Review

Oxytocin Conditions Intergroup Relations Through Upregulated In-Group Empathy, Cooperation, Conformity, and Defense

Carsten K.W. De Dreu and Mariska E. Kret

ABSTRACT

Humans live in, rely on, and contribute to groups. Evolution may have biologically prepared them to quickly identify others as belonging to the in-group (versus not), to decode emotional states, and to empathize with in-group members; to learn and conform to group norms and cultural practices; to extend and reciprocate trust and cooperation; and to aggressively protect the in-group against outside threat. We review evidence that these components of human group psychology rest on and are modulated by the hypothalamic neuropeptide oxytocin. It appears that oxytocin motivates and enables humans to 1) like and empathize with others in their groups, 2) comply with group norms and cultural practices, and 3) extend and reciprocate trust and cooperation, which may give rise to intergroup discrimination and sometimes defensive aggression against threatening (members of) out-groups. We explore the possibility that deficiencies in (components of) group psychology, seen in autistic spectrum disorder, schizophrenia, and borderline personality and social anxiety disorders, may be reduced by oxytocin administration. Avenues for new research are highlighted, and implications for the role of oxytocin in cooperation and competition within and between groups are discussed.

Keywords: Cognitive neuroscience, Cooperation, Intergroup discrimination, Neuropeptides, Psychopathology, Social cognition

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Humans are social animals and much of their evolutionary success has been attributed to their strong capacity for cooperation within groups (1,2). Relative to other species, humans are more likely to cooperate with unfamiliar and genetically nonrelated others and to create cohesive groups that include genetically unrelated others (3). It is within such groups, where members are interconnected and share a common fate, that humans developed artistic expressions, cultural rituals, and language (4); perfected ways to disseminate knowledge, insights, values, and preferences (5); learned to negotiate and trade (6); and designed and implemented social and technological innovations (7,8).

Because groups have been, and continue to be, pivotal to human survival and prosperity, evolution may have biologically prepared humans for developing a sophisticated group psychology that enables them to live in, rely on, and contribute to social groups (1). Such group psychology includes, but is not limited to, the ability to distinguish others on the basis of group membership, to signal and decode emotional states and empathize with others within one's group, to learn and comply with group norms and cultural practices, and, last but not least, to extend and reciprocate trust and cooperation with fellow group members (1,9–13). Importantly, these interrelated facets of human group psychology not only oil group functioning both absolutely and relative to other groups but also enable the individual to fit into a group, to profit from the safety and security it provides against outside threat, to be included

in potentially beneficial exchanges with others, and to receive social support. Vice versa, impairments in (components of) such group psychology undermine social inclusion and fitting in (14). Individuals chronically suffering from such impairments, including those diagnosed with autism spectrum disorder, schizophrenia, borderline personality disorder, or social anxiety disorder, risk lack of social support and have reduced well-being and poor health (15–17).

Here, we review evidence that key components of human group psychology rest on and are modulated by the evolutionary ancient hypothalamic neuropeptide oxytocin. We explore the role of oxytocin in combatting deficiencies in (components of) group psychology seen in autism spectrum disorder, schizophrenia, borderline personality disorder, and social phobia (18). We conclude that oxytocin motivates and enables tendencies to 1) like and empathize with others in their groups, 2) comply with group norms and cultural practices, 3) extend and reciprocate trust and cooperation, and 4) discriminate against and aggress rivaling out-groups and that oxytocin administration may effectively challenge dysfunctional deficiencies in these tendencies, as typically seen in a range of psychiatric disorders.

FEAR DAMPENING, SOCIAL SALIENCE, AND BIASED BIOBEHAVIORAL APPROACH AVOIDANCE

Oxytocin is a nine amino acid peptide hormone that is synthesized primarily in the paraventricular and supraoptic nuclei of the hypothalamus (19–22). Upon its release from neuronal soma, axons, and dendrites, oxytocin acts as a neuromodulator—it flows through neural tissue by a process termed volume transmission, which allows the oxytocin molecule to quickly modulate social emotional functions of the amygdala and brain stem (19,23,24). In addition, oxytocin targets the hippocampus and interacts with reward processing circuitries including the caudate nucleus, the nucleus accumbens, and the inferior frontal gyrus (20,21,25).

Through its interaction with the hypothalamic-pituitaryadrenal axis, oxytocin attenuates stress responses at both the body and neural level (19,26,27). For example, intranasal administration of oxytocin reduces cortisol levels after exposure to stressors (28-30) and inhibits cardiovascular stress responses (31,32). There is evidence too that intranasal oxytocin dampens amygdala responses to fear-provoking stimuli (33,34), although this is seen especially in male subjects (35,36) and may be contingent on early life experiences (16,37,38). Finally, oxytocin blunts attention to negative social cues such as angry faces and displays of dominance (38-41), and in patients with anxiety disorders, intranasal oxytocin attenuates hyperactivity in the amygdala when social cues conveying threat are displayed (42). Accordingly, in Vietnam veterans with posttraumatic stress disorder, oxytocin attenuated physiological responses during personal combat imagery (31). Oxytocin also protects against negative behavioral and autonomic consequences of long-term social isolation (43). The combination of intranasal oxytocin and social support reduces stress indexed by both self-report and endogenous cortisol (44).

In addition to its anxiolytic effects, oxytocin also modulates dopaminergic circuitries involved in reward processing and empathic responding (20,21,25,45–47). Accordingly, intranasal oxytocin strengthens general tendencies in social-cognitive processing. This social-salience account implies that what is usually considered positive and interesting becomes more positive and interesting under oxytocin, and what is commonly considered negative and aversive becomes more negative and aversive under oxytocin (48–50). Thus, when given oxytocin (versus matching placebo) and asked to recall memories of

maternal care and closeness, securely attached male subjects recalled more positive events, while anxiously attached male subjects recalled more negative experiences (48,51). Also, oxytocin stimulated positive responding to friendly faces and negative responding to unfriendly faces (49), and following an interpersonal competition, oxytocin enhanced envy when the competition was lost and Schadenfreude (gloating) when the competition was won (50).

Possibly through the combination of fear dampening and increased social salience, oxytocin 1) acts on the wanting mesocorticolimbic circuitry promoting (affiliative) approach, especially when (social) targets or events have positive valence; and 2) acts on the cortico-amygdala circuitry to reduce withdrawal from (social) threat, thus permitting alternative responses to danger and threat than flight (52-56) (Figure 1). Such oxytocin-biased biobehavioral approach avoidance resonates with a wealth of research showing that, first of all, oxytocin promotes social bonding between sexual partners (57-60) and enables positive parent-offspring interactions such as play and caring (61-63). This, as shown in Figure 1, translates also into enhanced tendencies to empathize, affiliate, conform, and cooperate with others, especially when these others are seen as familiar and in-group (Figure 1). Second, oxytocin-biased biobehavioral approach avoidance fits evidence that intranasal oxytocin potentiates startle reactivity to threat stimuli, especially when these are unpredictable (35,56,64) and the growing evidence that oxytocin prepares for and enables aggressive responding to threat, especially threat to offspring (viz. maternal defense) (65-69). One recent study showed that in humans, intranasal administration of oxytocin reduces calculated aggression to subordinate others and acquire their resources but does not incapacitate defensive aggression aimed at protecting against predation (53). Thus, through its dampening of the cortico-amygdala circuitry, oxytocin permits alternative responses to threat than flight and may upregulate vigilance and defense-motivated aggression aimed at protecting oneself and in-group members against outside threats, including those posed by human enemies (Figure 1).

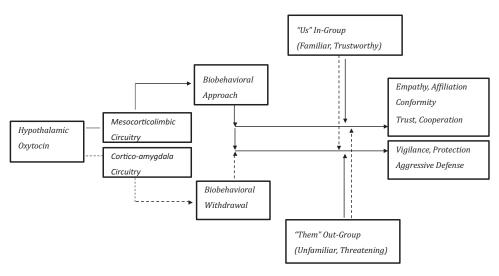


Figure 1. Oxytocin modulates group psychology through biased biobehavioral approach/withdrawal. Dashed (solid) lines are inhibitory (facilitating).

OXYTOCIN MOTIVATES INTERGROUP DISCRIMINATION BECAUSE OF ENHANCED IN-GROUP LOVE

As shown in Figure 1, oxytocin's biasing of biobehavioral approach/avoidance relates to a suite of motivational, cognitive, and behavioral tendencies within groups and toward individuals seen as belonging to (rivaling) out-groups. To fully appreciate this, it is important to emphasize that 1) groups rarely exist in isolation and often compare, cooperate, and compete with other groups; and 2) human group psychology is, therefore, concerned also with the comparative features of one's in-group relative to more or less salient out-groups (1,13). Human group psychology has a marked in-group bias: emotions from in-group members are encoded faster and more accurately than those from out-group members (9,10); in-group members are liked better and their shortcomings and defects are downplayed more (70); empathic responding is stronger when others are in-group rather than out-group (13,71); and trust and cooperation are extended to in-groups more than to out-groups (72). Thus, as shown in Figure 1, biobehavioral approach manifests in empathy, affiliation, conformity, and trust and cooperation, especially when targets are categorized as in-group and seen as familiar and essentially trustworthy. When targets are categorized as out-group and seen as unfamiliar and potentially threatening, prosocial responses are less likely, and instead, vigilance and protective shielding are enhanced.

Because human group psychology is in-group biased, it quickly gives rise to intergroup discrimination, where (members of) the in-group receive relatively beneficial treatment compared with (members of) more or less relevant out-groups (73–76). Theoretically, intergroup discrimination can be due to increased in-group love (behavior that benefits the in-group and its members) and/or out-group hate (behavior that hurts the out-group and its members). Evidence shows, however, that intergroup discrimination is mostly due to in-group love and rarely due to out-group hate (1,13,72–77). In Figure 1, this means that tendencies to empathize with and extend trust and cooperation toward in-group members explain the differential treatment of in-group and out-group members more than the vigilance vis-à-vis, and defensive aggression against, potentially threatening out-groups.

A number of studies suggest that oxytocin amplifies intergroup discrimination, that is, differential treatment of others classified as in-group rather than out-group. This work considered interpersonal decision making, where cooperation is personally more costly yet collectively more beneficial than noncooperation. In such situations, individuals given oxytocin extended more trust and made more cooperative choices than those given placebo, especially when participants familiarized with each other before decision making (78-80) or when the protagonist was depicted as trustworthy rather than potentially untrustworthy (81). For example, Ten Velden et al. (82) designed an incentivized two-player poker game with either an in-group or out-group protagonist. Seventy-two healthy male subjects received 24 IU oxytocin or matching placebo and played four rounds of poker with another individual from either their in-group or a rivaling out-group. Compared with placebo, participants under oxytocin settled more and competed less with an in-group compared with an out-group protagonist. These results suggest that oxytocin sensitizes humans to the group membership of their interaction partner, rendering them relatively more benevolent and less competitive toward those seen as belonging to their own group.

To unravel whether intergroup discrimination under oxytocin was due to increases in in-group love, out-group hate, or some combination, De Dreu et al. (83) gave indigenous Dutch male subjects oxytocin or placebo in a double-blind, randomized between-subjects design and, after 40 minutes, exposed them to images of in-group targets (Dutch male subjects) or out-group targets (male subjects from Middle-eastern descent or in other experiments, Germans). Across five experiments that used different methods to track intergroup discrimination, oxytocin motivated intergroup discrimination primarily because it promoted in-group love: in-group targets elicited stronger positive associations when participants received oxytocin rather than placebo. Others found that individuals receiving oxytocin attached greater value to and liked better their own nation's cultural symbols such as the national flag and its leadership (84) and that oxytocin increased in-group bias in neural responses (85) and intergroup discrimination not only in healthy control subjects but also in schizophrenia patients (86).

Across these studies, weak and inconclusive effects were found for out-group hate, suggesting that oxytocin produces intergroup discrimination primarily when and because it motivates in-group love and a shift in focus from the individual's self-interests toward the interests of the in-group. If true, we should see that oxytocin upregulates group-serving behavior even in the absence of any out-group. Evidence for this possibility was provided by a double-blind placebo-controlled experiment allowing individuals to lie privately and anonymously to benefit themselves and fellow group members (87). Results showed that healthy male subjects receiving intranasal oxytocin, rather than placebo, lied more to benefit their group and did so faster, yet not necessarily because they expected reciprocal dishonesty from fellow group members. In a control condition where dishonesty only benefited participants themselves but not fellow group members, oxytocin did not influence lying. Thus, oxytocin motivated group-benefitting behavior, even in the absence of intergroup competition.

Together, these studies suggest that 1) oxytocin promotes intergroup discrimination, because 2) oxytocin strengthens ingroup bounded empathy and in-group love and 3) oxytocin does not affect out-group hate. Results also suggest that oxytocin creates neither more benevolent views of others generally nor a tendency to develop more expanded and inclusive social categories. If that would have been the case, the data should have shown positive views and evaluations of in-group and out-group members alike, and this is not what was found (86,88,89).

OXYTOCIN MOTIVATES IN-GROUP CONFORMITY

Group psychology involves benevolent views of in-group members and willingness to cooperate with them. It also involves a tendency to conform to group rules and regulations, to adapt to preferences and opinions expressed by fellow

in-group members, and to adhere to in-group norms. Indeed, humans have a strong tendency toward in-group conformity (90–92), and this may be partly explained by its adaptive value (93). By conforming to the common behaviors and shared opinions of one's own group or community, members secure inclusion and avoid being ostracized, and they benefit from the wisdom of the group as a whole. Vice versa, groups with members that comply with group norms and practices may, across the board, function well and avoid within-group fighting and conflict.

Conformity can be with regard to attitudes and evaluations (henceforth opinions) and with regard to factual representations of the social and nonsocial world (henceforth beliefs) (94–97). It can take the form of compliance, when individuals go along with the majority view within their group in public but do not change their privately held opinions and beliefs. Sometimes, however, conformity is relatively deep in that individuals also adapt their privately held opinions and beliefs to those held by the majority view within their group (henceforth conversion) (98). This distinction is important because there is evidence that intranasal oxytocin motivates in-group conformity on both opinions and beliefs (99,100), yet also that such conformity is short-lived and not accompanied by conversion of structural changes in underlying cognitive structures (100). Specifically, Edelson et al. (100) showed participants an eyewitness styled documentary in groups of six to eight people who were told that their performance would be compared with that of other groups. Three days later, participants returned and were tested for their memory of facts and figures from the documentary. Four days thereafter, participants received placebo or oxytocin while being tested again for their memory. Importantly, before being tested, participants were given fabricated and, on some trials, explicitly erroneous answers from their in-group members. Results showed that individuals given oxytocin rather than placebo more often adopted the erroneous judgment by their in-group members, thus showing stronger in-group conformity. Interestingly, when tested again 1 week later, no effects of oxytocin on memory were found. This suggests that oxytocin motivates compliance but does not induce conversion.

OXYTOCIN MOTIVATES IN-GROUP COOPERATION AND DEFENSIVE OUT-GROUP AGGRESSION

That oxytocin motivates in-group liking and conformity but not out-group hate may appear inconsistent with animal literature showing that oxytocin prepares for and enables aggressive responding to threat, especially threat to offspring (so-called maternal defense) (65–69). However, out-group hate in the above works reflects attitudinal preferences rather than behavioral expressions, and out-group hate can be offensive (aimed at subordinating out-groups) or defensive (aimed at protecting oneself and others against out-group threat). Whereas offensive aggression is typically slow and calculated, defensive aggression is generally fast and impulsive (53,101).

The importance of distinguishing between defensive and offensive out-group aggression was revealed first in a study using a series of incentivized intergroup competition games (102). In two experiments, healthy male subjects received intranasal oxytocin or placebo, were assigned to one of two

groups, and then made decisions in an intergroup prisoner's dilemma-maximizing differences game (103). Each individual received €10 and was allowed to keep it, to invest it in a within-group pool benefiting other in-group members, or to invest it in a between-group pool benefiting other in-group members while simultaneously punishing out-group members. Within-group pool investments reflect (personally costly) ingroup love, whereas between-group pool investments reflect (personally costly) out-group hate that is symbolic and, if anything, reflective of offensive aggression. Results showed that 1) individuals who received oxytocin rather than placebo were less selfish; 2) in-group love was stronger than out-group hate, especially among individuals given oxytocin; and 3) ingroup love, but not out-group hate, was influenced by oxytocin [also see (104)].

In follow-up experiments (102,105), individuals represented their in-group in a competitive interaction with an out-group representative who either had strong or weak power to exploit the in-group (thus creating differential fear for exploitation in the in-group and a need for defensive aggression) or was easy or difficult to exploit (thus creating differential desire in the ingroup for greed and offensive aggression). Whereas oxytocin neither amplified nor reduced offensive aggression, it promoted defensive aggression when out-groups had high (versus low) power to exploit the in-group. These findings resonate with the literature on oxytocin and maternal defense, as well as with studies showing that wild meerkats infused with oxytocin (versus) placebo not only more strongly engage in cooperative behaviors, including digging, food sharing, and attending to offspring, but also spend longer time on guard, a particularly risky and personally costly but group-serving behavior (106).

In sum, oxytocin does not increase offensive aggression aimed at subordinating and exploiting the out-group but does prepare for defensive aggression aimed at warding off and neutralizing threat posed by rivaling out-groups (102,105–107) [also see (56,60,64,68)]. Combined with the finding that oxytocin also motivates in-group love and in-group conformity, this then suggests that oxytocin not only shifts the individual's focus from self-interest to group interest but, more specifically, enables a tend-and-defend functionality (102,105,107): oxytocin motivates tending toward the in-group and defending it against outside threat, human enemies included.

IMPLICATIONS FOR OXYTOCIN'S THERAPEUTIC POTENTIAL

Reduced capacity to empathize with others, to read and adapt to prevalent group norms and practices, and to extend and reciprocate trust and cooperation all make individuals vulnerable to social isolation and exclusion from the groups that provide shelter and opportunities for individual prosperity. This describes the daily life of individuals diagnosed with schizophrenia, autism, or borderline or social anxiety disorders, who tend to perform poorly on measures of empathic responding and encoding emotional expressions (17,108–111), have difficulty conforming to common group practices and cultural norms (14,112–114), and fail to trust and cooperate even with close others (115–117). Not surprisingly, therefore, many psychiatric patients have difficulty forming and maintaining

social bonds and suffer from social exclusion and isolation (15–17,118–121).

The linkage between (deficiencies in) group psychology on the one hand and the powerful effects of intranasal oxytocin on upregulating group psychology on the other hand suggests that treatment with oxytocin might be beneficial to a range of psychopathologies and psychiatric disorders, including schizophrenia, autism, and borderline and social anxiety disorders (16-18,24,122-138). To date, however, studies examining the potentially beneficial effects of oxytocin in various psychiatric disorders do not distinguish social targets and stimuli on the basis of in-group or out-group membership (16) [for an exception, see (86)]. Our review suggests that oxytocin is particularly potent in strengthening in-group bounded empathy, conformity, and trust and cooperation. Absent some familiarity, common fate, or shared group membership, oxytocin's effects on social cognition and biobehavioral approach-avoidance tendencies may be small, absent, or even counter-productive, increasing distrust and protective shielding [e.g., (138)]. One key implication of the present synthesis is that clinical trials examining effects of oxytocin on social cognition in psychiatric patients should either concentrate on responses to others with whom patients are familiar and share a common fate and/or group membership or explicitly compare familiar and in-group targets with unfamiliar strangers and out-group targets. Whether it concerns empathic responding, conformity, or trust and cooperation, we would expect stronger treatment effects in psychiatric patients when targets, including therapists and medical personnel, are familiar and considered in-group rather than unfamiliar or considered belonging to some (rivaling and/or threatening) out-group. In the latter case, oxytocin may even upregulate vigilance and protective shielding.

AVENUES FOR FUTURE RESEARCH

The studies reviewed here showed that oxytocin motivates ingroup favoritism and within-group, but not between-group, trust and cooperation. To the contrary, when the out-group constituted an imminent threat to the in-group, oxytocin stimulated competitive approach and defensive aggression. As such, oxytocin indirectly contributes to intergroup competition and conflict. First, in-group favoritism alone or in combination with out-group derogation creates intergroup discrimination: in-group members get relatively better treatment and receive benefits more readily than out-group members (73,76). Such unfair treatment triggers negative emotions, violent protest, and aggression among disfavored and excluded individuals (75). Accordingly, by stimulating ingroup love, oxytocin may trigger a chain reaction toward 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, the desire to defend themselves through preemptive strikes and aggression (1,101,102,105). Again, oxytocin's effects on within-group cooperation may, inadvertently, contribute to elevated levels of intergroup tension, competition, and conflict. This possibility that expected

escalatory spirals are set in motion by a combination of oxytocin-induced in-group love and imminent out-group threat needs direct testing in new research.

The current review is limited to studies using double-blind, placebo-controlled study designs in which humans receive intranasal oxytocin or placebo. However, studies tracking endogenous oxytocin from blood, urine, or saliva tend to produce similar findings, and although the underlying mechanisms are poorly understood, there is growing evidence that intranasal oxytocin increases both central and peripheral levels of endogenous oxytocin (139-141). For example, engaging in reciprocal cooperation associates with higher blood plasma oxytocin (142), receiving social support from close others associated with higher oxytocin levels than receiving identical support from unfamiliar strangers (143) and in chimpanzees sharing food among nongenetically related group members associated with higher urinary oxytocin levels (144). Together, these findings point to a recursive and reinforcing cycle between positive within-group exchange on the one hand and oxytocin release on the other (52).

Another issue to consider is that most studies reviewed here involved healthy male subjects and findings and conclusions may not generalize to female subjects. Social psychological studies of intergroup relations uncovered that women identify with their in-group more strongly than men (145) and that women show in-group favoritism regardless of whether they are dependent on the in-group, whereas men show in-group bias when they depend on in-group members for outcomes (146). Thus, oxytocin may have similar or stronger effects in female participants, but it is also possible that women would be less affected by oxytocin as their ingroup favoritism is already at a relatively high level. In addition, women given oxytocin more accurately identify interactions that involve affiliation, whereas men given oxytocin more accurately identify interactions that involve competition (147). Finally, robust sex differences in prenatal exposure to estradiol and testosterone may create strong differences in male and female subjects with regard to oxytocin receptiveness (148). Especially because some of the psychiatric disorders discussed here are more prevalent among male subjects (e.g., autistic spectrum disorder), whereas others tend to be seen more often in female subjects (e.g., social anxiety disorders), future research involving and comparing male and female subjects is needed. It may proceed with testing the hypothesis that oxytocin's in-group tending response is stronger among female subjects, whereas the in-group defending response may be equally strong or even stronger in male subjects.

CONCLUSION

Human groups are critical for individual survival and prosperity, and humans may have evolved neurocognitive architectures that allow them to contribute to their groups by extending trust and favors, by cooperating, by complying with rules and regulations, and if necessary, by engaging in protective aggression against threatening outsiders and rivals. There is mounting evidence that each of these facets of human group psychology is modulated by oxytocin. Intranasal administration of oxytocin (versus placebo) increases in-group favoritism, lying for one's team, costly contributions to

in-group welfare, conformity to in-group preferences, and aggressive protection against threatening outsiders. Evolution may have prepared humans for in-group bounded cooperation, and oxytocin may be the pivotal means biology provided to shift the individual's focus from being self-interested to being group serving and from being a lone wolf to being an included and appreciated group member.

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