Hormones and Behavior 85 (2016) 12–18

Contents lists available at ScienceDirect

Hormones and Behavior

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

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

ARTICLE INFO

Article history:
Received 25 April 2016
Revised 5 July 2016
Accepted 15 July 2016
Available online 18 July 2016

Keywords:
Fear
Greed
Oxytocin
Cooperation
Emotion

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

http://dx.doi.org/10.1016/j.yhbeh.2016.07.003
0018-506X/

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