Opposing Oxytocin Effects on Intergroup Cooperative Behavior in Intuitive and Reflective Minds

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People often favor ingroup over outgroup members when choosing to cooperate. Such ingroup-favored cooperation is promoted by oxytocin—a neuropeptide shown to facilitate social cognition and that has emerged as a pharmacological target for treatments of social functioning deficits. The current study applied a dual-process model to investigate whether and how intuitive and reflective cognitive styles affect the oxytocin-motivated ingroup favoritism in cooperation. We examined oxytocin effects on ingroup favoritism in a double-blind, placebo-controlled between-subjects design where cognitive processing (intuition *vs* reflection) was experimentally manipulated in healthy Chinese males ($n = 150$). We also supplemented this experimental manipulation with an individual difference analysis by assessing participants' inclination toward intuition or reflection in daily life. Intranasal administration of oxytocin (*vs* placebo) increased ingroup favoritism among participants primed to be intuitive or those who preferred intuition in daily life. In contrast, oxytocin *decreased* ingroup favoritism in participants primed to rely on reflective thinking or those who preferred reflective decision-making in daily life. Our results demonstrate that oxytocin has distinct functional roles when different cognitive styles (ie, intuition *vs* reflection) are promoted during social cooperation in a group situation. Our findings have implications for oxytocin pharmacotherapy of social dysfunction in that whether the effects of oxytocin on social functioning are facilitative, debilitative, or null, depends on an individual'

The current study applied a dual-process model to investigate whether and how one's cognitive style affected the oxytocin-motivated ingroup favoritism in cooperation. The dual-process model proposes two distinct cognitive systems to produce decisions. Individuals with intuitive cognitive style prefer frugal, heuristic, and fast responses, whereas reflective individuals favor deliberative, analytic, and slow responses (Kahneman, 2011; Evans, 2008). It has been shown that intuitive and reflective cognitive styles play opposing roles in cooperative decision-making (Rand *et al*, 2012) such that intuition tends to support cooperation while reflection favors selfishness (Rand *et al*, 2012; Zaki and Mitchell, 2013). Neuroscience research has documented that intuition is supported mainly by the limbic system, including the amygdala, striatum, midbrain, nucleus accumbens (NAcc), ventral medial prefrontal cortex (mPFC), and orbitofrontal (OFC; Lieberman, 2007; Dalgleish, 2004). In contrast, reflection is supported by the lateral prefrontal cortex, dorsal anterior cingulate cortex, medial temporal lobe, and posterior parietal cortex (Lieberman, 2007; Miller and Cohen, 2001). Oxytocin is synthesized in the hypothalamus and projects from the hypothalamus to the amygdala, striatum, suprachiasmatic nucleus, and brainstem (Ludwig and Leng, 2006; Donaldson and Young, 2008). Intranasal administration of oxytocin has been shown to mainly modulate neural activity in the amygdala (Domes *et al*, 2007; Petrovic *et al*, 2008; Baumgartner *et al*, 2008), midbrain/striatum/NAcc (Baumgartner *et al*, 2008; Gordon *et al*, 2013; Groppe *et al*, 2013), mPFC (Petrovic *et al*, 2008; Gordon *et al*, 2013), and OFC (Petrovic *et al*, 2008; Gordon *et al*, 2013). These findings suggested that the oxytocinergic system and the intuition system involved common neural underpinnings. In addition, behavioral studies have shown evidence for distinct oxytocin effects on fast and slow emotion recognition. Oxytocin facilitated recognition of happy expression during fast exposure but enhanced recognition of fearful expression during slow recognition (Shahrestani *et al*, 2013).

These behavioral and neuroscience findings allow us to hypothesize that oxytocin promotes ingroup favoritism when intuition is favored. Reflective deliberation, however, might overrule the effect of oxytocin or even reverse it. We tested this hypothesis in a double-blind, placebo-controlled between-subjects design by combining intranasal administration of oxytocin and cognitive-style manipulation. Two complementary approaches were adopted to test our hypothesis. First, we assessed whether conceptual priming that temporarily promoted intuition or reflection affected the oxytocin effects on ingroup favoritism during a public goods game (PGG) with ingroup or outgroup members. Second, given that people differ in the inclination toward intuition or reflection in daily life (Evans, 2008; Lieberman, 2007), we examined whether the oxytocin effect on ingroup favoritism during PGG differed between individuals who preferred intuition or reflection in daily-life decision-making.

MATERIALS AND METHODS

Participants

This study recruited 150 male Chinese college students as paid volunteers. Data analyses consisted ofhet4-1.501.2art9(icte)-19(ipant-1.-10.ocin)TJ0-1.0983TD3(the)-651.6((ntuition)-365.9rimiii

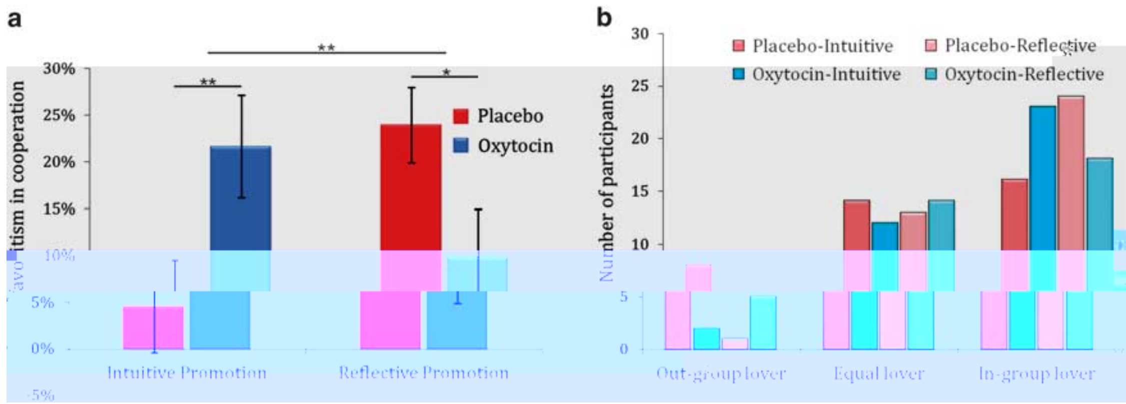

Figure 1 Distinct oxytocin effects on ingroup favoritism when intuition or reflection was promoted. (a) Oxytocin administration significantly enhanced ingroup favoritism when intuition was encouraged, whereas oxytocin significantly decreased ingroup favoritism when reflection was favored. (b) Distribution of outgroup-favored, equal, and ingroup-favored players. The distribution of 'ingroup-favored players' and 'outgroup-favored players' differed significantly across the four conditions. Oxytocin increased the number of ingroup-favored players among the individuals who were primed with intuition, whereas oxytocin decreased the number of ingroup-favored players among those who were primed with reflection.

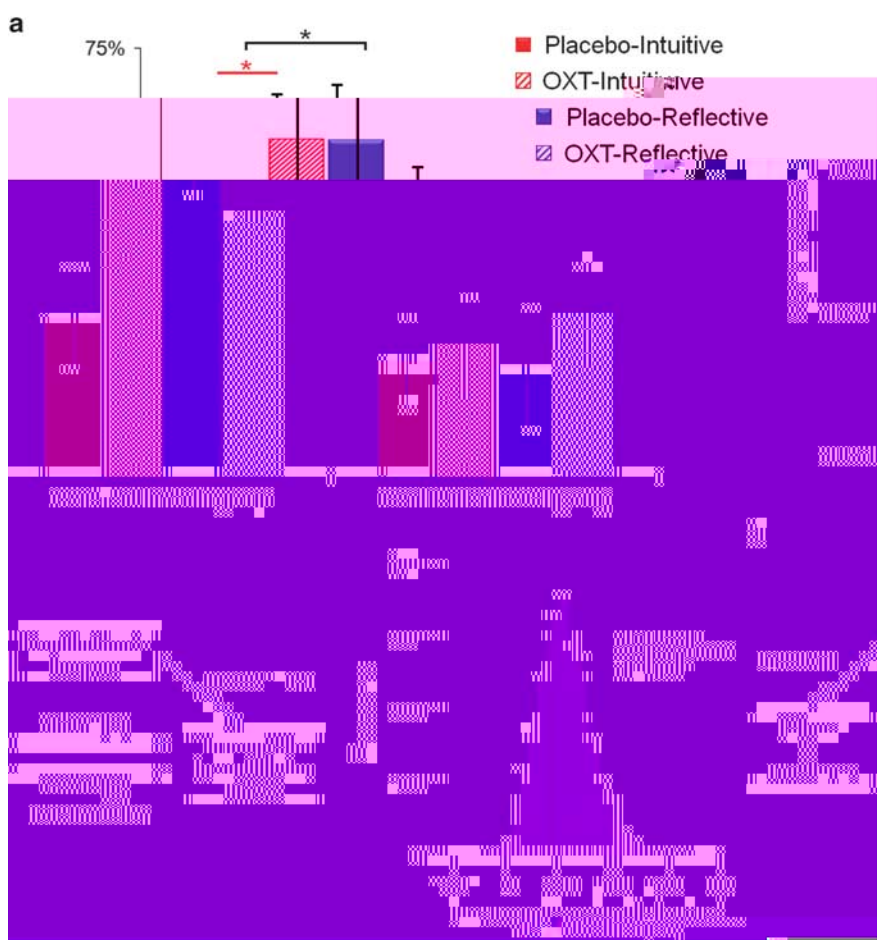

Figure 2 Effects on ingroup facilitation *vs* outgroup deterioration. (a) Oxytocin increased contribution to ingroup members when intuition was encouraged, but decreased ingroup cooperation when reflection was favored. However, there was no significant Treatment × Priming interaction when playing with outgroup members. (b) The Treatment × Priming interaction on ingroup favoritism was mediated by its effect on contribution amount to ingroup members. The bootstrapped sampling distribution of mediator effect was provided on the right panel.

through the intuitive system but *inhibits* ingroup favoritism when the reflective system is favored.

The Treatment × Priming interaction pattern was also evident in an analysis where we classified participants according to their differential contributions to ingroup and outgroup members. Among 150 participants, we identified 81 'ingroup-favored players' (who contributed more to ingroup compared with outgroup members) and

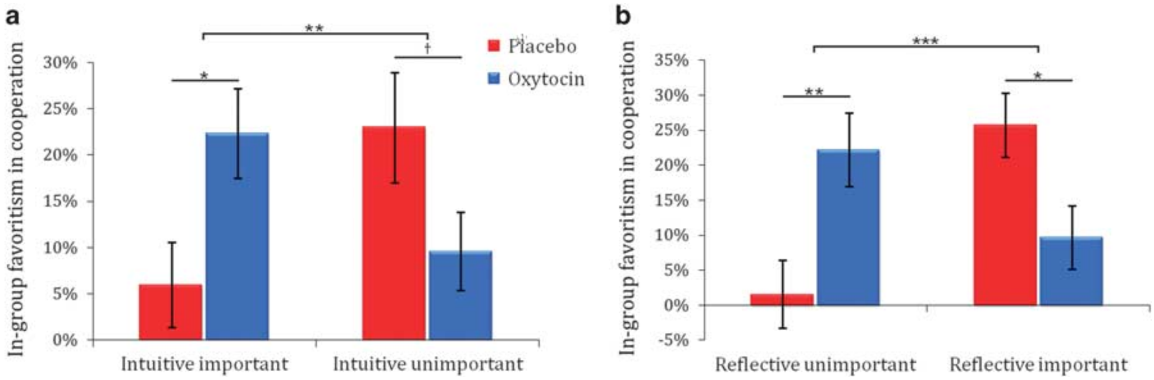

Figure 3 Influence of intuition *vs* reflection importance in daily life on ingroup favoritism during PGGs. Oxytocin administration increased ingroup favoritism on the contribution during PGG in individuals who thought intuition-important (a) or reflection-unimportant (b) in daily-life decision-making. However, oxytocin administration reduced ingroup favoritism during PGG in those who thought intuition-unimportant (a) or valued reflection-important (b) in daily-life decision-making. $^{\dagger}P<0.07$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

16 ‘outgroup-favored players’ (who contributed more to outgroup compared with ingroup members). The other 53 participants contributed equal amounts of money to ingroup and outgroup members. The distribution of ‘ingroup-favored players’ and ‘outgroup-favored players’ differed significantly across the four conditions ($\chi^2=9.543$, Cramer’s $V=0.314$ ($n=97$), $p=0.023$). Cramer’s V coefficient suggested a moderate association between ingroup-/outgroup-favored player categorization and different conditions, that is, oxytocin increased the number of ingroup-favored players among the individuals who were primed with intuition (number of ‘ingroup-favored players’ *vs* ‘outgroup-favored players’: placebo: 16 *vs* 8; oxytocin: 24 *vs* 1), whereas oxytocin decreased the number of ingroup-favored players among those who were primed with reflection (placebo: 23 *vs* 2; oxytocin: 18 *vs* 5; Figure 1b).

Treatment × Priming Interaction on Contributions to Ingroup *vs* Outgroup Members

To clarify whether the Treatment × Priming interaction on ingroup favoritism observed above was driven by cooperation with ingroup or outgroup members, we conducted separate analyses of contributions to ingroup and outgroup members. This analysis revealed a significant Treatment × Priming interaction on contributions when playing PGG with ingroup members ($F(1,146)=6.614$, $p=0.011$, $\eta^2=0.043$; Figure 2a and Supplementary Table S6) but not with outgroup members ($F(1,146)=0.127$, $p=0.722$, $\eta^2=0.001$; Supplementary Table S7). A mediation analysis further confirmed that the Treatment × Priming interaction on ingroup favoritism was mediated by its effect on contributions to ingroup members during PGG (Sobel test: $Z=-2.28$, $p=0.023$; Figure 2b, Supplementary Information, Section 4 and Supplementary Table S8) but not to outgroup members (Sobel test: $Z=-0.35$, $p=0.724$; Supplementary Table S9). A bootstrap resampling analysis of the effect size indicates that the mediator effects were different from zero with 95% confidence (Figure 2b and Supplementary Information, Section 4 for details of bootstrap resampling analysis). These results indicated that the interaction between cognitive style and oxytocin treatment on ingroup favoritism arose mainly from the influences on participants’ contributions towards ingroup members.

Intuitive *vs* Reflective Cognitive Styles in Daily Life

We next tested how cognitive styles in daily decision-making affect oxytocin effect on ingroup-favoritism. Ingroup-favoritism on contributions during PGGs was subjected to 2 (Treatment: oxytocin *vs* placebo) × 2 (Cognitive style: intuition-important *vs* intuition-unimportant group or reflection-important *vs* reflection-unimportant group) ANOVAs. These analyses revealed a similar pattern of results to those seen in our experimental manipulation by showing a significant interaction between Treatment and Cognitive style (Treatment × intuition importance: $F(1,146)=8.863$, $p=0.003$, $\eta^2=0.057$ (Figure 3a); Treatment × reflection importance: $F(1,146)=14.198$, $p<0.001$, $\eta^2=0.089$ (Figure 3b)). The Treatment × Cognitive style interaction on ingroup favoritism remained significant after controlling for age, education, ingroup/outgroup game orders, failing to understand the game, trait optimism, interpersonal trust, total contribution, and ingroup favoritism in other dimensions (Supplementary Tables S10–S13). Oxytocin (*vs* placebo) increased ingroup favoritism in the ‘reflection-unimportant’ group ($F(1,71)=9.272$, $p=0.003$, $\eta^2=0.116$) and ‘intuition-important’ group ($F(1,74)=5.714$, $p=0.019$, $\eta^2=0.072$), but decreased ingroup favoritism in the ‘reflection-important’ group ($F(1,75)=5.365$, $p=0.023$, $\eta^2=0.067$) and ‘intuition-unimportant’ group (although this latter effect was only marginally significant; $F(1,72)=3.411$, $p=0.069$, $\eta^2=0.045$). These results provided additional evidence for the opposing oxytocin effects on ingroup favoritism in participants favoring intuitive *vs* reflective systems.

Prosociality *vs* Expectations

Finally, we tested whether the Treatment × Cognitive-style interaction on ingroup favoritism during the PGG resulted from differential expectation of contributions from ingroup and outgroup members. We asked participants to report their expectations of other players’ contributions. Participants expected significantly more contributions from ingroup players compared with outgroup players ($F(1,144) = 81.867$, $p < 0.001$, $\eta^2 = 0.362$). However, neither the main effect of Treatment/Cognitive styles (either temporarily promoted or adapted in daily-life decision-making) nor their interaction was significant on expectations of differential contributions from ingroup compared with outgroup individuals (*ps* > 0.05; Supplementary Figure S3). Thus, the ingroup favoritism in expectations did not vary across treatment and cognitive-style and the Treatment × Cognitive-style interaction on ingroup favoritism cannot be simply caused by more optimistic expectations about the behaviors of ingroup members.

DISCUSSION

It has been documented that oxytocin motivates ingroup favoritism during social interaction (De Dreu, 2012; van IJzendoorn and Bakermans-Kranenburg, 2012). Here we revealed that oxytocin produced opposite effects on ingroup favoritism during social cooperation depending on individuals' cognitive styles. Specifically, intranasal administration of oxytocin (*vs* placebo) increased ingroup-favored cooperation among participants who were primed to be intuitive or preferred intuition in daily life but *decreased* ingroup favoritism in participants who were primed with reflection or preferred reflective decision-making in daily life. Our findings indicate that the biological and cognitive processes involved in social cooperation interact in a specific manner, that is, the adoption of intuition *vs* reflection qualitatively changes the oxytocin effect on social cooperative behavior. The distinct oxytocin effects on ingroup favoritism are evident both when intuition and reflection are temporarily promoted by an experimental manipulation, and when intuition and reflection are preferred in daily life.

Oxytocin did not affect ingroup favoritism simply by changing decision speed because oxytocin (*vs* placebo) administration did not affect participants' decision times (see Supplementary Information, Section 5) and the interaction of oxytocin and cognitive style remained salient after controlling for decision times during PGG. In addition, although participants expected more contributions from ingroup members compared with outgroup members, this ingroup biased expectation was not altered by oxytocin or cognitive style or their interaction. Thus, oxytocin and cognitive style interactively affected participants' prosocial preferences rather than simply making them more or less optimistic about others' increases selfish decisions (Rand *et al*, 2012). These results can be better understood when considering different meanings of a decision in a group or non-group situation. A person can act as either an individual self to pursue one's own goal/benefit or as a group self to pursue the goal/benefit of a social group (Leach *et al*, 2008; Ellemers, 2012). In a situation without group identity, reflection provides time to allow consideration of one's own benefit, leading to less contribution to the public pool (Rand *et al*, 2012). In a group situation, reflection provides time to ponder one's social group affiliation and the benefits of one's own group, leading to more contribution when playing with ingroup members (ie, stronger ingroup favoritism in the current work). There may also be an important cultural dimension to this finding—reflection may be more likely to lead to group affiliation among people from collectivist cultures (such as our participants), whereas those from individualistic cultures may favor selfishness when deliberating, regardless of group affiliation (Rand *et al*, 2015). These can be clarified in future research.

The current study was conducted on a sample of Chinese male adults. This raised the question whether and how the current effect can be generalized to other populations. Previous studies have shown differential or even opposing oxytocin effects between males and females (Macdonald, 2012; Fischer-Shofty *et al*, 2013; Rilling *et al*, 2014). Gender differences were also observed in ingroup favoritism (van Vugt *et al*, 2007; Charness and Rustichini, 2011). Another related issue is whether the current finding can be generalized to individuals from other cultures. The majority of literature on oxytocin effect has been conducted on non-Chinese (eg, European) populations. The current study of a Chinese population adds cultural diversity to the studied populations and raises an interesting question whether the effects of oxytocin on social cognition are sensitive to one's cultural background. On one hand, there were cultural differences in ingroup favoritism (Chen *et al*, 1998; Gelfand *et al*, 2012) and in oxytocin effect on affective responses to ostracism (Pfundmair *et al*, 2014). On the other hand, similar oxytocin effects on the promotion of ingroup favoritism were observed in European (De Dreu *et al*, 2010, 2011) and Chinese participants (Sheng *et al*, 2013). Moreover, similar to our finding, recent studies conducted on European participants showed that the oxytocin-driven group-serving dishonesty was relatively fast (Shalvi and De Dreu, 2014) and oxytocin reduced (deliberated) greedy decisions (De Dreu *et al*, 2015). It is important for future research to test directly whether and how the current findings can be generalized to females and other cultural populations.

It has been shown that the effects of oxytocin varied as a function of personal condition (such as psychopathology, personality trait, attachment style; Bartz *et al*, 2011a, b; Scheele *et al*, 2014). For example, the effect of oxytocin was discrepant in borderline personality disorder patients and healthy controls, as oxytocin decreased (rather than increased) trust and cooperation in patients (Bartz *et al*, 2011b). Moreover, oxytocin decreased trusting expectations for participants with anxious attachment but had no effect in less anxiously attached participants (Bartz *et al*, 2011b). Consistent with our findings in the context of

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