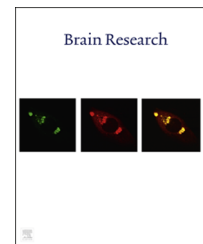


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Oxytocin differentially modulates compromise and competitive approach but not withdrawal to antagonists from own vs. rivaling other groups



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ABSTRACT

In humans, oxytocin promotes cognitive and motivational tendencies that benefit the groups on which humans depend for their survival and prosperity. Here we examined decision making in an incentivized two-player poker game with either an in-group or out-group antagonist. Sixty nine healthy males received 24 IU oxytocin or matching placebo, and played four rounds of a simplified poker game. On each round they received either low or high value cards to create differences in competitive strength, and then responded to a bet placed by their (simulated) (in-group or out-group) antagonist. Under placebo, participants withdrew and competed depending on their own (low vs. high) competitive strength, regardless of their antagonist's group membership. Under oxytocin, however, participants settled more and competed less with an in-group as compared to an out-group antagonist; withdrawal was unaffected by group membership. We conclude that oxytocin sensitizes humans to the group membership of their interaction partner, rendering them relatively more benevolent and less competitive towards those seen as belonging to their own group.

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1. Introduction

In their search for the neurobiological bases of social behavior, scientists across the behavioral and brain sciences turned their focus to oxytocin, an evolutionary ancient and structurally highly preserved neuropeptide (e.g., Bartz et al., 2010; Chang et al., 2012; Bos et al., 2012; Ross and Young, 2009; Striepens et al., 2012). Oxytocin is produced in the hypothalamus and released into the blood stream from axon terminals and into the brain from dendrites of hypothalamic neurons (Donaldson and Young, 2008; Ludwig and Leng, 2006). Functioning as both a neurotransmitter and hormone, oxytocin's targets are widespread and include the hippocampus and the amygdala

(Kirsch et al., 2005). Oxytocin interacts with dopaminergic, reward processing circuits in the nucleus accumbens shell and in the ventral tegmental area (Skuse and Gallagher, 2008), and exerts anxiolytic effects via direct activation of oxytocin receptors expressed in serotonergic neurons of the raphe nuclei (Veenema et al., 2010; Yoshida et al., 2009).

1.1. Social bond formation and maintenance

Oxytocin is perhaps best known for its critical role in parturition and reproduction on the one hand, and social bond formation and maintenance on the other (e.g., Carter et al., 2008). First, male rodents engineered to lack (fore-brain)

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oxytocin receptors no longer discriminate between familiar and unfamiliar females, whereas normal rodents spent more time investigating unfamiliar female rodents vs. female rodents with whom they had shared a cage for several days (Macbeth et al., 2009; also see Ferguson et al., 2000, 2002). Along similar lines, participants who memorized pictures of faces under oxytocin performed better one day later on measures of familiarity, indicating that oxytocin makes a face in memory more familiar (Rimmele et al., 2009).

In addition to social bond formation, oxytocin also appears to stimulate empathic responding, which is important also to social bond maintenance. For example, in women exposed to infant crying, intranasal oxytocin modulates activity in the inferior frontal gyrus (Riem et al., 2011), fathers given oxytocin rather than placebo stimulate their toddler's exploration more and show less hostility (Naber et al., 2010), and in males exposed to biological motion (a point-light figure representing a walking human), intranasal oxytocin modulates neural circuitries involved in affective perspective taking (Keri and Benedek, 2009; Perry et al., 2010). Other studies showed that participants given oxytocin rather than placebo have increased sensitivity to other's fear (Fischer-Shofty et al., 2010), empathize more with people depicted in emotionally charged situations (Hurlemann et al., 2010; but see Singer et al., 2008), and more accurately infer emotions expressed by others (Domes et al., 2007). Indeed, both humans and non-human mammals show increased benevolence under oxytocin, including tendencies to benefit con-specifics (Chang et al., 2012), to trust others (Baumgartner et al., 2008; Kosfeld et al., 2005), to make fair offers in bargaining (Zak et al., 2007), and to benefit others at a personal cost (e.g., Morhenn et al., 2008).

1.2. Indiscriminate benevolence vs. group-serving tendencies

Whereas the heretofore reviewed work suggest that oxytocin promotes indiscriminate benevolence and generosity (e.g., Zak et al., 2007), a more accurate conclusion appears that oxytocin promotes group-serving tendencies (De Dreu, 2012; Goodson, 2013). For example, meerkats live in clans and their survival and prosperity depends on successful in-clan cooperation and coordination and defense to predators and roving competing clans (Drewe et al., 2009). In free-living meerkats, peripheral administration of oxytocin rather than placebo increased an array of cooperative behaviors directed at the own clan, including digging, associating with pups, and *time-on-guard* (Madden and Clutton-Brock, 2011). Other studies documented that oxytocin is key in triggering so-called *maternal defense*, which occurs when a breast-feeding mother is faced with an unfamiliar intruder and lashes out to protect and defend its pups (Bosch et al., 2005; Pedersen et al., 1982).

In humans, similar tendencies have been documented as well. First, the hypothalamic release of oxytocin is promoted by displays of trust and cooperation by others, especially familiar others like parents and intimate partners (e.g., Ditzen et al., 2007; Feldman et al., 2010; Gordon et al., 2010; Holt-Lunstad et al., 2008; Morhenn et al., 2008; Uvnas-Moberg, 1998; Zak et al., 2005). Second, when given oxytocin rather than placebo, humans display more positive attitudes and empathize only with members of their own group and not

with those classified as rivaling out-group members (De Dreu et al., 2011, 2012b; Sheng et al., 2013). Third, individuals given oxytocin rather than placebo conform to opinions of in-group members more than to (identical) opinions voiced by out-group members (Stallen et al., 2012). Fourth, individuals given oxytocin self-sacrifice more, and contribute to their own group more than to the broader collective that includes both their own group and other groups (Israel et al., 2012). Finally, when their own group competes with an out-group, individuals given oxytocin prefer strong allies (De Dreu et al., 2012a; also see Kret and De Dreu, 2013) and display parochial altruism – a tendency to cooperate with the in-group and to compete against the out-group (De Dreu et al., 2010, 2012b; also see Choi and Bowles, 2007; Israel et al., 2012).

Taken together, it thus stands to reason that oxytocin does not promote indiscriminate pro-social tendencies. Instead, it appears that oxytocin promotes cognitive, motivational, and behavioral tendencies that are beneficial to the groups within which humans operate and upon which they depend for survival and prosperity (De Dreu, 2012; van Ijzendoorn and Bakermans-Kranenburg, 2012). Such tendencies include in-group love and, if necessary for in-group protection, out-group hate as well.

1.3. Current study: decision making in competitive interactions

The conclusion that oxytocin promotes group-serving tendencies rests on studies examining relatively cooperative situations where humans faced the choice to contribute to their group or not, to trust others or not, or to make (un)fair offers. However, in addition to these more benign situations, group life is marked also by conflict when, for example, individuals compete for status and scarce resources. Typically, such conflicts trigger a tendency towards (i) withdrawal and subordination, (ii) matching and compromise, or (iii) aggressive approach (De Dreu, 2010; Deutsch, 1973). Although individuals have an incentive to compete through aggressive approach, their overarching group fares better when conflict is mitigated through withdrawal and compromise (De Dreu, 2010). Accordingly, our conjecture that oxytocin promotes group-serving tendencies implies that in competitive interactions, oxytocin increases (i) costly withdrawal and/or settlement, and (ii) reduces aggressive approach, especially when (iii) antagonists are part of one's in-group rather than coming from rivaling out-groups.

We examined this possibility in an incentivized two-player poker game adapted from Ten Velden et al. (2012). Fig. 1 provides a schematic overview of the experimental procedures (see section 4 for further detail).

Participants received oxytocin or matching placebo, and were paired to a (simulated) antagonist from their own in-group, or from a rivaling out-group. In this simplified poker-game, participants are given chips with monetary value, and handed a card from a 52-card deck. Following an initial forced bet which starts the game, participants observe their antagonist's bet, to which they may respond by withdrawing from the game at a personal cost (i.e., “fold,” where the bet is lost and the pot is handed to the opponent), by (ii) *compromising* (i.e., “call,” they match their antagonist's bet and the player

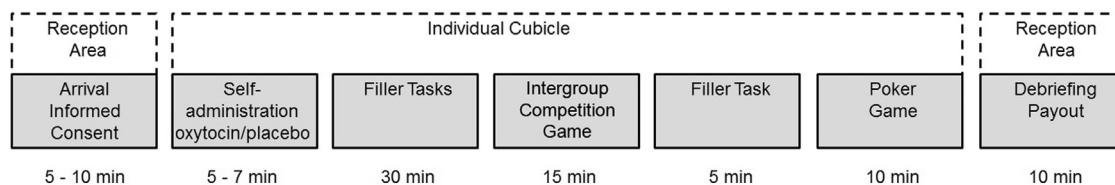


Fig. 1 – Time-line of the experiment; tasks taking place within individual cubicles were entirely computer-guided and participants worked alone at their own pace.

with the highest card wins the pot; in case of a draw, the pot is split between participant and antagonist), or (iii) *competing* (i.e., “raise,” in which case the participant increases the size of the pot). Raising is considered an aggressive approach strategy with which more chips can be gained or lost (depending on the strength of the card) if the competitor calls the bet; chips can be gained if the competitor folds. In terms of our hypotheses, we expected individuals to fold and/or call more, and to raise less when confronted with an in-group (vs. out-group) antagonist, especially when given oxytocin rather than placebo. We manipulated Competitive Strength by providing participants twice with a high value card, and twice with a low value card (Section 4), to explore whether competitive strength modulates predicted effects of oxytocin on decision making.

2. Results

2.1. Manipulation checks

To verify the adequacy of the manipulation of the antagonist's group membership, we cross-tabulated responses to the question whether the antagonist was a member of one's own group, or of the other group (1=my team, 2=other team) with Antagonist's Group, Treatment, and Group \times Treatment interaction. Responses only differed as a function of Antagonist Group, $\chi^2(1, 69)=68.108, p=0.0001$. Except for one mistake, the antagonist's group membership was accurately identified.

The competitive strength manipulation was verified after each decision, first, by asking participants to indicate on a slider whether their card was better (+60) to worse (–60) than their antagonist's card. Ratings were averaged across low value and high value cards, respectively, and submitted to a 2 (treatment) \times 2 (antagonist's group) \times 2 (high vs. low competitive strength) Mixed-Model ANOVA with competitive strength as within-subjects factor. Results showed only a main effect for competitive strength, $F(1, 65)=373.13, p=0.0001, \eta_p^2=0.852$, indicating that participants perceived themselves to be weaker than their antagonist when given a low value card ($M=-31.173, SD=13.488$, one-sample t-test, $t(69)=-20.605, p=0.001$), and stronger than their antagonist when given a high value card ($M=+18.185, SD=17.466$, one-sample t-test, $t(69)=8.194, p=0.001$). Second, we asked participants whether they felt they could win this round (1=not at all; to 5=very much). Ratings were averaged for low value and for high value cards, and submitted to a 2 (treatment) \times 2 (antagonist's group) \times 2 (high vs. low competitive strength) Mixed-Model ANOVA with competitive strength within-subjects. Results revealed the expected main effect for competitive strength,

$F(1, 65)=156.76, p=0.001, \eta_p^2=0.707$, and an unexpected competitive strength \times treatment effect, $F(1, 65)=4.51, p=0.037, \eta_p^2=0.065$. Inspection of the means showed that in both treatment conditions, low value cards induced less perceived competitive strength than high value cards, but this effect was weaker among participants given oxytocin ($M=2.14, SD=0.72$ vs. $M=3.51, SD=0.92$) rather than placebo ($M=1.82, SD=0.78$ vs. $M=3.75, SD=0.73$). In all, however, we concluded that our manipulation of competitive strength was successful and as intended.

2.2. Decision making

Across decision rounds, participants were given twice a low, and twice a high value card. For each value, we counted how often participants decided to fold, call, or raise (each ranges between 0 and 2). Decisions were submitted to a 2 (treatment) \times 2 (antagonist's group) \times 3 (decision: fold vs. call vs. raise) \times 2 (competitive strength: low vs. high) Mixed Model ANOVA with the last two factors within-subjects. This revealed, first of all, a main effect for Decision, $F(2, 65)=38.109, p=0.001, \eta_p^2=0.543$, and a Decision \times Competitive Strength interaction, $F(2, 65)=204.301, p=0.0001, \eta_p^2=0.864$. Fig. 2 shows that when given low value cards, participants more often decided to fold ($M=1.565, SD=0.606$), and less often to raise ($M=0.217, SD=0.449$), than when given high value cards ($M=0.014, SD=0.12$ for fold; $M=1.594, SD=0.577$ for raise). Decisions to call did not change as a function of competitive strength ($M=0.217, SD=0.449$ for low value; $M=0.391, SD=0.548$ for high value).

Treatment did not interact with Decision, $F(2, 65)=1.014, p=0.368, \eta_p^2=0.031$, indicating no overall preference change induced by oxytocin. However, as predicted, we did observe a significant Treatment \times Decision \times Antagonist's Group interaction, $F(2, 65)=4.045, p=0.022, \eta_p^2=0.112$. Follow-up analyses using the overall error term and associated degrees of freedom (Tatsuoka, 1988) indicated that whereas Decision and Antagonist's Group did not interact under placebo, $F(2, 65)=0.978, p=0.381, \eta_p^2=0.050$, they did under oxytocin, $F(2, 65)=3.848, p=0.026, \eta_p^2=0.214$. Fig. 3 (left panel) shows that when participants received placebo, their decision to fold, call, or raise did not depend on their antagonist's group membership. Fig. 3 (right panel) shows that when participants received oxytocin, however, they were more inclined to call when dealing with an in-group rather than out-group antagonist, $F(1, 66)=7.447, p=0.008, \eta_p^2=0.211$, and less inclined to raise when dealing with an in-group rather than out-group antagonist, $F(1, 66)=4.714, p=0.034, \eta_p^2=0.114$. These decision patterns did not differ for low vs. high value cards, in that the Treatment \times Decision \times Antagonist's Group \times Competitive Strength interaction was not significant, $F(2, 64)=2.079, p=0.14$.

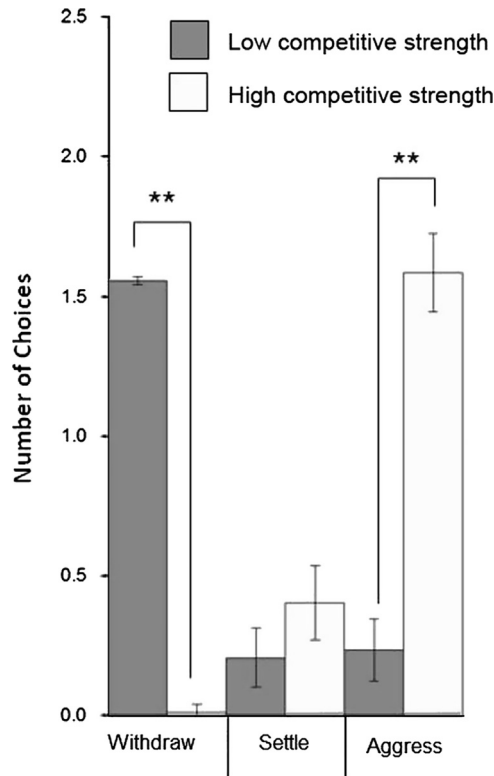


Fig. 2 – Decision Making depends on competitive strength such that individuals withdraw more and aggressively approach less under low competitive strength yet withdraw less and aggressively approach more under high competitive strength (range 0–2, displayed Means ± SE).

Another way of looking at this complex interaction among treatment, decision, and antagonist's group membership is by comparing oxytocin vs. placebo within each type of decision and for each antagonist. Treatment had no effect for costly withdrawal, regardless of whether the antagonist was in-group, $F(1, 66) = 2.382, p = 0.127$ or out-group, $F(1, 66) = 0.088, p = 0.767$. However, oxytocin compared to placebo led to more compromise when dealing with an in-group antagonist, $F(1, 66) = 8.837, p = 0.004, \eta_p^2 = 0.239$, and not when dealing with an out-group antagonist, $F(1, 66) = 1.037, p = 0.312, \eta_p^2 = 0.021$. Finally, oxytocin compared to placebo reduced competitive approach towards an in-group, $F(1, 66) = 2.808, p = 0.099, \eta_p^2 = 0.121$ (marginal), and non-significantly increased competitive approach towards an out-group, $F(1, 66) = 0.606, p = 0.441, \eta_p^2 = 0.012$. This corroborates earlier work showing that oxytocin compared to placebo increases benevolence towards in-group members and not, or to a much lesser extent, motivates competitiveness towards out-groups (De Dreu et al., 2010, 2011).

3. Conclusions and discussion

Results permit three conclusions. First, intranasal oxytocin does not increase indiscriminate benevolence in humans. This conclusion follows from the observation that in competitive interactions, humans given oxytocin reduce competitive approach only when their protagonist is an in-group

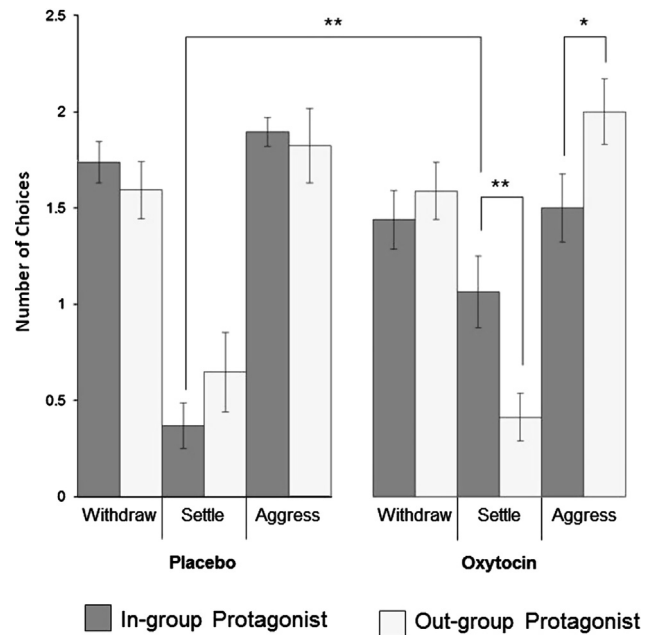


Fig. 3 – Decision Making as a function of Treatment and Antagonist's Group Membership range 0–4; displayed Means ± SE; Connectors indicate significant differences between means, with * $p < 0.10$ and ** $p < 0.05$ ($N = 69$, two-tailed tests). Under placebo, antagonist's group membership has no effect on withdrawal, compromise, or aggressive approach. Under oxytocin, individuals compromise more and aggressively approach less in-group compared to out-group antagonists.

member, and do not show an increased preference for settlement when protagonists are from a rivaling out-group. Second, and relatedly, intranasal oxytocin promotes cooperative conflict resolution in within but not between group competitions. This conclusion follows from the observation that, compared to placebo, oxytocin increased a preference for settlement with in-group protagonists, but not with out-group protagonists. Third, and finally, in competitive interactions, intranasal oxytocin does not influence preferences for withdrawal. This conclusion follows from the observation that regardless of competitive strength, and regardless of the protagonist's group membership, oxytocin exerted no influence whatsoever on the tendency to "fold" in the competitive poker-game studied here.

Results corroborate our conjecture that oxytocin plays a pivotal role in creating, maintaining, and promoting humans' bonds within the groups upon which they depend. Consistent with earlier studies on in-group favoritism (De Dreu et al., 2011; Sheng et al., 2013), social conformity (Stallen et al., 2012), and parochial altruism (De Dreu et al., 2010, 2012b), here we observed that oxytocin increases preferences for cooperative settlement and reduced preferences for competitive approach in interactions with in-group members, but not in interactions with out-group members.

The key finding that effects of oxytocin on competitive decision making are moderated by the antagonist's group membership subscribes to the general conclusion that, in humans, effects of oxytocin depend on both individual differences and personality characteristics, and on contextual

cues and situational constraints (Bartz et al., 2011). Scheele et al. (2012), for example, observed markedly different effects of oxytocin on interpersonal distance when participants were romantically engaged or not on the one hand, and the interaction target's sex. Other work observed effects of oxytocin to depend on early childhood experiences (Van IJzendoorn and Bakermans-Kranenburg, in press). Similar to the current findings, it thus appears that effects of oxytocin in humans are context-dependent, and that one key context involves (features of) the group setting within which the individual operates.

Our study involved healthy males engaging in a simple competition with a simulated protagonist. As such, current conclusions are limited, potentially, to males and may not generalize to female participants. There is some evidence that oxytocin up-regulates motivational attention to competition in males but not in females (Fischer-Shofty et al., in press). Future research should examine current hypotheses for both males and females. Second, competitive interaction was studied with a highly simplified poker game, in which participants made decisions without receiving feedback on the outcomes of these decisions. Accordingly, the current study contains no information about possible adaptation to the competitor's strategy, and about whether oxytocin increases flexible adaptation or not. There is some evidence that oxytocin, compared to placebo, promotes divergent thinking and flexible processing (De Dreu et al., in press), and it may thus be possible that humans given oxytocin more flexibly adapt to the outcomes of a competitive interaction, their opponent's strategy, and their combination. Herein lies another avenue for future research into the role of oxytocin in social behavior. Study limitations aside, our results inform an emerging debate about the fundamental mechanisms that account for the plethora of effects oxytocin seems to exert on social perception, social motivation, and social behavior. Three or more or less related accounts have been proposed. The first account rests on the well-documented anxiolytic effects of oxytocin. Oxytocin interacts with the hypothalamic-pituitary-adrenal axis to attenuate stress responses, and this has a pervasive influence throughout both the body and the brain (Neumann, 2008). Specifically, oxytocin reduces cortisol levels after exposure to stressors (Heinrichs et al., 2003), inhibits cardiovascular stress responses (Uvnas-Moberg, 1998), reduces the activation of the amygdala and attenuates its coupling to brainstem centers responsible for autonomic and behavioral components of fear (Kirsch et al., 2005; Petrovic et al., 2008). This, in turn, has been argued to allow the individual to consider alternatives to fight-or-flight – the typical autonomic response to (social) stressors – and permits pro-social approach (Lim and Young, 2006; Heinrichs et al., 2009; Taylor et al., 2000). This perspective fits the current finding that oxytocin increases a preference for settlement rather than aggressive approach with in-group competitors. However, it has difficulty accounting for the observation that oxytocin did not reduce aggressive approach towards out-group competitors, a finding that emerged in other work as well (De Dreu et al., 2010, 2011; Sheng et al., 2013; also see Declerck et al., 2010; Mikolajczak et al., 2010). A second possibility is that oxytocin increases attention to social cues and therefore it has widely varying effects on 'downstream' cognition and

behavior, depending on the social context (Bartz et al., 2011; Shamay-Tsoory et al., 2009). In the current competitive context, this "social salience hypothesis" would imply that oxytocin may increase competitive approach when antagonists belong to a rivaling out-group, yet when they belong to the in-group interaction oxytocin increases cooperation and reduce competitive approach. However, whereas we indeed observed that oxytocin increases in-group cooperation (increased compromise; reduced competitive approach), it did not increase out-group competition (reduced compromise; increased competitive approach).

The final perspective on oxytocin assumes its effects on social cognition and behavior emerge because oxytocin up-regulates social approach towards positive cues, and inhibits withdrawal from negative cues (Kemp and Guastella, 2011). Consistent with this is a recent study of rhesus macaques, showing that oxytocin increases attention to faces and eyes and, importantly, reduces social vigilance for unfamiliar, dominant, and emotional faces (Ebitz et al., 2013; also see Parr et al., in press). Along similar lines, intranasal oxytocin in humans facilitates recognition of and (empathic) responses to positive social cues, yet does not alter recognition of, and responses to aversive social stimuli. From this, Striepens et al. (2012, p. 18147) concluded that oxytocin prepares for "approach and protective behavior, but with heightened caution" (p. 18147), a conclusion that fits well the "tend-and-defend" response triggered by oxytocin in intergroup competition (De Dreu et al., 2010; De Dreu, 2012b). Current results also subscribe to this hypothesis. In competitive interactions among humans, oxytocin does not alter preferences for withdrawal, and increases pro-social preferences but with caution; only when dealing with in-group members and not with competitors from a rivaling out-group does oxytocin promote pro-social approach.

4. Experimental procedures

4.1. Participant recruitment

The study was approved by the Ethics Committee of the University of Amsterdam, and all participants provided informed consent prior to participation. Male participants were recruited via an on-line recruiting system and offered a monetary reward of €10 (approx. 13 USD) for participating in a study on the effects of medication on test scores and decision-making. They filled out an on-line medical screening – exclusion criteria were significant medical or psychiatric illness, medication, smoking more than five cigarettes per day, and drug or alcohol abuse. Seventy-three participants were retained and instructed to refrain from smoking or drinking (except water) for 2 h before the experiment. A total of sixty nine participants were included in the final sample and analyses (two participants were excluded because they indicated themselves as very experienced poker players, and two other participants were excluded because of technical failures and missing data). There were no differences between the two treatment groups in medical screening responses. Participants averaged 21.51 ($SD=3.078$) years of age, and age did not differ across experimental conditions, all

$F(1, 65) < 0.52$, all $p_s > 0.49$. On average, participants indicated they had moderate experience with poker ($M = 2.36$; with 5 = very much; $SD = 0.94$), and experience did not differ across experimental conditions, all $F(1, 65) < 2.10$, all $p > 0.15$.

4.2. Substance administration

Participants were randomly assigned to the oxytocin or placebo group (double-blind, placebo-controlled study design). Participants self-administered a single intranasal dose of 24 IU oxytocin (Syntocinon-Spray, Novartis; 3 puffs per nostril, each with 4 IU oxytocin) or placebo 30 min before the start of the experimental tasks (De Dreu et al., 2010; Kosfeld et al., 2005). To avoid any subjective effects (for example, olfactory effects) other than those caused by oxytocin, the placebo contained all the active ingredients except for the neuropeptide. The placebo was manufactured by Stichting Apothekers Haarlemse Ziekenhuizen (SAHZ) in coordination with the pharmacy at the Amsterdam Medical Centre (AMC), adhering to the guidelines on Good Manufacturing Practice (GMP) and Good Clinical Practice (GCP). The placebo was produced using the exact same recipes and procedures used by Novartis Inc. to produce the carrier of Syntocinon – the synthetic analog of oxytocin. Placebos were delivered in the same bottles as Syntocinon. In short, the only difference between the placebo and treatment was the absence vs. presence of the active neuropeptide.

4.3. Experimental procedures and materials

Fig. 1 provides the time-line of the experimental procedures and tasks. Participants came in groups of six individuals to the laboratory, where they were seated in individual cubicles in front of a computer displaying all instructions and recording responses. Participants could neither see nor communicate with other participants, and worked independently and at their own pace.

Participants self-administered oxytocin (or placebo) under experimenter supervision. Thereafter, the experimenter unlocked the participant's computer for them to work on a series of unrelated tests, for a total duration of 30 min (this was done because effects of oxytocin emerge approximately 30–35 min past administration; Baumgartner et al., 2008). Embedded in these unrelated tests was a measure of social value orientation, which asks participants in nine decomposed games to choose between a cooperative and a non-cooperative distribution of outcomes between themselves and an anonymous other (see for more detail, De Dreu et al., 2010). To verify that randomization across experimental conditions was successful, we analyzed the number of cooperative choices (range 0–9) in a 2 (Treatment) \times 2 (Antagonist's Group Membership) ANOVA. Neither factor had significant effects, alone or in combination, all $F(1, 65) < 2.34$, all $p_s > 0.16$, indicating that prior to the (effective) manipulation of our independent variables, and the decision game itself, no differences in cooperative preference existed across the four conditions.

Thirty minutes past self-administration of oxytocin or placebo, the computer switched to instructions for the main experimental tasks. Participants read that they were about to engage in a series of decision making tasks, some of which would require two three-person groups. Participants were

assigned to either Team “Triangle” or Team “Circle” on the basis of the order in which they signed-up for the experiment, and engaged in decision making in a between-group competition games (De Dreu et al., 2012b). This took approximately 15 min. Thereafter, they performed a short filler task asking about their current mood. They indicated for 8 positive and 10 negative mood states how they felt (e.g., concentrated; 1 = not at all, to 5 = very much). We created a positive affect index (8 items, $\alpha = 0.67$) and a negative affect index (10 items, $\alpha = 0.82$) and found no differences across the four conditions of our experimental design, all $F(1, 65) < 0.48$, $p_s > 0.49$. On average, participants felt more positive ($M = 2.96$, $SD = 0.58$) than negative ($M = 1.33$, $SD = 0.43$).

Following the short filler task, participants were introduced to the two-person simplified online poker game with another participant who would remain anonymous. Participants played four rounds of poker. In each round, they started with 25 chips and were reminded that the earned chips would be converted 1:1 into lottery tickets, which would go into a raffle for one of four 25€ Euro prizes. Before each round started, they had to place a forced bet of five chips and read that from a standard deck of 52 playing cards, they and their antagonist would randomly receive one card. The antagonist was (unknowingly to participants) simulated and said to be a member of their own Team “Triangle”, or of the rivaling other Team “Circle” (but different from the antagonist in the between-group competition games; we counter-balanced labels but this had no effects whatsoever). There was no feedback in between rounds—participants decided to fold, call or raise, and then immediately moved to the next round of the game.

After a practice trial, participants played four rounds of poker in which we varied participants' competitive strength. Participants received two low value cards (3 and 5), representing low competitive strength (the probability of winning, a draw, and losing, respectively, is 7.84%, 5.88%, and 86.27% for card value 3, and 23.53%, 5.88%, and 70.59% for card value 5). Participants received two high value cards (J and K), representing high competitive strength (the probability of winning, a draw, and losing, respectively, is 70.59%, 5.88%, and 23.53% for card value J, and 86.27%, 5.88%, and 7.84% for card value K). The color of the antagonist's chips was either red or white but because chip color did not interact with any of the variables, this variable is further ignored.

After the opponent placed a first bet of 10 chips, the participant had the choice between foldings (in which case the remaining 20 chips would be preserved, but five chips would be lost), calling (in which case 15 chips could be won, or 15 chips could be lost), or raising with a maximum of 10 chips in which case the opponent could either call the raise (depending on the amount raised, up to 25 chips could be won or lost), or fold, in which case the participant would win 15 chips. Note that the simulated poker game was an interpersonal (dyadic) game, with earnings from the game going only to the individual participant and not (also) to other members of his team and/or the (simulated) antagonist's team. Because no actual interaction took place, each participant received a fixed number of chips after the four rounds of the game, and each thus had the same probability of winning one of the raffle prizes.

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REFERENCES

- Bartz, J.A., Zaki, J., Bolger, N., Hollander, E., Ludwig, N.N., Kolevzon, A., Ochsner, K.N., 2010. Oxytocin selectively improves empathic accuracy. *Psychol. Sci.* 21, 1426–1428.
- Bartz, J.A., Zaki, J., Bolger, N., Ochsner, K.N., 2011. Social effects of oxytocin in humans: context and person matter. *Trends Cogn. Sci.* 15, 301–309.
- Baumgartner, T., Heinrichs, M., Vonlanthen, A., Fischbacher, U., Fehr, E., 2008. Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron* 58, 639–650.
- Bos, P.A., Panksepp, J., Bluthé, R.-M., Van Honk, J., 2012. Acute effects of steroid hormones and neuropeptides on human social-emotional behavior: a review of single administration studies. *Front. Neuroendocrinol.* 33, 17–35.
- Bosch, O.J., Meddle, S.L., Beiderbeck, D.I., Douglas, A.J., Neumann, I.D., 2005. Brain oxytocin correlates with maternal aggression: link to anxiety. *J. Neurosci.* 25, 6807–6815.
- Carter, C.S., Grippo, A.J., Pournajafi-Nazarloo, H., Ruscio, M.G., Porges, S.W., 2008. Oxytocin, vasopressin, and sociality. *Prog. Brain Res.* 170, 331–336.
- Chang, S.W.C., Barter, J.W., Ebitz, R.B., Watson, K.K., Platt, M.L., 2012. Inhaled oxytocin amplifies both vicarious reinforcement and self reinforcement in rhesus macaques (*Macaca mulatta*). *Proc. Natl. Acad. Sci. USA* 109, 959–964.
- Choi, J.-K., Bowles, S., 2007. The coevolution of parochial altruism and war. *Science* 318, 636–640.
- De Dreu, C.K.W., 2010. Social Conflict: the Emergence and Consequences of Struggle and Negotiation. In: Fiske, S.T. (Ed.), *Handbook of Social Psychology* 2nd ed. Wiley, New York, pp. 983–1023.
- De Dreu, C.K.W., 2012. Oxytocin modulates cooperation within and competition between groups: an integrative review and research agenda. *Horm. Behav.* 61, 419–428.
- De Dreu, C.K.W., Baas M., Roskes M., Sligte D.J., Epstein R.P., Chew S.H., Tong T., Jiang Y., Maysseless N. and Shamay-Tsoory S.G., Oxytonergic circuitry sustains and enables creative cognition in humans, *Soc. Cogn. Affect. Neurosci.*, <http://dx.doi.org/10.1093/scan/nst094>, in press.
- De Dreu, C.K.W., Greer, L.L., Handgraaf, M.J.J., Shalvi, S., Van Kleef, G.A., Baas, M., Ten Velden, F.S., Van Dijk, E., Feith, S.W.W., 2010. The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science* 328, 1408–1411.
- De Dreu, C.K.W., Greer, L.L., Van Kleef, G.A., Shalvi, S., Handgraaf, M.J.J., 2011. Oxytocin promotes human ethnocentrism. *Proc. Natl. Acad. Sci. USA* 108, 1262–1266.
- De Dreu, C.K.W., Greer, L.L., Shalvi, S., Handgraaf, M.J.J., Van Kleef, G.A., 2012a. Oxytocin modulates the selection of allies in intergroup conflict. *Proc. Biol. Sci.* 279, 1150–1154.
- De Dreu, C.K.W., Shalvi, S., Greer, L.L., Van Kleef, G.A., Handgraaf, M.J.J., 2012b. Oxytocin motivates non-cooperation in intergroup conflict to protect vulnerable in-group members. *PlosOne* 7, E46751.
- Declerck, C.H., Boone, C., Kiyonari, T., 2010. Oxytocin and cooperation under conditions of uncertainty: the modulating role of incentives and social information. *Horm. Behav.* 57, 368–374.
- Deutsch, M., 1973. *The resolution of conflict: Constructive and destructive processes*. Yale University Press, New Haven.
- Ditzen, B., Neumann, I.D., Bodenmann, D., Von Dawans, B., Turner, R.A., Ehlert, U., Heinrichs, M., 2007. Effects of different kinds of couple interaction on cortisol and heart rate responses to stress in women. *Psychoneuroendocrinology* 32, 565–574.
- Domes, G., Heinrichs, M., Michel, A., Berger, C., Herpertz, S.C., 2007. Oxytocin improves “mind-reading” in humans. *Biol. Psychiatry* 61, 731–733.
- Donaldson, Z.R., Young, L.J., 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 322, 900–903.
- Drewe, J.A., Madden, J.R., Pearce, G.P., 2009. The social network structure of a wild meerkat population: 1. Inter-group interactions. *Behav. Ecol. Sociobiol.* 63, 1295–1306.
- Ebitz, R.B., Watson, K.K., Platt, M.L., 2013. Oxytocin blunts social vigilance in the rhesus macaque. *Proc. Natl. Acad. Sci. U.S.A.* 110, 11630–11635.
- Feldman, R., Gordon, I., Schneiderman, I., Weisman, O., Zagoory-Sharon, O., 2010. Natural variations in maternal and paternal care are associated with systematic changes in oxytocin following parent-infant contact. *Psychoneuroendocrinology* 35, 1133–1141.
- Ferguson, J.N., Young, L.J., Insel, T.R., 2002. The neuroendocrine basis of social recognition. *Front. Neuroendocrinol.* 23, 200–224.
- Ferguson, J.N., Young, L.J., Hearn, E.F., Matzuk, M.M., Insel, T.R., Winslow, J.T., 2000. Social amnesia in mice lacking the oxytocin gene. *Nat. Genet.* 25, 284–288.
- Fischer-Shofty M., Levkovitz Y. and Shamay-Tsoory S.G., Oxytocin facilitates accurate perception of competition in men and kinship in women, *Soc. Cogn. Affect. Neurosci.*, <http://dx.doi.org/10.1093/scan/nsr100>, in press.
- Fischer-Shofty, M., Shamay-Tsoory, S.G., Harari, H., Levkovitz, Y., 2010. The effect of intranasal administration of oxytocin on fear recognition. *Neuropsychologia* 48, 179–184.
- Goodson, J.L., 2013. Deconstructing sociality, social evolution and relevant nonapeptide functions. *Psychoneuroendocrinology* 48, 465–478.
- Gordon, I., Zagoory-Sharon, O., Leckman, J.F., Feldman, R., 2010. Prolactin, oxytocin, and the development of paternal behavior across the first six months of fatherhood. *Horm. Behav.* 58, 513–518.
- Heinrichs, M., Baumgartner, T., Kirschbaum, C., Ehlert, U., 2003. Social support and oxytocin interact to suppress cortisol and subjective responses to psychological stress. *Biol. Psychiatry* 54, 1389–1398.
- Heinrichs, M., von Dawans, B., Domes, G., 2009. Oxytocin, vasopressin, and human social behavior. *Front. Neuroendocrinol.* 30, 548–557.
- Holt-Lunstad, J., Birmingham, W.A., Light, K.C., 2008. Influence of a “warm touch” support enhancement intervention among married couples on ambulatory blood pressure, oxytocin, alpha amylase, and cortisol. *Psychosom. Med.* 70, 976–985.
- Hurlmann, R., Patin, A., Onur, O., Cohen, M.X., Baumgartner, T., Metzler, S., Dziobek, I., Gallinat, J., Wagner, M., Kendrick, K.M., 2010. Oxytocin enhances amygdala-dependent, socially reinforced learning and emotional empathy in humans. *J. Neurosci.* 30, 4999–5007.
- Israel, S., Weisman, O., Ebstein, R.P., Bornstein, G., 2012. Oxytocin, but not vasopressin, increases both parochial and universal altruism. *Psychoneuroendocrinology* 37, 1341–1344.

- Kemp, A.H., Guastella, A.J., 2011. The role of oxytocin in human affect: a novel hypothesis. *Curr. Dir. Psychological Sci.* 20, 222–231.
- Keri, S., Benedek, G., 2009. Oxytocin enhances the perception of biological motion in humans. *Cogn. Affect. Behav. Neurosci.* 9, 237–241.
- Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., Gruppe, H., Mattay, V.S., Gallhofer, B., Meyer-Lindenberg, A., 2005. Oxytocin modulates neural circuitry for social cognition and fear in humans. *J. Neurosci.* 25, 11489–11493.
- Kosfeld, M., Heinrichs, M., Zak, P.J., Fischbacher, U., Fehr, E., 2005. Oxytocin increases trust in humans. *Nature* 435, 673–676.
- Kret, M.E., De Dreu, C.K.W., 2013. Oxytocin-motivated ally selection is moderated by fetal testosterone exposure and empathic concern. *Front. Neurosci.* 7, 1–9.
- Lim, M.M., Young, L.J., 2006. Neuropeptide regulation of affiliative behavior and social bonding in animals. *Horm. Behav.* 50, 506–517.
- Ludwig, M., Leng, G., 2006. Dendritic peptide release and peptide-dependent behaviors. *Nat. Rev. Neurosci.* 7, 126–136.
- Macbeth, A.H., Lee, H.J., Edds, J., Young III, W.S., 2009. Oxytocin and the oxytocin receptor underlie intrasrain, but not interstrain, social cognition. *Genes Brain Behav.* 8, 558–567.
- Madden, J.R., Clutton-Brock, T.H., 2011. Experimental peripheral administration of oxytocin elevates a suite of cooperative behaviours in a wild social animal. *Proc. Biol. Sci.* 278, 1189–1194.
- Mikolajczak, M., Gross, J.J., Lane, A., Corneille, O., de Timary, Ph., Luminet, O., 2010. Oxytocin makes people trusting, not gullible. *Psychol. Sci.* 21, 1072–1075.
- Morhenn, V.B., Park, J.W., Piper, E., Zak, P.J., 2008. Monetary sacrifice among strangers is mediated by endogenous oxytocin release after physical contact. *Evol. Hum. Behav.* 29, 375–383.
- Naber, F., Van IJzendoorn, M.H., Deschamps, P., Van Engeland, H., Bakermans-Kranenburg, M.J., 2010. Intranasal oxytocin increases fathers' observed responsiveness during play with their children: a double-blind within-subject experiment. *Psychoneuroendocrinology* 35, 1583–1586.
- Neumann, I.D., 2008. Brain oxytocin: a key regulator of emotional and social behaviours in both females and males. *J. Neuroendocrinol.* 20, 858–865.
- Parr L.A., Modi M, Siebert E. and Young L.J., Intranasal oxytocin selectively attenuates rhesus monkeys' attention to negative facial expressions, *Psychoneuroendocrinology*, <http://dx.doi.org/j.psyneuen.2013.02.011>, in press.
- Pedersen, C.A., Ascher, J.A., Monroe, Y.L., Prange Jr., A.J., 1982. Oxytocin induces maternal behavior in virgin female rats. *Science* 216, 648–650.
- Perry, A., Bentin, S., Shalev, I., Israel, S., Uzevovsky, F., Bar-On, E., Ebstein, R.P., 2010. Intranasal oxytocin modulates EEG mu/alpha and beta rhythms during perception of biological motion. *Psychoneuroendocrinology* 35, 1446–1453.
- Petrovic, P., Kalisch, R., Singer, T., Dolan, R.J., 2008. Oxytocin attenuates affective evaluations of conditioned faces and amygdala activity. *J. Neurosci.* 28, 6607–6615.
- Riem, M.M.E., Bakermans-Kranenburg, M.J., Pieper, S., Tops, M., Boksem, M.A.S., Vermeiren, R.R.J.M., Van IJzendoorn, M.H., Rombouts, S.A.R.B., 2011. Oxytocin modulates amygdala, insula, and inferior frontal gyrus responses to infant crying: a randomized Controlled Trial. *Biol. Psychiatry* 70, 291–297.
- Rimmele, U., Hediger, K., Heinrichs, M., Klaver, P., 2009. Oxytocin makes a face in memory more familiar. *J. Neurosci.* 29, 38–42.
- Ross, H.E., Young, L.J., 2009. Oxytocin and the neural mechanisms regulating social cognition and affiliative behavior. *Front. Neuroendocrinol.* 30, 534–547.
- Scheele, D., Striepens, N., Gunturkun, O., Deuschlander, S., Maier, W., Kendrick, K.M., Hurlmann, R., 2012. Oxytocin modulates social distance between males and females. *J. Neurosci.* 32, 16074–16079.
- Shamay-Tsoory, S.G., Fischer, M., Dvash, J., Harari, H., Perach-Bloom, N., Levkovitz, Y., 2009. Intranasal administration of oxytocin increases envy and schadenfreude (gloating). *Biol. Psychiatry.* 66, 864–870.
- Sheng, F., Liu, Y., Zhou, B., Zhou, W., Han, S., 2013. Oxytocin modulates the racial bias in neural responses to others' suffering. *Biol. Psychol.* 92, 380–386.
- Singer, T., Snozzi, R., Bird, G., Petrovic, P., Silani, G., Heinrichs, M., Dolan, R.J., 2008. Effects of oxytocin and prosocial behavior on brain responses to direct and vicariously experienced pain. *Emotion* 8, 781–791.
- Skuse, D.H., Gallagher, L., 2008. Dopaminergic-neuropeptide interactions in the social brain. *Trends Cogn. Sci.* 13, 27–35.
- Stallen, M., De Dreu, C.K.W., Shalvi, S., Schmidts, A., Sanfey, A., 2012. The herding hormone: oxytocin stimulates in-group conformity. *Psychol. Sci.* 23, 1288–1292.
- Striepens, N., Scheele, D., Kenrick, K.M., Becker, B., Schaefer, L., Schwalba, K., Reul, J., Maier, W., Hurlmann, R., 2012. Oxytocin facilitates protective responses to aversive social stimuli in males. *Proc. Natl. Acad. Sci. USA* 109, 18144–18149.
- Tatsuoka, M.M., 1988. *Multivariate analysis*. MacMillan, New York.
- Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A.R., Updegraff, J.A., 2000. Biobehavioral responses to stress in females: tend-and-befriend, not fight-or flight. *Psych. Rev.* 107, 411–429.
- Ten Velden, F.S., Baas, M., Shalvi, S., Preenen, P.Y., De Dreu, C.K.W., 2012. In competitive interaction displays of red increase actors' competitive approach and perceivers' withdrawal. *J. Exp. Soc. Psychol.* 48, 1205–1208.
- Uvnas-Moberg, K., 1998. Oxytocin may mediate the benefits of positive social interaction and emotions. *Psychoneuroendocrinology* 23, 819–835.
- van IJzendoorn, M.H., Bakermans-Kranenburg, M.J., 2012. A sniff of trust: meta-analysis of the effects of intranasal oxytocin administration on face recognition, trust to in-group, and trust to outgroup. *Psychoneuroendocrinology* 37, 438–443.
- Veenema, A.H., Blume, A., Niederle, D., Buwalda, B., Neumann, I.D., 2010. Effects of early life stress on adult male aggression and hypothalamic vasopressin and serotonin. *Eur. J. Neurosci.* 24, 1711–1720.
- Yoshida, M., Takaynagi, Y., Inoue, K., Kimura, T., Young, L.J., Onaka, T., Nishimori, K., 2009. Evidence that oxytocin exerts anxiolytic effects via oxytocin receptor expressed in serotonergic neurons in mice. *J. Neurosci.* 29, 2259–2271.
- Zak, P.J., Kurzban, R., Matzner, W.T., 2005. Oxytocin is associated with human trustworthiness. *Horm. Behav.* 48, 522–527.
- Zak, P.J., Stanton, A.A., Ahmadi, S., 2007. Oxytocin increases generosity in humans. *PlosOne* 11, e1128.