

Review

Oxytocin modulates cooperation within and competition between groups: An integrative review and research agenda [☆]

Carsten K.W. De Dreu

Department of Psychology, University of Amsterdam, Roetersstraat 15, 1018 WB Amsterdam, The Netherlands

ARTICLE INFO

Article history:

Received 16 June 2011

Revised 1 December 2011

Accepted 2 December 2011

Available online 20 December 2011

Keywords:

Hormones

Pro-social behavior

Theory of mind

Ethnocentrism

Aggression

Social dilemmas

Intergroup relations

ABSTRACT

The author reviews evidence that hypothalamic release (or infusion) of the neuropeptide oxytocin modulates the regulation of cooperation and conflict among humans because of three reasons. First, oxytocin enables social categorization of others into in-group versus out-group. Second, oxytocin dampens amygdala activity and enables the development of trust. Third, and finally, oxytocin up-regulates neural circuitries (e.g., inferior frontal gyrus, ventromedial prefrontal cortex, caudate nucleus) involved in empathy and other-concern. Consistent with an evolutionary perspective on the functionality of cooperation, it is concluded that oxytocin-motivated cooperation is mostly parochial—it motivates (i) in-group favoritism, (ii) cooperation towards in-group but not out-group members, and (iii) defense-motivated non-cooperation towards threatening outsiders. Thus, in addition to its well-known role in reproduction and pair-bond formation, oxytocin's primary functions include in-group "tend-and-defend." This review concludes with avenues for new research on oxytocin's functions in within-group cooperation and between-group competition.

This article is part of a Special Issue entitled Oxytocin, Vasopressin, and Social Behavior.

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[☆] Preparation of this work was supported by the UvA-FMG Research Priority Grant on Affect Regulation, and Grant 432-08-002 of The Netherlands Science Foundation. The author declares no conflict of interest.

E-mail address: c.k.w.dedreu@uva.nl.

Introduction

“Groups with a greater number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other ... would spread and be victorious over other tribes” (Darwin, 1873, p. 156).

Humans have an extraordinary capacity to create and promote social life: They form long-term attachments to close others (Bowley, 1973; Mikulincer and Shaver, 2007), empathize with others (Batson, 1998), and sacrifice their immediate self-interests to promote the overarching interests of the groups and communities they belong to (Dawes, 1980; Penner et al., 2005; Komorita and Parks, 1995; Ostrom, 1998). Humans may even sacrifice their lives, for example as soldiers or suicide bombers, to promote a common cause, or to protect their group against enemy forces (Arrow, 2007; Kruglanski et al., 2009; Stouffer et al., 1949; Tobena, 2009). Together, these and related observations fit Darwin's insight that, throughout evolution, pro-social behavior served individual survival and prosperity: Through self-sacrifice and cooperation humans promote the functioning of their in-group that provides for levels of security and prosperity well beyond what individuals could possibly achieve alone (Alexander, 1990; Shinada et al., 2004; Trivers, 1985).

If self-sacrifice and cooperation has survival functionality, the human brain must have evolved to motivate such pro-social tendencies, and we should be able to identify neurobiological systems and circuitries that modulate cooperative decision making (Rilling and Sanfey, 2011). Indeed, studies in neuroendocrinology and social neuroscience provide mounting evidence for an intimate link between pro-sociality and the evolutionary ancient and highly preserved neuropeptide oxytocin (Bos et al., 2012; Donaldson and Young, 2008; Madden and Clutton-Brock, 2011; Ross and Young, 2009). Oxytocin is a nine amino-acid, cyclic neuropeptide produced in the brain, and has a well-established role in reproduction and pair-bond formation (e.g., Carter et al., 2008). Recent work suggests, however, that its functions are broader, and that oxytocin plays a critical role also in the formation and maintenance of social groups more generally, including non-cooperation towards rivaling out-groups.

Here I review these and related insights, and the evidence from studies focusing on acute effects of oxytocin in healthy volunteers.¹ The first section of this review examines how hypothalamic release of oxytocin modulates three critical functions underlying parochial cooperation, namely (i) social categorization of others into in-group versus out-group; (ii) in-group trust, and (iii) concern for (members of) the in-group. The second and third sections review the research evidence for these three propositions and additionally reveal that oxytocin motivates (iv) non-cooperation towards rivaling out-groups especially when out-groups threaten one's in-group. The final section summarizes the main conclusions and identifies avenues for new research into the link between oxytocin, and the regulation of intra- and intergroup relations.

Why and how oxytocin modulates cooperation

Harvard economist and Nobel Laureate Thomas Schelling (1960/1980; also Deutsch, 1973; Luce and Raiffa, 1957) observed that most group settings contain incentives to compete with others so as to defend and promote immediate self-interest (e.g., personal gains and status) as well as incentives to cooperate with others so as to establish well-functioning long-term relationships that provide greater benefit

¹ Because of space constraints, studies on the relationship between polymorphism in oxytocin receptor genes and social behavior (e.g. Apicella et al., 2010; Israel et al., 2009), and empathy (Roderigues et al., 2009; Tost et al., 2010) are excluded from this review, as are studies on the relationship between oxytocin and autism spectrum disorders (e.g., Andari et al., 2010).

to all than mutual competition. Put differently, social systems like families, small groups, communities and work organizations all share two basic properties: (i) each individual member serves personal interests best by opting for non-cooperation; and (ii) when all members opt for non-cooperation, each is worse off than when all had opted for cooperation (Bornstein, 2003; Dawes, 1980; De Dreu et al., 2008; Komorita and Parks, 1995).

Given these structural features of most social systems, individuals would be expected to sacrifice immediate self-interest and to cooperate only when they have, first of all, *trust*—the positive expectation that others will reciprocate one's cooperative effort (Coombs, 1973; Berg et al., 1995; Pruitt and Kimmel, 1977).² Second, individuals cooperate to the extent that they have *other-concern*—the care for others' outcomes, interests, and well-being (Carnevale and Pruitt, 1992; De Dreu et al., 2000; De Dreu, 2010; Komorita and Parks, 1995; Weber et al., 2004; Pruitt and Kimmel, 1977). Other-concern includes a desire for fairness and to benefit the collective rather than oneself (Bohnet and Frey, 1999; De Dreu et al., 2000).

In general, people have stronger trust in and concern for others they like and feel close to (Wu et al., 2011), with whom they share common goals and values (Burnham, 2003), with whom they anticipate future interaction, or with whom they share group membership (for reviews, e.g., Batson, 1998; De Dreu, 2010; De Dreu et al., 2000, 2008; Komorita and Parks, 1995; Pruitt and Kimmel, 1977). Thus, cooperation is primarily *parochial*—people more readily cooperate with members of their in-group than with members of more or less rivaling out-groups (Bernhard et al., 2006; Brewer and Kramer, 1986; Choi and Bowles, 2007a, 2007b; Darwin, 1873; Hammond and Axelrod, 2006; Polzer, 1996; Wit and Kerr, 2002; Wildschut et al., 2003).

Because parochialism serves individual and group survival both in ancestral and contemporary societies (Darwin, 1873), it may have its root cause in evolved neurobiological circuitries. Fig. 1 shows that oxytocin is a likely neurohormonal modulator of parochialism because of three reasons: (i) it facilitates social categorization of others as in-group versus not in-group, (ii) it enables trust to develop, and (iii) it up-regulates other-concern. These three critical functions are now briefly elaborated upon, and in the next sections evaluated in light of the existing research evidence.

Social categorization

Humans have evolved capacity to quickly distinguish others into in-group versus out-group (Allport, 1954; Brewer and Kramer, 1986; Kurzban et al., 2001; Mahajan et al., 2011), and such social discrimination may be modulated by oxytocin. Specifically, when a bond is formed between a mother and her offspring, or between sexual partners in monogamous species, an olfactory memory is forged in the olfactory bulb. In mothers, oxytocin released in the brain during parturition helps to establish the olfactory signatures of the offspring as memorable (Ferguson et al., 2000; Brennan and Kendrick, 2006; Tobin et al., 2010). Male rodents engineered to lack (fore-brain) oxytocin receptors no longer discriminated between familiar and unfamiliar females—compared to normal rodents, these knock-out rodents spent equal time investigating female rodents with whom they had shared a cage for several days, but less time investigating novel females who they met for the first time (Macbeth et al., 2009; also see Ferguson et al., 2000, 2002).

With regard to social categorization in humans, evidence is exceedingly sparse. However, some first indications derive from a study by Rimmele et al. (2009) who gave participants intranasal oxytocin or placebo and showed them a series of pictures of faces. One day later,

² Trust as defined here is inversely related to fear of being exploited by others, and betrayal aversion (Baumgartner et al., 2008; De Dreu, 2010; De Dreu et al., in press). There are other, broader and multifaceted definitions of trust discussed elsewhere (e.g., Rousseau et al., 1998).

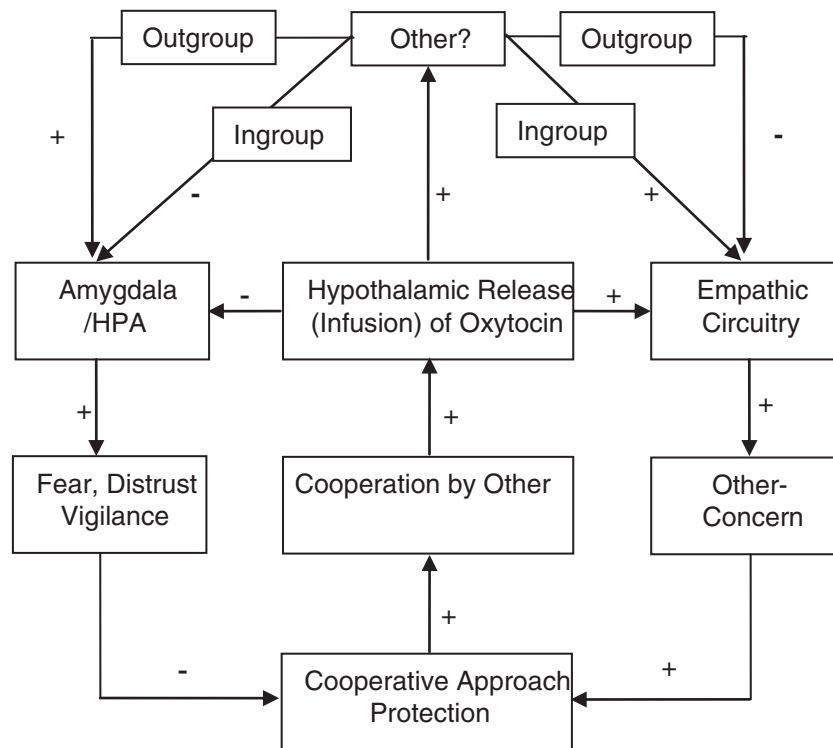


Fig. 1. Hypothalamic release of oxytocin motivates cooperation with in-group others because of lower distress and higher other-concern. *Note:* Arrows reflect causal pathways. Up-regulating (down-regulating) effects are denoted with positive (negative) signs.

participants returned to the laboratory and were given a surprise recognition task, where they had to indicate for a series of pictures whether they had seen the picture before. Interestingly, results showed that participants who learned pictures of faces under oxytocin performed better one day later than those who had learned the pictures under placebo. Effects were particularly strong on measures of familiarity and weak on measures of mere recollection – oxytocin makes a face in memory more familiar.

Familiarity in turn is a key driver of social categorization (Mateo, 2004; Tang-Martinez, 2001), with familiar others being more likely to be categorized as in-group than unfamiliar others (Castelli and Zogmeister, 2000; Castelli et al., 2004). However, research is needed to test the claim that hypothalamic release of infusion of oxytocin mediates the mere categorization of others into in-group and out-group (also see Kavaliers and Choleris, 2011).

Trust and other-concern

People develop trust in, and concern for members of their in-group, and these tendencies are modulated by two distinct neurological systems. The development of trust, and the reduction of fear and vigilance, is mediated by amygdala activity (Baumgartner et al., 2009; LeDoux, 2000; Phelps, 2006), and in humans, amygdala activity is lower when exposed to in-group rather than out-group targets (Beer et al., 2008; Hein et al., 2010; Van Bavel et al., 2008). Hypothalamic release of oxytocin dampens neural circuitries involved in fear-signaling and the regulation of distress (e.g., amygdala; hypothalamic–pituitary–adrenal axis; LeDoux, 2000; Phelps, 2006). Accordingly, as shown in Fig. 1, hypothalamic release of oxytocin promotes the development of trust in in-group others (and may counter-act the tendency to fear out-group others). Research evidence for this proposition is reviewed below.

Concern for others is mediated by neural circuitries involved in empathy and reward processing, including the inferior frontal gyrus and the inferior parietal lobe necessary for emotion recognition and

contagion, as well as the evolutionary and phylogenetically more recent ventromedial prefrontal cortex, and the temporoparietal junction and the medial temporal lobe (Baumgartner et al., 2009; Decety and Chaminade, 2003; Halko et al., 2009; Keuken et al., 2011; Shamay-Tsoory, 2011; Schnell et al., 2011).³ Empathy refers to the individual's capacity to experience affective reactions to the observed or anticipated experiences of another individual, and to take another person's perspective (Batson, 1998; Frith and Singer, 2008). The neural circuitries involved in empathy are activated more when individuals are exposed to in-group rather than out-group members (Harris and Fiske, 2007; Hein et al., 2010; Van Bavel et al., 2008) and, importantly, these circuitries are up-regulated by hypothalamic release (or infusion) of oxytocin.⁴ Accordingly, as shown in Fig. 1, hypothalamic release of oxytocin promotes the development of other-concern for in-group others (and may counter-act the tendency to withhold other-concern from out-group others).

Self-sustaining spiral of (in-group) cooperation

The combination of increased trust and other-concern enables individuals to engage in cooperation and to benefit others at a personal cost. Importantly, such self-sacrifice may include tendencies to risk oneself to protect others (e.g., by aggressing against threatening

³ In addition to empathy, other-concern may be driven by strategic considerations. For example, when the individual expects future interaction with the protagonist and sees the protagonist as relatively powerful, the individual may be motivated to care of other's outcomes to ensure personal interests in the longer run, or to avoid the protagonist becomes angry and lashes out. Such strategic considerations for other-concern are not further discussed here (see e.g., Bazerman et al., 2000; De Dreu et al., 2000).

⁴ A distinction has been made between affective and cognitive empathy (e.g., Frith and Singer, 2008), with oxytocin being involved primarily in affective empathy through its influence on the inferior frontal gyrus and the inferior frontal lobe, and indirectly in cognitive empathy through its interaction with dopaminergic circuitries (striatum, ventromedial prefrontal cortex). For a review and discussion, see Shamay-Tsoory (2011).

outsiders). From Fig. 1 it follows that these tendencies emerge especially when protagonists are categorized as in-group, and that hypothalamic release (or infusion) of oxytocin amplifies such parochial cooperation and (in-group) protection. This key hypothesis is examined here in light of the available evidence.

Finally, Fig. 1 shows that in-group protection and cooperation begets cooperation (Axelrod, 1984; De Dreu, 2010; Pruitt and Kimmel, 1977), and there is some evidence that displays of trust and cooperation by others, especially familiar others like parents and intimate partners, promotes hypothalamic release of oxytocin (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). In addition, intranasal oxytocin augments activity in the caudate nucleus following reciprocated cooperation, suggesting that oxytocin enhances the reward from reciprocated cooperation and facilitates the learning that the protagonist can be trusted (Rilling et al., 2012). In all, there is reason to assume a spiral of oxytocin-mediated and mutually reinforcing cooperation among the individual and his or her protagonist(s) and that such positive spirals are more likely when protagonists are categorized as in-group rather than out-group.

Oxytocin down-regulates fear-signaling and enables trust

Produced in the hypothalamus and functioning as both hormone and neurotransmitter, oxytocin's targets are widespread and include the amygdala, hippocampus, and regions of the spinal cord that regulate the parasympathetic branch of the autonomic nervous system (Ludwig and Leng, 2006; Neumann, 2008; Roderigues et al., 2009). 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; Roderigues and Sapolsky, 2009). Specifically, oxytocin reduces cortisol levels after exposure to stressors (Heinrichs et al., 2003), inhibits cardiovascular stress responses (Uvnas-Moberg, 1998), and modulates brain areas and neural circuitries involved in the processing of fear-related information. For example, in a neuro-imaging study, Kirsch et al. (2005) gave participants either an intranasal dose of oxytocin or placebo, and showed them fearful or neutral stimuli while brain activity was being registered. Results showed that oxytocin reduced the activation of the amygdala and attenuated its coupling to brainstem centers responsible for autonomic and behavioral components of fear (see also Petrovic et al., 2008).

Fearful, anxiety-provoking stimuli and situations typically motivate an immediate and automatic fight-or-flight response (LeDoux, 2000; Phelps, 2006). However, because of its anxiolytic effects at both the physiological and neurological level, oxytocin may allow the individual to consider alternatives to fight-or-flight, including pro-social approach (Lim and Young, 2006; Heinrichs et al., 2009; Taylor et al., 2000). Indeed, individuals given oxytocin rather than placebo respond less fearfully to angry faces (Evans et al., 2010), and couples given intranasal oxytocin rather than placebo engage in more constructive discussions of relationship conflicts (Ditzen et al., 2009).

Direct evidence for the possibility that oxytocin enables the individual to consider pro-social approach derives from studies infusing exogenous oxytocin (versus placebo) before participants make monetary donations to a protagonist in a (variation of) the so-called trust-game (Berg et al., 1995). The Trust Game involves two participants, each with a \$10 endowment. Player 1 (henceforth Investor) is asked to choose an amount to be transferred to Player 2 (henceforth Trustee). As explained to both participants, the amount transferred by Investor is tripled on the way to Trustee. Trustee is then asked to choose an amount to back-transfer to Investor. The back-transfer is not tripled, and the final amounts in the two accounts are paid. In this game, the main reason for Investors to transfer is trust: the positive expectation that Trustee will reciprocate and transfer back. To Trustees, the main reason to back-transfer is other-concern.

A pioneering study by Kosfeld et al. (2005) showed that oxytocin influences Investor's transfer. Healthy males self-administered through nasal spray either 24 IU placebo or oxytocin and, after 45 min, engaged in a Trust Game. More Investors in the oxytocin group than in the placebo group transferred the maximum amount, and the average transfer was also somewhat higher among participants given oxytocin rather than placebo. A follow-up study by Baumgartner et al. (2008) considered Investor transfers both before and after they learned about their Trustee's back transfer (set at a constant 50% back transfer in 6 trials of the trust game). Intranasal oxytocin did not influence pre-feedback transfers by Investors. However, after Investors learned that Trustees back-transferred in 50% of the trials, Investors given oxytocin continued to make substantial transfers whereas those given placebo significantly decreased their transfers. Thus, oxytocin inoculated betrayal aversion among Investors (also see Rilling et al., 2012).⁵

The effects of oxytocin on trust and betrayal aversion not only pertain to monetary, but also social decisions. For example, Keri and Kiss (2011) observed higher levels of blood plasma oxytocin among participants when they released an important secret to their experimenter, compared to when they exchanged a neutral message. Mikolajczak et al. (2010a) gave male participants either oxytocin or placebo and asked them to complete a sexual fantasies questionnaire that inquired about purposefully very intimate sexual fantasies typically not shared with strangers. Forty minutes later participants were asked to put their sexual fantasies questionnaire in an envelope and to hand it to the experimenter. Participants were free to seal the envelope or not, and whether the envelope was sealed was taken as reflecting (dis)trust in the experimenter (i.e., that he might violate his instructions not to look at the participant's answers). Sixty percent of the participants given oxytocin did not seal their envelope, whereas only 3% of the participants given placebo left their envelope open. This suggests that oxytocin increases trust not only in financial but also in social exchange.

Evidence that oxytocin-modulated trust is parochial

Research findings thus far are consistent with the proposition in Fig. 1 that because oxytocin dampens amygdala activity, it enables trust to develop. An important qualifier in Fig. 1 is that these effects emerge especially when protagonists are categorized as in-group. Indirect support for this proposition derives from studies showing stronger effect of oxytocin on trust and cooperation when protagonists are (displayed as) benign and trustworthy, or are familiar rather than unfamiliar to the individual (with familiarity promoting in-group categorization; Castelli et al., 2004). Specifically, when trustees were anonymous strangers, effects of oxytocin on average Investor transfer were statistically weak (Kosfeld et al., 2005), and absent (on pre-feedback trials; Baumgartner et al., 2008). Furthermore, in both the Mikolajczak et al. (2010a) and the Keri and Kiss (2011) studies did the experimenter serve as protagonist and perhaps experimenters are perceived as more benign than anonymous strangers. Using the trust game, Mikolajczak et al. (2010b) indeed showed that Investors given oxytocin rather than placebo transferred more money to Trustees that were described as a pro-social person (e.g., studying philosophy, practicing first aid). When Trustees were described in less pro-social terms (e.g., studying marketing, practicing violent combat sports), oxytocin no longer influenced Investor behavior. Finally, Declerck et al. (2010) studied cooperation in an Assurance Game where the only reason not to cooperate is distrust (Colman, 2003; Bornstein, 2003), and found that individuals given oxytocin expected more cooperation and cooperated

⁵ An important side-result in both the Kosfeld et al. and the Baumgartner et al. studies is that when Investors were told that transfer-back decisions would be determined by a random mechanism, no effects of oxytocin were found. This rules out that trust and trust betrayal responses merely reflect risk-tolerance and that oxytocin modulates risk-tolerance rather than trust (see Kosfeld et al., 2005).

more but only when they had familiarized themselves with their protagonist. Absent such positive prior interaction, oxytocin actually led to less cooperation than placebo.

Taken together, oxytocin reduces fear and anxiety at both the neural and the behavioral level. It seems that especially with familiar and relatively benign protagonists this translates in greater trust, and more cooperation. When protagonists were described in less benign terms, or when prior interaction was absent and protagonists were fully anonymous, oxytocin had no or even negative effects on trust and cooperation. These findings provide indirect support for the proposition in Fig. 1 that oxytocin modulates trust and cooperation towards in-group members, and not towards out-groups. More direct evidence for this proposition will be discussed in the next section, after we have reviewed work indicating that oxytocin (also) modulates cooperation and other-concern partly because it up-regulates neural and behavioral expression of empathy.

Oxytocin up-regulates empathic other-concern

Other-concern more readily develops for others that are in-group, rather than out-group (Hein et al., 2010; Van der Schalk et al., 2011; Wu et al., 2011). Furthermore, people feel empathic and develop high other-concern when in-group others, with whom one seeks to align and cooperate, are perceived to be sad, distressed, embarrassed, disappointed, or guilty (Batson, 1998; Van Kleef et al., 2010). Interestingly, there is reason to assume empathy and other-concern is mediated by oxytocin. 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 are more stimulating of their toddler's exploration and showed less hostility (Naber et al., 2010), and in males exposed to biological motion, intranasal oxytocin modulated neural circuitries involved in affective perspective taking (Keri and Benedek, 2009; Perry et al., 2010; also see Gallese et al., 2004). Other studies showed that participants given oxytocin rather than placebo have increased sensitivity to other's fear (Fischer-Shofty et al., 2010), empathize more for persons depicted in emotionally charged situations (Hurlemann et al., 2010; but see Singer et al., 2008), rate images of neutral faces as more trustworthy and attractive (Theodoridou et al., 2009), and more accurately infer emotions expressed by others (Domes et al., 2007; also see Roderigues et al., 2009).

Consistent with these findings, there is evidence also that oxytocin modulates behavioral expressions of other-concern and motivates fairness. Following trust-signaling by their Investors, Trustees' back-transfers were positively correlated with oxytocin levels in their blood plasma (Zak et al., 2005; Morhenn et al., 2008). Likewise, individuals given oxytocin rather than placebo were more willing to interact again with others who previously included the participant in a ball-tossing game, but not with others who previously ostracized the individual (Alvares et al., 2010; also see Andari et al., 2010). Finally, individuals given oxytocin rather than placebo make more generous offers in two-party ultimatum bargaining where a proposer is asked to propose a split of \$10 into P for the responder and \$10-P for himself (Zak et al., 2007). The responder can accept the proposal in which case payments were made, or the responder can reject the proposal, in which case the proposer and the responder are paid nothing.⁶ However, whereas proposers in the Zak et al. study were more generous when given oxytocin, responders' punishment thresholds (i.e., the

level at which they would reject offers) were unaffected by oxytocin. Also, when asked to split \$10 into D for the other person and \$10-D for oneself (the other person had no decision to make), oxytocin had no effect on the amount offered (Zak et al., 2007).

In all, the research evidence suggests that oxytocin up-regulates neural and behavioral expressions of other-concern. It should be noted, however, that other-concern is a multifaceted construct that includes a concern for other's outcomes and interests, a desire for fairness, and a desire for mutual rather than personal benefit (see Footnotes 3 and 4). Targeted research is needed to increase our understanding of the specific facets of other-concern that are influenced by oxytocin. For example, in some of the above works (e.g., Zak et al., 2007), oxytocin seemed to influence fairness considerations (as measured through offers in the Ultimatum Game) but not concern for other's outcomes (as measured through offers in the Dictator Game). Such new research could also test for alternative interpretations, in that some findings may reflect increased adherence to pro-social norms, or strategic maneuvering, rather than "genuine" other-concern.

Oxytocin motivates in-group favoritism and parochial cooperation

Fig. 1 proposed that the effects of oxytocin on empathy and concomitant cooperation emerge especially when protagonists are categorized as in-group, and not when they are categorized as out-group. This proposition was tested in De Dreu et al. (2011a). Based on the well-established finding that humans positively value and evaluate in-group members (henceforth "in-group favoritism"), and sometimes negatively value and evaluate out-group members (henceforth "out-group derogation;" Dovidio and Gaertner, 2010; Yzerbyt and Demoulin, 2010), De Dreu et al. hypothesized that oxytocin motivates in-group favoritism and, perhaps, out-group derogation. In five experiments, indigenous Dutch males received oxytocin or placebo in a double-blind, randomized between-subjects design and, after 40 min, were exposed to images of in-group targets (Dutch males) or out-group targets (males from Middle-Eastern descent or, in other experiments, Germans). Using different methods, De Dreu et al. indeed found that oxytocin motivated stronger in-group favoritism – in-group targets elicited stronger positive and more benevolent associations when participants received oxytocin rather than placebo. Weak and possibly unreliable effects were found on out-group derogation.

Two aspects of these results are noteworthy. First, and consistent with Fig. 1, these data suggest that oxytocin up-regulates empathy for in-group members but does not create more benevolent views of others generally, or expanded social categories. If that would have been the case, the data should have shown not only increased in-group favoritism but also more positive views and evaluations of out-group members. In none of the experiments reported in De Dreu et al. (2011a) this was the case (also see Chen et al., 2011; De Dreu et al., 2011b). Second, these results imply that oxytocin motivates parochial cooperation with in-group members, and not with individuals belonging to out-groups. Two experiments reported in De Dreu et al. (2010) tested this implication directly. Males self-administered through nasal spray 24 IU oxytocin or placebo. Forty minutes later they were, on the basis of a trivial criterion, categorized into two three-person groups, and engaged in an Intergroup Prisoner's Dilemma—Maximizing Differences Game (IPD-MD; Halevy et al., 2008). Each individual received €10 and was allowed to invest all or part of it in a within-group pool, and in a between-group pool. Within-group pool investments were multiplied by 1.5 and equally distributed among in-group members (i.e., for each Euro invested, each member received €0.50). Within-group pool investments thus reflect in-group love—the motivation to benefit in-group members at a cost to oneself. Between-group pool investments had the same consequence to the in-group as within-group pool investments, but also reduced the endowments of the three out-group members by a factor of 1.5 (i.e., for each Euro invested, each in-group member gained €0.50, and each

⁶ Proposers motivated by greed should offer the smallest possible portion to the responder and responders motivated by greed should accept anything greater than zero. Empirically, few individuals in this type of setting are motivated by greed only: Proposers commonly propose (close to) equal splits ($P \approx \$10-P$), and recipients commonly reject too strong deviations from equal split. Such tendencies toward equal split proposals reflect other-concern (sometimes referred to as inequity aversion, Fehr and Gächter, 2002): Proposers desire to be fair in and of itself, or anticipate their responder to respond to unfairness with spite; Responders punish unfairness because of spite and reputation concerns (e.g., Pillutla and Murnighan, 1996; Van Dijk et al., 2004).

out-group member lost €0.50). Between-group pool investments thus reflect out-group hate—the motivation to hurt the out-group at a cost to oneself (Haley et al., 2008).

Fig. 2 summarizes the number of participants predominantly contributing to in-group love, or out-group hate, as a function of treatment. It shows that across the two experiments reported in De Dreu et al. (2010), more participants in the oxytocin than placebo condition opted for an in-group love allocation strategy, whereas more participants in the placebo than oxytocin condition kept the bulk of their endowment to themselves (no effects were found on the number of participants investing in out-group hate). De Dreu et al. reported that males given oxytocin rather placebo (i) displayed more in-group love; (ii) expected other in-group members to contribute more to in-group love; (iii) did not invest more or less in out-group hate; and (iv) had similar levels of distrust for the out-group.

Taken together, in both humans and non-humans, oxytocin enables social discrimination (Ferguson et al., 2000; Macbeth et al., 2009), motivates in-group favoritism (De Dreu et al., 2011a, 2011b), and increases parochial altruism and cooperation. Oxytocin neither increases nor decreases distrust and spiteful behavior towards rivaling out-groups.

Oxytocin motivates non-cooperation towards rivaling out-groups

Other-concern not only promotes in-group love but also tendencies to help and protect those others through increased competition towards outsiders (Arrow, 2007). In intergroup competition, one's in-group is served well not only by in-group love, but also by (i) defensive aggression such as launching pre-emptive strikes that reduce or even neutralize the threat posed by out-groups (Darwin, 1873; Jervis, 1976); and (ii) offensive aggression aimed at winning the competition and exploiting rivaling out-groups (Boyd and Richerson, 1982). There is indeed substantial evidence that in intergroup competition, humans promote their in-group through increased cooperation with in-group members (Bornstein, 2003; Puurtinen and Mappes, 2009) and increased competition towards the out-group (Wildschut et al., 2003).

The above results on in-group favoritism and parochial cooperation suggested that oxytocin does not motivate out-group derogation and out-group hate. However, it cannot be excluded that oxytocin motivates in-group protection through defense-motivated non-cooperation. Three lines of research support this possibility. First, there is evidence that lactating Wistar rats selectively bred for high anxiety-related behaviors (HAB) show more maternal aggression against a virgin intruder compared to Wistar rats bred for low anxiety-related behaviors (LAB) (Bosch et al., 2005). In this study, maternal aggression was positively correlated with oxytocin release in the paraventricular nucleus among HAB-rats, and negatively

correlated in LAB-rats. Finally, blockade of endogenous oxytocin action by infusion of an oxytocin receptor antagonist reduced maternal aggression among HAB dams, and increased aggression among LAB dams. Bosch et al. (2005) conclude that maternal aggression serves to protect offspring, and from this study it thus follows whereas oxytocin reduces defense-motivated aggression towards outsiders among low-anxiety individuals, it up-regulates aggression among high-anxiety individuals.

Second, De Dreu et al. (2010, Exp. 3) provided a conceptual replication and extension of the results reported in Bosch et al. (2005). Participants played a Prisoner's Dilemma between their own in-group, and a three-person out-group—they choose between cooperation and non-cooperation, with outcomes from their decision accruing to the in-group (the decision maker included). The cardinal payoffs of the Prisoner's Dilemma were manipulated so that out-group non-cooperation (rather than cooperation) had either strong or weak negative effects on in-group outcomes.⁷ In this game, to prevent negative effects of possible out-group non-cooperation, individuals should choose the non-cooperative rather than cooperative alternative themselves. Results showed that the variation in out-group threat interacted with whether participants received intranasal oxytocin or placebo. When out-group threat was low, treatment had no effect on non-cooperation towards the out-group; when out-group threat was high, however, group members were significantly more non-cooperative towards the out-group when they had been given oxytocin rather than placebo. From these results, De Dreu et al. concluded that oxytocin motivates humans to be non-cooperative with rivaling out-groups especially when the out-group represents a threat to the individual's in-group.

The third and final piece of evidence for the notion that oxytocin motivates non-cooperation towards out-groups comes from a study on coalition-formation (De Dreu et al., *in press*). In this study, participants engaged in an intergroup competition and were then asked to select allies into their team. They were shown faces of potential allies that were morphed into either high threat (low on trustworthiness and high on dominance) or low threat (high on trustworthiness and low on dominance; see e.g. Oosterhof and Todorov, 2008). Males that were given oxytocin rather than placebo selected more high-than low-threat allies into their team, and rated these high-threat targets as more useful. The authors concluded that in intergroup competition, oxytocin motivates humans to select allies that have high threat potential and appear aggressive rather than friendly, presumably to make their in-group a stronger and more threatening competitor to rivaling out-groups.

Conclusions and avenues for future research

The research reviewed here shows that hypothalamic release (or infusion) of oxytocin (i) down-regulates fear and anxiety, and enables trust to develop especially with protagonists that are familiar and/or categorized as in-group; (ii) motivates empathic other-concern, in-group favoritism, and parochial cooperation; and (iii) motivates non-cooperation towards potentially threatening out-groups. These conclusions subscribe to the emerging insight that oxytocin-induced goodwill (empathy, trust, cooperation) is far from indiscriminate and highly contingent upon the perceived features and characteristics of goodwill's targets (Chen et al., 2011; De Dreu et al., 2011a, 2011b; Bartz et al., 2010). Conclusions also fit the Darwinian insight that human self-sacrifice and cooperation serve in-group functioning and thereby enhance individual prosperity and survival. Accordingly, the oxytocinergic

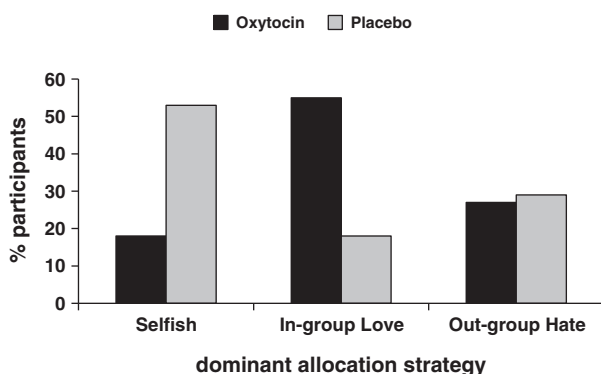


Fig. 2. In intergroup competition oxytocin increases contributions to benefit the in-group but not to hurt the out-group. Bars reflect percentage of participants in De Dreu et al. (2010; Exp. and 2 combined; $N = 116$ males) keeping their endowment (selfish), donating most to benefit the in-group (in-group love), and donating most to hurt the out-group (out-group hate).

⁷ The experiment also manipulated the extent to which it was rewarding to exploit out-group cooperation. Consistent with the finding that oxytocin does not modulate out-group derogation (De Dreu et al., 2011a, 2011b), or spiteful tendencies to hurt the out-group (De Dreu et al., 2010 Exp. 1 and 2), oxytocin did not modulate out-group exploitation.

circuitry may have evolved to sustain within-group cooperation, in-group protection, and if needed, competition towards rivaling out-groups. In the remainder of this section, I elaborate on these conclusions, and point out gaps in our understanding of the link between oxytocin on the one hand, and human cooperation on the other.

Opening the black box

The insights and conclusions just summarized emerge when we take a bird's eye perspective on the emerging research literatures, yet allow ourselves some leaps of faith too. In fact, there are a number of concerns with the existing evidence that require new research. First, the link between oxytocin and brain-level responses in empathy-related brain circuitries, including the inferior frontal gyrus and the ventromedial prefrontal cortex needs further testing, especially when targets are categorized as in-group versus out-group. Related, the link between oxytocin and expressions of trust, other-concern, and cooperation toward in-group versus out-group targets remains elusive. There are important gaps in our understanding of the transfer from hypothalamic release of oxytocin, and expressions of complex social behaviors like cooperation. Research is needed to fill these voids, and in doing so needs to take into account the features and characteristics of the targets of cooperation—we need brain imaging research that takes seriously the notion that human cooperation and non-cooperation is modulated by the interaction between neuropeptides and features of the social environment within which cooperation takes place (for an example, see [Rilling et al., 2012](#)).

An issue of broader concern is that all studies on oxytocin and human cooperation forced individuals to decide cooperatively or not, with non-cooperation being taken as indicative of distrust and competitive motivation. Such an inference overlooks the fact that in many social settings individuals prefer leaving the situation rather than either cooperating with, or competing against their protagonist. Although oxytocin seems to promote social approach and not social avoidance ([Kemp and Guastella, 2011](#)), it cannot be excluded that with not-so-benign protagonists, oxytocin associates with increased withdrawal—when given the choice, oxytocin may actually motivate people to not playing the trust game, the ultimatum bargaining game, or the intergroup prisoner's dilemma game. Future research on oxytocin and human cooperation would benefit from research paradigms that include a broader repertoire of behavioral options, withdrawal being one of them (e.g., [Miller and Holmes, 1975](#); [Shalvi et al., 2011](#)).

From social recognition to social discrimination

The research discussed here suggested that effects of oxytocin on behavioral expressions of trust, empathy, and cooperation may be stronger when protagonists are categorized as in-group, and may even reverse when others are seen as out-group. Furthermore, based on studies into social amnesia in rodents and voles ([Ferguson et al., 2000, 2002](#); [Macbeth et al., 2009](#)), it was hypothesized that oxytocin facilitates classification of others as in-group versus out-group. Such social discrimination in non-human mammals involves the olfactory bulb, which is dense with oxytocin receptors ([Ferguson et al., 2000](#)). However, while similar processes may be operating in humans, humans also discriminate others on the basis of perceptual and cognitive cues such as physical appearance and attitude similarity, and auditory cues such as native language spoken (for reviews, see [Dovidio and Gaertner, 2010](#); [Yzerbyt and Demoulin, 2010](#)). Research is needed to test the proposition that oxytocin guides social discrimination in humans, and to uncover whether and how oxytocin modulates the neural circuitries involved in classifying others into in-group versus out-group on the basis of perceptual and/or auditory cues. Such research is needed also to clearly distinguish between mere

categorization, and the motivation to treat familiar/in-group others more positively than unfamiliar/out-group others.

From parochial cooperation to in-group maintenance

The studies reviewed here suggest that oxytocin plays a particularly important role in a broad variety of behaviors aimed at sustaining, maintaining, and improving social life within one's in-group. To date, research almost exclusively focused on either social cognition measures of facial recognition and liking, or behavioral measures of trust and cooperation. However, if indeed oxytocin serves as a single neurohormonal mechanism underlying these and related forms of within-group cooperation, it follows that a broader variety of social behaviors should be affected by oxytocin as well. In free-living meerkats, for example, peripheral administration of oxytocin increased a suite of cooperative behaviors, including digging, guarding, pup-feeding, and associating with pups ([Madden and Clutton-Brock, 2011](#)). In humans, oxytocin motivates the selection of high rather than low threat allies that are particularly instrumental in protecting the in-group against outside dangers, including those posed by rivaling out-groups ([De Dreu et al., in press](#)).

To support group life, humans enforce and comply with group norms, exchange information, and create and invent ideas and problem solutions that facilitate group survival and prosperity ([Alexander, 1990](#); [De Dreu et al., 2008](#); [Rilling and Sanfey, 2011](#)). An intriguing question for new research is whether, in humans, oxytocin indeed modulates a broader variety of group maintenance behaviors, including norm compliance and enforcement, information sharing, and perhaps even group problem solving and creativity. If true, this would further support and underline the emerging insight that one of the primary functions of oxytocin includes sustaining and promoting group life.

From in-group love to intergroup tension

Evolutionary theory suggests that intergroup competition fuels within-group cooperation, and that within-group cooperation serves survival in intergroup competition and conflict. Throughout this review, it became clear that oxytocin modulates other-concern for benign protagonists, in-group favoritism, and within-group but not between-group trust and cooperation. Moreover, oxytocin stimulated non-cooperation towards the out-group when the out-group constituted an imminent threat to the in-group.

These findings suggest that oxytocin indirectly contributes to intergroup competition and conflict. First, in-group favoritism alone or in combination with out-group derogation creates intergroup bias – in-group members get relatively better treatment and receive benefits more readily than out-group members ([Brewer, 1999](#); [Dovidio and Gaertner, 2010](#); [Fiske, 2002](#)). Because such unfair treatment triggers negative emotions, violent protest, and aggression among disfavored and excluded individuals ([Hewstone et al., 2002](#)), by stimulating in-group favoritism oxytocin may trigger a chain reaction towards intense between-group conflict. Second, through its effects on within-group cooperation, oxytocin contributes to making the in-group well-functioning and strong, not only in absolute terms but also relative to rivaling out-groups. Perceiving such effective and relatively strong groups may trigger, among rivaling out-groups, pre-emptive strikes and aggression ([De Dreu, 2010](#); [Deutsch, 1973](#); [Jervis, 1976](#)). Again, oxytocin's effects on within-group cooperation may, inadvertently, contribute to elevated levels of intergroup tension, competition, and conflict.

That oxytocin is involved in, and may even indirectly promote intergroup tension and conflict, is thought-provoking and potentially relevant to our understanding of the broader social functions of oxytocin. However, the supporting evidence is limited, and replications and extensions are needed. First, in humans oxytocin motivated

inter-group competition when out-group threat was high and not when out-group threat was low (De Dreu et al., 2010). In nursing rats, oxytocin motivated aggression against intruders when rats were bred for high anxiety; among those bred for low anxiety, oxytocin actually reduced aggression against intruders (Bosch et al., 2005). Thus, there may be important individual differences and contextual factors that temper or even reverse effects of oxytocin on inter-group competition, and research is needed to uncover and document these moderators. Second, current evidence is limited to one-shot interactions, in which competing groups had no history or future together. Theoretically, one would expect escalatory spirals set in motion by oxytocin-induced in-group favoritism and parochial cooperation. Research is needed, however, to test such unfolding of cooperation and aggression over time. Furthermore, there is a wealth of factors associated with intergroup relations known to affect intergroup competition and cooperation, including power and status differences, and history of conflict or cooperation (for reviews see e.g., De Dreu, 2010; Dovidio and Gaertner, 2010; Fiske, 2010).

Coda

In humans, the evolutionary ancient and highly preserved neuropeptide oxytocin modulates a range of cognitive and behavioral functions related to affiliation and pair bonding. Close scrutiny of recent experiments on social judgment and decision making in humans reveals that oxytocin's effects on trust, other-concern, and cooperation emerge especially with benign protagonists and those seen as belonging to one's in-group. Oxytocin also modulates protection of in-group members through the selection of high rather than low threat allies and through competition against threatening outsiders. Thus, in addition to reproduction and pair-bond formation, the oxytocinergic circuitry serves to "tend-and-defend" the in-group.

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