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Us against them: oxytocin response to competition in a small-scale human society

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Cooperation can be an effective way to compete. The neurohormone oxytocin (OT) may modulate this by enhancing both cooperation and competition. However, studies of endogenous OT reactivity during real-world competition are scarce. Here, we tested the hypothesis that OT modulates inter-group competition in a human subsistence society, the Tsimane' of Bolivia, by measuring urinary OT in football players before and after matches. Matches varied in group salience, involving intra-community, inter-community and interethnic opponents. Urinary OT was quantified using radioimmunoassays. We observed an increase in urinary OT levels following competition among men, but not among women. OT responses were strongest during both intra-community and interethnic matches. This pattern suggests sensitivity to familiar rivalries, consistent with the 'nasty neighbour effect', as well as heightened responses to out-groups. Our results support the hypothesis that OT mediates group-level competition in humans and reveal that OT reactivity varies by group salience. Moreover, our results showed a sex-specific response, with OT increases in men but not in women.

1. Introduction

Social organisms display some of the most striking forms of cooperation in the animal kingdom, while simultaneously adopting resolutely antisocial behaviour, especially when confronted with rival groups. Many cooperative breeders such as meerkats (*Suricata suricatta*), for instance, maintain high levels of cooperation within family groups, while frequently engaging in intense inter-group conflict [1]. Similarly, chimpanzees (*Pan troglodytes*) cooperate within their communities in collective hunting and meat sharing [2–4], yet they also regularly engage in border patrols and lethal inter-group attacks [5–7]. Humans are also a prime example of this duality: large-scale cooperation undergirds food production, technological innovation and institutions, while organized warfare remains an indelible feature that has shadowed humankind across recorded history [8,9].

Rather than occupying opposite ends of a behavioural spectrum, cooperation and competition appear to be two facets of the same adaptive strategy, sometimes described as parochial cooperation, i.e. the tendency to combine costly in-group cooperation with antagonism towards outsiders [10,11]. Theoretical work suggests that neither in-group cooperation nor out-group aggression is likely to persist in isolation over evolutionary time. However, both traits can become stable when they coevolve, mutually reinforcing each other's adaptive value [12]. In this view, parochial cooperation is a composite strategy through which individuals increase group-level success and, in turn, individual fitness, especially in contexts where inter-group competition makes cohesive and cooperative groups more likely to succeed.

Building on this conceptual foundation, the practical success of parochial cooperation appears to depend on a capacity for rapid, group-wide adjustments in behaviour, emotion and physiology whenever external hostility arises [13]. The endocrine system provides precisely this integrative machinery, aligning neurocognitive processing with peripheral physiological shifts that sharpen competitive readiness [14]. More specifically, in mammals, the oxytocinergic system is a prime candidate regulator of parochial altruism, able to modulate prosocial and antisocial responses concurrently [15–18].

Oxytocin (OT) is a nonapeptide, highly conserved in mammals, produced primarily by the hypothalamus. It then diffuses in two ways: centrally, by modulating neuronal activity, and peripherally, via the blood. When released peripherally, OT circulates in plasma and is eliminated by renal filtration, while a small fraction reaches saliva through transfer via the salivary glands [19,20]. While it is therefore possible to quantify OT production in plasma, saliva or urine, urinary OT has the advantage to provide an integrated measure of peripheral exposure accumulated since the last urination, rather than a momentary snapshot, thus offering better detection of pulsatile events [21].

Long heralded as the 'love hormone', oxytocin's reputation is now more nuanced as it may also facilitate ethnocentrism and domestic violence [22,23]. This apparently paradoxical duality becomes clearer if we consider OT not as intrinsically prosocial or antisocial, but as an adaptive coordination system. In the context of inter-group conflict, an increase in OT can simultaneously (i) enhance in-group cooperation, trust and synchrony, and (ii) increase vigilance or aggression towards the out-group [15,24]. One potential mechanism which could facilitate this is social salience, defined as the contextual relevance given to social stimuli [25]. Indeed, intranasal OT increases attention to out-group faces and enhances processing of relevant social cues, whether positive or negative [25–28]. OT could also facilitate group cooperation and competition by encoding the valence (positive or negative) of a situation and motivate approach or avoidance [29,30]. Thus, OT is a strong candidate for an adaptive coordination system underlying group cooperation and competition [17,18].

Human OT research has been dominated by laboratory studies using exogenous OT administration, which is key to demonstrating causality and identifying specific mechanisms; however, measuring naturally occurring hormone variation in ecologically valid contexts may be more informative about the evolutionary functions of endocrine systems [31]. In several non-human species, experimental manipulations and field endocrinology are more explicitly integrated. While laboratory studies establish causal behavioural effects, field research shows that hormone concentrations fluctuate predictably in contexts such as mating, territorial defence or inter-group conflict. Although findings are not always convergent, such discrepancies have clarified the context-dependence and socioecological specificity of oxytocinergic effects. To date, very few studies have examined whether natural social stressors in humans, including group-level cooperation or rivalry, are sufficient to elicit a comparable physiological response [32]. Field evidence from non-human primates supports the hypothesis that OT regulates parochial cooperation. For instance, in chimpanzees, border patrols and hostile confrontations result in a significant rise in urinary OT, detected both before and during the confrontation [7]. In bonobos (*Pan paniscus*), however, there is no OT response to inter-group encounters [33], consistent with their lower levels of between-group competition [34–36]. In humans, who engage in both peaceful and hostile inter-group relations [11], it has not yet been demonstrated that an external threat is sufficient to trigger the release of OT and, in so doing, to influence cooperation or competition.

From an evolutionary perspective, hormonal systems should be examined under the energetic and immunological constraints of ancestral lifeways [17]. Indeed, hormones are often viewed as mediators of competing demands such as growth, immune defence and reproduction, and accordingly hormone profiles vary predictably with local ecology [37–39]. For instance, testosterone levels decline during illness or nutritional shortfalls [40,41], and consequently men in subsistence societies, who experience such energetic stress more frequently, exhibit substantially lower baseline testosterone than men in industrialized societies [42–44]. In recent work among the Tsimane', it has been shown that breastfeeding was the dominant predictor of variation in OT levels in women, and higher OT was associated with better self-rated health, consistent with OT's beneficial effects on various physiological systems [4546–48] . However, the degree to which OT mediates energetic trade-offs involved in cooperation and competition remains poorly understood [46–48].

Here, we tested the hypothesis that OT mediates parochial cooperation among the Tsimane' forager-horticulturalists of the Bolivian Amazon. The Tsimane' resemble the aforementioned ancestral conditions insofar as they live with high pathogen burdens, limited caloric surpluses and structure their social relationships predominantly around kinship ties within relatively small communities. These communities are generally composed of several dozen households loosely linked by shared facilities such as a school or road and an elected community representative (*corregidor*) [49–51]. Within these communities, clusters of related households and extended family networks cooperate in daily tasks and (re)production, while also competing with others for status and resources. Relationships with members of neighbouring communities are generally less frequent and less central to everyday cooperation, even though people often have some kin in other villages and may move between communities a few times in their lives while trying to remain near close relatives [52–56]. Crucially, football matches, which occur with relative regularity and have been ethnographically documented as emotionally intense and socially salient competitions [43], provide a naturalistic yet ethically acceptable proxy for inter-group conflict that simultaneously requires coordinated cooperation within teams. We therefore predicted that engaging in between-group competition, such as a football match, will elicit a rise in OT compared with pre-match levels, above and beyond the effects of physical activity. Additionally, given that previous research has identified sex differences in OT responses to social stimuli [57,58], we investigated whether OT responses to inter-group competition differ between men and women, thus allowing us to explore potential sex-specific mechanisms underlying parochial cooperation. Furthermore, organizing football matches allowed us to experimentally vary the level of out-group salience, which has been rarely explored in studies on OT and parochial cooperation, with few exceptions [28].

In this study, we focused on three levels of out-group salience: teams from the same community (close, regular in-group opponents drawn from distinct extended-family coalitions), different communities (co-ethnic opponents who are less central to everyday cooperation despite some kin ties and occasional mobility) and non-Tsimane' (a clearly bounded ethnic out-group, e.g. non-governmental organization (NGO) workers or town footballers, often perceived as socially and economically more distant) and we hypothesized two competing patterns of OT release. First, we predicted a strong OT response to teams from the same community, who regularly compete outside of the football context, as proposed by the 'nasty neighbour effect' [59]. Among the Tsimane', opposing teams from the same community map onto distinct extended-family networks that typically cooperate internally but compete over resources such as land and local status, making these kin-based coalitions natural candidates for 'neighbouring groups' in this context. Second, we expected a strong response against non-Tsimane' teams, as Tsimane' may sometimes experience discrimination and economic exploitation from outsiders and have a strong ethnic identity [60,61]. As a result, we predicted the lowest OT response to teams from other communities, who share an ethnic identity but are not in direct competition in daily life.

2. Material and methods

(a) Study population

Hormonal and behavioural data were collected from 90 Tsimane' participants (56 men, 34 women) aged 13–57 (mean age = 26.1; s.d. = 9.1) and comprise 188 urine samples (pre-football: 93 samples; post-football: 95 samples) collected across two fieldwork seasons in March–April 2023 ('FW1') and October–December 2023 ('FW2').

The Tsimane' are forager-horticulturalists of the Amazonian Bolivian basin (Beni region) who reside mainly along the Maniqui River and its tributaries. They are spread across around 95 communities, each ranging from a few dozen to several hundred individuals [50].

Tsimane' social organization centres around tightly knit clusters of nuclear and extended families, within which daily labour, meals and other resources are routinely pooled [53,54]. Largely isolated from wider Bolivian society until the mid-twentieth century, they became more connected after missionaries arrived and a road linked them to the highlands [62]. Unlike other Amazonian horticulturalists such as the Shuar or Yanomamo, they have no documented history of inter-community warfare. Collective endeavours instead include communal feasts, group hunting/fishing, infrastructure projects and occasional football matches [43,49,63]. Although ethnically homogeneous, Tsimane' interact with outsiders through trade in market towns, work for ranchers or logging companies, and occasional visits by NGOs or anthropologists. Since government resettlement programmes in the 1960s, nearby settlement by Andean descendants (*Interculturales*) has been associated with reported discrimination and conflict [60,61].

Although increasingly exposed to the market economy, the Tsimane' maintain a lifestyle relatively similar to that of subsistence populations prior to the emergence of mechanized agriculture and industrialization more widely. Accordingly, daily activities continue to centre on subsistence horticulture, hunting and fishing; lack of access to clean water and limited hygiene also expose individuals to a substantial pathogen burden, therefore placing consistently high energetic demands on immune function [44,50]. Moreover, unlike Western populations, Tsimane' women experience very high fertility and nearly all infants are breastfed for extended periods [64].

(b) Physical inter-group competitive context

Tsimane' men play football on average 3.1 times per week (s.d. = 1.5) [43]. Women also participate in football matches but less frequently [65]. On typical days, matches are played between players from the same community, often with relatively random teams, while Sundays may see matches between neighbouring communities.

Participants were recruited from four Tsimane' communities. To vary group salience, matches were organized at three distinct competitive levels: intra-community fixtures (players from the same community), inter-community fixtures (players from different Tsimane' communities) and Tsimane' versus non-Tsimane' (against ethnically distinct outsiders). Players participating in inter-community fixtures were recruited from neighbouring communities and travelled to the hosting community on the morning of the tournament. Non-Tsimane' participants included NGO workers and a team from the nearby town of San Borja. Non-Tsimane' opponents were not sampled as part of this study.

For all matches, players independently formed their teams prior to data collection, reflecting natural social divisions within their communities and between neighbouring communities. Consequently, teams consisted of individuals sharing geographical proximity and strong familial or social ties. In total, 11 male teams (mean age = 28.4; s.d. = 9.3) and eight female teams (mean age = 22.3; s.d. = 7.2) participated in the study. The team compositions remained unchanged across all fixtures and competition levels, and no player transferred between teams.

To further raise competitive stakes, matches were organized as tournaments, with each player receiving a prize increasing with final ranking. The top prize was equivalent to roughly 1 day's wages, with lower-ranked prizes proportionally smaller.

(c) Sample collection

Matches lasted 40 min. Each half lasted 15 min with a 10 min break. Pre-match urine samples were collected 10 min before kick-off, while post-match samples were collected 10 min after the end of the match. In humans, it has been reported that urinary OT concentrations peak approximately 30–60 min after systemic administration [19,66]. Accordingly, by imposing a minimum interval of 1 h between pre- and post-match urine collections, any oxytocin fluctuations resulting from football participation should be reliably detectable.

We collected 1.5 ml (FW1) or 3 ml (FW2) of urine per participant. Following collection, and in order to prevent OT degradation, urine samples from FW2 were immediately acidified with 10 µl of phosphoric acid per ml of sample. All samples were stored in liquid nitrogen in the field within minutes of collection, and shipped on dry ice to the laboratory, where they were kept at −80°C prior to OT quantification [67].

Across all fixtures, most players contributed a single pair of samples (one pre- and one post-football sample from one match), and only a small subset of players were sampled in more than one match (five duplicate pre-football samples and seven duplicate post-football samples). Importantly, all repeat-sampled participants were sampled within the same team and never appeared in multiple teams.

(d) Oxytocin measurements

Urinary oxytocin concentrations (pg ml^{-1}) were assessed by the Wisconsin National Primate Research Centre at the University of Wisconsin-Madison by performing radioimmunoassay (RIA). Phoenix Pharmaceuticals Oxytocin RIA kits were employed for the analysis. The samples underwent a solid-phase extraction procedure in order to reduce molecular interference, lessen the impacts of the sample matrix, and get a 12-fold analyte concentration [67,68]. Wherever possible, pre- and post-football samples from the same participant were assayed within the same batch to reduce variability arising from inter-assay differences and to better isolate football-related changes in oxytocin levels. The intra-assay coefficient of variation (CV) ranged from 3.1% to 5.8%, and the inter-assay CV ranged from 6.4% to 7.9%.

(e) Physical activity

OT levels may be affected by physical activity [69]. To adjust for this, the physical activity of a subset of players ($n = 30$), from the second field season, was assessed using wrist-worn Actigraph wGT3X accelerometers [70]. Physical activity was quantified as steps per minute over the 40 min match duration (minimum: 23.1; maximum: 74.8; mean = 53.1; s.d. = 10.8).

(f) Specific gravity correction

To control for hydration status, specific gravity (SG), defined as the ratio of the density of urine to that of distilled water, was measured immediately after collection using an ATAGO™ Master-URC/NM refractometer. Urine concentrations were then normalized by applying a specific gravity correction, according to the following formula [71]:

$$\text{Corrected OT Concentration} = \text{Raw OT Concentration} \times \frac{\text{mean}SG_{\text{pop}} - 1.0}{SG_{\text{sample}} - 1.0}$$

where $\text{mean}SG_{\text{pop}}$ represents the mean specific gravity of all samples, and SG_{sample} is the specific gravity of the sample to which the correction is applied.

The specific gravity correction has been preferred to the conventional creatinine correction to ensure the stability and reliability of our hormone assays based on punctual samples. Specific gravity accurately reflects the total concentration of urinary solutes under normal physiological conditions and remains stable during storage, whereas creatinine degrades during extended storage and repeated freeze–thaw cycles. Furthermore, creatinine excretion varies considerably according to intrinsic and behavioural factors; including sex, age, muscle mass, physical activity, dietary intake and time of day; which undermines its reliability as a correction method, particularly at low urinary concentration [72,73].

(g) Statistical analyses

All statistical analyses were conducted within a Bayesian framework. This allows probabilistic interpretation of parameter estimates and transparent quantification of uncertainty [74]. Rather than relying on p-values or dichotomous significance tests, the results are presented in the form of full posterior distributions for all parameters of interest.

For each variable of interest we present the posterior mean (b), the 95% credible interval (lower and upper bounds: l-95% CrI and u-95% CrI), and the posterior probability ($p > 0$) that the effect lies in the expected direction. The ($p > 0$) is calculated as the proportion of the posterior distribution falling above zero, which provides a direct measure of our confidence in the presence and direction of an association.

To support interpretation, we also visualize model predictions using conditional effect plots. These plots illustrate the estimated relationship between each predictor and the outcome variable, while holding other covariates constant.

Main model (Competition Model): We modelled corrected OT concentration using lognormal Bayesian mixed-effects models in the so called 'competition model'. This approach accounts for the positively skewed distribution of hormonal data and allows for hierarchical structuring of sources of variation, including individual identity and technical factors (such as field season or assay batch). Fixed effects included Sex (women versus men), Sample Type (pre-football versus post-football sample), Breastfeeding (no versus yes), standardized Age (Age), Extraction Lot (Lot), and Fieldwork (FW). To account for possible differential responses between men and women players, an interaction between Sex and Sample Type was included. Full model specifications are provided in the electronic supplementary materials, Methods.

Extended model (Group salience model*)*: To test whether the salience of social context modulated OT concentrations, we extended the main model to include a three-way interaction between Sex, Sample Type (pre-football versus post-football sample) and out-group Type (intra-community, inter-community, Tsimane' versus non-Tsimane'). Full model specifications are provided in the electronic supplementary material, Methods.

Physical activity model: To assess whether changes in physical activity could explain variation in OT levels, we modelled post-football OT concentration as a lognormal Bayesian mixed-effects function of average steps per minute during the match with a sex interaction, while adjusting for pre-football OT and relevant covariates, and accounting for technical clustering and censoring.

All models were implemented in RStudio (v. 4.2.1), with Bayesian mixed-effects models implemented through the *brms* and *rstan* packages [75]. Model convergence was assessed using R-hat statistics (all = 1), effective sample sizes and visual inspection of trace plots. For models that exhibited divergent transitions with default settings, we increased the Stan target acceptance rate (adapt_delta) to 0.99 to improve sampling efficiency; this tuning step affects only sampling efficiency and does not change the posterior estimates.

3. Results

(a) Effect of competition

Football competition was associated with an increase in men's urinary OT levels (b = 0.39; 95% CrI = 0.09–0.7; posterior probability of a positive effect $P(>0)$ = 0.99; table 1, figure 1). By contrast, OT levels in women did not change after the match (b = 0.01; 95% CrI = −0.22 –0.24; $P(>0)$ = 0.52; table 1, figure 1). Breastfeeding was the strongest predictor of OT levels. Indeed, on the log-scale, breastfeeding women showed an increase of b = 0.77 (95% CrI = 0.38–1.17; $P(>0)$ = 1.00; table 1) compared with non-breastfeeding women (reference category). This corresponds to an average OT concentration approximately exp(0.77) ≈ 2.16 times higher in breastfeeding women, thereby providing strong biological validation for our measurements.

No other covariates in the model yielded credible effects (table 1).

(b) Effect of group salience

In the extended model including out-group type, intra-community football matches among men were associated with a rise in urinary OT (b = 0.41; 95% CrI: 0.06–0.76; $P(>0)$ = 0.99 ; electronic supplementary material, table S1, figure 2), supporting a robust effect of competition in familiar, within-community contexts. By contrast, women showed little evidence for any change in oxytocin levels following intra-community competition (b = 0; 95% CrI: −0.23–0.23; $P(>0)$ = 0.51 ; electronic supplementary material, table S1, figure 2), once again following the sex-differentiated result in section 6(a).

When examining out-group contexts, results indicated that the OT response in men was smaller in inter-community matches (b = 0.13; $P(>0)$ = 0.71), and with less credibility than for intra-community fixtures. More notably, matches opposing Tsimane' players to non-Tsimane' out-groups yielded a pronounced rise in men's OT (b = 0.56; $P(>0)$ = 1), similar in magnitude and certainty to intra-community fixtures.

(c) Effect of physical activity

We found evidence that physical activity positively influenced changes in OT following competitive interaction. Posterior distributions placed high probability mass above zero for both men ($P(>0)$ = 0.99) and women ($P(>0)$ = 0.98). The estimated main effect of steps per minute on post-football OT was small though (b = 0.05, 95% CrI = 0.01–0.1), indicating a directionally positive but weak association (Supplementary materials, figure 2).

4. Discussion

(a) Oxytocin's response to group competition

Our study investigated whether the human oxytocinergic system responds to group competition, using football matches as an example. We hypothesized that this system plays a key role in parochial cooperation. Consequently, we anticipated an increase of endogenous OT concentration following football matches. In support of this hypothesis, the first model revealed a positive effect of competition on OT concentration in men, but not in women (table 2, figure 1). This sex-specific pattern indicates that

OT release in competitive contexts is not a uniform response to physical activity or social interactions *per se*, but might be conditioned by how the competitive environment is perceived, particularly in terms of social incentives and threat dynamics (see section 7(c) and section 7(d)). The OT response to football is in line with observations made in chimpanzees, in which increases in endogenous OT accompany inter-group patrols and are correlated with greater behavioural cohesion [7]. In both contexts, group-level competition is inseparable from within-group cooperation and coordination.

As mentioned in the introduction, one mechanism by which OT could facilitate parochial cooperation is by increasing social salience [25,26]. For example, OT increases attention to faces and particularly eye contact in species where the latter conveys social information, such as humans and rhesus macaques [76,77]. Furthermore, intranasal injection of OT improves the recognition of emotional expressions and the interpretation of complex social relationships, such as kinship or rivalry dynamics [78,79]. In inter-group contexts, OT appears to enhance the social salience of the out-group by increasing sensitivity to threatening and non-threatening signals from that group [80]. These neuromodulatory functions appear crucial in group competition where it is necessary to quickly categorize allies and adversaries, decode intentions and respond to threats, which requires rapid and effective reading of the social environment. In addition to social salience, behavioural coordination and synchronization are essential for success in group competition. OT increases sensitivity to human movement and biological motion, which can promote team coordination and the reading of opposing actions in real time, especially in our football competition setting [81]. Moreover, in humans OT improves joint performance in coordinated tasks and increases neuronal synchronization between partners in regions related to social processing [82,83]. In highly interdependent contexts, such as combat simulations or collaborative tasks, OT promotes the alignment of intentions and behaviours, increasing mutual trust and shared attention [84]. Synchronization itself appears to lead to an endogenous release of OT, creating a positive feedback loop that strengthens cohesion [85].

In sum, OT may facilitate parochial cooperation through several plausible mechanisms, though field studies like ours are not well suited to identify specific mechanisms. Moreover, it is important to emphasize that oxytocin does not exert a fixed behavioural effect, but operates within species-specific social structures. Work in voles has shown that closely related species with different mating systems display distinct patterns of oxytocin receptor distribution, leading to divergent affiliative and bonding behaviours despite sharing a homologous endocrine system [86]. Conversely, recent work in canids suggests that similar outward behaviours in competitive inter-group contexts may be supported by different endocrine profiles depending on socioecological conditions [87]. Furthermore, endogenous OT levels respond to male–female sexual consortships in chacma baboons (*Papio ursinus*) [88], but only to female–female (not male–female) sexual interactions among bonobos (*Pan paniscus*) [89]. More broadly, similar behaviours can emerge from different endocrine pathways across taxa [90]. Hence, further comparative and integrative work is needed to clarify how oxytocin contributes to parochial cooperation under different socioecological conditions.

(b) Physical activity contributes but does not fully account for men's post-match oxytocin rise

Analyses incorporating physical activity indicated that average steps per minute were positively associated with post-football OT concentration for both sexes. Posterior evidence favoured a positive slope in both men and women, although the average effect on the log scale appeared modest. This suggests that physical activity contributes to the increase of OT concentration after group competition, but that it alone cannot explain the entire post-match effect observed in men.

If physical activity were the principal driver of the post-match increase, a similarly positive activity–OT association in men and women should have produced comparable pre- to post-match responses in the competition model; instead, only men showed a rise. In comparable intra-community fixtures, women also exhibited a slightly higher mean step rate than men (50.79 versus 48.99 steps min^{-1}), suggesting that a stronger OT response might have been expected in women rather than in men based solely on physical activity. Moreover, among men, inter-community matches were on average associated with slightly higher activity than intra-community matches, yet the OT response was stronger for intra-community ones.

Taken together, the evidence indicates that physical activity positively contributes to OT variation, yet the competitive social context remains decisive. The male post-match increase cannot be attributed to physical activity *per se* and aligns with the view that the oxytocinergic system reacts to cooperation and/or competition cues during football fixtures.

(c) Oxytocin's response to group salience

The observed differences in OT responses across the three levels of group salience among male participants suggest nuanced neuroendocrine adaptations to varying competitive contexts. Men displayed the strongest increase in OT concentration after engaging in intra-community matches (figure 2A), and in Tsimane' versus non-Tsimane' matches (figure 2C). Conversely, they displayed the weakest response after playing against players from a neighbouring community (figure 2B).

In intra-community matches, opponents were familiar rivals within the same community, and team selections often followed extended-family lines. Among the Tsimane', these clusters form cohesive cooperative units that share resources but also compete over land, labour and social status. As a result, intra-community fixtures effectively pitted neighbouring kin-based coalitions against one another, which we view as the closest analogue in this setting to the 'nasty neighbour effect' described as a competitive dynamic documented in several species including humans, where rivalry and hostility are more pronounced toward familiar individuals due to frequent and direct competition, particularly regarding social status [59]. More generally, humans routinely navigate nested and intersecting group identities, allowing 'neighbour' competition to arise between subgroups within a shared community rather than only between clearly bounded groups. Among Tsimane'

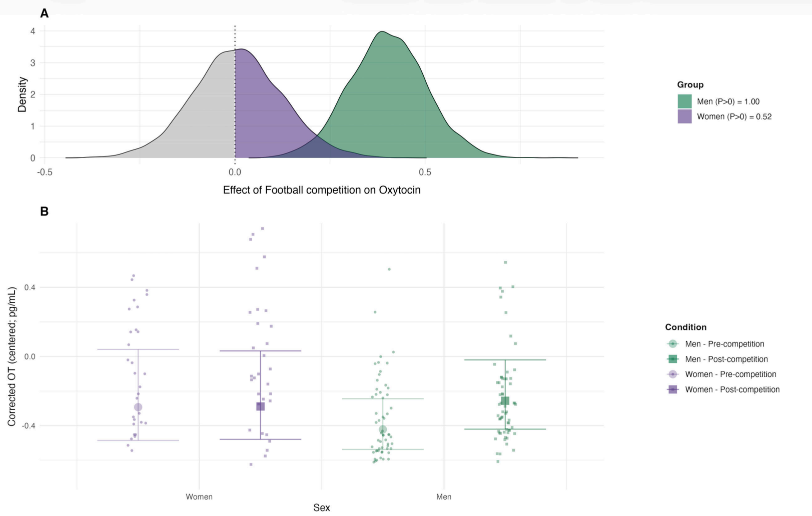

Figure 1. Oxytocin levels respond to competition in men but not women. (A) Posterior probability distribution of the effect of football competition on endogenous urinary oxytocin levels in men and women. The posterior distributions represent the predicted change in OT levels post-football compared with the pre-football levels, indicated by the dotted line at 0. Posterior probabilities *P*(>0) represent the proportion of the distribution that is greater than 0, directly quantifying the support for the predicted rise in oxytocin levels post-competition. (B) Conditional effects of sex and sample type (pre- versus post-competition) on oxytocin concentration, illustrating changes in oxytocin levels before and after competition for both men and women. OT concentrations are grand-mean centred (i.e. values are expressed as deviations from the overall mean corrected OT level; 0 corresponds to the global mean). Small circles (pre-competition) and squares (post-competition) represent individual grand-mean–centred corrected OT values for each urine sample; some points fall outside the plotted range. Larger circles and squares represent predicted mean oxytocin concentrations, while bars indicate the 95% credible intervals.

Table 1. Results of competition model predicting OT response to football competition. For each parameter, we reported the mean of the posterior probability distribution, the estimate error and the 95% credible intervals. *P*(>0) represents the proportion of the posterior distribution above zero, indicating the probability of a positive effect.

predictor	estimate (*b*)	est. error	l-95% CrI	u-95% CrI	*P*(>0)
intercept (Sex = W, sample type = Pre, BF = No, FW = FW1, Lot = 1)	−0.83	0.27	−1.36	−0.3	0.00
sex = M	−0.33	0.24	−0.81	0.15	0.09
sample type = post-football	0.01	0.12	−0.22	0.24	0.52
breastfeeding = Yes	0.77	0.2	0.38	1.17	1.00
age (standardized)	−0.02	0.08	−0.17	0.13	0.39
lot 2	−0.36	0.3	−0.96	0.24	0.11
lot 3	0.15	0.59	−1	1.3	0.60
lot 4	−0.07	0.59	−1.24	1.07	0.45
fieldWork = FW2	0.04	0.6	−1.13	1.23	0.52
sex = M : sample type = post-football	0.39	0.16	0.09	0.7	0.99

men, status competition is closely linked to mating success and social prestige, often achieved through public displays of competence and dominance [52,91]. Therefore, football matches could be an opportunity, among others, to display status to other community members, in addition to representing direct competition over valuable resources (tournament prizes). In this sense, OT reactivity in intra-community matches may reflect both cooperation within familiar teams and competition with rival teams, i.e. parochial cooperation.

Conversely, Tsimane′ versus non-Tsimane′ matches correspond to competition against complete outsiders, from a different ethnic group, that might trigger intensified inter-group rivalries. According to theories of parochial cooperation and in-group favouritism [10,92], competition against clearly defined outsiders is likely to strengthen intra-group cohesion and cooperation, triggering a robust OT response that supports coordinated group defence and competition against external threats [15]. In the context of the Tsimane′, competition with non-Tsimane′ players is likely to promote a unified and strong group-level response given their perceived discrimination and overall rather negative experiences with outsiders.

Inter-community matches, which involved competitors from neighbouring Tsimane′ communities who are neither regular competitors nor complete strangers (co-ethnics with occasional kin ties and limited day-to-day interactions), produced the weakest OT response. This intermediate response suggests that the competitive imperative at this level may be perceived as less critical for immediate social status or direct group defence, even though the material resources at stake were the same as in the other matches.

Another possible explanation for this intermediate OT response might have been the visiting status of footballers from nearby communities. Such status might imply greater physical activity as well as social interaction and coordination prior

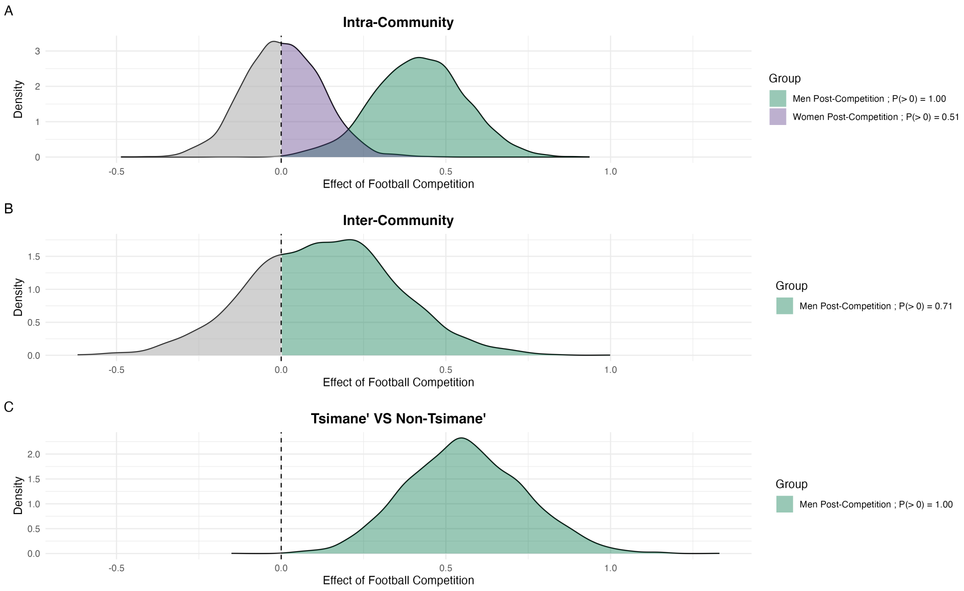

Figure 2. Oxytocin response varies according to group salience—posterior distributions of the competition effect (Post-football–Pre-football on log urinary oxytocin) from the extended model for three levels of group salience: (A) intra-community (men and women), (B) inter-community (men only) and (C) Tsimane′ versus non-Tsimane′ (men only). The vertical dashed line at 0 indicates no change. *P*(>0) denotes the posterior probability that the effect is positive, directly quantifying support for a rise in oxytocin after engaging in football competition.

to matches and, therefore, elevated pre-game OT levels. To address this potential alternative explanation, we conducted a supplementary analysis comparing pre-football OT levels between visiting and local players (electronic supplementary material, figure S1). Results showed no evidence for any pre-football OT level difference between these two groups (b = 0.05; 95% CrI = −1.61–1.7) suggesting that the observed intermediate OT responses are unlikely to be driven by systematically elevated baseline levels.

(d) Sex difference in oxytocin's response to group competition

By contrast to men, women did not exhibit an increase in OT concentration following football competition. On the surface, this result is consistent with the 'male warrior hypothesis', which posits that males are more sensitive to group-level competition, and is supported by evidence from social psychology and the fact that males engage more in between-group competition than females across mammals [93,94]. However, another plausible explanation is that Tsimane′ women started from higher baseline OT levels, leading to a ceiling effect. Indeed, in our data, men tended to have lower baseline than women (b = 0.39; 95% CrI = 0.09–0.7; $P(>0)$ = 0.99), even after adjusting for breastfeeding. A higher baseline may reduce the scope for detectable pre–post changes in peripheral OT, even if central oxytocinergic activity is modulated by competition.

More broadly, experimental and comparative work suggests that oxytocin operates within a sex-differentiated neuroendocrine context. Studies in humans report sex-specific behavioural effects of intranasal OT, with men showing enhanced sensitivity to competitive and status-related cues, whereas in women OT more reliably amplifies the recognition of kinship and affiliative bonds [28,95]. In addition, oestrogen and progesterone modulate OT receptor expression and neuronal responsiveness to OT in limbic and hypothalamic networks, leading to phase-dependent variation in OT sensitivity across the menstrual cycle [96, 97, 98,99, 100, 101]. Such findings imply that social cues that trigger OT release, and the functions of that release, may differ between sexes.

These considerations are consistent with ethnographic observations among the Tsimane′. Women are deeply involved in food production and processing, the maintenance of social ties and domestic care, and rivalries are often expressed in relational rather than overtly coalitional forms. Field studies show that Tsimane′ women compete through gossip, reputational attacks and social exclusion that can restrict access to mutual aid, emotional support and food-sharing networks [102,103], and women's status has measurable fitness consequences [55]. It is therefore plausible that competitive contexts most relevant to women's oxytocinergic responses differ from the male-dominated, physically confrontational setting of football matches. Although women do participate in football matches, they do so less frequently, and football is often more strongly associated with male sociality, public competition and reputation [43,65]. This context may be more socially salient for men than for women, potentially amplifying endocrine responses in men without necessarily implying a general sex difference in responses to inter-group competition.

Evidence from non-human primates further suggests that sex differences in oxytocinergic responses to inter-group competition are not fixed, but contingent on socioecology and sex roles. For example, in Taï Forest chimpanzees, where both males and females participate actively in territorial defence, individuals of both sexes show increased OT following inter-group encounters [7]. Future work in other populations and contexts, and with competitive settings more typical of women's everyday rivalries, will be needed to clarify the mechanisms underlying these sex differences.

Table 2. Sample distribution across fieldwork seasons and out-group types. Bold numbers indicate the number of unique players sampled in each condition. Values in parentheses show the number of pre-football and post-football urine samples, respectively. The 'breastfeeding samples' column reports the number of pre- and post-football samples provided by breastfeeding women, and 'total samples' corresponds to the total number of pre- and post-football samples in each cell.

fieldwork	out-group type	men	women	breastfeeding samples	total samples
FW1	intra-community	**14** (pre: 11, post: 14)	**11** (pre: 11, post: 10)	pre: 6, post: 6	**46**
	Tsimane' versus non-Tsimane'	**10** (pre: 10, post: 10)	—	—	**20**
FW2	intra-community	**19** (pre: 19, post: 18)	**25** (pre: 25, post: 25)	pre: 11, post: 11	**87**
	inter-community	**9** (pre: 9, post: 9)	—	—	**18**
	Tsimane' versus non-Tsimane'	**8** (pre: 8, post: 8)	—	—	**16**

(e) Limitations

It is important to note that the naturalistic team-sport paradigm used here inherently combines within-team cooperation and between-team competition. These two aspects cannot be dissociated. Thus, the observed patterns reflect oxytocin responsiveness to this joint context rather than to either process in isolation. The sample size for inter-community contexts is modest, leading to relatively wide credibility intervals for certain contrasts. Nevertheless, the use of Bayesian rather than frequentist models allows us to express results probabilistically and maintain appropriate caution without disregarding observed patterns and tendencies. Furthermore, the dual pathway of OT release (central and peripheral) means that its spectrum of action extends from behavioural modulation to physiological function modulation. Although it has been shown that central and peripheral OT concentrations respond similarly in stressful situations, peripheral OT measurement remains only an indicator of central OT [104]. Therefore, we cannot rule out the influence of physiological demands on measured OT levels, although controlling for known physiological parameters such as physical activity or breastfeeding should improve the reliability of our measurements. Finally, our data come from a single small-scale population with its own unique intra- and inter-community relationships. Consequently, any extrapolation to other human groups or species must be cautious and based on explicit comparative studies.

5. Conclusion and perspectives

Our results provide unique field evidence that endogenous oxytocin responds to group-level competition in humans. In Tsimane' men, OT levels increased selectively in contexts of high social importance; whether competing against familiar group rivals or ethnically distinct strangers; whereas women showed no such comparable hormonal changes. This sex-specific response suggests that OT may play a key role in coordinating competitive behaviour in groups, particularly when coalition dynamics and social threat are most prominent and recurrent.

These results have potential implications for the evolution of social neuroendocrinology, but it remains an open question whether similar OT responses occur in other human populations or in other species. In species characterized by strong inter-group competition, particularly in the sex that most often engages in inter-group aggression—typically males in many mammals (but females in some taxa such as hyenas) [94]—one might expect comparable patterns, although this is likely to depend strongly on socioecological context [7,33]. The role of OT in mobilizing social cohesion, vigilance and coordination during group conflict may therefore represent a more general feature of mammalian sociality [105,106], but this hypothesis requires explicit comparative tests across taxa, with the caveat of potential phylogenetic diversity in endocrine mechanisms underlying the same phenotypes [90].

In addition, interactions between OT and sex hormones (testosterone, oestrogen, progesterone), which have been shown to influence threat reactivity and affiliative behaviour [107], may shape gendered patterns in social neuroendocrine responses. An integrative study of OT and its dynamics with other hormones could shed light on this matter.

Ethics. This study received approval from the Ethics Committee of the Faculty of Science and Social Science at the University of Zurich, Switzerland, under the approval number 23.03.13, issued in March 2023 and valid for a period of 4 years. Participants were given detailed verbal and written information about the study procedures and gave verbal consent to take part in the experiments.

Data accessibility. Data availability is restricted for ethical reasons, in accordance with the CARE Principles for Indigenous Data Governance (https://www.gida-global.org/care) and the FAIR Principles for scientific data management (https://www.go-fair.org/fair-principles/). Requests for data reuse should be addressed to Prof. Adrian Jaeggi (adrian.jaeggi@iem.uzh.ch) or Dr. Camila Scaff (camila.scaff@iem.uzh.ch). Code for all models and figures are publicly available on OSF [108].

Supplementary material is available online [109].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.C.C.D.: conceptualization, formal analysis, investigation, writing—original draft, writing—review and editing; A.E.C.: investigation; J.S.M.: investigation, writing—review and editing; V.B.: investigation, writing—review and editing; D.J.: investigation, writing—review and editing; A.C.I.: conceptualization, investigation; L.C.T.: conceptualization, investigation; B.T.: investigation, writing—review and editing; C.S.: investigation, writing—review and editing; A.V.J.: conceptualization, funding acquisition, investigation, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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