The Neuropeptide Oxytocin Regulates Parochial Altruism in Intergroup Conflict Among Humans

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Materials and Methods
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Figs. S1 to S16
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The Neuropeptide Oxytocin Regulates Parochial Altruism in Intergroup Conflict Among Humans

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Humans regulate intergroup conflict through parochial altruism; they self-sacrifice to contribute to in-group welfare and to aggress against competing out-groups. Parochial altruism has distinct survival functions, and the brain may have evolved to sustain and promote in-group cohesion and effectiveness and to ward off threatening out-groups. Here, we have linked oxytocin, a neuropeptide produced in the hypothalamus, to the regulation of intergroup conflict. In three experiments using double-blind placebo-controlled designs, male participants self-administered oxytocin or placebo and made decisions with financial consequences to themselves, their in-group, and a competing out-group. Results showed that oxytocin drives a "tend and defend" response in that it promoted in-group trust and cooperation, and defensive, but not offensive, aggression toward competing out-groups.

Intergroup conflict is among the most pervasive problems facing human society, giving rise to such phenomena as prejudice, terrorism, ethnic cleansing, and interstate war (*1*, *2*). Results can be devastating: Governmental genocidal policies killed more than 210 million people during the 20th century alone, and since 2000 more than 30,000 people have been killed by terrorists (*3*). Individuals contribute to these atrocities and their less violent but no less pervasive counterparts through parochial altruism: They self-sacrifice (i) to benefit their own group ("in-group love") and (ii) to derogate, hurt, and sabotage competing out-groups ("out-group aggression") (*4*, *5*). As in-group love furthers the power and effectiveness of one's own group vis-à-vis the competing out-group, in-group love is an indirect way of competing with the out-group. Out-group aggression undermines the out-group's power and effectiveness and thus is an indirect form of cooperation toward one's own group that is often honored and publicly recognized by in-group leaders as heroic, loyal, and patriotic behavior (*6*, *7*). Out-group aggression may be driven by the desire to increase the in-group's relative status and power in the intergroup competition (henceforth "out-group hate"). Alternatively, it may be driven by the vigilant desire to defend and protect the in-group against real or perceived out-group threat (*8*, *9*).

Parochial altruism figures prominently in evolutionary explanations of human social behavior. As noted by Darwin (p. 156) (*10*), "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." The pivotal implication is that the human brain evolved to sustain motivated cognition and behavior critical to the survival of one's own group, to facilitate contributions to in-group welfare, and to defend against outside threats, including competing groups (*1*). We examine whether parochial altruism has its biological basis in brain oxytocin—a peptide of nine amino acids that is produced in the hypothalamus and released into both the brain and the bloodstream (*11*). Functioning as both a neurotransmitter and a hormone, oxytocin's targets are widespread and include the amygdala, hippocampus, brainstem, and regions of the spinal cord that regulate the autonomic nervous system (*12*). Its manifold effects include the promotion of trust and cooperation. For example, affiliating with close kin associates with the release of blood plasma oxytocin (*13*), and larger numbers of oxytocin receptors (OXTR) in the human brain associate with greater empathy, generosity, and other-regarding preferences (*12*, *14*). Finally, exogenous oxytocin (e.g., administered through nasal spray) promotes general trust and cooperation and reduces the tendency to take advantage of others' cooperation (*15*–*18*).

Oxytocin has not been implicated in the way humans regulate intergroup competition and conflict, and perhaps oxytocin stimulates trust and cooperation toward other in-group and out-group members alike. However, compared with the interpersonal exchanges in which oxytocin has been studied thus far, cooperation takes on a radically different purpose and meaning in intergroup competition and conflict. As noted, cooperation directed toward the in-group functions to preserve, defend, and strengthen the in-group and indirectly reduces the effectiveness and power of competing out-groups; noncooperation and aggression directed at the out-group hurts the out-group and indirectly protects and strengthens the in-group (*4*–*7*). Accordingly, we hypothesized that when humans are organized in in-groups and competing out-groups, oxytocin modulates parochial altruism. It increases (i) in-group trust—the positive expectation that in-group members self-sacrifice to promote in-group welfare, (ii) in-group love, (iii) out-group hate—the inclination to aggress against the out-group to increase relative standing, and (iv) defensive out-group aggression—hostility aimed at warding off out-group threat (e.g., preemptive strike). The latter two hypotheses resonate with the notion that aggression against the out-

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group indirectly promotes the welfare of one's own group (*6*, *7*), that oxytocin in nonhuman mammals promotes territoriality and aggression toward intruders (*19*–*21*), and that exogenous oxytocin in humans stimulates envy when interpersonal competition is lost and gloating when the game is won (*22*).

To address these issues, we designed three experiments. Experiments 1 and 2 tested whether oxytocin stimulates in-group love, out-group hate, or both. Experiment 2 addressed whether the effects of oxytocin are limited to individuals with cooperative personalities, who may respond more strongly to oxytocin than individuals with noncooperative personalities (*12*, *14*). Experiment 3 manipulated out-group threat to examine oxytocin's influence on preemptive strikes, a form of defense-motivated aggression. All experiments were computer-mediated and used a double-blind, placebo-controlled design in which participants received intranasal administration of oxytocin (or placebo containing the carrier without the neuropeptide). Thirty minutes later, participants were assigned, on the basis of a trivial criterion, to two three-person groups (the group they were assigned to being the in-group, the other being the out-group) and introduced to an intergroup game in which they made confidential decisions that had financial consequences for themselves, their fellow in-group members, and the competing out-group (*23*).

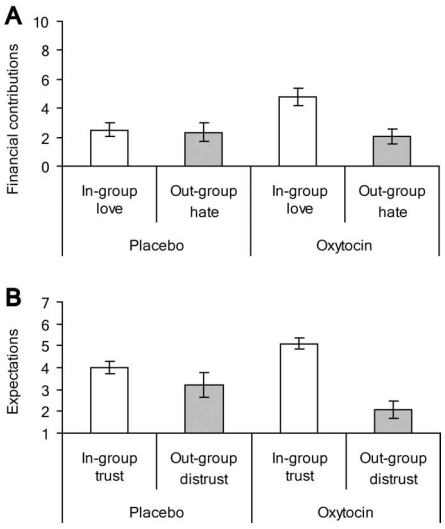

Fig. 1. (**A**) Financial contributions made in the IPD-MD game (displayed ±SE). (**B**) Participant's in-group trust and out-group distrust [measured on a seven-point Likert scale, ranging from 1 (low) to 7 (high), displayed ±SE].

In Experiment 1, 49 healthy males were introduced to the intergroup prisoners' dilemma–maximizing differences game (IPD-MD) (*23*, *24*). Each individual was given €10. Each Euro kept was worth €1 for the individual; each Euro contributed to the within-group pool added €0.50 to each in-group member, including the contributor; each Euro contributed to the between-group pool added €0.50 to each in-group member, including the contributor and, in addition, it subtracted €0.50 from each out-group member. The game captures those intergroup conflicts in which contributing nothing yields the highest personal outcomes regardless of what others do. Contributing to the within-group pool yields the highest benefit to the in-group (and the larger collective) and thus reflects a cooperative motivation to benefit the in-group without hurting the out-group (in-group love). Contributing to the between-group pool, in contrast, reflects spiteful out-group hate.

Participants indicated how much of their €10 they contributed to the within-group pool, to the between-group pool, and how much they kept for themselves. Contributions to the within-group and between-group pools were submitted to a 2 (treatment: oxytocin/placebo) × 2 (pool: within/between) mixed-model analysis of variance (ANOVA). Results showed that in-group love exceeded out-group hate [$F_{1,47}$ = 5.54, $P < 0.025$]. This effect was qualified by a treatment × pool interaction [$F_{1,47}$ = 4.38, $P < 0.05$]: Oxytocin amplified in-group love [$F_{1,47}$ = 8.18, $P < 0.001$] and neither increased nor decreased spiteful out-group hate [$F_{1,47} < 1$] (Fig. 1A). This also follows from an analysis in which we classified participants according to their dominant strategy. Those who gave more to themselves than to in-group love or out-group hate were classified as egoists. In-group lovers gave more to in-group love than to out-group hate or themselves. Out-group haters gave more to the between-group pool than to in-group love or themselves. Oxytocin influenced the distribution of participants across these three strategies [Cramer's $V = 0.431$ ($N = 49$), $P < 0.011$]. In the placebo condition, 52% pursued the egoist strategy, and only 20% were in-group lovers. In the oxytocin condition, however, 17% of the participants were egoistic and 58% were in-group lovers. The number of out-group haters was similar in the oxytocin (25%) and placebo (28%) conditions. Thus, oxytocin led people away from shortsighted selfishness to in-group love but did not affect spiteful out-group hate.

After allocation decisions, participants stated whether they expected (i) their in-group members to contribute to the within-group pool (in-group trust) and (ii) out-group members to contribute to the between-group pool (out-group distrust). A 2 (treatment: oxytocin/placebo) × 2 (focus: in-group trust/out-group distrust) ANOVA showed that in-group trust exceeded out-group distrust [$F_{1,47}$ = 19.90, $P < 0.001$]. A treatment × focus interaction [$F_{1,47}$ = 6.81, $P < 0.015$] showed that oxytocin increased in-group trust [$F_{1,47} = 6.56$, $P < 0.015$] and neither increased nor decreased out-group distrust [$F_{1,47}$ = 2.47, $P < 0.13$] (Fig. 1B).

Experiment 1 revealed that oxytocin influenced participants' allocation strategy. Because humans differ in their natural inclination to cooperate (*25*), perhaps cooperative individuals respond more strongly to oxytocin than noncooperative individuals (*12*, *14*). Experiment 2 examined whether effects of oxytocin on parochial altruism found in Experiment 1 generalize across cooperative and noncooperative individuals or remain limited to cooperative individuals. Before oxytocin administration, 67 males completed the standard social value orientations test in which they chose nine times between distributions of outcomes to oneself and an anonymous other (*25*). An example is the choice between (i) 40 to self and 40 to other (the cooperative choice), (ii)

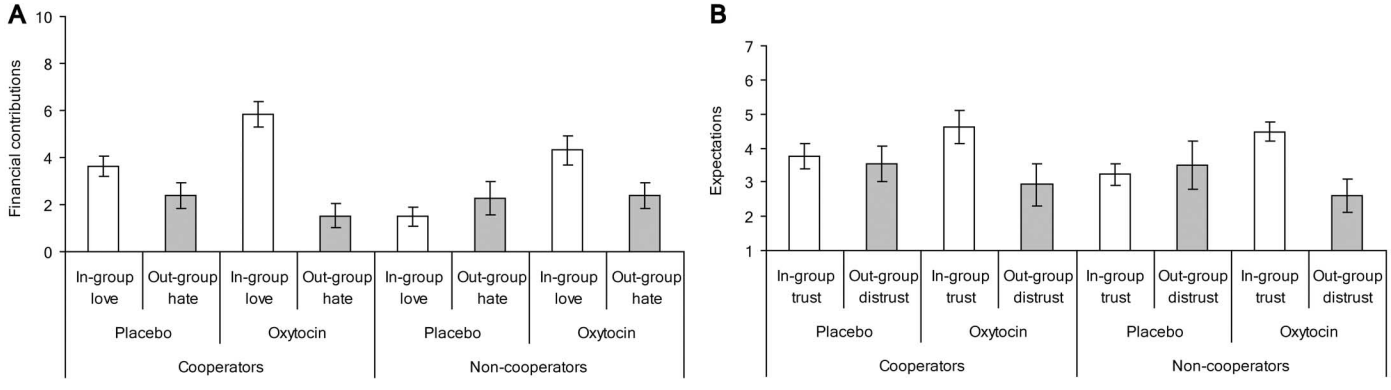

Fig. 2. (**A**) Financial contributions made in the IPD-MD game (displayed ±SE). (**B**) Participant's in-group trust and out-group distrust [ranging from 1 (low) to 7 (high), displayed ±SE].

50 to self and 20 to other, and (iii) 40 to self and 0 to other (ii and iii are noncooperative choices) (*23*, *25*). Participants were classified as cooperator if they made at least six out of nine cooperative choices ($N = 25$) or as noncooperator if they made at least six out of nine noncooperative choices ($N = 42$) (*23*).

Experiment 2 was otherwise identical to Experiment 1. Contributions to the within-group and between-group pools were analyzed in a 2 (treatment: oxytocin/placebo) × 2 (disposition: cooperators/noncooperators) × 2 (pool: within/between) ANOVA. This revealed effects for treatment [$F_{1,63} = 6.62$, $P < 0.012$] and pool [$F_{1,63} = 11.47$, $P < 0.001$] and treatment × pool [$F_{1,63} = 8.49$, $P < 0.005$] and disposition × pool interactions [$F_{1,63} = 4.94$, $P < 0.030$]. Compared with placebo, oxytocin increased in-group love among both cooperators [$t(23) = 2.98$, $P < 0.008$] and noncooperators [$t(40) = 3.81$, $P < 0.001$]. Oxytocin did not affect out-group hate [for cooperators, $t(23) = 0.96$, $P < 0.35$; for noncooperators, $t(40) = -0.11$, $P < 0.92$] (Fig. 2A). Because no interactions involving both treatment and disposition were significant [all $F_{1,63} < 0.48$, all $P > 0.40$], treatment and disposition have parallel but independent effects on parochial altruism. This conclusion also applied to in-group trust and out-group distrust (Fig. 2B). Specifically, submitting in-group trust and out-group distrust to a 2 (treatment: oxytocin/placebo) × 2 (disposition: cooperators/noncooperators) × 2 (focus: in-group trust/out-group distrust) ANOVA showed no effects for disposition [all $F_{1,63} < 1$, all $P > 0.29$] but replicated the effect for focus [$F_{1,63} = 6.62$, $P < 0.012$] and the treatment × focus interaction [$F_{1,63} = 3.27$, $P < 0.075$]. Compared with placebo, oxytocin increased in-group trust [$M = 3.43$ versus $M = 4.51$, $t(65) = -3.19$, $P < 0.01$] but did not influence out-group distrust [$M = 3.30$ versus $M = 2.82$, $t(65) = 1.08$, $P < 0.28$].

In the IPD-MD, contributions to the between-group pool reflect aggression oriented toward downgrading the well-being of the out-group both absolutely and relative to the in-group. Oxytocin did not motivate such out-group hate. However, the IPD-MD provides in-group members with no direct means to protect (payoff to) the in-group against out-group aggression. It thus remains possible that in addition to in-group love, oxytocin modulates defensive aggression against threatening out-groups. In Experiment 3, after intranasal administration of oxytocin or placebo, 75 males were randomly assigned to one of four different between-group prisoner dilemmas (BG-PD). Participants decided, on behalf of their in-group, to cooperate or not with another participant representing the out-group (*26*). The participant's choice to cooperate or not combined with the out-group's decision to cooperate or not yields four possible payoffs (Fig. 3A): temptation (T), reward (R), punishment (P), and sucker (S), which are ordered as T > R > P > S (*27*). This ordering has several consequences. Figure 3B shows that if both participant and out-group cooperate, both in-group and out-group obtain the reward payoff of 1.00, which exceeds the punishment payoff for mutual noncooperation of 0.60 [i.e., R – P = 1.00 – 0.60 = 0.40 (henceforth cooperator's gain)]. The dilemma occurs because both the participant and the out-group representative obtain even higher payoffs for their own group by noncooperation. Noncooperation may reflect the greedy desire to exploit the out-group and/or the defensive desire to protect the in-group against out-group noncooperation. First, if the out-group were to cooperate, participants would obtain higher outcomes for their in-group by noncooperation (T) than by cooperation (R) [in

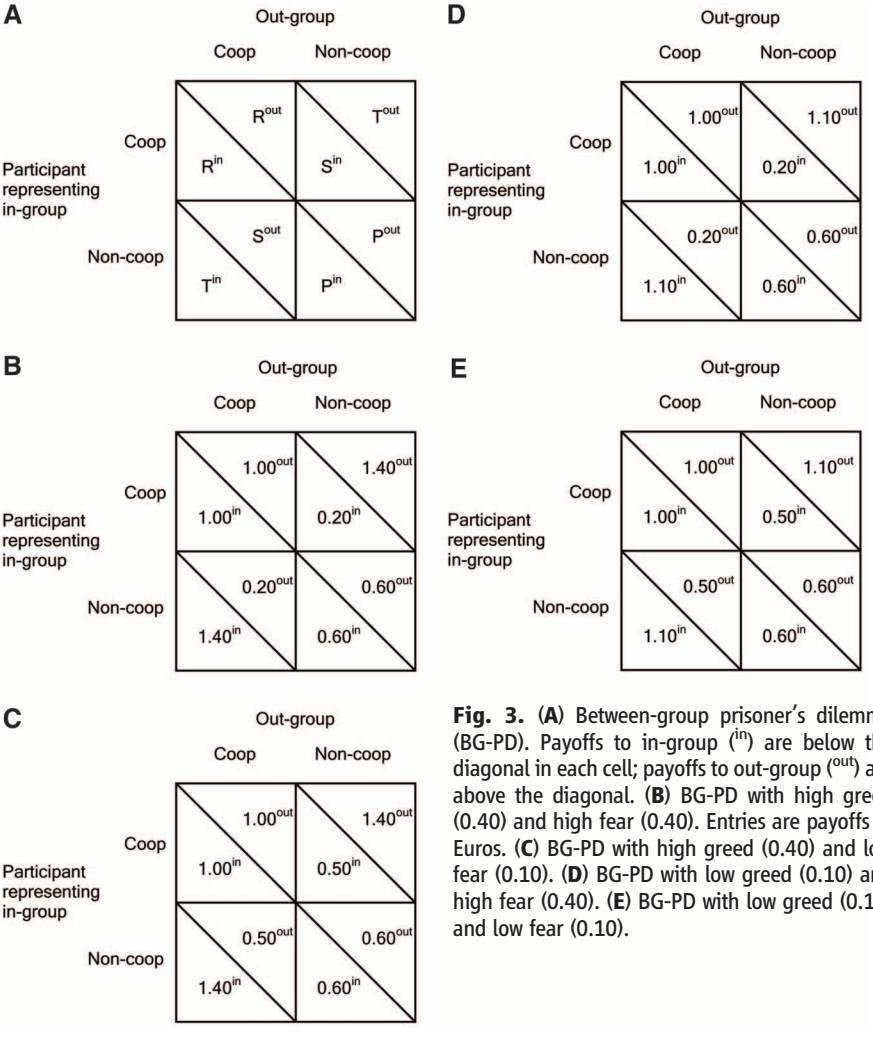

Fig. 3. (**A**) Between-group prisoner's dilemma (BG-PD). Payoffs to in-group (^{in}) are below the diagonal in each cell; payoffs to out-group (^{out}) are above the diagonal. (**B**) BG-PD with high greed (0.40) and high fear (0.40). Entries are payoffs in Euros. (**C**) BG-PD with high greed (0.40) and low fear (0.10). (**D**) BG-PD with low greed (0.10) and high fear (0.40). (**E**) BG-PD with low greed (0.10) and low fear (0.10).

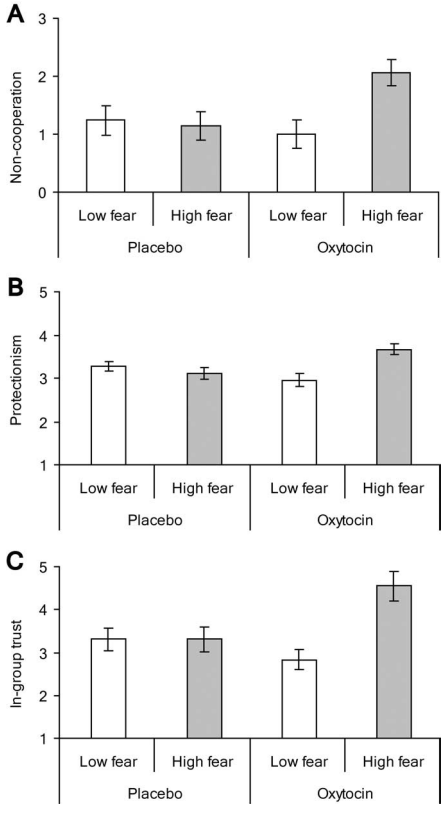

Fig. 4. (**A**) Noncooperation in the BG-PD (range 0 to 3, displayed ±SE). (**B**) Motivation to protect in-group members [ranging from 1 (low protectionism) to 7 (high protectionism), displayed ± SE). (**C**) Participant's in-group trust [ranging from 1 (low) to 7 (high), displayed ± SE).

Fig. 3B: T – R = 1.40 – 1.00 = 0.40 (henceforth greed)]. Second, if the out-group were to noncooperate, participants obtain higher outcomes for their in-group by noncooperation (P) than by cooperation (S) [in Fig. 3B: P – S = 0.60 – 0.20 = 0.40 (henceforth, fear)]. In Experiment 3, we manipulated payoffs so that the magnitude of greed and fear varied independently (*28*, *29*). Greed was set at a high 0.40 in Fig. 3, B and C, and at a low 0.10 in Fig. 3, D and E. Because across these games cooperator's gain and fear are held constant, higher noncooperation in the games in Fig. 3, B and C, compared with those in Fig. 3, D and E, must reflect a greedy desire to exploit the out-group. Fear was set at a high 0.40 in Fig. 3, B and D, and at a low 0.10 in Fig. 3, C and E. Because cooperator's gain and greed are held constant, higher noncooperation in the games in Fig. 3, B and D, compared with those in Fig. 3, C and E, must reflect an anxious desire to protect the in-group against a possibly aggressive out-group.

Participants made three confidential decisions between cooperation and noncooperation (the choices by out-group members were not revealed) (*23*). Given that noncooperation promotes in-group welfare and hurts the out-group, and because oxytocin promotes in-group love, we hypothesized that oxytocin triggers noncooperation and explored whether this tendency would be stronger under high greed. More important, and following animal research (*19*, *20*), we expected oxytocin to motivate protectionism: It promotes noncooperation especially when out-group fear is high. To test these hypotheses, noncooperation was submitted to a 2 (treatment: oxytocin/placebo) × 2 (greed: low/high) × 2 (fear: low/high) between-subjects ANOVA. More noncooperation was observed among individuals given oxytocin compared with placebo [$F_{1,67} = 3.98$, $P < 0.05$]. This effect was qualified by the treatment × fear interaction [$F_{1,67} = 7.51$, $P < 0.01$]: More noncooperation was seen among individuals given oxytocin rather than placebo when out-group fear was high rather than low (Fig. 4A). No effects involving greed were significant [all $F_{1,67} < 2.03$, $P > 0.16$]. If anything, the treatment × fear interaction was stronger under low greed. Overall, this shows that oxytocin promotes defense-motivated aggression in intergroup conflict.

To substantiate that noncooperation was related to the desire to protect one's in-group, participants rated whether they (i) tried to defend their in-group against possible out-group noncooperation (protectionism), (ii) expected fellow in-group members to serve in-group interests by noncooperation toward the out-group (in-group trust), and (iii) expected out-group noncooperation (out-group distrust) (*23*). A 2 (treatment) × 2 (greed) × 2 (fear) ANOVA showed that protectionism was stronger among individuals given oxytocin rather than placebo [$F_{1,67} = 4.27$, $P < 0.047$], especially when out-group fear was high [$F_{1,67} = 11.59$, $P < 0.001$]; no other effects were significant (Fig. 4B). Likewise, in-group trust was stronger among individuals given oxytocin rather than placebo [$F_{1,67} = 8.19$, $P < 0.006$], especially when out-group fear was high [$F_{1,67} = 6.36$, $P < 0.014$]; no other effects were significant (Fig. 4C). Both protectionism and in-group trust correlated with participant noncooperation toward the out-group [Pearson $r(75) = 0.35$, $P < 0.002$, and $r(75) = 0.48$, $P < 0.001$, respectively]. Consistent with the previous experiments, a 2 (treatment) × 2 (greed) × 2 (fear) ANOVA on out-group distrust showed no effects [all $F_{1,67} < 1.22$, all $P > 0.28$ ($M = 5.73$)]. This shows that noncooperation toward the out-group was driven less by expectations about out-group aggression than by the extent to which such aggression would hurt the in-group. Put otherwise, these findings reflect a "tend and defend" pattern in which oxytocin stimulates humans to aggress against out-group threat in order to protect their in-group.

When in-groups face competing out-groups, humans are motivated to display parochial altruism, and such parochial altruism has strong survival functions. We have shown that specific forms of parochial altruism have their biological roots in oxytocin; across three experiments we found that compared with those given placebo, individuals given oxytocin displayed more in-group trust and in-group love but did not display more out-group hate and out-group distrust. We also showed that oxytocin (compared with placebo) led to defensive forms of out-group aggression when out-group threat was eminent. These findings generalized across dispositional cooperators and noncooperators. Recent work has linked such phenotypic differences with genetic differences in OXTR (*12*, *14*), and new research may examine how genetic differences in OXTR relate to the regulation of intergroup conflict and competition. However, because our experiments involved males only, it is unknown whether oxytocin in females triggers the "tend and defend" form of parochial altruism uncovered here (*30*). This notwithstanding, because violent intergroup conflict more often involves males rather than females (the "male warrior hypothesis") (*31*), findings pertain to the most relevant half of the human species.

Others before us emphasized that parochial altruism contributes to individual survival (*1*, *10*) and speculated that the human brain evolved to maintain and promote social life and to protect against eminent threats, including competing out-groups. Merging insights and techniques from the biological, economic, and psychological sciences, we uncovered a biological cause of intergroup competition and conflict. Our findings show that oxytocin, a neuropeptide functioning as both a neurotransmitter and hormone, plays a critical role in driving in-group love and defensive (but not offensive) aggression toward out-groups. Perhaps offensive forms of out-group hate have their biological roots elsewhere, or perhaps these tendencies are primarily grounded in perceived in-group love and protectionism in competing out-groups. After all, if competing out-groups become strong and powerful, they become a threat to the in-group, and this in and of itself not only motivates in-group members to display in-group love but also motivates protectionism and preemptive strike. As shown here, this "tend and defend" form of parochial altruism is precisely what oxytocin modulates.

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Materials and Methods
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