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Testosterone reduces the threat premium in competitive resource division

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Like other animals, humans are sensitive to facial cues of threat. Recent evidence suggests that we use this information to dynamically calibrate competitive decision-making over resources, ceding more to high-threat individuals (who appear more willing/able to retaliate) and keeping more from low-threat individuals. Little is known, however, about the biological factors that support such threat assessment and decision-making systems. In a pre-registered, double-blind, placebo-controlled, cross-over testosterone administration study ($n = 118$ men), we show for the first time that testosterone reduces the effects of threat on decision-making: participants ceded more resources to high-threat (versus low-threat) individuals (replicating the 'threat premium'), but this effect was blunted by testosterone, which selectively reduced the amount of resources ceded to those highest in threat. Thus, our findings suggest that testosterone influences competitive decision-making by recalibrating the integration of threat into the decision-making process.

1. Introduction

Competitions over resources can be deadly. The ability to accurately assess the threat potential of conspecifics and appropriately regulate fight-or-flight decision-making is thus paramount to survival. Many species use visual information to make such assessments, with the lethality and duration of agonistic contests reduced when there is (versus is not) opportunity to visually assess one's opponent before the bout (reviewed in [1]). Although information regarding body size is important, advertisement and assessment of threat across many species depends on features of the face, specifically. For example, paper wasps high in threat have more (versus less) broken black facial patterning, and other wasps use this cue when competing over resources—preferentially appropriating food guarded by wasps with less (versus more) broken black facial patterning [2,3].

Humans also assess threat based on features of the face (e.g. [4–9]), and recent work suggests that threat-related facial structure and assessments modulate competitive decision-making over resources: across several studies, participants submissively ceded more resources to those with more (versus less) threatening facial structure [10] (see Methods below for more details about this resource division task). This tendency to submissively cede more resources to high-threat (versus low-threat) individuals—an effect coined the 'threat premium'—was large, overall, but relatively smaller for male than female participants. Furthermore, within the male participants, it was relatively smaller for those who were physically stronger (versus weaker) [10].[1]

Whereas this work provides evidence that humans, like other animals, calibrate competitive decision-making over resources based on threat, the biological factors that govern such threat-based decision-making remain unknown. One important biological factor may be the steroid hormone testosterone.

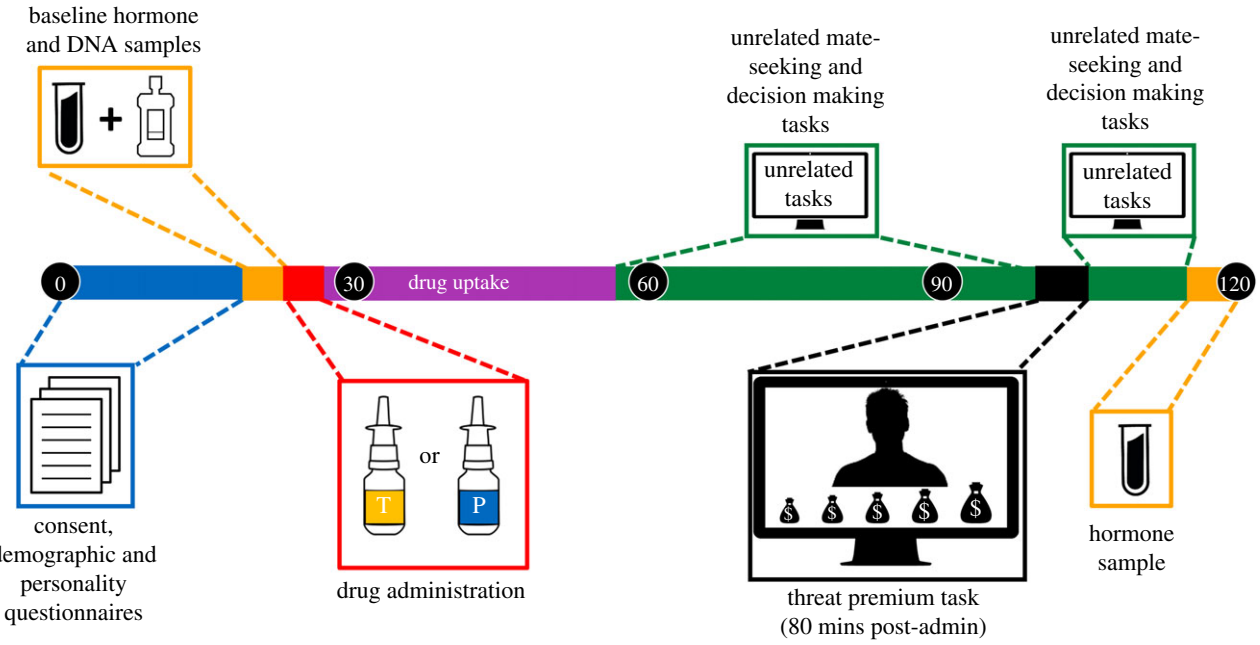

Figure 1. Experimental timeline. White numbers represent minutes from the start of the study. (Online version in colour.)

Concentrations of the hormone surge in response to social challenges, and these surges are posited to prepare the organism for resource-related competitions important to survival and mating [13]. Concentrations of the hormone are also higher in men than in women (e.g. [14]) and higher in physically stronger than weaker men (e.g. [15,16]). Because men, and especially physically stronger men, are those that exhibit smaller threat premiums—a reduced tendency to submissively cede resources based on threat—it stands to reason that testosterone may diminish the threat premium. In additional support of this idea, there is evidence that testosterone reduces socially submissive behavioural responses to facial displays of threat. For example, although people tend to avert their gaze from, and physically avoid, faces displaying angry (versus neutral or happy) facial expressions, testosterone reduces these submissive tendencies (e.g. [17,18]).

Based on these findings—that testosterone is higher in groups/individuals exhibiting smaller threat premiums, and that it reduces socially submissive behavioural responses to facial threat—we preregistered (see osf.io/wmrb2 and osf.io/gpt95) and tested the novel prediction that it would reduce resource ceding to high-threat (versus low-threat) individuals, thus abolishing or buffering against the threat premium. We also used this opportunity to replicate and extend the initial threat premium effect, employing a new and naturalistic—yet tightly controlled—stimuli set of faces manipulated to vary on threat.

2. Methods

(a) Participants

One hundred and twenty male participants were recruited through an online student participant pool, through campus posters and through online advertisements (Facebook, Instagram and Kijiji, a classified advertisement website). All participants met the eligibility criteria (i.e. were 18–40 years of age; not members of sports teams for which testosterone supplementation is banned; not taking hormone-disrupting prescription medication; not dependent on drugs or alcohol; not currently diagnosed with psychological or developmental disorders) and provided informed consent to the procedures of the study, which were approved by the research ethics board of Nipissing University. Because of time limitations, two participants did not complete the competitive resource division task on either testing day and were excluded from the analyses. Three participants did not return for the second day of testing, so we include data from their first day only. Furthermore, because of errors in assigning participants to the correct conditions (one participant received the same drug treatment on both days, three participants viewed the wrong stimuli sets for the bargaining tasks on the second week), we removed their data from the second testing day, but retained it for their first testing day. Therefore, our final sample included 118 male participants, seven of whom had data for the first day of testing only.

(b) Procedure

See the experimental timeline in figure 1. Participants were tested individually, in separate testing rooms, with test sessions starting between 9.30 and 5.30. On the first testing day, participants completed consent forms and demographic and personality questionnaires (20 min),[2] provided a saliva sample for the determination of baseline testosterone concentrations, and then provided a mouthwash sample for genotyping (androgen receptor CAG repeat length, not used here). Next, in a double-blind administration procedure, participants received nasal gel delivered in two syringes, each of 5.5 mg (one for each nostril, 11 mg total) and containing either testosterone or placebo. After a 30 min wait (allowing for drug uptake), participants began the behavioural testing protocol which involved mate preference, perception, cooperation and generosity tasks. Next, participants played a series of competitive resource division tasks involving male faces manipulated to vary on threat.[3] These tasks started 80 ($\pm$5) min after drug administration, and took approximately 5 min to complete, thus occurring well within the window during which the nasal gel elevates testosterone concentrations (for pharmacokinetics, see [24]). Afterwards, participants rated the same male faces used in the competitive resource division tasks on perceived threat, to ensure our manipulation of the faces successfully modulated these perceptions in this sample of men. We had participants provide these ratings after the resource division task to avoid priming them and artificially enhancing the association between perceptions of threat and decision-making in the resource division

task. Finally, participants completed a virtual dating task (again for testing other hypotheses related to mate-seeking) and, at the end of the study session, provided a second saliva sample (approx. 95 min after the drug administration). On the second day of testing—which occurred two weeks later, often on the same day of the week and same time of day—participants completed the same procedures but were assigned to receive the opposite drug treatment. At the end of the second session, participants guessed the drug they received during the second session, and these guesses were no better than chance accuracy (50.44%, $t_{112} = 0.094$, $p = 0.926$), suggesting that the drug did not induce physiological, psychological or other changes that were consciously detectable by the participant.

(c) Drug manipulation

Under the supervision of research assistants—using a double-blind procedure—participants self-administered 11 mg of gel containing either testosterone (Natesto) or placebo, by applying it to the lateral sides of their left and right nostrils (5.5 mg per nostril, separated into two syringes). After application, participants pinched their nostrils shut to evenly distribute the gel around the nostril walls, and then waited for absorption. Pharmacokinetic data in eugonadal men showed this manipulation to increase blood concentrations of testosterone to the high-normal range within 15 min, and to maintain this elevation until 180 min post-administration or longer [24].

(d) Salivary hormone measures

Salivary hormone measures can also be used to confirm a drug-induced testosterone increase at the group level [24], but are prone to contamination from gel administration (e.g. [19]), limiting our ability to model individual differences in baseline testosterone and testosterone reactivity. Therefore, salivary measures used here functioned primarily as a manipulation check. Nevertheless, to limit contamination, keyboards and computer mice were covered with disposable protective sheets at the beginning of each session, and participants were instructed to thoroughly sanitize their hands after self-administration and before touching any surfaces. After each testing session, the disposable protective sheets were discarded, and the keyboards, mice and other potentially contaminated surface areas (e.g. door knobs) were wiped with a cleaning solution containing 70% alcohol.

For the collection of saliva, participants chewed Salivette swabs for 30 s, until they were saturated with saliva. The samples were then stored at −20°C until hormone determination, at which point they were thawed and centrifuged, and the supernatant was analysed (in duplicate) with enzyme immunoassay kits from DRG International (mean coefficients of variation: intra-assay = 9.34%; inter-assay = 6.87%). A mixed-factorial ANOVA with two within-subject factors (time: pre versus post-administration; drug: placebo versus testosterone) and one between-subject factor (order: testosterone first versus placebo first) revealed a significant drug by time interaction ($F_{1,109} = 10.589$, $p = 0.002$, $\eta_p^2 = 0.089$): testosterone concentrations differed at post- (testosterone > placebo, $t_{110} = 3.310$, $p = 0.001$, $dz = 0.437$) but not pre-administration ($t_{110} = 1.153$, $p = .251$, $dz = 0.153$), confirming that the drug successfully increased testosterone concentrations.[4]

(e) Stimulus faces

To create realistic yet controlled faces that varied on threat, we extracted the facial structure (fiducial points) from Oosterhof & Todorov's [4] computational models of facial threat, and then transformed a set of 20 base images of Caucasian males (taken from the Chicago Face Database [25]) along this structural threat dimension. Therefore, 40 images were used in total: 20 low-threat and 20 high-threat versions of the 20 different facial identities.[5] The structure of the faces was delineated and transformed using PSYCHOMORPH [26]. Although the Chicago Face Database includes 93 Caucasian male faces, we used only a subset of 20 base images because of time constraints in the testing protocol. We selected this specific subset based on earlier validation work showing that the distribution of mean ratings of threat (made by a different set of 95 observers; S.N.G. 2017, unpublished data) of the low- and high-threat versions of these faces did not overlap.

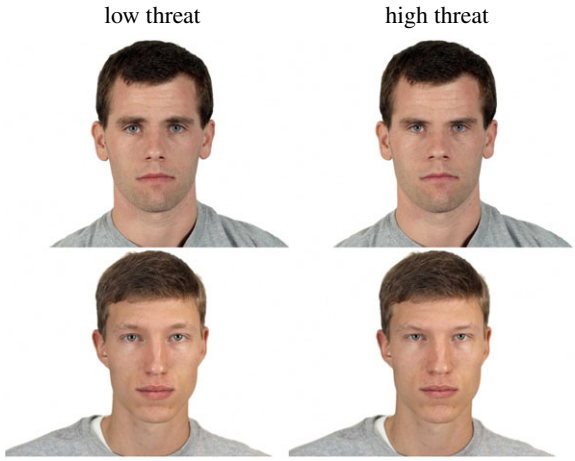

Figure 2. Examples of the low- and high-threat stimuli used in the current study. Edited versions of photographs reproduced with permission from [25]. (Online version in colour.)

The manipulation of threat employed here was less extreme—in terms of mean difference between high- and low-threat faces—and more representative of the typical variation in threat we may see in the real-world, compared with manipulations employed previously ($M_{\text{difference}} = 1.24$ versus 3 standard deviations in [10]). Furthermore, the manipulation involved real rather than avatar faces. Therefore, this stimuli set may produce estimates and allow for inferences that are more generalizable than those produced by other, previously used stimuli sets (e.g. [4]). See figure 2 for examples of the low- and high-threat versions of the faces; the stimuli set is available from the first author upon request.

To ensure our threat manipulation successfully modulated participants' perceptions, we had them rate the faces—one at a time, and in random order—on threat ('How THREATENING does this person look?'; task programmed in E-PRIME with 7-point response key: 1 = not at all threatening, 7 = very threatening), with threat defined as a willingness and ability to cause harm to others. Participants were told to use their gut instincts and, once they formed an impression regarding threat, to press the response key as quickly as possible. A robust multilevel model on these ratings confirmed that the manipulation was successful, with the participants in the current study rating the high-threat faces as more threatening than the low-threat faces (estimate = 0.901 points higher on 7-point scale, s.e. = 0.070, $t_{53} = 12.790$, $p < 0.001$; see additional details about multilevel models in the 'Statistical analyses' subsection and additional analyses involving these ratings of threat in electronic supplementary material).

(f) Competitive resource division task

The ultimatum game was competitively framed (as in [10]) such that participants were told their goal was to make as much money as possible, which could be achieved by offering the lowest amount to each responder, without having the offer rejected. Specifically, participants proposed how to split a separate 10 dollars for each of the 20 fictitious male responders. Before beginning the task, they were reminded that although they could split the 10 dollars any way they wanted, the responder could either accept the proposal—in which case each player would be paid their

corresponding amounts—or reject the offer—in which case each player would receive nothing (0 dollars). To enhance believability, participants were told that the responders had already indicated, in a previous study, the minimum amount that they would be willing to accept, and thus any offers lower than this amount would be rejected. Participants were also told that only one of the other responders would be selected at random to receive the participant's proposal, and that only one of the two offers made to that specific participant (one offer was made on the first testing day and one offer was made on the second testing day), chosen at random, would be proposed. Thus, participants were again encouraged to treat each offer, on both testing days, as if it would be the one to determine their payout at the end of the study. Participants saw each face one at a time (order randomized) and were asked to indicate how much of the 10 dollars they would be willing to offer the individual. The specific offer prompt was 'Use the keyboard and percentages below to indicate the amount of your 10 dollars you propose to offer this man.' Participants could press any numerical key from 0 to 9, corresponding to the percentage of the 10 dollars they wished to offer (e.g. 0 = 0%, 5 = 50%, 9 = 90%), or could press the enter key to cede the full amount (100%). See electronic supplementary material, table S1 for the full on-screen instructions.

(g) Statistical analyses

To investigate whether testosterone reduced the threat premium, we regressed the resources ceded in the competitive resource division task onto drug (testosterone versus placebo), facial threat (low versus high) and their interaction. We also included order of drug administration (order; testosterone versus placebo first), and its interactions with the other variables, in a separate model to rule out order-dependent effects. Robust mixed-level models [27] were used, including random intercepts and random slopes for the highest order interactions and/or the main effects not captured by these interactions [28]. Participant and stimulus ID were grouping factors.[6] Significance was determined using Satterthwaite approximations of degrees of freedom, limiting Type I error inflation but maintaining power [29]. Using alternative (but less reliable and more biased [30]) statistical models produced a similar pattern of results (see electronic supplementary material).

3. Results

A robust mixed-level model revealed that testosterone reduced the threat premium (i.e. decreased the effects of threat on resource ceding; figure 3): participants ceded more to high-threat (versus low-threat) faces (main effect of threat), but this effect was blunted by testosterone administration (drug × threat interaction), which selectively reduced ceding to high-threat faces (see figure 4 for more detailed plots of these effects; see table 1 for full model results). This drug by threat interaction was not further moderated by the order of drug administration (estimate = −0.039, s.e. = 0.093, $t_{102} = -0.420$, $p = 0.675$) and appeared to influence decision-making implicitly or unconsciously, rather than through changes to explicit perceptions of threat (see electronic supplementary material for exploratory analyses involving explicit threat perceptions; also see [17]).

4. Discussion

Like other animals (e.g. [2]), humans appear to rely on assessments of threat when competing over resources [10]. Here, we show that testosterone disrupts this link between threat and resource-related, competitive decision-making; whereas

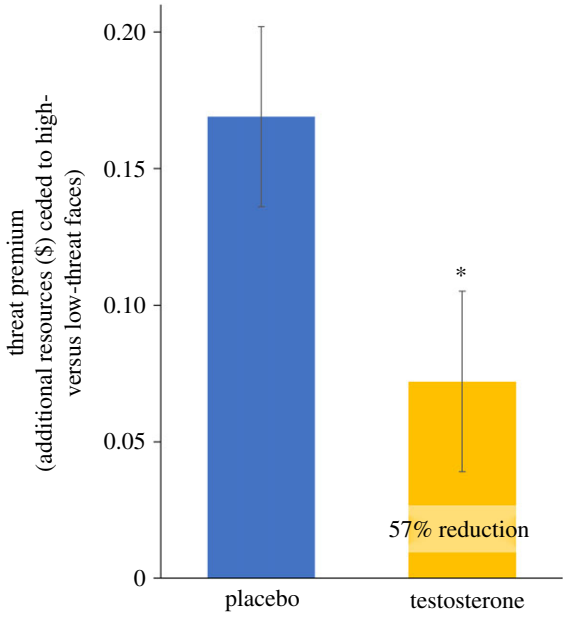

Figure 3. Bar graph showing the threat premium—the tendency to cede more resources to high than to low threat individuals—as a function of drug administration. Values on the *y*-axis indicate the amount of additional resources ceded to high relative to low threat faces. This tendency to cede additional resources to high relative to low threat faces was reduced by 57% after testosterone compared with placebo administration. *$p < 0.05$. (Online version in colour.)

participants submissively ceded more resources to high (versus low) threat individuals, this effect was blunted by testosterone administration.

At first glance, testosterone may appear to promote maladaptive decision-making that can lead to costly conflicts. It is important to note, though, that whereas we artificially elevated testosterone in all participants, surges in testosterone that occur in the real world would presumably be tuned to the actual threat potential and fight history of the individual. Specifically, such surges occur during challenges (reviewed in [13,31,32]), with the largest increases evident in winners (meta-analyses in [32,33]). Because high-threat individuals with better fight history and capabilities are more likely to win such contests, they would be more likely to experience these surges. Therefore, such surges are probably experienced by those who can afford the potential social or survival costs associated with reduced threat integration.[7] In fact, for high-threat individuals, reduced threat integration may promote more appropriate decisions to dominantly protect rather than submissively cede resources, given the greater ability for such individuals to successfully defend these resources. Reduced threat integration may also promote success in subsequent contests by reducing apprehension and increasing confidence and the decisiveness of attacks. Such effects of reduced threat integration may explain, for example, how outcome-dependent surges in testosterone increase aggression and success in future contests across various species (i.e. the winner effect [34–36]).

Our findings also raise important questions about how testosterone recalibrates threat's integration into the decision-making process. One possibility is that it modulates certain appearance-based inferences about the target. For example, humans may infer that high-threat (versus low-threat) individuals are more prone to retaliation after unfair treatment, but testosterone may reduce this retaliation-related inference. If

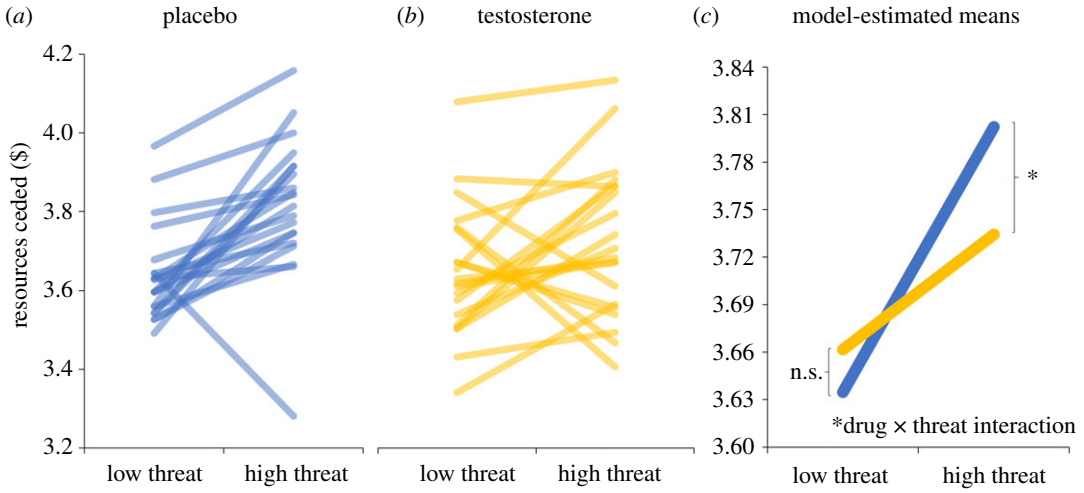

Figure 4. Line graphs showing the threat premium—the tendency to cede more resources to high-threat (versus low-threat) individuals—under placebo (*a*) versus testosterone (*b*). Each line represents the change in resources ceded, from the low- to the high-threat version of a given face identity (i.e. each of the 20 lines corresponds to a different face identity; 20 face identities total). Stronger increases from the low- to the high-threat version of a given face (steeper positive slopes) indicate larger threat premiums, whereas weaker increases (moderate positive slopes) or decreases (negative slopes) indicate smaller threat premiums or threat penalties. (*c*) Shows the results of the robust multilevel model, with the two lines representing the amount of resources ceded to the high- versus low-threat versions of the faces after placebo (blue) versus testosterone (yellow) administration. The testosterone slope is not as steep as the placebo slope, in part because testosterone selectively decreased resource ceding to the high-threat versions of the faces, thus reducing the threat premium. *$p < 0.05$. (Online version in colour.)

Table 1. Results of robust mixed-level model predicting amount of resources ceded ($) in the competitive resource division task. Conditional effects of drug and of threat were tested by transforming these variables (e.g. by $\pm \sim 0.5$) so that a score of 0 reflected one of the two conditions (threat: low versus high; drug: placebo versus testosterone) and rerunning the model.

		95% CIs[a]					
predictors	estimate	lower	upper	s.e.	*t*	d.f.	*p*-value
intercept	3.712	3.510	3.914	0.103	36.010	124	<0.001
drug	−0.023	−0.069	0.024	0.024	−0.970	4315	0.332
threat	0.121	0.075	0.167	0.023	5.190	4412	<0.001
drug × threat	−0.098	−0.189	−0.006	0.047	−2.090	102	0.039
conditional effects of drug							
at low threat	0.026	−0.039	0.091	0.033	0.780	102	0.437
at high-threat	−0.072	−0.137	−0.006	0.033	−2.150	102	0.034
conditional effects of threat							
after receiving placebo	0.169	0.105	0.234	0.033	5.160	102	<0.001
after receiving testosterone	0.072	0.007	0.137	0.033	2.160	102	0.033

[a]Wald 95% CIs.

so, the hormone may be modulating neural networks that support mentalizing (e.g. [37–39]). Reduced mentalizing capabilities [40] and lower activation in brain regions that subserve mentalizing [41] predict lower offers in the ultimatum game, suggesting that this process is critical for anticipating responder aversion to, and thus rejection of, low offers.

Another possibility is that testosterone acts by decreasing not the anticipation, but rather the fear, of retaliation when proposing low offers to high-threat (versus low-threat) faces. Fear of retaliatory punishment drives higher offers in the ultimatum game [42] and testosterone reduces fear-potentiated startle [43] and sensitivity to punishment in decision-making tasks [44] (see also [45]). Such fear reduction could be further associated with, or driven by, testosterone's upregulation of self-perceived threat [22]. Consistent with this idea, previous studies suggest that threat's effects on resource ceding is reduced as the physical strength of the perceiver/proposer increases [10]. Thus, competitive resource division depends on the threat of both individuals in the interaction, with physically stronger proposers caring less about the responder's threat. Ultimately, by increasing the proposer's perceptions of their own threat [22], testosterone may buffer against the fear-inducing process of low-balling high-threat individuals and risking retaliation.[8] Relatedly, to the extent that offering less money to high-threat faces is a form of risk-taking, testosterone may have operated through the modulation of risk-taking (e.g. [46,47]).

Testosterone is also posited to promote status- and dominance-related concerns, which may drive the hormone's effects on social behaviour (reviewed in [48,49]). Dominance and resources are tightly linked, with dominance often defined by one's access to and control of resources (see [50]). Some have suggested that having one's offer rejected in the ultimatum game, which results in a loss of resources, compromises status [51]. Submissively ceding resources for fear of retaliation may be even more compromising to status though, especially when ceding to high-threat individuals with whom people are less willing to share [10]. Therefore, ceding resources to high-threat (versus low-threat) individuals may be especially compromising to status and—by increasing concerns about status—testosterone may reduce one's willingness to make such a compromise.[9]

It is important to note that although our effects appeared relatively small, with threat increasing offers by $0.17 after placebo—but $0.07 after testosterone—these changes signify more than a 50% reduction in the threat premium after testosterone administration. Additionally, more than half of the offers in this task were within a 1-dollar range (4–5 dollars), suggesting a rather restricted zone within which testosterone and threat could modulate decision-making. Our study was also conducted using a mild, more ecologically valid and representative manipulation of testosterone and threat (see Method section) than has been used in the past. Therefore, the estimates reported here are probably more conservative than those that would emerge using other more common (but extreme) manipulations.

5. Conclusion and future directions

Our data support the idea that testosterone regulates competitive decision-making over resources by recalibrating the integration of threat-related information into the decision-making process. Ultimately, future studies will be required to determine at which phase of threat assessment and decision-making testosterone has its effects and whether these effects are driven through (a) the enhancement of self-perceived threat and subsequent reduction of fear of retaliation, (b) an increased concern about status (and thus unwillingness to cede resources to high-threat individuals), (c) greater perceived social challenge in high-threat faces (and thus activation of more competitive decision-making, as discussed in the electronic supplementary material), or other psychological mechanisms.

Ethics. All procedures were approved by the Nipissing University Research Ethics Board and consistent with the provisions of Canada's Tri-Council Policy Statement: Ethical Conduct for Research Involving Humans.

Data accessibility. See electronic supplementary material for data and analysis code.

Authors' contributions. S.N.G., V.P., B.M.B., N.V.W. and J.M.C. conceived of and designed the study, S.N.G., J.M.C. and V.P. participated in data analysis. S.N.G. wrote the initial manuscript, which was critically revised by V.P., B.M.B., N.V.W. and J.M.C. T.L.O. coordinated data collection, which was medically supervised by P.L.B. and B.G. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing Interests. We declare we have no competing interests.

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Endnotes

[1]Note that these findings emerged even though the competitive decision-making task was completed online and anonymously and using facial photographs of the opponent—a context in which own- and opponent-threat should be irrelevant (for other findings linking threat to bargaining and negotiation see [11,12]).

[2]See electronic supplementary material for additional details regarding personality.

[3]Although we conducted several other tasks before and after the threat premium paradigm, these other tasks were used to test separate hypotheses. This practice is common in pharmacological challenge studies and—as others have pointed out (see [19–21])—is viewed favourably by ethics committees given it increases the scientific knowledge gained from the study, better offsetting the invasiveness of administration procedures and financial costs. Furthermore, although we positioned some of these other tasks before the threat premium, we previously found similar testosterone effects on face-processing and decision-making tasks regardless of whether the tasks occurred earlier or later in the testing protocol and the number and types of other, preceding tasks (e.g. [22,23]), suggesting the hormone acted over and above potential fatigue and carry-over effects.

[4]Note that these analyses do not include the seven participants for whom we excluded data from the second testing day (see Participants section).

[5]This set of 40 images was divided into two smaller subsets of 20 images. In each subset, all 20 identities were shown, but in one subset half were of the high-threat versions and half were of the low threat versions. In the other subset, the opposite versions of each identity were shown. Therefore, each participant saw each identity, but only one version of the identity (low or high-threat), depending on the subset to which they were assigned, which was counterbalanced across participants.

[6]Structure of final model for predicting resource ceding: rlmerRcpp (ResourcesCeded~drugc * threatc+(1+drugc:threatc|| ParticipantID)+(1+drugc:threatc || StimulusID), data=[DATAFRAME NAME], method="DASvar"). Variable names ending with 'c' indicate centred variables, which were coded with a one-unit difference between the two conditions (thus, their estimates represent the difference between the two conditions, controlling for the other variables in the model). Correlations involving the random intercepts were dropped given the algorithms from our initial models did not converge or, if they did converge, the estimating equations were not satisfied. For data and analysis code, see electronic supplementary material.

[7]These social or survival costs associated with reduced threat integration (e.g. greater likelihood of costly conflicts) may, in fact, explain why humans (and other species) show outcome-dependent changes in testosterone. Specifically, losers—who presumably lost because they are lower in threat and, further, may be injured as a result of the loss—would be less able to afford the costs of reduced threat integration that would otherwise accompany a testosterone surge. Although speculative, these costs may have, over time, contributed to the blunted testosterone responses seen in losers (meta-analyses in [32,33]).

[8]Although we speculate on a fear-related mechanism, resource ceding is influenced by generosity as well, which may also explain the diminished threat premium after testosterone administration. An exploratory analysis involving an additional task that indexed generosity did not support this generosity-related mechanism, however (see electronic supplementary material).

[9]Our findings are also consistent with the challenge hypothesis [13] and the fitness model of testosterone dynamics [31], and may explain inconsistencies across ultimatum game studies that have examined the effects of testosterone on proposer decision-making (e.g. [51,52]), points we discuss further in the electronic supplementary material. In the electronic supplementary material, we also speculate on potential neural mechanisms underlying the effects reported here.

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