Oxytocin promotes synchronized out-group attack during intergroup conflict in humans

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Abstract

Intergroup conflict contributes to human discrimination and violence, but persists because individuals make costly contributions to their group's fighting capacity. Yet how groups effectively synchronize their contributions during intergroup conflict remains poorly understood. Here we examine whether the evolutionary ancient neuropeptide oxytocin provides a neurobiological mechanism underlying group synchronization to attack or defend during real-time intergroup conflict. In a double-blind placebo-controlled study with *N*=480 males in Attacker-Defender intergroup conflicts, we found that oxytocin reduced attackers' contributions and over time increased attacker's within-group synchronization of contributions. However, rather than becoming peaceful, oxytocin enabled attackers to track rivals' defense-history and synchronize their contributions into well-timed (when defenders were weak) and hence more profitable attacks. Combined, results reveal behavioral synchronization and coordinated action as critical components of successful attacks, subscribe to the possibility that oxytocin enables individuals to contribute to in-group efficiency and prosperity, even when such implies outsiders are excluded or harmed.

Key words: Oxytocin; Intergroup conflict; Group synchronization; Out-group attack; collective action

Introduction

Conflict between groups of people can profoundly change their demographic, economic and cultural outlook. Across human history, intergroup conflict functioned as a critical change agent and selection pressure that may have shaped the biological preparedness for in-group cooperation and self-sacrifice for one's own group (Bar-Tal et al., 2007; Boyd and Richerson, 1982; Choi and Bowles, 2007; De Dreu et al., 2010; Macfarlan et al., 2014). Recent work decomposed such in-group serving cooperation into contributions to attacks of rivaling out-groups, and the willingness to defend one's own group against such possible attacks (De Dreu et al., 2016a; Halevy et al., 2008; Rusch, 2014a, b; Lopez, 2017; Wrangham, 2018). It showed that individuals are more strongly motivated to contribute to defend own group than to attack out-group and, importantly, that out-group attacks frequently fail because individual contributions to out-group attack are poorly coordinated (De Dreu et al., 2016a). Indeed, attacking enemies who are expected to have strong defenses more likely results in failure and waste, than attacking groups expected to be weak and defenseless (De Dreu et al., 2016b; Grossman and Kim, 2002; Goeree et al., 2003). Thus, to be successful in intergroup conflict, group members not only need to contribute to intergroup fighting, but they also need to be able to coordinate both the level of attack and its timing.

How group members coordinate and synchronize behavior into effective joint actions during intergroup conflict remains poorly understood (De Dreu et al., 2016a; Packer and Ruttan, 1988) and we lack a mechanistic understanding of its underlying neurobiological and behavioral processes. Here we address this issue, targeting the neuro-hormone oxytocin as an evolved neurobiological mechanism underlying group-level coordination of out-group attack in dynamic intergroup conflicts. Indeed, studies in ethnography and anthropology have shown that small

groups preparing for intergroup conflict build cohesion and commitment through social bonding routines and rituals. Groups selectively invite friends to join a raid (Schelling, 1960), bond like family (Macfarlan et al., 2014; Wilson and Wilson, 2007), and engage its warriors in cultural rituals that simulate self-sacrifice and synchronized behaviors (Glowacki et al., 2016; Xygalatas et al., 2013). Furthermore, neuroendocrine studies (Burkett et al., 2016; Carter, 2014; Ma et al., 2016; Samuni et al., 2017) have linked these and related social bonding and cultural rituals to the release of oxytocin, a nine-amino acid neuropeptide that, upon its endogenous production in the hypothalamus (Donaldson and Young, 2008; Hatton, 1990) or especially following intranasal administration (Donaldson and Young, 2008; Lee et al., 2018; Tanaka et al., 2018), targets the brainstem and various sub-cortical brain regions involved in threat detection and reward processing (Burkett et al., 2016; Carter, 2014; Ma et al., 2016; Paloyelis et al., 2016; Wang et al., 2017). Moreover, in both non-human and human primates, elevated levels of oxytocin via intranasal administration have been linked to a range of cognitive and behavioral effects including within-group conformity, trust, affiliation, and cooperation (Arueti et al., 2013; Aydogan et al., 2017; Bartz et al., 2011; Burkett et al., 2016; De Dreu et al., 2010; Hurlemann et al., 2010; Madden and Clutton-Brock, 2011; Mu et al., 2016; Rilling et al., 2012; Samuni et al., 2017; Stallen et al., 2012; Yan et al., 2018).

Whereas these works together point to oxytocin as a possible neurobiological mechanism underlying behavioral synchronization and group coordination, three issues remain. First, we lack empirical evidence for the possible role of oxytocin in the group-level coordination of collective action in general, and during intergroup conflict in particular. Second, we poorly understand what group members use to coordinate collective action during intergroup conflict, and whether oxytocin directly influences the group-coordinated behavior or changes the strategy

group members coordinated on. Third, and finally, we do not know whether and how oxytocin modulates these distinctly different forms of tacit coordination within groups attacking out-groups, or defending against such out-group attacks.

Here we addressed these issues in eighty interactive, multi-round contests between three-person attacker and three-person defender groups. Group members on each side made individual contributions to their group's fighting capacity (aimed at attacking the other side, or aimed at defending against such possible attacks). We provided individuals with real-time feedback on group investments and success after each contest round, which allowed group members to learn and adapt to their rival's past contributions, and use the history of play as a prominent focal point to coordinate their future attacks and defenses. Indeed, when lacking explicit coordination mechanisms such as a directive leader or decision-making protocols (De Dreu et al., 2016a; Gavrilets et al., 2014; Hermalin, 1998), groups tacitly coordinate on social norms and focal points (Halevy and Chou, 2014; Schelling, 1960) which, in on-going intergroup conflict can be the rival's history of play. For example, when attacking out-groups, groups may coordinate their contributions on the historical level of defense displayed by their target, so that groups attack when historical defense was low and the target appears vulnerable; and not attack when historical defense was high and the target appears strong and difficult to beat.

We expected oxytocin to elevate contributions to in-group defense but because in-group defense is tacitly well-coordinated—individuals fight towards the same goal of self-preservation and group survival—elevating oxytocin may not further contribute to the coordination of joint in-group defense. Whereas defenders may adapt to their attacker's past aggressiveness, we did not anticipate a modulating effect for oxytocin. Conversely, we expected oxytocin to influence

contributions and coordination within attacker groups. In general, coordination of out-group attack is inherently more difficult (De Dreu et al., 2016) and we anticipated two possible effects of oxytocin. On the one hand, oxytocin has been linked to enhanced prosociality (Carter, 2014; Kosfeld et al., 2015; Madden and Clutton-Brock, 2011; Rilling et al., 2012; Yan et al., 2018), empathy (Hurlemann et al., 2010; Bartz et al., 2010) and consolation (Burkett et al., 2016). From this it follows that if oxytocin also facilitates behavioral synchronization, it should enable attacker groups to coordinate on a peaceful no-attack strategy that is independent of the rivals' history of defense. On the other hand, oxytocin has been linked to enhanced in-group conformity (Aydogan et al., 2017; Stallen et al., 2012; De Dreu and Kret, 2016), suggesting that oxytocin can facilitate behavioral synchronization on social norms and shared focal points that emerge during group interaction. From this perspective, and fitting anthropological work on bonding rituals prior to group raiding (Glowacki et al., 2016; Macfarlan et al., 2014; Schelling, 1960; Wilson and Wilson, 2007), oxytocin may (i) facilitate the use of rival's history and enable attacker groups to coordinate better on the level and timing of their attacks, and (ii) to efficiently appropriate resources from out-group rivals. Evidence for this possibility would be consistent with earlier findings that oxytocin facilitates learning from feedback (Ma et al., 2016) and shifts the focus from self-interest to in-group interests (De Dreu and Kret, 2016), limits trust and cooperation to in-group members (De Dreu et al., 2010; Ma et al., 2015; Ten Velden et al., 2017), and promotes aggression toward threatening rivals (Madden and Clutton-Brock, 2011; Samuni et al., 2017; Striepens et al., 2012; Ne'eman et al., 2016).

Methods Summary

We examined these possibilities using a dynamic, fully incentivized Intergroup Attacker-Defender Contest game (IADC, De Dreu et al., 2016a). The IADC is an all-pay contest (Abbink et al., 2010; Dechenaux et al., 2015; De Dreu et al., 2016a) involving 6 individuals randomly assigned to a 3-person attacker and a 3-person defender group. We created 80 IADC sessions (with $N = 480$ healthy males); in 40 (40) sessions, participants received intranasal oxytocin (matching placebo) (*Materials and Methods*; *SI* Fig. S1). Each IADC session involved two blocks of 15 investment rounds with real-time feedback in between rounds. For each investment round, individuals received 20 MU (Monetary Units) from which they could contribute g ($0 \leq g_i \leq 20$) to the group's pool C ($0 \leq C \leq 60$). Contributions were wasted, but when $C_{attacker} \leq C_{defender}$, defenders survived and all 6 individuals kept their remaining endowment (leftovers, $20\text{-}g_i$). However, when $C_{attacker} > C_{defender}$, the attackers won the defenders' remaining resources (spoils from winning, $60 - C_{defender}$). Spoils were divided equally among attacker group members and added to their remaining endowments ($20\text{-}g_i$) and defenders earned 0. Thus, individual contributions in attacker (defender) groups reflect out-group attack (in-group defense). In one 15-round block, individuals made their decisions individually and simultaneously without communication. In the other block (order counterbalanced), individuals within groups made their decisions in sequence: one randomly drawn member made his decision first, followed by the second randomly selected member who was informed about the first member's contribution, and then the third and final member made their decision (De Dreu et al., 2016a; Gavrilets et al., 2014, *SI* Fig. S2).

The sequential decision-making protocol acts as a 'coordination device' and has been shown to facilitate behavioral synchronization within groups (De Dreu et al., 2016a; Gavrilets et al., 2014;

Hermalin, 1998), thus providing a benchmark to compare groups in the simultaneous decision-protocol who lack an explicit coordination mechanism and have to find other means—such as a shared social norm or the rival's past defense—to synchronize and turn contributions into effective joint action (De Dreu et al., 2016a). We operationalized within-group coordination as the variance in contributions to group fighting, with lower group-level variance reflecting better coordination (De Dreu et al., 2016a) and expected that possible effects of oxytocin on group coordination would emerge especially under simultaneous rather than sequential decision-making.

Results

Before examining within-group coordination, we examined treatment effects on contributions to group fighting. Individual contributions were averaged across the three members within each rivaling group, and submitted to a 2 (Treatment: Oxytocin vs. Placebo) × 2 (Role: Attack vs. Defense) × 2 (Procedure: Simultaneous vs. Sequential) × 15 (Rounds) mixed-model Analysis of Variance (ANOVA) with Treatment between-sessions. Individuals contributed more under sequential than simultaneous decision-making ($M \pm SE$ = 6.89±0.20 *vs.* 6.47±0.24; $F(1,78) = 5.109$, $p = 0.027$, $\eta^2 = 0.061$), and somewhat less when given oxytocin rather than placebo ($M \pm SE$ = 6.28±0.29 *vs.* 7.08±0.29; $F(1,78) = 3.719$, $p = 0.057$, $\eta^2 = 0.046$). Fig. 1A shows higher contributions to in-group defense than to out-group attack, especially in earlier rounds (Role, $F(1,78) = 287.903$, $p < 0.001$; $\eta^2 = 0.787$; Role × Round, $F(14,1092) = 4.299$, $p < 0.001$, $\eta^2 = 0.054$).

Treatment effects also emerged when we examined the number of non-contributors. There were more non-contributors in attacker compared to defender groups ($M \pm SE$ = 20.23±0.92 *vs.* 4.25±0.44; $F(1,78) = 408.489$, $p < 0.001$; $\eta^2 = 0.840$), and more non-contributors in groups given

oxytocin than placebo ($M \pm SE$ = 13.46±0.90 *vs.* 11.01±0.75; $F(1,78) = 4.345$, $p = 0.040$; $\eta^2 = 0.053$). Crucially, oxytocin increased the number of non-contributors in attacker groups but not in defender groups (Role × Treatment, $F(1,78) = 5.043$, $p = 0.028$, $\eta^2 = 0.061$, Fig. 1B). This Role × Treatment effect is especially true when decisions were made simultaneously ($F(1,78) = 5.712$, $p = 0.019$, $\eta^2 = 0.068$) but less so when sequentially ($F(1,78) = 2.143$, $p = 0.147$; $\eta^2 = 0.027$). To further reveal how oxytocin influences the non-contributing decisions, we examined participants' decision time by calculating the decision time separately for the round that participants decided to or not to contribute. We showed that attacker groups made their decisions not to contribute faster than to contribute (Contribute: $F(1,78) = 137.679$, $p < 0.001$, $\eta^2 = 0.641$). Interestingly, oxytocin sped up attacker groups to make their non-contributing decisions (Treatment × Contribute : $F(1,77) = 4.857$, $p = 0.031$; $\eta^2 = 0.059$, *SI*, Fig. S3).

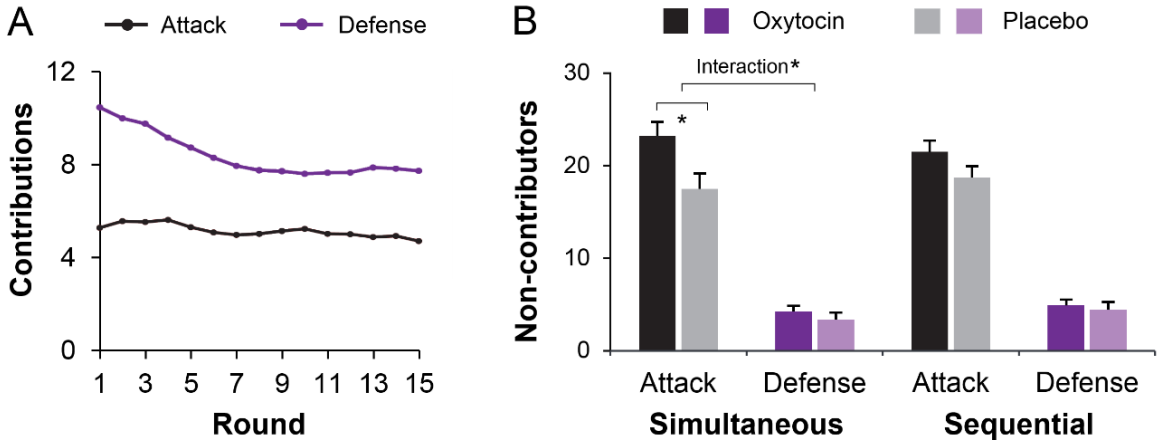

Fig. 1. *Oxytocin modulates contributions to group fighting.* **(A)** Attacker groups contribute less than defender groups, especially in early rounds of the conflict (range 0 – 20). **(B)** Giving individuals oxytocin rather than placebo increases the number of non-contributing members in attacker groups especially under simultaneous decision-making (with 0-3 members per round across 15 rounds; range 0 – 45; displayed M ± 1SE). Connectors indicate $p \leq 0.05$.

Next we analyzed group-level coordination operationalized as the within-group variance in contributions, with lower variance indicating stronger coordination (De Dreu et al., 2016a). First, there was a Procedure x Role interaction ($F(1,78) = 101.978$, $p<0.0001$, $\eta^2= 0.567$). The sequential decision-protocol facilitated coordination for attack ($F(1,78) = 77.852$, $p<0.0001$, $\eta^2= 0.500$) and reduced coordination for defense ($F(1,78) = 39.268$, $p<0.0001$, $\eta^2= 0.335$). Importantly, as predicted, oxytocin facilitated group-level coordination (i.e., reduced within-group variance for contributions, see *SI*, Fig. S4 for another index) of out-group attack but not of in-group defense, especially in earlier rounds (Role x Treatment x Round, $F(14,1092) = 1.753$, $p = 0.041$, $\eta^2 = 0.022$; Fig. 2A).

To examine what strategy attackers given oxytocin coordinated on we first examined the contest outcomes. As noted, oxytocin may enable groups to coordinate on a peaceful "no-attack strategy," in which case we should find lower victories in attacker groups given oxytocin rather than placebo, and no effect of oxytocin on tracking rival s' defense history. This was not the case: the number of victories was similar in attacker groups given oxytocin (M±SE: 24.8% ± 1.8%) and placebo (M±SE: 26.6% ± 1.5%)($F(1,78) = 0.572$, $p = 0.452$; $\eta^2 = 0.007$). Furthermore, rather than making groups coordinate on a peaceful no-attack strategy, oxytocin may enable groups to coordinate on attacking at the right moment with the right force. To facilitate the illustration of the oxytocin effect on the relationship between investment and payment (leftover and spoils), the investment and payment for each condition were respectively highlighted in Fig. 2B using a standard bootstrapping procedure. As illustrated in Fig. 2B, we observed that while oxytocin decreased contribution to attack, oxytocin increased payment (t(78)=1.882, p=0.063, Cohen d'=0.421, 95% CI, -0.049 to 1.768), especially when decisions were made simultaneously (black dots vs. gray dots). Statistical analysis separately on the spoils and leftover, further showed that,

groups given oxytocin rather than placebo had higher spoils when attacks were successful ($t(74)=1.819$, $p=0.073$, Cohen d'=0.419, 95% CI, -0.086 to 1.888, Fig. 2C), and higher leftovers when attacks failed ($t(78)=2.609$, $p=0.011$, Cohen d'=0.583, 95% CI, 0.475 to 3.522, Fig. 2D).

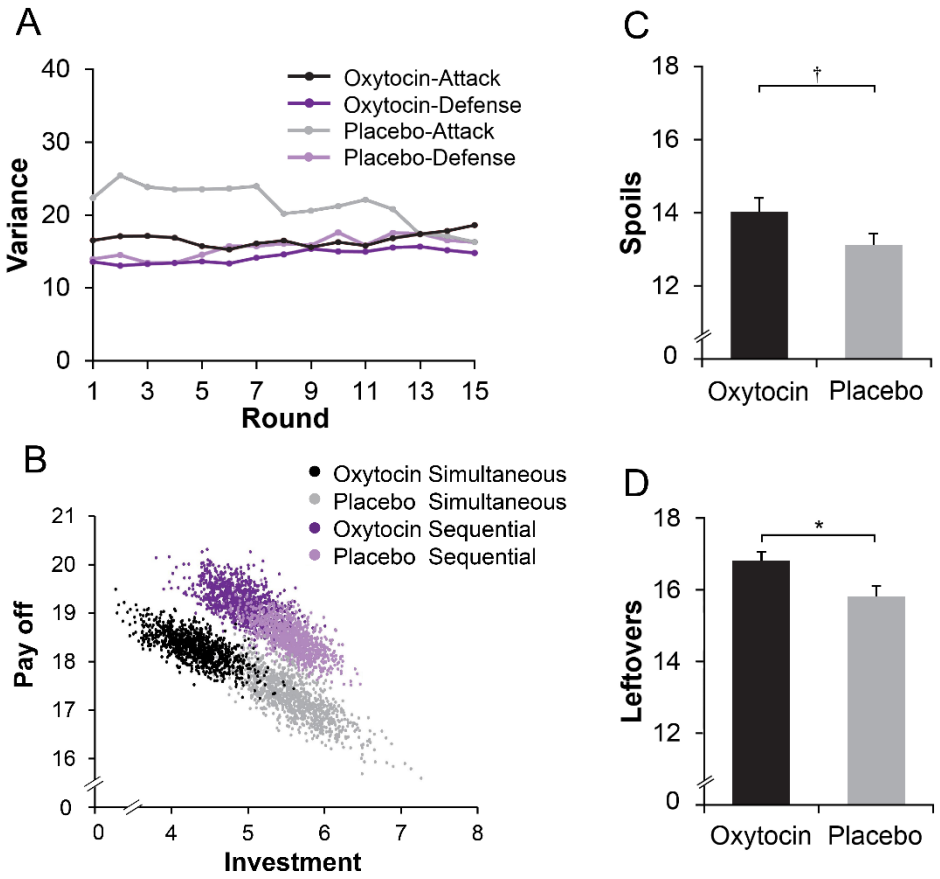

Fig. 2. *Oxytocin modulates within-group coordination*. **(A)** Giving individuals oxytocin rather than placebo enables better coordination (lower within-group variance) in attacker groups, especially in early rounds of the conflict; **(B)** Bootstrapping illustration of the oxytocin shifts on the investment and payment. Bivariate distributions of 1,000 bootstrapped sample means for each condition (Treatment x Procedure) plotted against the investment and payment. **(C/D)** Giving attacker groups oxytocin rather than placebo increases their spoils from winning conflicts (C) and the leftovers (D) when not winning the conflict (N=76 because 4 attacker groups never won).

Second, we examined how attacker groups collectively identified when to attack by creating a

past defense parameter α (average defender's investment in the last two rounds, i.e., $(D_{i-1}+D_{i-2})/2$ on round i) and regressed attacker group's investments onto α (attack increased when defender groups were vulnerable rather than strong, as indicated by α approaching -1). It showed that attacker groups given oxytocin tracked their rival's past defense and attacked especially when defenders appeared more rather than less vulnerable (i.e., attack regressed *negatively* on rival's historical defense). Specifically, when decisions were made simultaneously, attack regressed more strongly on α when groups received oxytocin (M±SE: -0.30 ± 0.05) rather than placebo (M±SE: -0.01 ± 0.13) ($F(1,78) = 4.683$, $p = 0.034$, $\eta^2 = 0.057$), and under oxytocin but not placebo, the regression on α was also stronger in simultaneous rather than sequential decision-making (Treatment × Procedure interaction, $F(1,78) = 7.397$, $p = 0.008$, $\eta^2 = 0.087$, Fig. 3A).

Combined, results suggest that groups given oxytocin created more spoils from winning and had higher leftovers when attacks failed because they better coordinated attack at the right time and with the proper force. Indeed, when decisions were made simultaneously, the more strongly attacker groups relied on tracking parameter α, the lower their within-group variance when contributing ($r = 0.222$, $p = 0.048$, Fig. 3B), and the lower within-group variance when contributing, the higher the attacker's spoils when winning the conflict ($r = -0.328$, $p = 0.004$, Fig. 3C). Indirect mediation analyses confirmed that the attacker's higher spoils under oxytocin was mediated by (i) increased tracking of defenders' past investments and (ii) concomitant increased within-group coordination (indirect effect = 0.120, SE = 0.860; 95% *Confidence Interval* = 0.018-0.401, Fig. 3D).

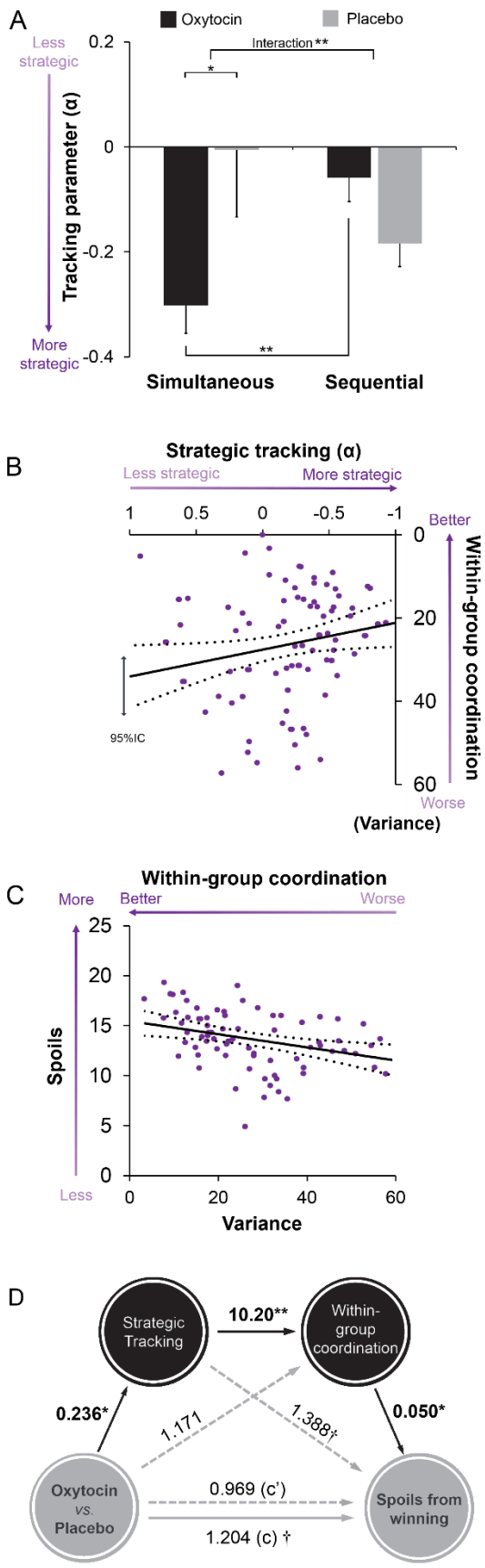
A
Oxytocin
Placebo
Less strategic
More strategic
Tracking parameter (α)
0.2
0
-0.2
-0.4
Interaction**
*
**
Simultaneous
Sequential
B
Strategic tracking (α)
Less strategic
More strategic
1
0.5
0
-0.5
-1
Better
Worse
Within-group coordination
(Variance)
0
20
40
60
95%IC
C
Within-group coordination
More
Better
Worse
Spoils
Less
25
20
15
10
5
0
0
20
40
60
Variance
D
Strategic Tracking
10.20**
Within-group coordination
0.236*
1.171
1.388†
0.050*
Oxytocin vs. Placebo
0.969 (c')
1.204 (c) †
Spoils from winning

Fig. 3. *Oxytocin enables a track-and-attack strategy (probability of attack increases when defender groups are vulnerable rather than strong, as indicated by α → -1).* **(A)** When attacker groups are given oxytocin investments regress negatively on α (the rival's historical contributions to defense), especially during simultaneous than sequential decision-making. **(B)** Stronger negative regression of attack on rival's defense history (α → -1) among attacker groups associates with better coordination (i.e., lower within-group variance). **(C)** Better coordination (i.e., lower within-group variance) associates with higher spoils when winning the conflict. (**D**) Oxytocin's effect on spoils from successful attacks is mediated by treatment effects on tracking α (more strategic when α → -1) and better within-group coordination.

Conclusion and Discussion

To be victorious in intergroup conflict, group members not only need to contribute to their group's fighting capacity. They also need to coordinate collective action so that they attack when their rival is expected to be weak, and avoid wasting resources on attacking tough defenders. Here we found, using a dynamic intergroup contest between attackers and defenders, that those groups who tracked their defender's history of play and coordinated their attacks of weak rather than strong defenders wasted less resources on failed attacks and enjoyed greater spoils when winning. In addition, we uncovered that oxytocin serves as a neurobiological mechanism underlying such well-timed and coordinated attacks, as it enabled individuals within attacker groups to converge their individual contributions on each other more, and to collectively refrain from attacking apparently strong defenders, and effectively attacking apparently weak defenders. Finally, we found that providing attacker groups with a sequential decision-making protocol as an explicit coordination device substituted oxytocin-induced tacit coordination.

Our result that oxytocin enables behavioral synchronization of contributions and makes groups effectively coordinate their attacks on out-groups resonates with two heretofore disconnected sets of findings—that small groups of warriors engage in social bonding and cultural rites (Glowacki et al., 2016; Macfarlan et al., 2014; Schelling, 1960; Wilson and Wilson, 2007; Xygalatas et al., 2013), and that social bonding and synchronized action can trigger the release of oxytocin (Burkett et al., 2016; Carter, 2014; Ma et al., 2016; Samuni et al., 2017). Here we simulated different levels of oxytocin through intranasal administration and observed that oxytocin may be a neurobiological mechanism through which social bonding and performing synchronization rituals such as war dances can help warrior groups to better coordinate their attacks, and become victorious. We also found that such basic mechanisms for coordination can be substituted by institutional arrangements, like a sequential decision-making protocol, that enable groups to explicitly coordinate the timing and force of their attacks on out-groups. We speculate that related institutional arrangements, like appointing a directive leader or having open communication channels can have similar effects. Our findings suggest that oxytocin plays less of a role when such explicit coordination mechanisms are in place, and which neurobiological mechanisms mediate explicit coordination of collective action in groups remains an open question.

Neither oxytocin nor the sequential decision-protocol contributed to coordination in defender groups. One possibility is that in-group defense is tacitly well-coordinated because of the stronger alignment of individual interests within defender groups. After all, when defender groups survive an enemy attack, those who did not contribute to in-group defense come out relatively wealthy. But when in-group defense fails, all group members lose regardless of whether they contributed or not. As a result of this stronger common fate in defender groups,

individuals contribute spontaneously and tacitly coordinate well on avoiding collective defeat. Exogenous enhancers, whether at the neurobiological or institutional level, are needed nor contributing.

Previous studies provided evidence for the role of oxytocin in intergroup interaction: It can increase the positive view and benign approach of the in-group and has been linked to subtle forms of intergroup discrimination (De Dreu et al., 2010; De Dreu and Kret, 2016; Ma et al., 2015; Stallen et al., 2012; Ten Velden et al., 2017). Without exception, this early evidence was limited to individual-level decision-making, and did not clearly distinguish the distinct motives for contributing to in-group efficiency and out-group aggression. It remains unknown whether and how oxytocin differentially affects attack and defense behavior during intergroup conflict. Using a dynamic attack-defense contest we revealed selective effect of oxytocin on group attacking. As such, the present study provides a new perspective on oxytocin in intergroup conflict by highlighting its functionality for strategic attack (rather than defense). In doing so, we also obtained first-time evidence that in-group coordination for collective action can be tracked to evolutionary ancient neurobiological factors.

Our study involved Chinese males as study participants, which may limit generalization. At the same time, however, findings for the comparison between sequential and simultaneous decision making protocols during out-group attack and in-group defense strongly resonate with findings obtained in Western culture, with both male and female participants (De Dreu et al., 2016a). Furthermore, recent work on the role of oxytocin in in-group cooperation suggests similar effects for both male and female participants (Ten Velden et al., 2017). How exogenous administration of oxytocin operates at the neurophysiological level is more open to debate. Whereas some have

questioned whether intranasal administration of oxytocin can have significant impact on brain and behavior (Leng and Ludwig, 2016), recent studies in rodents (Neumann et al., 2013; Tanaka et al., 2018), rhesus macaques (Lee et al., 2018; Modi et al., 2014) and in humans (Paloyelis et al., 2016) collectively suggest that intranasal oxytocin elevates brain-level presence of oxytocin, and impacts behavioral decisions through targeted neural networks involved in threat detection and reward processing (Carter, 2014; Hurlemann et al., 2010; Ma et al., 2016; Rilling et al., 2012; Stallen et al., 2012; Wang et al., 2017). In addition, there is mounting evidence that higher levels of oxytocin in saliva, blood, or urine relate to in-group affiliation and cooperation (Madden and Clutton-Brock, 2011; Samuni et al., 2017) and intergroup discrimination (Levy et al., 2016).

Intergroup conflict shapes the economic and cultural outlook of groups and societies, and interferes with individual life-trajectories. These impacts of intergroup conflict depend on the personally costly contributions of group members and, as shown here, on the ability of groups to coordinate collective attacks. Both institutional arrangements, such as leading-by-example, and neurobiological mechanisms, such as oxytocin, facilitate behavioral synchronization and, as such, effective exploitation of out-groups. Indeed, as shown here, providing group members with oxytocin or an explicit coordination device enables them to waste less on failed attacks, and to earn more from their victories.

Materials and methods

Participants. We recruited 486 healthy males, mostly science and engineering students, as paid volunteers. One IADC session (N=6) was dropped from data analysis because of technical failure. Data from 480 participants (80 IADC sessions, age 18-29 years; $M \pm SE$= 20.37 $\pm$0.07

years) were included in the final data analysis. The data analysis on the current study was conducted on a 6-person-group level, thus we conducted sample size estimation by G*Power to determine the number of groups sufficient to detect a significant effect. Based on an estimated average small-to-medium effect size of oxytocin effect on social behaviors (d=0.28, Walum et al., 2016), 80 6-person groups were needed to detect a significant effect ($\alpha = 0.05$, $\beta = 0.85$, ANOVA: repeated measures, within-between interaction, G-Power, Faul et al., 2009). All participants were healthy and had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. Those who majored in psychology or economics or participated in any other drug study in recent weeks were excluded from participation. Participants were instructed to refrain from smoking or drinking (except water) for 2h before the experiment.

Ethics Approval. All participants provided written informed consent to participate after the experimental procedures had been fully explained, and were acknowledged their right to withdraw at any time during the study. All experimental procedures adhered to the standards set by the Declaration of Helsinki and were approved by the Institutional Review Board at the State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing, China (protocol number: ICBIR_A_0107_001).

Procedure. The experiment followed a randomized double-blind placebo-controlled between-subjects design (*SI*, Fig. S1). For each IADC session, 6 strangers were invited to the lab at the same time and randomly assigned to 6 individual cubicles within the same room. Upon arrival, participants first completed questionnaires that measured current mood, empathic capacity,

prosocial personality, impulsiveness, subjective socio-economic status and cooperative personality. Participants then self-administered oxytocin or placebo. After 35 min, participants were given instructions for the IADC game and completed two practice rounds. When they also passed a comprehension check, they played 15 simultaneous rounds and 15 sequential rounds of IADC investments (*SI*, Fig. S2). All the experimental instructions used neutral language (e.g., contribution was labeled investment; defense and attack were avoided, and groups were labeled to as group A or B). Finally, participants filled out a post-survey for mood measurement and manipulation check. The attacker and defender groups under oxytocin or placebo did not differ in mood change, empathic capacity, prosocial personality, impulsiveness, subjective socio-economic status and cooperative personality (*SI*, Table S1, S2).

Oxytocin administration. The procedure of oxytocin and placebo administration was similar to previous work, that showed significant oxytocin effects on decision-making behaviors or in-group favoritism (De Dreu et al., 2010; Ma et al., 2015; 2016; Rilling et al., 2012; Yan et al., 2018). A single intranasal dose of 24 IU oxytocin or placebo (containing the active ingredients except for the neuropeptide) was self-administered by nasal spray about 35 min before the experimental task under experimenter supervision. A 24 IU dosage is employed as it is the most commonly used dosage in oxytocin literature (Wang et al., 2017) and recently shown having more pronounced effects (compared with 12 or 48 IU dose of oxytocin) on behavioral and neural responses (Spengler et al., 2017). The spray was administered to participants three times, and each administration consisted of one inhalation of 4 IU into each nostril. Six participants in the same IADC session were assigned to the same treatment (oxytocin or placebo), so as to avoid potential influence of oxytocin to placebo between individuals.

Data analysis. Data were aggregated to the group level, with Role (Attacker vs. Defender), Procedure (Simultaneous vs. Sequential) and Round as within group variables, and Treatment (Oxytocin vs. Placebo) as between-group factor. Analyses were performed on (i) contribution (the averaged investment of each round, range: 0-20), (ii) the number of non-contributors (the number of group members making a 0 investment across a 15-round block, range: 0-45), (iii) variance (within-group variance of each round), (iv) success rate for attack (range 0-100%), (v) the attackers' leftovers when losing a conflict, and (vi) the attackers' spoils when winning a conflict and, finally, (vii) inter-group tracking. Analyses for (i) – (vii) are reported in the Main Text and shown in Fig. 1-3. In addition, to complement and validate these analyses, we analyzed (viii) decision time for investment decisions (log 10-transformed decision time), and (ix) within-group coordination as reflected in the Intra-class correlation coefficient. The results for these complementary analyses are reported below in *SI*, Fig. S3-S6.

Game-theoretic Analysis. The IADC is an all-pay contest with a single mixed-strategy Nash equilibrium (Abbink et al., 2010; Dechenaux et al., 2015; De Dreu et al., 2016a). With two three-person groups, each member assumed to have risk-neutral preferences and having a discretionary resource of $e = 20$ to invest from, the IADC game has unique mixed-strategy Nash equilibrium with out-group attack (in-group defense) expected to average 10.15 (9.77), and attackers (defenders) should win (survive) 32.45% (67.55%) of the episodes. Across the 15 rounds of simultaneous decision-making under placebo, both out-group attack ($M \pm SE = 5.58 \pm 0.40$) and in-group defense ($M \pm SE = 8.27 \pm 0.36$) fell below the Nash-equilibrium ($t(39) = -11.30$, $p < 0.001$ and $t(39) = -4.18$, $p < 0.001$). Attackers defeated defenders in 22.08% (SE=2.2%) of their attacks, which is below the Nash success-rate ($t(39) = -4.734$, $p < 0.001$). Oxytocin did not influence deviations from rationality (attack: $t(39) = -15.78$, $p < 0.001$; defense: $t(39) = -6.022$, p

< 0.001; success-rate: $t(39) = -6.615$, $p < 0.001$).

Response Time for Decisions to (Not) Contribute. We showed that oxytocin increases the number of non-contributors in attacker groups. To further reveal how oxytocin influences the non-contributing decisions, we examined participants' decision time by calculating the response time separately for the round that participants decided to or not to contribute. This analysis was conducted only on the attacker group because 1) there were very few rounds (9%) in which defenders decided not to contribute; 2) oxytocin only influenced the number of non-contributors in attacker groups. Since the distribution of decision times is heavily right skewed, linear regression is not appropriate. Similar to a previous study (Ma et al., 2015), we first log 10-transformed decision times in all the analyses that involved decision times. The log 10-transformed decision time was submitted into a 2 (Contribute: Yes vs. No) × 2 (Treatment: Oxytocin vs. Placebo) ANOVA for the attacker group. The decisions of which the response time exceeded 180 seconds were excluded in final data analysis (0.51% of the decisions, due to network problem during the experiment). Fig. S3 shows that attacker groups make their decisions to not contribute faster than to contribute (Contribute: $F(1, 78) = 137.679$, $p < 0.001$, $\eta^2 = 0.641$). Interestingly, oxytocin speeds up attacker groups to make their decisions to not contribute (Treatment × Contribute : $F(1,77)=4.857$, $p=0.031$; $\eta^2= 0.059$).

Within-Group Coordination. To complement and cross-validate the results for within-group variance as an indicator of within-group coordination, we computed another related index—the intra-class correlation. The intraclass correlation (ICC2, De Dreu et al., 2016a; LeBreton and Senter, 2008) operates on a data structured as groups, describing how strongly individuals in the same group resemble each other. Higher ICC2 values in essence mean group members are more

similar to each other in the contributions made to their group's fighting capacity. A Treatment × Role × Procedure ANOVA showed that effects for role ($F(1,78)=43.090$, $p < 0.001$, $\eta^2= 0.356$), procedure ($F(1,78)=166.199$, $p < 0.001$, $\eta^2= 0.681$) and the role x procedure interaction were significant ($F(1,78)=147.586$, $p < 0.001$, $\eta^2= 0.654$). Furthermore, fitting the results for within-group variance reported in the Main Text (see Fig. 2A), results further showed that oxytocin increased attacker groups' intraclass correlation under simultaneous decision-making ($t(78)=-2.057$, $p=0.043$, Cohen's $d=0.230$, *SI*, Fig. S4).

Tracking on historical contribution. To test whether attacker groups made their investment decision based on tracking of their rival's historical level of defense, we built a multiple linear regression of attacker groups' average contribution on round i (referred as A_i, with i range from 3 to 15) as a function of average level of defense of last rounds (calculated as $(D_{i-1}+D_{i-2})/2$, regression weight referred as α). The regression weight α was Fisher's z transformed for statistical analysis. Similar to previous study (De Dreu et al., 2016b), we also included another parameter: defense change of the last and before-last rounds, calculated as $(D_{i-1}-D_{i-2})$, regression weight referred as β. However, the analysis on β failed to show significant main effects of Treatment/Procedure or their interaction (*p*s>0.1). To complement the analysis of attacker groups, we also examined whether and how defender groups tracked the historical level of attack in their rivals. This showed that defender groups relied more on α to track attacker groups under simultaneous (relative to sequential) decision-making. The main effect of Treatment and its interaction with Procedure was not significant (*p*s>0.05, *SI*, Fig. S5).

Mediation analysis. We performed formal mediation analyses to examine though which route oxytocin increased attacker group's spoils from winning a conflict. Two potential mediators were

included in the mediation model: one is tracking coefficient (α) the other is within-group variance. Four different regression models were constructed, as shown below:

$$Y = \beta_{11}X + \beta_{10} \quad (1)$$

$$M1 = \beta_{21}X + \beta_{20} \quad (2)$$

$$M2 = \beta_{31}X + \beta_{32}M1 + B_{30} \quad (3)$$

$$Y = \beta_{41}X + \beta_{42}M1 + B_{43}M2 + B_{40} \quad (4)$$

In these models, X is the independent variable (Treatment, dummy-coded, 0 for Placebo and 1 for Oxytocin), M1 is the first mediator (the weight for attacker group's tracking of the historical defense, the tracking coefficient, α), M2 is a second mediator (attacker group's within-group variance), and Y is the dependent variable (attacker groups' spoils from winning a conflict, reported in the Main Text, and DV with the sum of attacker groups' spoils from winning a conflict and leftovers from losing a conflict reported in the *SI*). A resampling method known as bootstrapping was used to test the direct and indirect path. Bootstrapping is a nonparametric approach to effect-size estimation and hypothesis testing that is increasingly recommended for many types of analyses, including mediation (Mackinnon et al., 2004; Shrout and Bolger, 2002). Rather than impose questionable distributional assumptions, bootstrapping generates an empirical approximation of the sampling distribution of a statistic by repeated random resampling from the available data, and uses this distribution to calculate p-values and construct confidence intervals (5,000 resamples were taken for these analyses). Moreover, this procedure supplies superior confidence intervals (CIs) that are bias-corrected and accelerated (Preacher et al., 2007). Results are summarized in *SI*, Fig. S3 and S6 and in *SI*, Table S3, S4. As can be seen, multistep mediational analysis showed that the oxytocin effect on increasing attacker group's spoils from winning the conflict *plus* leftovers from losing the conflict was mediated by its effect on increasing tracking of defenders' history so as to increase within-group coordination.

The authors declare no conflict of interest.

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Author Contributions: YM and CKWDD conceived of the project, discussed analyses and results, wrote the paper and incorporated co-author revisions. HZ and JG programmed the experiment and computing scripts, and HZ implemented the experiment and coordinated data collection. HZ and YM analyzed the data.

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Supplementary Information

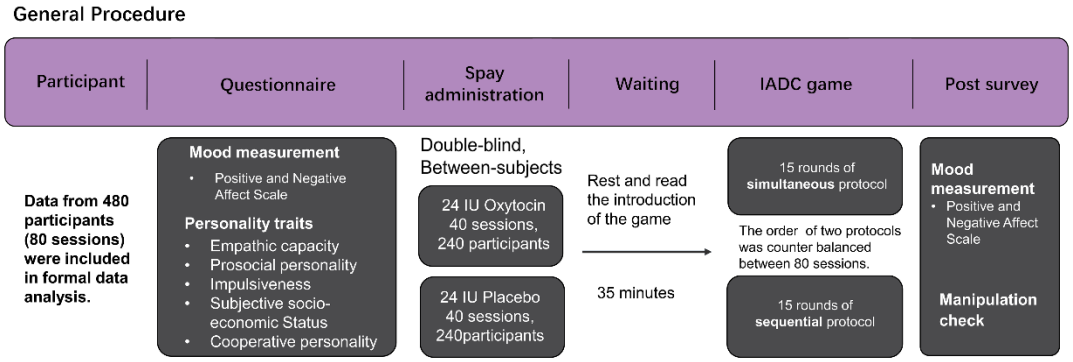

Fig. S1. Time-line of the Experimental Procedure and Treatments.

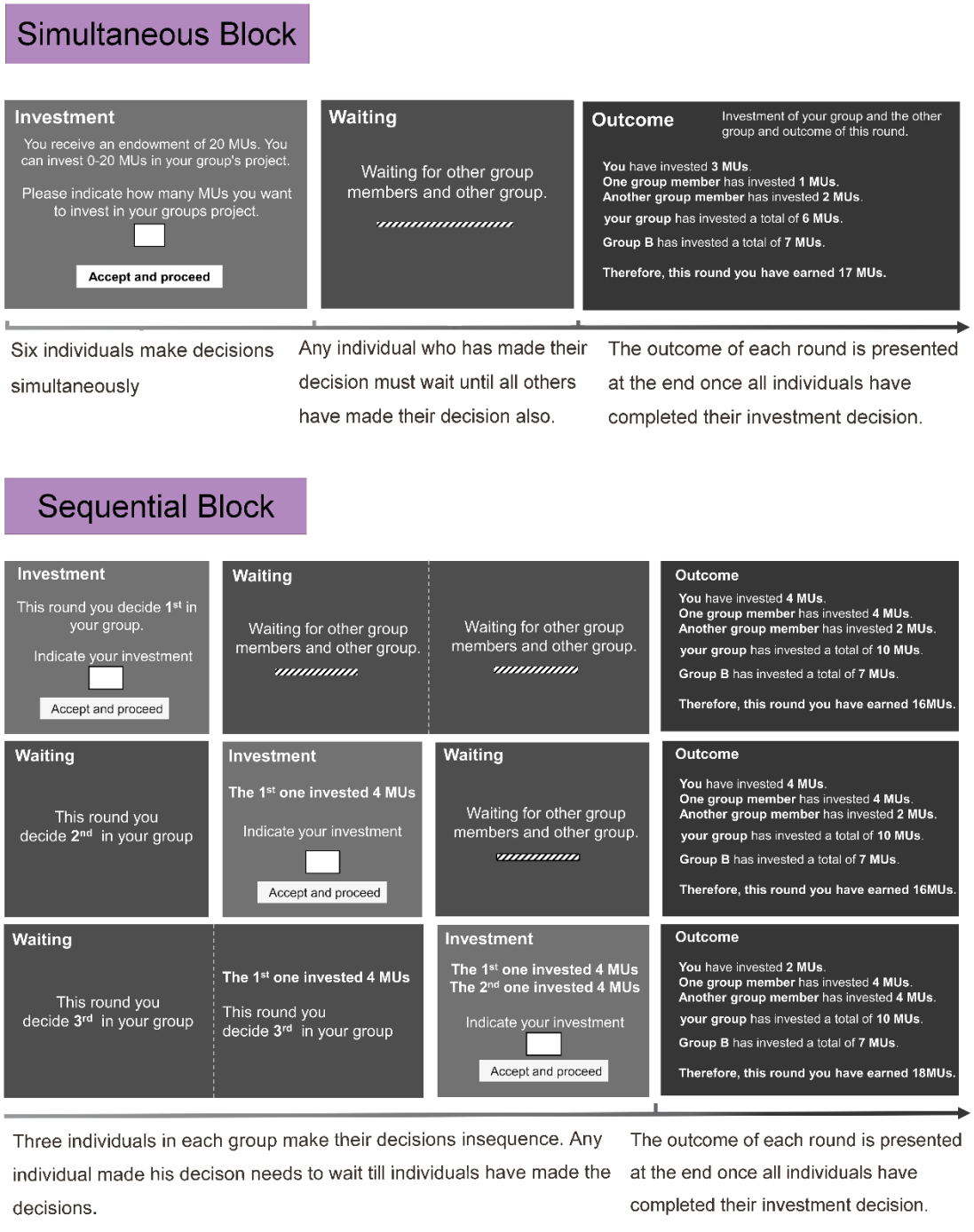

Fig. S2 Illustration of one round of the IADC game in the simultaneous and sequential decision-making blocks.

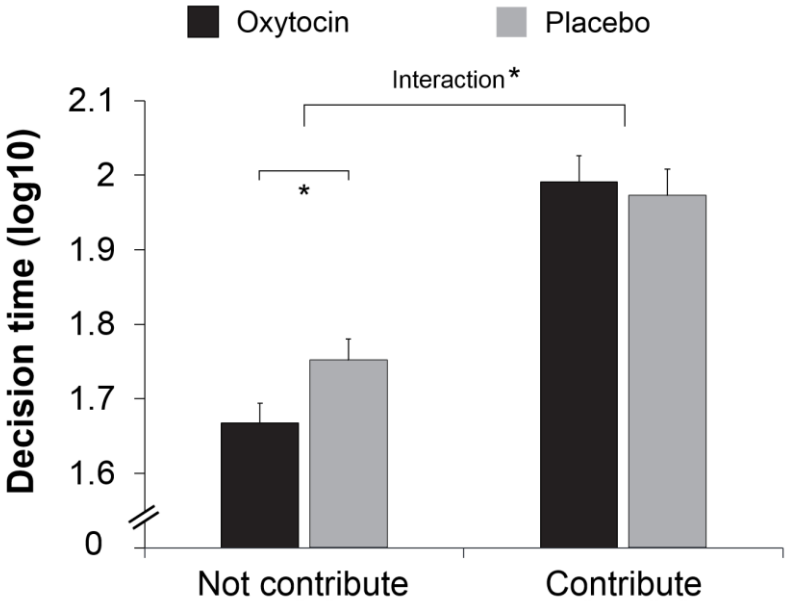

Fig. S3 Response Time for Decisions to (Not) Contribute.

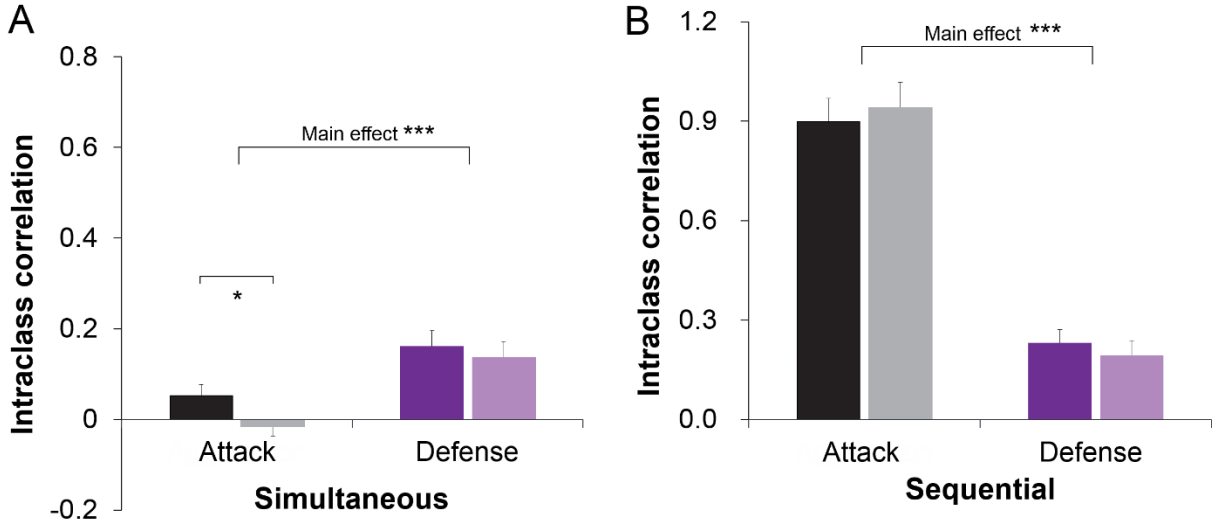

Fig. S4 Oxytocin increases attacker group's within-group coordination especially in the simultaneous decision-making block.

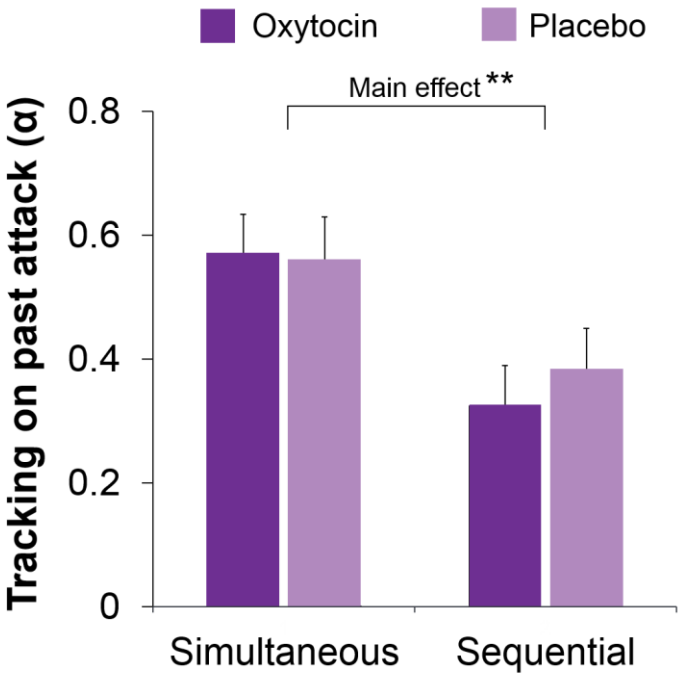

Fig. S5 Defender groups tracked on attacker groups' historical contributions better under simultaneous (relative to sequential) decision-making.

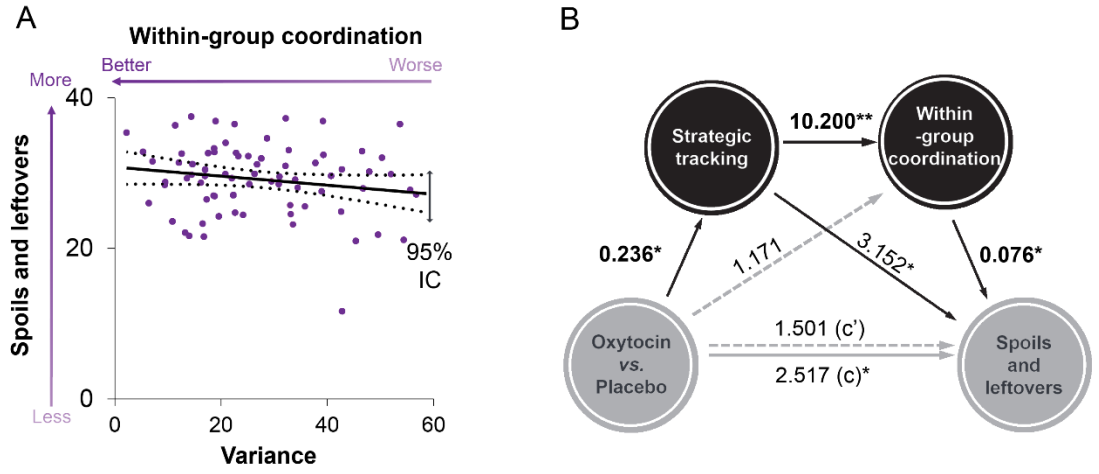

Fig. S6 (A) Better coordination (i.e., lower within-group variance) associates with higher spoils and leftovers. (B) Oxytocin's effect on attacker groups' spoils from successful attacks and leftovers from attack failure is mediated by treatment effects on tracking α and better within-group coordination. Significant pathways were highlighted in bold. (†p<0.1; *p<0.05; **p<0.01).

Table S1.

Match personality traits.

	Oxytocin		Placebo		Interaction
	Attack	Defense	Attack	Defense	
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	F (*p*)
Empathic capacity	3.50 (0.39)	3.48 (0.40)	3.51 (0.40)	3.51 (0.39)	0.068 (0.794)
Cooperative personality	3.55 (0.43)	3.54 (0.41)	3.55 (0.40)	3.55 (0.39)	0.103 (0.749)
Social value orientation	27.14 (12.40)	27.73 (12.93)	25.99 (12.97)	26.23 (13.45)	0.021 (0.886)
Prosocial personality	41.20 (4.80)	41.51 (4.72)	40.96 (5.34)	40.86 (4.94)	0.218 (0.641)
Impulsiveness	19.32 (2.38)	19.46 (3.02)	19.02 (2.85)	18.81 (2.75)	0.498 (0.481)
Socio-economic status	5.25 (1.52)	5.31 (1.58)	5.49 (1.61)	5.09 (1.53)	2.679 (0.102)

Table S2.

Mood changes from pre-experiment to post-experiment.

	Oxytocin		Placebo		Interaction
	Attack	Defense	Attack	Defense	
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)	F (*p*)
Interested	1.33 (2.15)	1.07 (2.13)	1.54 (2.22)	1.11 (2.11)	0.198 (0.656)
Distressed	0.63 (1.63)	0.67 (1.43)	0.87 (1.40)	0.72 (1.49)	0.515 (0.473)
Excited	1.21 (1.81)	0.87 (1.83)	1.23 (1.85)	0.91 (1.85)	0.002 (0.969)
Upset	0.71 (1.42)	0.62 (1.36)	0.93 (1.63)	0.83 (1.49)	0.001 (0.976)
Strong	1.01 (1.78)	0.89 (1.74)	1.09 (1.93)	1.14 (1.76)	0.250 (0.617)
Guilty	0.58 (1.51)	0.53 (1.37)	0.79 (1.30)	0.75 (1.49)	0.002 (0.960)
Scared	0.34 (1.45)	0.22 (1.23)	0.48 (1.32)	0.36 (1.38)	0.001 (0.972)
Hostile	0.56 (1.34)	0.56 (1.08)	0.88 (1.28)	0.67 (1.51)	0.747 (0.388)
Enthusiastic	1.10 (1.99)	0.85 (1.83)	1.25 (1.98)	1.08 (1.83)	0.047 (0.828)
Proud	1.30 (1.71)	0.10 (1.66)	1.28 (1.71)	1.18 (1.84)	0.393 (0.531)
Irritable	0.71 (1.52)	0.48 (1.50)	0.86 (1.49)	0.72 (1.77)	0.089 (0.766)
Alert	1.28 (1.92)	1.10 (1.78)	1.29 (2.03)	1.06 (1.91)	0.023 (0.880)
Ashamed	0.61 (1.44)	0.40 (1.32)	0.67 (1.25)	0.70 (1.40)	0.932 (0.335)
Inspired	1.08 (1.72)	0.92 (1.66)	1.09 (1.83)	0.86 (1.93)	0.041 (0.839)
Nervous	0.39 (1.61)	0.21 (1.44)	0.51 (1.52)	0.48 (1.61)	0.277 (0.599)
Determined	1.23 (1.83)	1.06 (1.71)	1.33 (2.00)	1.21 (1.84)	0.017 (0.897)
Attentive	1.34 (2.10)	1.07 (1.91)	1.404 (2.12)	1.20 (1.89)	0.026 (0.872)
Jittery	0.56 (1.59)	0.42 (1.26)	0.65 (1.44)	0.57 (1.49)	0.053 (0.818)
Active	1.23 (1.94)	1.02 (1.88)	1.36 (1.98)	1.19 (1.76)	0.014 (0.905)
Afraid	0.40 (1.35)	0.23 (1.22)	0.38 (1.31)	0.34 (1.39)	0.269 (0.604)
Positive	-1.40 (6.07)	-0.84 (4.48)	-1.77 (5.65)	-1.61 (6.42)	0.154 (0.695)
Negative	-1.33 (7.04)	-0.22 (5.60)	-0.02 (6.16)	-0.58 (6.76)	2.013 (0.157)
All	-1.78 (8.86)	-1.75 (6.52)	-2.18 (9.58)	-0.83 (8.87)	0.473 (0.492)

Table S3.

Point estimates for indirect effects and bootstrapped 95% bias-corrected confidence intervals for multiple mediational analysis in which attacker group's tracking (*strategic tracking when α → -1*) and within-group variance (*variance*) were represented as mediators in the association between *Treatment* and *spoils from winning* a conflict during simultaneous decision-making.

Path	Estimate	LLCI	ULCI
Treatment > Attackers track defenders (α) > Spoils from winning	0.327	-0.099	1.132
Treatment > Variance > Spoils from winning	0.058	-0.264	0.518
Treatment > Attackers track defenders (α) > Variance > Spoils from winning	**0.120**	**0.018**	**0.401**
Total indirect effect	0.506	0.022	1.396

Notes. Treatment was a dichotomous variable (0 for Placebo and 1 for Oxytocin); Confidence intervals for indirect effect are bias-corrected and accelerated bootstrap resamples=5000; *N=76* for all tests.

Table S4.

Point estimates for indirect effects and bootstrapped 95% bias-corrected confidence intervals for multiple mediational analysis in which attacker group's tracking (*strategic tracking when α → -1)* and within-group variance (*variance*) were represented as mediators in the association between *Treatment* and *spoils and leftovers* during simultaneous decision-making.

Path	Estimate	LLCI	ULCI
Treatment > Attackers track defenders (α) > Spoils & leftovers	**0.743**	**0.031**	**3.186**
Treatment > Variance > Spoils and leftovers	0.089	-0.406	0.779
Treatment > Attackers track defenders (α) > Variance > Spoils and leftovers	**0.183**	**0.024**	**0.692**
Total indirect effect	**1.015**	**0.156**	**2.416**

Notes. Treatment was a dichotomous variable (0 for Placebo and 1 for Oxytocin); Confidence intervals for indirect effect are bias-corrected and accelerated bootstrap resamples=5000; *N=76* for all tests.