who defects can get the "temptation" (T) and the one who cooperates can only receive the "sucker" (S). Additionally, the following criteria must be fulfilled: $T > R > P > S$ and $2R > T + S$ (Ahn et al., 2001). Payoff relationship $R > P$ indicates that mutual cooperation is better than mutual defection, while the payoff relationship $T > R$ and $P > S$ shows that defection can bring oneself a larger reward! From the viewpoint of a self-interested "rational" agent, the relatively optimal choice for participants is to defect in the PDG, in other words, the only "Nash equilibrium" is mutual defection.

There are two kinds of motivations to defect. First, assuming that your opponent decides to cooperate, you can get higher payoffs for yourself by defection than cooperation (henceforth considered as greed). Next, assuming that your opponent decides to defect, you can get higher payoffs as well by defection than cooperation (henceforth considered as fear). So you should choose to defect in both of these scenarios. Therefore, here we define the size of greed motivation as the difference between T and R (greed = T − R). Similarly, size of fear motivation is given by the differences between P and S (fear = P − S). The respective impact on greed and fear is investigated by manipulating payoff parameters. So we manipulated the cardinal payoffs to create variations in the motivation of Greed and Fear (Ahn et al., 2001; De Dreu et al., 2010). Greed is set at high ¥4 (14–10 = 4, approximately $ 0.64, Fig. 1b and c) and at low ¥1 (11–10 = 1, approximately $ 0.16, Fig. 1d and e). Fear is set at high ¥4 (6–2 = 4, Fig. 1b and d) and at low ¥1 (6–5 = 1, Fig. 1c and e). Therefore, there are four conditions in this game: High Greed/High Fear (HH), High Greed/Low Fear (HL), Low Greed/High Fear (LH), and Low Greed/Low Fear (LL), see Fig. 1b, c, d, and e. One of the four payoff matrices was randomly presented in each trial and each kind of payoff matrix was repeated 8 times, thus leading to 32 trials in total.

In this study participants are asked to make their decision simultaneously and independently. Their outcomes are based on the

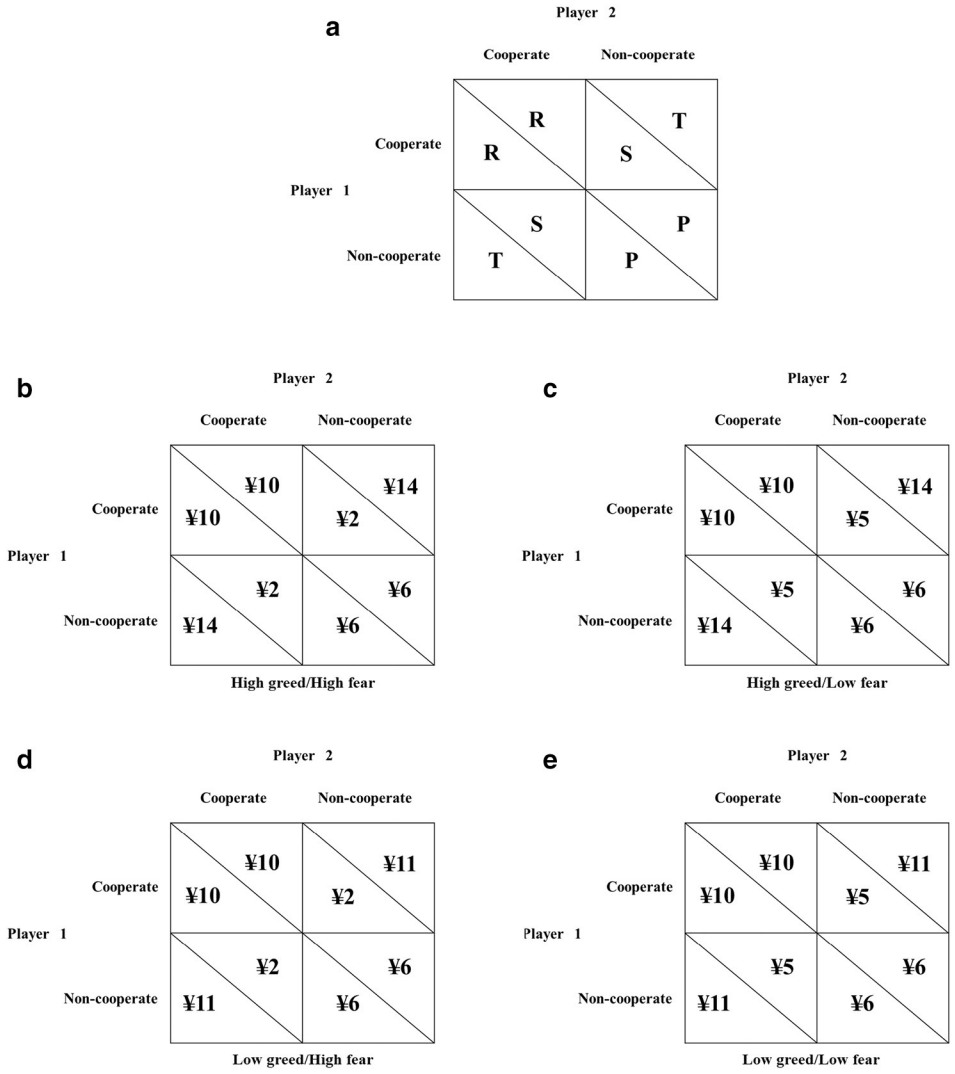

Fig. 1. (a) The payoff matrix of the PDG. If Player 1 and Player 2 both cooperate, they gain the reward (R). If Player 1 cooperates but Player 2 does not cooperate, then Player 1 receives the sucker (S) while Player 2 obtains the temptation (T), and vice versa. If both players defect, they receive the punishment (P). The payoffs hold for: $T > R > P > S$. Greed = T − R, and Fear = P − S. The PDG (b) is set with high greed (T − R = ¥14 − ¥10 = ¥4, approximately $ 0.64) and high fear (P − S = ¥6 − ¥2 = ¥4). The PDG (c) is set with high greed (¥4) and low fear (¥1). The PDG (d) is set with low greed (¥1) and high fear (¥4). The PDG (e) is set with low greed (¥1) and low fear (¥1).

interaction of their mutual choices. To insure the independence of each trial and eliminate the potential effect of a player's decision on the next trial, no feedback is shown which makes the game a series of one-shot interactions. Therefore, what the opponent has chosen is unknown to both players and complete anonymity is guaranteed. That is to say, the potential impact of expectation of reciprocity (Axelrod and Hamilton, 1981), threat of punishment (Kandori, 1992), and mutual identification (Simpson, 2006) are dispelled.

2.4. Procedures

Participants sat about 1 m in front of a computer screen in individual cubicles preventing them from seeing others and communicating. They were first randomly assigned to either intranasal administration of oxytocin (n = 39) or placebo (n = 38). To ensure the homogeneity of the two treatment groups and rule out any possible contributions from anxiety differences on choice preferences, after the treatment administration the experimenter left the room, and participants completed two questionnaires (Chinese versions) including the State-Trait Anxiety Inventory (STAI) and the Tridimensional Personality Questionnaire (TPQ) (Duan et al., 2006). The STAI contains 40 items to measure the state anxiety (Cronbach's $\alpha = 0.797$) and trait anxiety (Cronbach's $\alpha = 0.828$). The TPQ consists of 100 items which measure three higher order dimensions of temperament: novelty-seeking (Cronbach's $\alpha = 0.578$), reward dependence (Cronbach's $\alpha = 0.557$), and harm-avoidance (Cronbach's $\alpha = 0.525$).

Participants were informed that the task would involve two players. The participant was assigned as "Player 1" and an anonymous opponent, playing in the next laboratory, was denoted as "Player 2". In each trial the participant would play with the same player. Unknown to participants, opponents were simulated by a computer program. Both players were assigned their own surnames with their first names replaced by "Mr". We selected very common surnames for the computer player and participants could not identify who they were. Participants were given comprehensive instructions on the PDG task (see below) before the formal test. The participant was "quizzed" about the payoffs and the instructions were explained again if there was any misunderstanding. Next, a practice block (including 3 trials) was administered before the formal test. It was emphasized to participants that they would make their decisions simultaneously and independently of the other player, so they would not receive any feedback. When they finished the task, they were told that one round would be randomly selected at the end of the experiment to determine payment and so every choice

they made might bring them monetary consequences and they should therefore take all their decisions seriously.

The experimental task started 45 min post administration of oxytocin or placebo and lasted about 7 min. The experiment was implemented in E-prime version 2.0 (Psychology Software Tools Inc., Pittsburgh, USA; www.pstnet.com/eprime). At the beginning of each trial, an asterisk was presented on the screen for 1 s to engage attention. Then participants were shown a payoff matrix to Player 1 (the participant) and Player 2 (the opponent) as a function of four possible combinations of choices (1 or 3 by Player 1; 1 or 3 by Player 2; 1 = Cooperate, and 3 = Non-cooperate) for 6 s. As shown in Fig. 1a, if two players both choose "1", they gain the R, otherwise they receive the P if they both choose "3". Besides, if Player 1 decides to choose "3" but Player 2 adopts "1", then Player 1 receives T while Player 2 obtains S, and vice versa. The payoffs hold for: T > R > P > S. Greed Level = T − R, and Fear Level = P − S. The PDG (Fig. 1b) is set with high greed (T − R = ¥14 − ¥10 = ¥4, approximately $ 0.64) and high fear (P − S = ¥6 − ¥2 = ¥4). The PDG (Fig. 1c) is set with high greed (¥4) and low fear (¥1). The PDG (Fig. 1d) is set with low greed (¥1) and high fear (¥4). The PDG (Fig. 1e) is set with low greed (¥1) and low fear (¥1). Following this, one line of words "Make A Choice" were presented above the payoff matrix. The participant was asked to press one of the buttons on a keyboard to indicate whether he would like to cooperate (pressing 1) or not (pressing 3) within 6 s, otherwise this round would be regarded as invalid. Each participant completed 32 trials in all. After participants finished the task, they received a base payment (¥35) plus the extra bonus they had gained in the experiment.

Following the PDG task, we asked the participants a series of post-experiment questions to ensure credibility: (i) whether the participant had identified they had received the oxytocin or placebo treatment; (ii) whether he had participated in the same economic games previously; (iii) whether he believed the task was real (i.e. that the other participant was real). All 70 participants (not including excluded ones) met these three criteria: they were unable to identify which administration contained the treatment above chance levels, had never engaged in similar games before, and believed they were interacting with real humans. Importantly, all participants (not including excluded ones) were not suspicious of the scenario and believed that they were interacting with real humans during the task, confirming that our social manipulation was successful.

2.5. Data analysis and results

Data were statistically analyzed using SPSS version 16.0. We excluded trials in which reaction time (RT) was <400 ms (about 2 SD below the mean RT). About 12.5% trials per participant were excluded. We also did the analysis without excluding any trials and found similar behavioral patterns. The oxytocin and placebo groups did not differ in demographic, anxiety, or tridimensional personality measures (all $p > 0.10$). In statistical testing, we used eta squared (partial η^2) for ANOVAs and Cohen's d for pair-wise comparisons to analyze effect sizes.

For each participant, we were interested in the greed and fear levels in defection choice. We computed the greed level as the defection rate (percentage of choosing non-cooperation) differences between high greed (i.e. HH and HL) and low greed conditions (i.e. LH and LL). Similarly, the fear level is defined as the differences in defection rate under high fear (i.e. HH and LH) compared to low fear conditions (i.e. HL and LL). The higher greed level the participant shows in the task, the more we consider he is motivated by greed. Likewise, the higher fear level the participant shows the more he is thought to be motivated by fear. To test our hypotheses, we conducted a repeated measures analysis of variance with the defection rate as dependent variable, and the treatment (oxytocin/placebo), greed level (high/low) and fear level (high/low) as independent variables with treatment as a between-subject factor, and greed and fear as two within-subject factors, see Fig. 2a. Analysis yielded a main effect of treatment, $F(1, 75) = 5.34$, $p = 0.02$, partial $\eta^2 = 0.07$. A higher defection rate was observed among participants who were given oxytocin (M ± SD = 0.676 ± 0.33) rather than placebo (M ± SD = 0.576 ± 0.30). There was a main effect of greed, $F(1, 75) = 53.70$, $p < 0.001$, partial $\eta^2 = 0.42$, and fear, $F(1, 75) = 69.18$, $p < 0.001$, partial $\eta^2 = 0.48$. We compared effects on greed and fear in the oxytocin vs. placebo groups respectively. The treatment × greed interaction was not significant, $F < 1$. There was no significant difference of greed in the oxytocin and placebo group. Importantly, the treatment × fear interaction was significant which means the fear difference between oxytocin and placebo groups was significant, $F(1, 75) = 11.41$, $p = 0.001$, partial $\eta^2 = 0.13$, see Fig. 2b. Post-hoc comparisons (using Sidak test) revealed that in the high fear condition, participants in the oxytocin group showed significantly higher levels of defection than the placebo group, $p < 0.001$. In the high fear condition, participants given oxytocin (M ± SD = 0.828 ± 0.22) defected more than the placebo group (M ± SD = 0.640 ± 0.22), Cohen's d = 0.85, $p < 0.001$. In the low fear condition, there was no such difference, $p = 0.805$. Additionally, we also conducted a repeated measures analysis of variance with the defection rate as dependent variable, and the treatment (oxytocin/placebo) and condition level (greed level/fear level) as independent variables, with treatment as a between-subject factor, and condition level as a within-subject factor. Analysis showed that the treatment × condition level was significant, $F(1, 75) = 5.15$, $p = 0.026$, partial $\eta^2 = 0.06$. Post-hoc comparisons (using Sidak test) revealed that in the fear condition, participants in the oxytocin group showed significantly higher levels of defection than the placebo group, $p = 0.001$. In the fear condition, participants given oxytocin (M ± SD = 0.607 ± 0.46) defected more than the placebo group (M ± SD = 0.256 ± 0.46), Cohen's d = 0.76, $p < 0.001$. In the greed condition, there was no such difference, $p = 0.757$. These results showed that oxytocin promotes the individual's defection out of fear but not greed.

RT for defection and cooperation decisions was also analyzed (seventeen participants did not defect in some conditions, so there were no defection RTs for them in these cases). The main effect of fear on defection RT was significant, $F(1, 58) = 5.38$, $p = 0.024$, partial $\eta^2 = 0.09$, showing that RT in high fear conditions (M ± SD = 1416 ± 95 ms) was lower than that in low fear conditions (M ± SD = 1570 ± 129 ms). Besides, analysis showed that fear × treatment was significant, $F(1, 58) = 5.02$, $p = 0.029$, partial $\eta^2 = 0.08$. Post-hoc comparison (using Sidak test) revealed that in the oxytocin group, RT in the high fear condition showed significantly lower than the low fear condition, $p = 0.002$. In the oxytocin group, participants in high fear (M ± SD = 1381 ± 88 ms) responded faster than low fear (M ± SD = 1684 ± 120 ms), Cohen's d = 2.88, $p = 0.002$. In the placebo group, there was no such difference, $p = 0.955$. No other effects were significant.

3. Experiment 2: assessment of the social relevance of the task

Since participants did not meet the other player in person, one concern about the behavioral effects in Experiment 1 is that they may be driven by pure economic motivations rather than social motivations such as fear and greed. Participants may approach this task as a pure economic task rather than a social situation. We conducted a behavioral study to demonstrate the social nature of the experimental task. We employed a non-social version of the same experimental paradigm in which participants were informed that they played the game with a computer rather than a real-life player. Rational decision theory would predict that participants would always choose the 'non-cooperation' option since this option always generates better outcomes than the 'cooperation' option, regardless what the computer would choose in a non-social context (Coleman and Fararo, 1992; Geanakoplos et al., 1989).

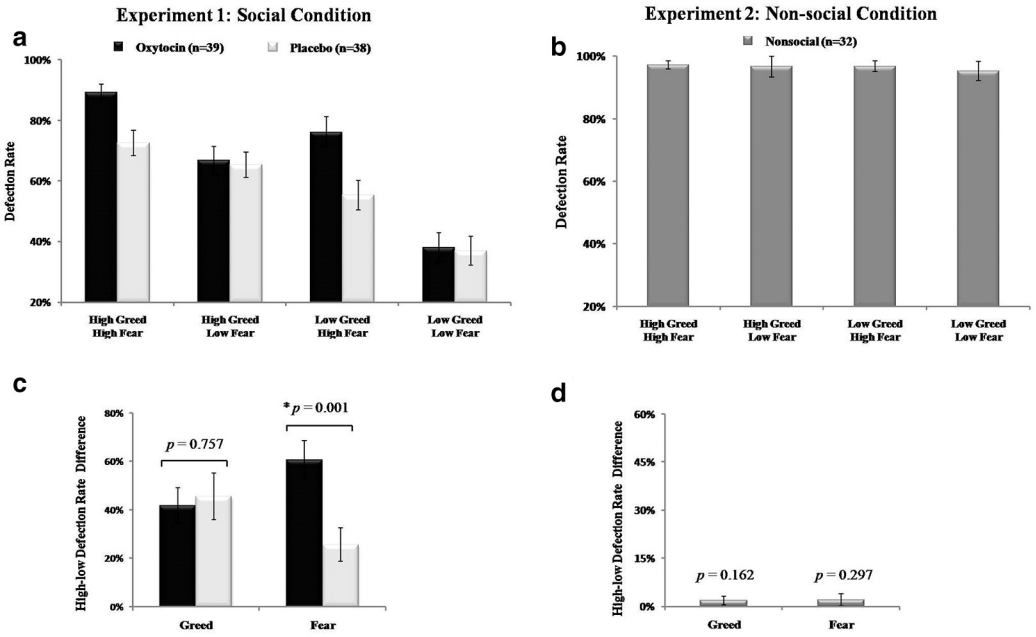

Fig. 2. Defection rate in the four experimental conditions (a) in PDG for the Oxytocin (n = 39) and Placebo (n = 38) group in Exp.1 (Social Condition). Defection rate in the four experimental conditions (b) in PDG for the Nonsocial (n = 32) group in Exp. 2 (Non-social Condition). Defection rate differences (c) as a function of greed/fear in the Oxytocin and Placebo group. Defection rate differences (d) as a function of greed/fear in the Nonsocial group. Error bars represent standard errors of the means.

3.1. Participants and experimental paradigm

Thirty-two healthy, right-handed, male students (mean age ± SD, 21.32 ± 1.16 years) from the South China Normal University participated in Experiment 2 in return for monetary compensation. We employed a non-social version of the same experimental paradigm with a different cover story. Participants were told that they would play with a computer which would randomly choose one of the two options. The two options were labeled as choice A and choice B, corresponding to 'Cooperate' and 'Non-cooperate' in Experiment 1. We predicted that in the non-social context, participants would always choose non-cooperation.

3.2. Data analysis and results

Calculation of greed level and fear level is similar to Experiment 1. We excluded 139 trials in the non-social group (RT < 400 ms). Consistent with our prediction, participants choose non-cooperation with 0.965 ± 0.07 (M ± SD) in the non-social context. Defection rate was submitted to a 2 (greed level: high/low) × 2 (fear level: high/low) repeated measures analysis of variance see Fig. 2c. Results showed that there were no main effects of greed ($p = 0.162$, partial $\eta^2 = 0.062$) or fear ($p = 0.297$, partial $\eta^2 = 0.035$) and no interaction between greed and fear ($p = 0.707$, partial $\eta^2 = 0.005$).

Thus, in the non-social context, participants almost always choose the 'Non-cooperate' option to maximize their own rewards. The control experiment thus confirmed that participants' decisions in Experiment 1 were sensitive to social factors.

4. Conclusions and discussion

We found that the oxytocin-exposed male participants cooperated less than the placebo group in the PDG at the interpersonal level. Specifically, oxytocin only enhanced fear motivation. Critically, our study informs research on cooperation in social dilemmas that oxytocin not only functions to regulate inter-group conflict but also inter-individual conflict, where it enhances fear motivation but not greed motivation in men. Furthermore, despite the fact that participants did not meet prior to the social experiment, results from Exp 2 indicate that our social interaction manipulation is effective. Participants in the non-social context almost always choose noncooperation, suggesting that defection is the dominate strategy when participants play with a non-human agent.

Previous research has shown that after prior contact with the opponent, oxytocin increases cooperative behavior, and even in the absence of social information it can increase intrinsic self-interested behavior, and especially greed (Declerck et al., 2014). Likewise, our experiment did not present social information or feedback, and oxytocin decreased cooperation. On the other hand, these results are relevant to the dominant strategy of the PDG in which greed and fear drive people to defect (Declerck et al., 2010). Therefore, contrary to its known role in prosocial behaviors (trusting-building and social cognition), it appears that oxytocin can actually decrease cooperation by increasing social fear in conditions of inter-individual conflict. It has been found that oxytocin promotes the "tend and defend" pattern between groups—cooperate more with in-groups while defending against outsiders (De Dreu et al., 2010; De Dreu et al., 2012). Such parochial altruism has essential survival functions: to foster in-group survival and to prevent potential threat from out-groups (De Dreu, 2012). Likewise, when it comes to competitive interaction, oxytocin only reduces competition against in-group protagonists but not out-groups (Ten Velden et al., 2014). However, since group members also benefit when their own group thrives, it is unclear whether the in-group favoritism is driven by in-group concern or purely by self-interest. A recent study pitted self-interest against other in-group members' interest and found that non-cooperation was unaffected by oxytocin treatment when self-interest was greatly compromised (De Dreu et al., 2012). Only when personal vulnerability was low, oxytocin motivated non-cooperation in intergroup conflict to protect vulnerable in-group members. Thus, whether and how much self-interest is involved seems to determine the effects oxytocin on cooperation in intergroup conflict (Ma et al., 2015), thereby motivating the need to investigate oxytocin's influences on cooperation in inter-individual conflict. Our results showed that oxytocin enhanced social fear and thus reduced cooperation. The oxytocin effects we found resemble the "tend and defend" pattern reported by De Dreu et al. (2010), in that we observed more non-cooperation in participants

given oxytocin when fear motivation was high. Our findings may suggest that the "tend and defend" model may also apply to inter-individual situations where group processes are not involved. This is consistent with recent findings that oxytocin facilitates 'tend and befriend' behaviors by increasing the general level of social conformity, regardless of whether others are in-group or out-group members. (Huang et al., 2015). Taken together, these complementary findings confirm that oxytocin may not only modulate fear in "we and them" inter-group conflict, but also in "me and you" inter-individual conflict.

On the other hand a recent study also examining inter-individual conflict, but using the predator-prey game (PPG), showed instead that oxytocin selectively tempered greed but not fear (De Dreu et al., 2014). In PPG, the predator decides how much initial money to invest in plunder, while the prey decides how much to invest in defense with an equal amount of money. The PPG resembles natural predator-prey interactions where both predator and prey have to struggle for their very existence (Hoppensteadt, 2006). Loss by predators results in no extra bonus, and the disappearance of upfront costs like money and effort. Therefore, in the PPG, predators' investment might not only result from greed motivation but also fear of appropriating nothing in such a competitive context. The fear of loss inherent in the predator-prey contest leads predators to invest more for an extra bonus, which is similar to loss contemplation (Delgado et al., 2008). Thus, we argue that fear of losing and greed cannot be fully disentangled in the PPG paradigm. Even though the modified PDG we utilized here inherently contains fear and greed as well, we separated greed and fear by manipulating the cardinal payoffs (see Fig. 1). The PDG may offer a more valid inference of oxytocin effects on inter-individual conflict. What is more, the PPG is a fixed sum game and there are no joint gains to achieve. This is not the case for the PDG, where it is possible for people to make a choice for personal gain or exploitation, but they might also consider collective reward when there is risk of destroying a sharing system (Fehr and Fischbacher, 2003). This strengthens the validity of the PDG in examining inter-individual conflict as a collective reward motivates participants to engage in the task socially. Critically, when participants were informed that their partner was a computer (Exp. 2), participants no longer perceived a collective reward, therefore leading to high levels of defection across all conditions. Hence, it may be the case that oxytocin modulated greed but not fear in the PPG setup because a lack of collective reward among competitors motivates participants' self-interest to maximize their own gains with minimal consideration of the outcome on the other. It is also important to emphasize that De Dreu et al. (2014) reported that oxytocin reduced the frequency of greed among predators, $p = 0.026$, one-tailed. However, previous studies had found no effect of oxytocin on greed (De Dreu et al., 2010; Israel et al., 2012; Kosfeld et al., 2005). As a consequence, it may be more appropriate to use two-tailed tests until more research has been conducted.

Although oxytocin has anxiolytic effects (MacDonald and Feifel, 2014), it does not necessarily follow that it should reduce the readiness to fight and protect oneself or promote trust and cooperation (De Dreu et al., 2014). Conversely, across many species, plasma oxytocin in breast-feeding mothers predicts heightened aggressive behavior against potentially threatening conspecifics or predators in defense of their young (Hahn-Holbrook et al., 2011). From an evolutionary perspective, fear detection functions as a warning system, therefore detecting threat and preserving oneself outweighs accumulating personal gain (Delgado et al., 2008). When danger is not imminent, oxytocin may encourage individuals to be more cooperative by reducing fear (Marsh et al., 2007). However, in the context of intense social conflict, such as competing with strangers, the exaggerated social fear induced by oxytocin may be adaptive as it reduces the risk of putting oneself in dangerous situations. It has been found that participants given oxytocin can recognize fearful expressions and judge trustworthiness more accurately (Fischer-Shofty et al., 2010; Lambert et al., 2014), and relative to placebo groups they showed faster perception of disgusted expression faces and health and sickness cues (Preckel et al., 2014; Theodoridou et al., 2013). Our study further supports the role of oxytocin in vigilance toward potential social threats from other individuals. Thus, oxytocin may serve to protect individuals from social threat in certain social contexts where conflict is relatively intense (Declerck et al., 2010).

Several caveats need to be mentioned about the current study. First, to guarantee anonymity, we did not arrange participants to meet their co-players in person, unlike some previous studies in which subjects briefly met prior to the experiment in order to strengthen their belief that they were interacting with real partners in the game (even though they were in fact computer generated). Prior research suggests that this social context defines how people respond to oxytocin (Declerck et al., 2010; Stallen et al., 2012). However, our debriefing results did confirm that participants in general believed that they were playing with a real person and results from Experiment 2 also confirmed the social elements in the PDG. Nevertheless, it is still possible that prior social interaction might have influenced the oxytocin effect observed in the current study. Second, it is well established that gender differences modulate oxytocin effects (Fischer-Shofty et al., 2013; Palgi et al., 2014). For instance, oxytocin facilitates perception of competition in males but not in females (Fischer-Shofty et al., 2013). Current human research has a largely male bias because of the potential variability of oxytocin effects based on levels of female hormones and also because of the increased potential health risks of oxytocin for females (e.g., induction of uterine contractions) (MacDonald and MacDonald, 2010). For these reasons, we only recruited male participants. However, there are several studies examining sex differences in oxytocin function (Preckel et al., 2014; Scheele et al., 2014; Yao et al., 2014). Whether our findings can be extended to females awaits future research. Third, we did not examine the effect of oxytocin on decision making in the non-social context. We did not find any effect of fear or greed on defection rate when participants played the game with computers. Moreover, participants chose noncooperation most of the time, indicating a ceiling effect in the non-social condition. Thus, it is unlikely oxytocin would have any effect in the non-social context since defection is the dominate strategy in all experimental conditions. Fourth, we used common surnames in Exp 1 and this may enhance participants' self-awareness. The greater self-awareness from the use of the participants' surname prior to engaging in a cooperative task could potentially impact decision-making in social tasks. Future studies may use symbols to represent participants. Finally, most evidence about oxytocin effects on social dilemmas is based on male Caucasian subjects from western cultures (as stated above), and has provided inconsistent results (De Dreu, 2012; De Dreu et al., 2010; De Dreu et al., 2014; De Dreu et al., 2012; Israel et al., 2012; Ten Velden et al., 2014). The current study in a Chinese population adds the empirical bases from Asian background and eastern culture and poses an interesting question whether one's cultural background can influence oxytocin effect on social decision making. Moreover, previous research has shown that there are cross-culture differences in social dilemmas per se (Morris and Peng, 1994). Therefore, culture might have a strong influence on responses to social dilemmas and in especially inter-individual conflict (De Dreu et al., 2012).

In conclusion, our results are both consistent with and complementary to previous findings (De Dreu et al., 2010; De Dreu et al., 2014; De Dreu et al., 2012). We have shown that the relation between oxytocin and cooperation is not unitary, and provide the first demonstration that in an inter-individual context, oxytocin boosts individuals' defection out of specific motivation: fear but not greed. The results have implications for conceptualization of oxytocin and inter-individual conflict by demonstrating how greed/fear motivation and oxytocin may be integrated at the behavioral level.

Author contributions

R. Yu developed the study concept. H. Zheng collected and analyzed the data under the supervision of R. Yu. H. Zheng wrote a first draft that

R. Yu and K. M. Kendrick revised. All authors approved the final version of the manuscript for submission.

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Declaration of conflicting interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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