Preliminary Evidence that Acute Stress Moderates Testosterone's Association with Retaliatory Behavior

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Abstract

Theories suggest that testosterone should increase retaliation after social provocation. However, empirical evidence in support of these theories is mixed. Building on the *dual hormone hypothesis*, the present research investigated whether acute stress would causally suppress testosterone's association with retaliatory social behavior. We also explored sex differences in behavioral responses to acute stress. Thirty-nine participants (51.28% male) provided saliva samples to measure basal testosterone and were randomly assigned to a high- or low-stress condition. Participants then engaged in 20 one-shot rounds of the ultimatum game, an economic decision-making paradigm that assesses retaliatory behavioral responses to unfair treatment (rejection of unfair offers). Results revealed a positive association between basal testosterone and retaliation in the low-stress condition, but not in the high-stress condition. Further analyses showed that cortisol change from before to after the experimental manipulation moderated the association between basal testosterone and retaliatory behavior. These associations between basal testosterone and retaliation under varying levels of stress were similar in men and women. However, there was a sex difference in behavioral responses to the stress manipulation that was independent of testosterone. In women, the stress condition reduced retaliation compared to the control condition, whereas in men the opposite pattern emerged. Collectively, this study (i) provides preliminary evidence that experimentally manipulated stress blocks basal testosterone's association with retaliation, and (ii) reveals a sex difference in retaliation under varying levels of stress. Discussion focuses on mechanisms, limitations, and the need for follow-up studies with larger sample sizes.

Keywords: testosterone, stress, cortisol, ultimatum game, retaliation, sex differences

Introduction

Provocation that threatens one's social status can lead to retaliation. For example, an employee who is denied a promotion that is long overdue may react aggressively towards coworkers. Neuroendocrine theories have posited that in the face of threats to status, testosterone should be associated with greater retaliatory behavior as a means to restore lost status (Mazur and Booth, 1998; Archer, 2006). In support of this theory, studies have found a positive relationship between testosterone and status-seeking behaviors such as aggression, competitive behavior, and dominance, especially when status is threatened (Archer, 2006; Carré et al., 2011). However, several other studies have only found weak or null effects (Archer, 2006; Archer et al., 2005; Carré et al., 2011). For example, meta-analyses reveal only a weak positive association between basal testosterone and human aggression (r = .08 in Archer, et al., 2005). Although there is some evidence that testosterone is related to increased retaliation in response to social provocation, findings across studies are mixed.

A possible reason for these inconsistencies is that testosterone's effect on aggressive, competitive, and dominant behaviors may depend on environmental stress. Testosterone may be positively related to retaliatory behavior only in low-stress contexts, whereas high-stress contexts may block testosterone's influence on behavior. Some studies provide initial support for the hypothesis that stress blocks testosterone's behavioral effects. One study measured self-reported dispositional anxiety — a psychological marker of chronic stress (van Eck et al., 1996) — and found that an acute increase in testosterone was related to aggressive behavior only among individuals low in trait anxiety (Norman et al., 2014). Among individuals high in trait anxiety, there was a null association between testosterone responses and aggressive behavior. Other research on the dual hormone hypothesis also provides support for this perspective (Mehta and

Josephs. 2010; reviewed in Mehta and Prasad, 2015). The dual hormone hypothesis proposes that testosterone's role in status-relevant social behavior should depend on cortisol — a hormone released as part of the hypothalamic-pituitary-adrenal (HPA) axis response to physical and psychological stress (Dickerson and Kemeny, 2004). Specifically, the dual hormone hypothesis predicts that higher concentrations of cortisol should inhibit testosterone's positive impact on status-seeking behaviors. In support of this hypothesis, several studies have demonstrated that basal testosterone is positively related to measures of aggression, dominance, and social status when basal cortisol is low but not when basal cortisol is high (aggression: Dabbs et al., 1991; Popma et al., 2007; Tackett, et al., 2014; see also social inclusion condition of Geniole, et al., 2011; dominance: Mehta and Josephs, 2010; social status: Edwards and Casto, 2013; Ponzi, et al., 2016; Sherman, et al., 2016; group performance: Akinola, et al., in press; for a recent review, see Mehta and Prasad, 2015). However, other research revealed non-significant dual-hormone interaction effects on aggressive behavior (Geniole, et al., 2013; Mazur and Booth, 2014).

Taken together, there is some indirect support for the moderating role of stress on the testosterone-behavior relation, but one key limitation of these prior studies is that they are all correlational. To date, it remains unknown whether stress has a *causal* impact on the testosterone-behavior relation. To address this large gap in knowledge, we designed a study in which we experimentally increased or decreased stress and examined the influence of this manipulation on the relationship between basal testosterone and subsequent retaliation. We hypothesized that testosterone would be positively related to retaliatory behavior in the low-stress condition, but not in the high-stress condition. Such a pattern of results would provide promising evidence that acute stress causally blocks testosterone's behavioral effects.

The ultimatum game is a laboratory decision-making paradigm that assesses retaliatory behavioral responses to social provocation (Güth, 1995; Wang et al., 2011). This game involves two players: a proposer and a responder. The proposer decides how to split a sum of money (e.g., $10) with the responder. The responder then decides whether to accept or reject the proposer's offer. If the responder accepts the offer, the money is split as proposed. If the responder rejects the offer, both players receive $0. A round concludes once the responder makes a decision to accept or reject. Responders generally accept fair offers (e.g., $5: $5 split), but they often reject unfair offers (e.g., $8: $2 split) even though accepting these unequal offers guarantees financial reward. These unfair offer rejections — a retaliatory behavioral response designed to punish the proposer in the face of perceived provocation (unfair treatment) — can be considered a measure of aggressive behavior. Indeed, receiving an unfair offer increases feelings of anger and spite, emotions strongly related to aggressive motivation (Brañas-Garza et al., 2014; Espín et al., 2015; Pillutla and Murnighan, 1996; Raihani and Bshary, 2015). In addition, evidence from social neuroscience suggests that several brain regions linked to impulsive aggression — such as the insula, amygdala, and ventromedial prefrontal cortex — are related to rejection of unfair offers (Gospic et al., 2011; Koenigs and Tranel, 2007; Mehta and Beer, 2010; Moretti, et al., 2008; Sanfey et al., 2003). Further, experimental depletion of serotonin, which has been linked to impulsive aggression in prior research, increases rejections of unfair offers (Crockett et al., 2008). Finally, personality traits that are related to aggressive behavior — high trait aggression and low trait agreeableness — also predict increased unfair offer rejections (Mehta, 2008; Mehta, et al., 2015a; Nguyen et al., 2011). Together, these studies provide convergent evidence supporting the construct validity of the ultimatum game as a paradigm to investigate aggressive behavioral responses to unfair treatment.

Other research suggests that competition and status motives may also underlie retaliatory behaviors in the ultimatum game (Brañas-Garza et al., 2014; Espín et al., 2015; Nowak, 2000; Pillutla and Murnighan, 1996; Raihani and Bshary, 2015; Yamagishi et al., 2009, 2012). Responders concerned with their social status relative to the other player may perceive the ultimatum game as a competition over money, whereby the player who earns more money can be considered the winner (or having higher status) and the player who earns less money can be considered the loser (or having lower status). Therefore, accepting an unfair offer would result in a loss of status because the responder earns less money than the proposer in this situation. In contrast, rejecting an unfair offer could be a behavioral strategy to prevent a loss of status because the responder earns the same amount of money as the proposer in this situation (both players earn $0). Consistent with this logic, some research indicates that high concern for status, such as concern over managing one's reputation and preventing inferior status, motivates unfair offer rejections (Brañas-Garza et al., 2014; Espín et al., 2015; Nowak, 2000; Pillutla and Murnighan, 1996; Raihani and Bshary, 2015; Yamagishi et al., 2009, 2012). Collectively, there is evidence across disparate fields suggesting that motives linked to aggression, competition, and social status may underlie rejection of unfair offers in the ultimatum game.

As reviewed earlier, there is mixed evidence regarding the direct association between testosterone and status-relevant social behaviors. Consistent with this broader literature on testosterone and human social behavior, studies that examined the association between testosterone and unfair offer rejections in the ultimatum game also yielded mixed results (positive associations in studies with basal testosterone: male-only sample - Burnham, 2007; mixed-sex sample - Mehta and Beer, 2010; positive association with basal testosterone in intergroup competition setting: male-only sample - Diekhof et al., 2014; null effect with basal testosterone: Mehta, et al., 2015a; positive effect of exogenous testosterone in males - Zak et al., 2009; trend-level negative effect of exogeneous testosterone in a mixed-sex sample: Kopsida, et al., 2016; non-significant effects of exogenous testosterone in females - Eisenegger et al., 2010; Zethraeus et al., 2009). These equivocal results, combined with correlational evidence suggesting that markers of stress moderate testosterone's behavioral effects, led to our hypothesis that acute stress would causally inhibit basal testosterone's association with unfair offer rejections. We tested this key hypothesis by measuring basal testosterone, experimentally manipulating levels of acute stress using standard methods (Kirschbaum et al., 1993; Ventura et al., 2012), and then measuring retaliatory behavioral responses to unfair treatment in the ultimatum game. We hypothesized that basal testosterone would be positively related to unfair offer rejections at lower levels of stress, but not at higher levels of stress. In other words, we expected that acute stress would block testosterone's behavioral effects.

A second goal of the present research was to explore possible hormonal mechanisms through which acute stress may alter the testosterone-behavior association. One likely mechanism is through changes in cortisol levels, a mechanism consistent with the predictions of the dual-hormone hypothesis (Mehta and Josephs, 2010). As reviewed above, there is some evidence that basal cortisol moderates the relationship between testosterone and behavior (Mehta and Prasad, 2015) and there is robust evidence that acute stress increases cortisol concentrations (Dickerson and Kemeny, 2004). Thus, we explored whether experimentally elevated acute stress would block testosterone's effect on retaliatory behavior via acute increases in cortisol.

In addition to exploring the role of cortisol change as a mechanism for the moderating effects of acute stress, we also explored two additional psychological factors: perceived unfairness and anger. Both have been linked to unfair offer rejections in the ultimatum game

(Pillutla and Murnighan, 1996; Sanfey et al., 2003; van 't Wout et al., 2006), but little is known about how testosterone and its interaction with stress may be related to these psychological variables. In fact, prior studies found null effects of exogenous testosterone on perceived anger (Eisenegger et al., 2010) and fairness (Zak et al., 2009; Kopsida, et al., 2016) in the ultimatum game. These null effects of testosterone on self-reported psychological measures are consistent with evidence suggesting that testosterone influences behavior primarily outside of conscious awareness (Josephs, et al., 2006; Schultheiss et al., 2005; Terburg, et al., 2012). Hence, we examined whether testosterone interacted with acute stress to predict perceived unfairness and anger, but we did not formulate specific predictions for these additional analyses.

Finally, we conducted exploratory analyses that tested for sex differences. Prior research has found mixed evidence for sex differences in testosterone's behavioral effects (Carré et al., 2011; Mehta and Josephs, 2010), and there is initial evidence for sex differences in behavioral responses to acute stress (Lighthall, et al., 2009; van den Bos, et al., 2009). Therefore, we explored the role of sex as a moderator of the effects of acute stress and testosterone on retaliatory behavior in the ultimatum game.

Materials and Methods

Participants

Thirty-nine (20 males and 19 females[1]; M_{age} = 21.69 years, *SD* = 1.96) undergraduate students enrolled for an introductory management course at a large Singaporean University participated in the study in exchange for course credit towards research requirements. In addition

[1] Out of the 19 women in our study, we had information from 16 women who reported not being on oral contraceptives (OCs). Given that OCs are known to depress basal testosterone levels (Edwards and O'Neal, 2009), we compared basal testosterone levels in these 3 women with the other 16 women and found no evidence for differences in testosterone levels in our sample (p=.97).

to the 1.5 credits that they received for their participation, they also had the opportunity to earn real monetary payoffs up to $5 in the Ultimatum Game (described below).

Ethics Statement

The ethical review committee of the National University of Singapore approved the experimental protocol.

Procedure

Participants reported to the lab in the afternoon between 1300-1600 hours to minimize the effects of circadian fluctuations in testosterone and cortisol levels (Touitou and Haus, 2000). Upon their arrival the experimenter obtained written informed consent and had participants fill out a short survey about their biological health and other individual differences.

Baseline saliva sample

A baseline saliva sample was collected once participants completed the initial survey, approximately 10 minutes after arrival to the laboratory. Before providing the sample participants were asked to rinse their mouths with water to remove any remnant food particles. To further avoid contamination of the saliva samples, prior to the actual day of the experiment participants were requested to refrain from eating, drinking and brushing their teeth at least an hour before their timeslot. Participants were also asked to refrain from consuming any caffeinated products like coffee, tea and cocoa. Saliva samples were collected using an oral swab (Salivette®) that was placed under the tongue for 1.5 minutes to allow sufficient saliva to accumulate[2] (see footnote 1 for validation studies that demonstrate strong correlations between

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[2] The Salivette® method was used because our experiment focused on cortisol responses to the stress manipulation, but the samples were also analyzed for testosterone concentrations. Earlier research found that Salivettes® (oral cotton swabs) inflate testosterone values (Shirtcliff et al., 2001), but new research suggests that even with this inflation there are very high correlations between samples collected with oral swabs and passive drool (rank-ordered *Spearman's rho* =.82 in Giltay et al. (2012) and *Spearman's rho* =.87 in van Caenegem et al. (2011)). We also replicated these findings in our lab across two validation

testosterone levels collected via cotton Salivette® and passive drool). Participants were then asked to gently replace the swabs into the containers without any physical contact with their hands. The samples were immediately transferred into an icebox to avoid degradation of hormones and precipitate mucins. At the end of each day's data collection period, the samples were transported from the icebox to the in-house biomarker laboratory (at Saw Swee Hock School of Public Health, National University of Singapore) where they were immediately stored in a long-term freezer at -70°C until subsequently assayed for testosterone and cortisol (see below for details). At the time participants provided their baseline saliva sample, they were not aware of the subsequent social stress or relaxation task that they would be assigned to. This was done to eliminate any anticipatory effects of the social stressor or relaxation task on testosterone and cortisol concentrations; therefore these samples likely reflect stable, basal concentrations of these hormones (Liening et al., 2010).

Stress Manipulation

After completing the baseline saliva sample participants were randomly assigned to either a high- or low-stress condition. The high-stress condition consisted of the Trier Social Stress Task, a psychological stress induction paradigm involving performance of a speech and completion of challenging math problems in front of an evaluative audience (Dickerson et al., 2008; Kirschbaum et al., 1993; Kudielka et al., 2007). This paradigm has been shown to reliably increase cortisol concentrations approximately 20-30 minutes after the manipulation (Dickerson

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studies with a larger mixed-sex sample (Study 1: N= 36 (19 females)) and sample with only males (Study 2: N= 19 men). There was inflation of testosterone values at the lower end of the distribution (ostensibly in female participants). Despite this inflation, we found similar correlations between testosterone levels collected via cotton swabs and passive drool (Study 1: *Spearman's rho*=.71, p<.001; Males: *Spearman's rho* =.78, p<.001; Females: *Spearman's rho* =.67, p<.001; Study 2: *Spearman's rho* =.78, p<.001). This new evidence suggests that there will be very similar testosterone-behavior associations from samples collected with Salivettes® and passive drool. We encourage further methodological studies on collection methods as well as replication and extension of the present findings.

and Kemeny, 2004; Kirschbaum et al., 1993). To a large extent, the protocol that was used was similar to the original TSST paradigm, apart from minor modifications that were made which included: (i) a preparatory time of 5 minutes instead of 3 minutes or 10 minutes used in other studies (Haushofer et al., 2013), (ii) confederates dressed in business casual clothes instead of white lab coats to increase ecological validity to a business setting, (iii) a more complex math task so that it was challenging for a sample of Asian undergraduate students who participated in this study (see Frisch et al., 2015; Kudielka et al., 2007, for research that modified the difficulty of the math task based on the population).

Participants were informed that they were required to participate in a mock job-interview as part of the study. They were escorted to a conference room where they were introduced to a male and female confederate, dressed in business attire, and seated across a table. The confederates provided them with standardized instructions about the task. Participants were informed that they would adopt the role of a job applicant applying for a vacant job, and that the confederates formed the selection panel for the mock interview. They were told that they have to speak for 3 minutes about why they would make a good applicant for the position and that the selection panel might ask them additional questions after the speech. They were also informed that the whole process would be video-recorded, which was done to increase perceptions of social evaluation. Participants were then escorted to another room where they were given 5 minutes to prepare their speech.

After the preparatory period, the experimenter led the participant back to the interview room. During the course of the entire interview, the participant stood at a marked spot approximately 2 meters from where the interviewers were seated. Before the interview began, one of the interviewers stood up to switch on a camera so that the participant believed the speech was being video-recorded (in reality, the participants were not being recorded). The interviewers then reiterated the instructions; they specifically went over the timeline of the interview and subsequently asked the participants to begin their speech. If the participants ran out of things to say, they were prompted to keep going until 3 minutes were up. The interviewers followed this up with three prepared questions: (i) what are your greatest strengths? (ii) what would you consider your weaknesses? and (iii) what makes you special? Finally, during the last 5 minutes of the interview, participants were asked to perform a complex mathematical task in which they counted down prime numbers starting with 300. If they provided an incorrect response, they interviewer stopped them saying: “Wrong. Start again!”, and were asked to start from the beginning. Over the course of the interview, the panel maintained neutral affect and did provide any verbal or non-verbal feedback when the participant was talking. The entire task including the time taken to provide instructions lasted approximately 20 minutes.

The low-stress condition consisted of a relaxation task in which participants listened to instrumental music and read travel magazines. The experimenter provided the participants with a set of travel magazines, turned on the music, and left the room. Participants stayed in the room alone for the entire duration of the relaxation condition. This condition also lasted for 20 minutes, which was approximately the same overall duration as the high-stress condition. We modeled the low-stress condition on relaxation-induction interventions that have been previously used in alternative medicine research to alleviate anxiety and lower cortisol levels (Khalfa et al., 2003; Ventura et al., 2012). Ventura et al. (2012) had participants either read a magazine or listen to music to induce relaxation, but we combined the two conditions to maximize the effect of this intervention on reduced cortisol concentrations. This design in which we compared a social stress to a relaxation condition allowed us to maximize differences in cortisol, a theorized mechanism for the impact of stress on the testosterone-behavior association.

Ultimatum game

Immediately after the social stress or relaxation manipulation, participants were escorted to another room, where they played a computerized version of the ultimatum game (Güth, 1995; Koenigs and Tranel, 2007; Sanfey et al., 2003). Participants believed that that they would play the ultimatum game with 20 players in one-shot interactions but in reality they were playing with the computer. At the start of the game, all participants were assigned to the role of a responder and were made to believe their assignment to this role was completely random. In each of the 20 rounds that the participant played, they were required to split S$10 (~8USD) with another individual (the fictitious proposer). At the start of each round, participant first saw the proposer's unique user id, followed by the offer they made. Proposers made offers of a pre-determined offer value of S$5, S$4, S$3, S$2, or S$1 out of the S$10. Each offer value was presented four times across the 20 rounds that the participant played, and was randomized across each participant. After the offer was made, participants were asked if they would like to accept or reject the offer. If they accepted the offer, the $10 would be split in the manner proposed. If they rejected the offer, both players would receive $0. Every round concluded once the responder made the decision to accept or reject the proposed offer. At the end of the 20 rounds, a random trial was selected, and participants were compensated for that trial based on their decision to reject or accept the offer in that round. Prior to playing the game, participants were informed their compensation would be based on their decision to accept or reject offers in a randomly selected trial. The ultimatum game took about 20 minutes to complete.

Post-stress saliva sample

At the end of the ultimatum game, a second saliva sample was taken. The timing of this second sample was approximately 20 minutes after the completion of the high- or low-stress manipulations, and served to measure acute cortisol fluctuations from before to after the social stress or relaxation tasks. We waited for 20 minutes after the end of social stress/relaxation tasks to collect the second saliva sample because it takes several minutes for hormones in serum to reach saliva (Riad-Fahmy et al., 1987) and because cortisol levels tend peak approximately 15-20 minutes after laboratory stressors (Kirschbaum et al., 1993; Wirth et al., 2006).

Self-reported fairness and anger ratings

After the participants completed the ultimatum game and provided the second saliva sample, they were given a second survey in which they self-reported perceptions of the game and the offers that they were presented. For each offer value ($5, $4, $3, $2, $1) they rated how fair they perceived the offers to be on a 7-point scale (1= very unfair and 7 = very fair) and the anger they experienced towards these offers on a 5-point scale (1= not at all angry and 5= very angry) (Pillutla and Murnighan, 1996; Sanfey et al., 2003). After completing the questionnaire, participants were debriefed about the true purpose of this study and were dismissed. The entire study took 1 hour and 20 minutes to complete. See Fig. 1 for the sequence of tasks along with the time taken to for each component of the protocol.

<<Insert Figure 1>>

Fig. 1. Timeline for the study

Hormone Assays

The samples that were collected in the laboratory were transported to an in-house biomarker lab where they were analyzed for testosterone and cortisol concentrations using salivary enzyme immunoassay (EIA) kits purchased from Salimetrics (Salimetrics LLC, State College, PA, USA). Standard procedures and protocol were followed during the assay process (Schultheiss and Stanton, 2009). All the standards and controls were assayed in duplicate, and 30% of the samples on that plate were randomly chosen and assayed in duplicates. Both the average intra-assay coefficient of variation (CV) and inter-assay CV for testosterone and cortisol were below 10%.

Statistical Analyses

We standardized testosterone levels within sex of participants (Josephs et al., 2006; Mehta and Beer, 2010; Mehta et al., 2009; Newman et al., 2005; Zyphur et al., 2009). This data analysis strategy was used to increase statistical power of our analyses and to examine if there were any sex differences in our hormone-behavior results. Consistent with what is reported in other literature (Mehta and Josephs, 2006; Mehta et al., 2008; Wirth et al., 2006), the cortisol scores showed a positive skew and therefore were log-transformed and then standardized. Cortisol reactivity was calculated as a percent change in raw cortisol scores from baseline to after the stress manipulation. Similarly acute testosterone change was calculated as a percent change in raw testosterone from baseline to after the stress manipulation. In all analyses, we dummy coded the stress condition (1 as high-stress and 0 as low-stress) and sex (1 as female and 0 as male). To test the interaction between levels of stress and testosterone, we conducted moderated regressions using standardized basal testosterone scores with the dummy coded variable of stress condition and standardized cortisol reactivity scores (Aiken et al., 1991). To interpret significant interactions, we plotted the relationship between testosterone and the rejection of unfair offers, across the levels of the stress manipulation and one standard deviation above and below the mean for cortisol reactivity scores. The simple slopes of the relationship between testosterone unfair offer rejection rate were also tested using standard procedures (see Aiken et al., 1991).

Results

Preliminary analyses

First we conducted analyses to verify that there were no differences in baseline hormone levels as a function of the stress manipulation. As expected, participants did not differ in their basal cortisol levels across the low and high stress conditions ($F(1, 37)=2.74$, $p=.11$). We also did not find sex differences in basal levels of cortisol across all participants ($F(1, 37)= .85$, $p=.36$). As expected, there was a sex difference in basal testosterone concentrations ($F(1,37)=23.60$, $p<.001$). When controlling for participant sex, there were non-significant differences in basal testosterone between the low and high stress conditions ($F(1,36)=1.12$, $p=.30$). See Table S1 for means and SDs of untransformed testosterone and cortisol concentrations before and after the stress manipulation, and across sexes.

Next we examined associations between testosterone and cortisol. Our standardized basal testosterone and basal cortisol scores were positively correlated ($r=0.46$, $p=.003$), which is consistent with previous research (Mehta and Josephs, 2010; Mehta et al., 2008.; Popma et al., 2007). Additionally, the standardized cortisol reactivity and testosterone reactivity scores were also positively correlated ($r=0.44$, $p=.005$), which is also consistent with prior research (correlation between hormone change scores: Mehta & Josephs, 2006; Mehta, et al., 2015; evidence of positive co-variation between HPA-HPG axes: Dismukes, et al., 2015; Marceau et al., 2014).

Stress-induced changes in cortisol and testosterone

To ascertain if the experimental manipulation of stress influenced cortisol or testosterone changes, we computed percent changes in raw cortisol and testosterone. The change in cortisol for participants in the high stress condition differed from the change in cortisol for participants in the low-stress condition ($t(27.28)=-3.23$, $p=.003$, $d=1.02$, *95% CI*: -111.40, -25.01). Comparing the means of cortisol change revealed that the individuals in the high-stress condition demonstrated greater increases in cortisol ($M=43.40$, $SD=84.87$, *95% CI*: 3.68, 83.12) relative to those in the low-stress condition ($M=-24.80$, $SD= 39.80$, *95%CI*: -43.99, -5.62). Follow-up one-sample t-tests revealed that the cortisol increase in the high-stress condition and the cortisol decrease in the low-stress condition were both significantly different from zero (high stress: $t(19)=2.29$, $p=.03$; low stress: $t(18)=-2.72$, $p=.01$).These findings indicate that our stress and relaxation manipulations successfully altered cortisol levels in the expected direction consistent with prior research (Kudielka et al., 2007; Ventura et al., 2012). Supplementary analyses using repeated measures GLM analyses showed the same pattern of cortisol changes (see Supplementary Results and Table S1).

We also found that changes in testosterone in the high-stress condition only marginally differed from the low-stress condition ($t(36.98)=-1.91$, $p=.06$, *95% CI*: -23.24, .71). Comparing the means of testosterone change indicated that those in the high-stress condition ($M= 5.93$, $SD= 19.14$, *95% CI*: -3.02, 14.90) marginally rose in testosterone relative to the low-stress condition ($M= -5.32$, $SD= 17.76$, *95% CI:* -13.88, 3.23). Supplementary analyses using repeated measures GLM also showed marginally significant results (see Supplementary Results and Table S1). The simultaneous activation of both the HPA and HPG axis is consistent with prior research that provides evidence their co-activation, especially in stressful contexts (Dismukes, et al., 2015; Lemarie et al., 1997).

Additional analyses revealed non-significant main effects of sex and non-significant sex X condition interactions for both cortisol and testosterone reactivity scores (*ps*>.10).

Ultimatum game preliminary analyses

The average rejection rates in the present study ($5 offers: *M* = 7.05%, *SD* =21.42; $4 offers: *M* = 21.79%, *SD* = 38.55; $3 offers: *M* = 55.77%, *SD* = 46.40; $2 offers: *M* = 69.87%, *SD* = 42.21; $1 offers: *M* = 80.13%, *SD* = 35.90) were similar to behavioral results found prior research on the ultimatum game (Koenigs and Tranel, 2007; Mehta and Josephs, 2010; Sanfey et al., 2003). To test our main hypotheses, we categorized $3, $2 and $1 offers as *unfair offers*, and we averaged across these offer types to create an overall index of the percentage of unfair offers rejected (*M*= 68.59%, *SD* = 37.7). This classification was done for two reasons. Firstly, previous research used the same grouping (see Koenigs and Tranel, 2007; Mehta and Josephs, 2010). Therefore, this classification allows us to compare the present results to prior studies. Secondly, self-reported fairness perceptions were consistent with this classification. Specifically, the $4 and $5 offer values received fairness ratings above the mid-point of the 7-point scale ($5 offer: 6.5 (*SD*= .88); $4 offer: 4.9 (*SD*= 1.56)), whereas the $3, $2, and $1 offers received fairness ratings below the midpoint indicating that these offers were indeed perceived as unfair ($3 offer: *M* = 3.2 (*SD*= 1.61); $2 offer: *M* = 2.1 (*SD*= 1.39); $1 offer: *M* =1.69 (*SD*= 1.36)).

Confirmatory analyses were also conducted in which we compared psychological and behavior reactions to the aggregated categories of unfair (average of $3, $2, and $1 offers) and fair offers (average of $5 and $4 offers). As expected, paired-samples t-tests revealed that unfair offers were perceived as less fair (*M*= 2.35, *SD*=1.34) than fair offers (*M*=5.75, *SD*=1.02) (*t*(38)=

-15.51, $p<.001$, *95% CI*: -3.84, -2.95), unfair offers elicited more anger ($M=2.72$, $SD=1.16$) than fair offers ($M=1.24$, $SD=.39$ ($t(38)= 9.31$, $p<.001$, *95% CI*: 1.15, 1.79), and unfair offers were more likely to be rejected ($M= 68.59\%$, $SD = 37.7$) than fair offers ($M= 14.51\%$, $SD= 26.57$) ($t(38) = 9.25$, $p<.001$, *95% CI*: 42.31, 65.02).

Basal testosterone, stress, and unfair offer rejections

We tested the hypothesis that basal testosterone's role in unfair offer rejections would depend on environmental stress. Specifically, we expected that testosterone would be positively associated with unfair offer rejections in the low-stress condition, but in the high-stress condition, this relationship between testosterone and unfair offer rejections would be suppressed. To test this hypothesis, we conducted a hierarchical multiple regression in which we entered the stress condition (dummy coded: 1 as high-stress and 0 as low-stress condition) and basal testosterone in Step 1, and the basal testosterone x stress condition interaction in Step 2 (Aiken et al., 1991). This analysis revealed no main effects in Step 1, but there was a statistically significant basal testosterone x stress interaction in Step 2 ($\Delta R^2=.13$, $\beta=-.57$, $b=-28.75$, $t(35)= -2.28$, $p=.028$, *95% CIs*: -54.28, -3.22). Fig. 2 demonstrates the pattern of this interaction. An analysis of simple slopes (Aiken & West, 1991) revealed that the relationship between testosterone and unfair offer rejection rate was positive in the low-stress condition ($b= 19.92$, $t(35)=2.05$, $p=.05$, *95% CI*: .20, 39.64). In support for the hypothesis that stress blocks testosterone's behavioral effects, there was a non-significant association between basal testosterone and unfair offer rejection rate in the high-stress condition ($b=-8.83$, $t(35)=-1.12$, $p=.28$, *95% CI*: -25.05, 7.39). Follow-up analyses revealed that this effect was robust when controlling for relevant covariates; the basal testosterone x stress interaction remained statistically significant when controlling for participant sex ($\Delta R^2=.16$, $\beta=-.71$, $b= -35.52$, $t(34)=-$

2.57, *p*=.015, *95% CI*: -63.65, 7.39), the time of the basal hormone sample (ΔR^2=.16, β=-.65, *b*=-32.47, *t*(34)=-2.67, *p*=.012, *95% CI*: -57.24, -7.71), wake-up time (ΔR^2=.096, β=-.51, *b*=-25.74, *t*(34)=-1.20, *p*=.057, *95% CI*: -52.24, .76), and time from awakening (in minutes calculated by subtracting the time of the baseline saliva sample from the time the participant woke up) (ΔR^2=.097, β=-.51, *b*=-25.44, *t*(34)=-2.01, *p*=.05, *95% CI*: -51.14, .26)[3].

<<Insert Figure 2>>

Fig. 2. The interaction between basal testosterone and stress condition in predicting the rejection of unfair offers.

Participant sex moderation analyses

Follow-up regression analysis explored if sex moderated the basal testosterone x stress condition interaction on unfair offer rejections. There was a non-significant sex x basal testosterone x stress condition interaction (β=-09, *b*= 8.14, *t*(31)=.28, *p*=.78, *95% CI*: -50.85, 67.14). Despite not finding a significant sex x basal testosterone x condition interaction, we conducted additional analyses to confirm that the interaction pattern was similar across both sexes. We did not expect to find significant results because of reduced statistical power in these analyses. Separate analyses for each sex confirmed a similar basal testosterone x stress condition interaction pattern in males (β = -78, *p* = .08) and females (β = -.53, *p* = .13) (see Fig. S1 for the basal testosterone x stress condition interaction patterns in males and females separately; in both men and women, there were positive slopes between basal T and unfair offer rejection rates in the low-stress condition but not in the high-stress condition). These analyses suggest that there were no sex differences in the pattern of the basal testosterone x stress condition interaction.

[3] In the supplementary materials, we report analyses that test for interactions among basal testosterone, basal cortisol, and the stress condition.

Even though we did not find a significant sex x basal testosterone x stress interaction, our analyses did reveal a sex x stress condition interaction ($F(1, 35)= 5.24$, $p=.03$, $\eta_p^2=.13$). As shown in Fig. 3, post-hoc analyses indicated that females rejected more unfair offers in the low-stress condition (*M*= 84.17, *SD*=23.06) compared to the high-stress condition (*M*= 50.93, *SD*=37.14) ($t(17)= 2.37$, $p=.03$, $d= 1.07$, *95% CI*: 3.67, 62.81). The opposite pattern was found in males, although these behavioral differences in males were non-significant (high-stress condition: *M*= 78.03, *SD*= 39.31; low-stress condition: *M*= 57. 41, *SD*=44.18; $t(18)= -1.10$, $p=.28$, $d= .49$, *95% CI*: -59.86, 18.61). This pattern of results conceptually replicates and extends previous work that has examined sex differences in the impact of stress on risky decision-making (Lighthall, et al., 2009; van den Bos et al., 2009).

<<Insert Figure 3>>

Fig. 3. The interaction between sex of the participant and stress condition in predicting the rejection of unfair offers.

Basal testosterone, cortisol reactivity, and unfair offer rejections

Next, we explored whether the basal testosterone x stress interaction reported above was driven by acute cortisol fluctuations in response to the stress manipulation. A possible mechanism involving cortisol activity is consistent with the predictions of the dual-hormone hypothesis (Mehta and Josephs, 2010). We conducted a hierarchical multiple regression in which we entered the standardized basal testosterone and standardized percent cortisol change scores in Step 1, and the basal testosterone x cortisol reactivity (measured as % change in cortisol from baseline to post the stress manipulation) interaction in Step 2. This analysis revealed no main effects in Step 1, but there was a statistically significant basal testosterone x cortisol reactivity interaction in Step 2 ($\Delta R^2=.16$, $\beta= -.44$, $b= -15.54$, $t(35)= -2.57$, $p=.01$, *95% CIs*: -27.82, -3.26).

The pattern of this interaction was similar to the interaction between testosterone and stress condition (see Fig. 4). An analysis of simple slopes indicated a positive relationship between basal testosterone and rejection of unfair offers only among individuals who decreased in cortisol (-1SD: b= 15.40, t(35)= -1.98, p=.056, *95% CIs*: -.41, 31.21), but not among individuals who increased in cortisol (+1SD: b= -15.17, t(35)= -1.56, p=.13, *95% CIs*:-34.93, 4.60). The statistically significant interaction term indicates that these slopes statistically differed from each other.

Further, we found that the basal testosterone x cortisol reactivity interaction remained statistically significant even when controlling for the stress condition (ΔR^2=.15, β= -.44, b=-15.50, t(34)= -2.48, p=.018, *95% CIs*: -28.19, -2.81), the sex of the participant (ΔR^2=.16, β= -.45, b=-15.92, t(34)= -2.57, p=.015, *95% CIs*: -28.51, -3.32) and when controlling for the stress condition and participant sex in the same analysis (ΔR^2=.16, β= -.45, b=-15.88, t(33)= -2.48, p=.02, *95% CIs*: -28.91, -2.86). In other follow-up analyses, the basal testosterone x cortisol reactivity interaction remained significant when controlling for time of the basal hormone sample (ΔR^2=.17, β= -.47, b= -16.37, t(34)= -2.80, p=.008, *95% CIs*:-28.27, -4.48), wake-up time (ΔR^2=.15, β= -.44, b= -15.40, t(34)= -2.58, p=.01, *95% CIs*: -27.52, -3.28), and time from awakening (ΔR^2=.16, β= -.45, b= -15.72, t(34)= -2.69, p=.01, *95% CIs*: -27.59, -3.85). We also conducted analyses using an alternate metric of cortisol reactivity — residualized cortisol change — and found a similar interaction pattern to the one noted above (ΔR^2= .06, β= -.28, b= -.14, t(34)= -1.59, p=.12, *95% CIs*:-.32-.039).

<<Insert Figure 4>>

Fig. 4. The interaction between basal testosterone and cortisol change in predicting the rejection of unfair offers.

Participant sex moderation analyses

We again tested for sex differences in the basal testosterone x cortisol reactivity interaction and again found a non-significant sex X basal testosterone x cortisol reactivity interaction (β= -.04, *b*=-1.95 *t*(31)= -.13, *p*=.90, *95% CIs*: -31.90, 27, 99). There were also non-significant sex x basal T and sex x cortisol reactivity interactions in this analysis. Despite not finding a significant sex x basal testosterone x cortisol reactivity interaction, we conducted additional analyses to confirm that the basal testosterone x cortisol reactivity interaction pattern was similar across both sexes. Subsequent analyses confirmed that the this interaction term showed a similar pattern across males (β = -.47, *p* = .054) and females (β = -.73, *p* = .058) (see Fig. S2 for the basal testosterone x cortisol reactivity interaction patterns in males and females separately). These analyses indicate that there were no sex differences in the pattern of the basal T x cortisol reactivity interaction.

Moderated Mediation Analyses

We conducted moderation mediation analyses to explore whether cortisol reactivity was a potential mechanism through which acute stress causally inhibited basal testosterone's association with rejection of unfair offers. Using the PROCESS macro (v 2.12.1), Model 15 template in SPSS (v21, IBM Corp), we tested a moderated mediation model with stress condition as the independent variable, cortisol reactivity as the mediator, basal testosterone as the moderator of both the stress condition and cortisol reactivity, and rejection of unfair offers as the dependent variable. This analysis revealed non-significant moderated mediation (ω =-10.32, SE= 8.64, 95% CI: -26.12, 5.40). Because this study was not designed to test moderated mediation, the lack of statistical significance in these analyses was likely due to insufficient statistical power. Given that the basal testosterone x cortisol reactivity interaction remained significant even after controlling for the stress condition, we conclude that the present study provides preliminary evidence that cortisol reactivity may be a potential mechanisms through which heightened stress causally inhibits basal testosterone's association with unfair offer rejections. Future studies with larger sample sizes should be conducted to test for moderated mediation more rigorously.

Self-reported anger and fairness

Although unfair offer rejection rates were positively correlated with perceptions of anger ($r(39)= .39$, $p=.014$) and negatively correlated with perceptions of fairness ($r(39)=-.61$, $p<.001$) multiple-regression analyses indicated that basal testosterone and the stress manipulation did not predict perceptions of anger or fairness (no main effects or interactions, all *ps*>.10). These results are consistent with prior research that also found null associations between testosterone and self-reported psychological measures (Eisenegger et al., 2010; Kopsida, et al., 2016; Zak et al., 2009). Further, these findings provide additional support for the claim that testosterone's behavioral effects likely operate outside of conscious awareness (Josephs, et al., 2006; Schultheiss et al., 2005; Terburg, et al., 2012).

Testosterone reactivity and unfair offer rejections

Our primary analyses focused on basal testosterone to be consistent with most prior research on endogenous hormone concentrations in the ultimatum game (Burnham, 2007; Diekhof et al., 2014; Mehta and Josephs, 2010; but see also Mehta, et al., 2015a). However, other research that used different behavioral paradigms found that acute fluctuations in testosterone are related to subsequent aggressive behavior especially in men (Carré et al., 2011). Thus, we conducted follow-up analyses in which we examined associations between acute fluctuations in testosterone from before to after the stress manipulation and ultimatum game decision-making. While testosterone marginally rose in the stress condition compared to the relaxation condition (reported above), there were non-significant associations between acute fluctuations in testosterone and unfair offer rejections (r = .07, p = .65), fairness perceptions (r = .19, p = .24), and anger (r = .09, p = .60), and acute testosterone fluctuations did not significantly interact with the stress condition or cortisol reactivity to predict unfair offer rejections, fairness, perceptions, or anger (all p's>.10).

While we did not find statistically significant testosterone reactivity x stress or testosterone reactivity x cortisol reactivity interactions, we found that the testosterone reactivity x sex interaction significantly predicted anger reported in response to receiving unfair offers (ΔR^2=.10, β= -.44, b= -.75, t(34)= -2.31, p=.028, *95% CIs*:-1.41, -.09) and marginally predicted unfair offer rejections (ΔR^2=.09, β= -.43, b= -23.50, t(34)= -1.89, p=.067, *95% CIs*: -48.70, 1.71), while controlling for the stress condition[4]. Analyses of simple slopes indicated that testosterone increases in men were associated with greater anger (b=15.32, t(34) = 1.74 , p=.09, *95% CI*: -2.56, 33.20) and higher rates of unfair offer rejections (b= 19.92, t(35)=2.05 , p=.05, *95% CI*: .20, 39.64). In women, there were non-significant associations between testosterone change and anger or rejections of unfair offers (ps > .30). These results are consistent with

[4] The sex x testosterone reactivity interaction remained statistically significant even with excluding the stress condition as a covariate for anger experienced towards unfair offers (ΔR^2=.10, β= -.44, b= -.74, t(34)= -2.31, p=.027, *95% CIs*:-1.39, -.09), and was marginally significant for unfair offer rejections (ΔR^2=.10, β= -.43, b= -23.77, t(35)= -1.94, p=.06, *95% CIs*: -48.68, 1.15). The analyses were also robust to other covariates for both anger experienced towards unfair offers: time of the basal hormone sample (ΔR^2=.09, β= -.42, b= -.71, t(34)= -2.19, p=.036, *95% CIs*:-1.36, -.05), wake-up time (ΔR^2=.10, β= -.44, b= -.75, t(34)= -2.31, p=.027, *95% CIs*:-1.41, -.09), and time from awakening (ΔR^2=.10, β= -.44, b= -.75, t(34)= -2.29, p=.028, *95% CIs*:-1.41, -.09), and rejection of unfair offers: time of the basal hormone sample (ΔR^2=.08, β=-.40, b=-21.98, t(34)=-1.81, , p= .08, *95% CI*: -46.71, 2.75), wake-up time (ΔR^2=.09, β=-.42, b=-23.05, t(34)=-1.88, p= .068, *95% CI*: -47.92, 1.82), and time from awakening (ΔR^2=.084, β=-.41, b=-22.33, t(34)=-1.84, , p= .075, *95% CI*: -47.02, 2.36).

previous research highlighting an association between acute fluctuations in testosterone and subsequent aggression that is specific to males and is not found in females (Carré et al., 2011).

Collectively, the primary results of the present study indicate that (i) acute stress causally inhibits the association between basal testosterone and retaliatory behavioral responses to unfair treatment in the ultimatum game (unfair offer rejections), and (ii) the mechanism for this effect may involve stress-induced cortisol increases. Although not the primary focus of our study, we also found some sex differences that are consistent with prior research (discussed below).

Discussion

The present study provides the first piece of empirical evidence that experimentally manipulated stress moderates the relationship between basal testosterone and behavior. Basal testosterone was positively related to unfair offer rejections in the low-stress condition, but this testosterone-behavior relationship was blocked in the high-stress condition. This pattern of results was observed in both men and women. Previous studies found inconsistent associations between basal testosterone and retaliatory behavior in the ultimatum game (Burnham, 2007; Diekhof et al., 2014; Eisenegger et al., 2010; Mehta and Josephs, 2010; Kopsida, et al., 2016; Zethraeus et al., 2009). The present study suggests that variability in acute environmental stress may be one potential explanation for these null and inconsistent effects. Indeed, our data support the hypothesis that acute stress causally inhibits basal testosterone's effect on retaliation in response to unfair treatment (unfair offer rejections).

Additional analyses suggest that an acute stress-induced cortisol increase might be one likely mechanism through which stress blocks testosterone's behavioral effects. In support of this hypothesis, we found that the social stress condition increased cortisol concentrations compared to the relaxation condition. Further analyses revealed that basal testosterone interacted with these cortisol changes to predict unfair offer rejections, even when controlling for the stress condition. Previous studies on the dual hormone hypothesis found that basal cortisol inhibits the association between basal testosterone and behaviors such as aggression and dominance (Dabbs et al., 1991; Edwards and Casto, 2013; Mehta and Josephs, 2010; Popma et al., 2007; Tackett et al., 2014, see also social inclusion condition in Geniole et al., 2011). The present study advances this body of research by demonstrating that acute stress causally suppresses the association between basal testosterone and retaliatory behavior, and that this effect may be driven by acute stress-induced activation of the HPA axis (increased cortisol). Although we found some initial support for acute cortisol change as a plausible mechanism, our study did not find clear evidence for mediation. Evidence for mediation will require additional studies with greater statistical power.

At the molecular level, high levels of cortisol have the capability of inhibiting the pathways between testosterone and behavior at multiple levels, an effect that may be accomplished via reduction in androgen receptors and the suppression of testosterone's effects on target tissues (Burnstein et al., 1995; Chen et al., 1997; Johnson et al., 1992; Smith et al., 1985; Tilbrook et al., 2000; Viau, 2002). While the effects of chronic stressors suppressing testosterone's functioning are well documented, there is variability surrounding the effects of acute stressors on HPG-axis activity (Tilbrook et al., 2000). It is possibile that acute stress *may* inhibit testosterone's impact on retaliation via cortisol suppression of the HPG axis at the molecular level. However, this hypothesis remains highly speculative, and direct tests of it will require additional research.

Although we found preliminary evidence for acute cortisol change as a possible mechanism for the moderating effects of stress on testosterone's role in social behavior, there are other related mechanisms that should be investigated in future research. Neuroimaging studies have revealed that activation in the amygdala — a region implicated in aggressive motivation in response to social provocation — is positively related to unfair offer rejections (Gospic et al., 2011), whereas activation in the ventromedial prefrontal cortex (vmPFC) — a region implicated in self-regulation and impulse control — is negatively related to unfair offer rejections (Koenigs and Tranel, 2007; Mehta and Beer, 2010). Further research suggests that testosterone enhances amygdala reactivity to social threat cues (e.g., angry faces- Gospic et al., 2011; Hermans et al., 2008) and inhibits vmPFC activity when receiving an unfair offer in the ultimatum game (Mehta and Beer, 2010). Most relevant to the present research are two neuroimaging studies that examined basal profiles of testosterone and cortisol. A profile of high testosterone and low cortisol was associated with enhanced amygdala activity to angry faces in one study (Hermans et al., 2008). In another study, the high testosterone low cortisol profile was associated with increased connectivity between the amygdala and vmPFC in response to social provocation (a verbal insult - Denson, Ronay, von Hippel & Schira, 2013). Thus, it is possible that acute stress may block testosterone's effect on unfair offer rejections in the ultimatum game through interactions between testosterone and cortisol in these subcortical and prefrontal regions (for a related theory that predicts testosterone/cortisol ratio effects instead of statistical interaction effects, see Montoya et al., 2012; Terburg et al., 2009).

A broader psychological mechanism for the present findings may involve interactions between approach and avoidance motivational systems. Testosterone has been associated with approach motivation (e.g., dominance motivation- Mazur and Booth, 1998), whereas social stress and acute cortisol increases enhance threat vigilance and are associated with behavioral inhibition as well as avoidant behaviors (Dickerson and Kemeny, 2004; Gray and McNaughton, 2003; Roelofs et al., 2009). A combination of high approach motivation (high testosterone) and low behavioral inhibition (low-stress social context) may encourage status-seeking behaviors such as aggression, whereas the increased avoidance tendencies in high-stress contexts may counteract the influence of high approach motivation (high testosterone), resulting in the inhibition of aggression (Dabbs et al., 1991; for similar arguments, see Carré et al., 2011; Maner et al., 2012; Mehta and Josephs, 2010; Montoya et al., 2012; Popma et al., 2007; Terburg et al., 2009). More broadly, it may be evolutionarily adaptive for high environmental stress to block the effects of increased testosterone activity on approach-oriented status-seeking behaviors such as retaliation because such behaviors are metabolically costly and potentially dangerous (Buchanan et al., 2003; Carré and Mehta, 2011; Haselton and Buss, 2000; Maner et al., 2012). And only when environmental stress is low may it be beneficial for a high-testosterone individual to adopt retaliatory behaviors in pursuit of status.

Another related psychological mechanism may involve cognitive appraisals of unfair offers as posing either a challenge or a threat (Mendes et al., 2001; Seery, 2011). Challenge appraisals are defined as perceptions that available resources outweigh situational demands and are associated with approach-oriented behavioral responses to social stress (Blascovich et al., 2004; Blascovich, 2013). Threat appraisals are defined as perceptions that situational demands outweigh available resources and are associated with avoidant behavioral responses to stress (Mendes et al., 2007). It is plausible that a high-testosterone individual in a low-stress environment may appraise unfair offers as being a challenge: that there are adequate resources to deal with the situational demands of the social provocation. This challenge appraisal may lead to retaliatory behaviors (i.e., rejection of unfair offers). However, a high-testosterone individual in a high-stress environment may perceive the unfair offer as being a threat: that the social provocation poses greater demands relative to available resources. This threat appraisal may lead to conciliatory behaviors (i.e., acceptance of unfair offers). Follow-up research should test these psychological mechanisms directly by measuring challenge versus threat appraisals (Mendes et al., 2001; Mendes, et al., 2007; Skinner and Brewer, 2002) and approach-avoidance motivation (Craver and White, 1994) in the ultimatum game.

Sex Differences

There were no sex differences for our primary results. In both men and women, there were positive associations between basal testosterone and unfair offer rejection rates in the low-stress condition but not in the high-stress condition. These non-significant sex differences for basal testosterone's association with behavior in our study aligns well with prior research, which also found similar basal T-behavior associations in men and women (Josephs et al., 2006; Newman et al., 2005, Mehta & Josephs, 2010). However, we did find a sex difference in ultimatum game decision making under varying levels of stress that was independent of basal testosterone. Women engaged in less retaliation (reduced rejection of unfair offers) in the high-stress condition compared to the low-stress condition, whereas men showed the opposite pattern (increased rejection of unfair offers in the high stress-condition compared to the low-stress condition, though these differences in men were not statistically significant). According to the tend-and-befriend theory, stressful contexts should encourage women to inhibit behaviors such as aggression and risk-taking and instead engage in affiliative and conciliatory behaviors (e.g. accept unfair offers). In contrast, stressful contexts should prompt men to engage in fight-or-flight behaviors such risk taking and social aggression (e.g., reject unfair offers) (Taylor, 2006; Taylor et al., 2000). Previous studies have provided initial support for the tend-and-befriend theory on measures of risk-taking. Women showed reduced risk-taking in the stress condition compared to the control condition, whereas men showed increased risk-taking in the stress condition compared to the control condition (Lighthall, et al., 2009; van den Bos, et al., 2009; see also footnote 4 of Mehta, et al., 2015b). The current findings provide additional support for the tend-and-befriend theory by revealing a previously unknown sex difference in the impact of stress on behavioral responses to social provocation in the ultimatum game.

Our primary analyses focused on basal testosterone's association with retaliatory behaviors under varying levels of stress, but we also measured acute testosterone reactivity in our study. In doing so, we uncovered a sex difference in the association between testosterone reactivity and behavior in both the low- and high-stress conditions, with a pattern that aligns well with previous research. Specifically, men who rose in testosterone reported greater anger after receiving unfair offers and rejected these offers at higher rates. Women, on the other hand, did not demonstrate these associations. These sex differences in the relationship between testosterone reactivity and behavioral responses to social provocation are consistent with prior research, which found that increased testosterone reactivity in competitive contexts predicts men's - but not women's - status-relevant behaviors in other behavioral paradigms besides the ultimatum game (mixed-sex sample: Carré et al., 2009, 2013; male only sample: Apicella, et al., 2014; Carré & McCormick, 2008; Mehta and Josephs, 2006). These new findings on retaliatory behavior in the ultimatum game provide further support for the claim that acute testosterone increases are related to aggressive, competitive, and dominant behaviors following social provocation in men but not in women.

Limitations and Future Directions

Despite the contribution that these findings make, there are some limitations of the present study that should be addressed in future research. Firstly, in the present study we manipulated stress by randomly assigning participants to a relaxation condition in which cortisol dropped or a stress condition in which cortisol increased. This manipulation was employed in order to maximize differences in cortisol concentrations between the two conditions. However, it remains unclear to what extent the moderating effect of this stress manipulation was driven by the social stress condition, the relaxation condition, or both. Future research should include additional control conditions in order to better understand the mechanisms for the impact of stress and relaxation on the relationship between testosterone and behavior (e.g., a non-evaluative control condition that can be compared to the socially evaluative stress condition- Het et al., 2009; a control condition in which participants sit alone that can be compared to the relaxation condition- Ventura et al., 2012). Relatedly, to elicit a cortisol response we employed a social evaluative stress paradigm that is designed to create a context of uncontrollability and increase threats to the self (Dickerson et al., 2008; Kirschbaum et al., 1993; Kudielka et al., 2007). It is not clear whether the behaviors we observed in the ultimatum game were a product of the interpersonally threatening nature of the stressor, or other aspects of the stressor. Additional studies comparing social and non-social stressors (e.g., the standard cold pressor task- Hines and Brown, 1932) can help further elucidate the mechanisms underlying the impact of causal stress manipulations on the association between basal testosterone and aggression.

Secondly, the present study included 39 participants (20 men, 19 men) who were randomly assigned to a low- or high-stress condition prior to the ultimatum game. In line with our theorizing, we found that acute stress moderates the association between basal testosterone retaliatory behavior in both men and women. However, there may not been have been sufficient statistical power to detect three-way interactions between participant sex, the stress condition, and testosterone, and direct tests of moderated-mediation models will also require greater statistical power. Therefore, the present study must be directly and conceptually replicated with larger mixed-sex samples before firm conclusions are drawn.

Thirdly, in addition to replicating these effects in larger samples, future studies should test these effects using more accurate methods of hormone assessment, such as mass spectrometry. Mass spectrometry may yield more reliable and valid salivary hormone concentrations compared to immunoassays, especially with estimating sex hormones (see Welker, et al., 2016; Soldin and Soldin, 2009). Apart from being a superior method for estimating salivary testosterone in general, mass spectrometry also provides greater sensitivity and accuracy in detecting low concentrations of testosterone - for example those found in women. There is evidence of enzyme-linked immunoassays (EIAs) inflating female testosterone concentrations, and this systematic bias in hormone measurement may inflate type 2 errors by obscuring the strength of the effects currently being reported in social neuroendocrinology studies. Therefore, we advocate the use of mass spectrometry as a more precise method of hormone measurement for future research, especially in mixed-sex samples, when feasible.

Fourthly, given that oral contraceptives (OCs) are known to decrease basal salivary testosterone, their use by female participants in our study may have been a confounding factor (Edwards and O'Neal, 2009). Though most of the women in our sample did not report using OCs, it is possible that these women were on other forms of hormonal-based contraception, which may have influenced their basal testosterone levels. Further, we did not screen for participants with endocrine disorders or those who used hormonal medications (e.g. corticosteroids), both of which may have influenced basal testosterone and cortisol levels. Therefore, future studies should control for the use of hormone-based contraception, endocrine conditions, and hormonal medication in their examination of the relationship between basal testosterone and retaliatory behaviors.

Fifth, in this study we used rejection of unfair offers in the ultimatum game as a measure of retaliatory aggression. Future research can employ well-validated metrics of retaliation and aggression from other related paradigms - for example, the Point Subtraction Aggression Paradigm (PSAP). Past research has generally revealed null effects of basal testosterone on reactive aggression in the PSAP (Carré et al., 2011), but these studies did not examine the moderating role of acute environmental stress. The results of the present study suggest that reducing acute environmental stress (e.g., with relaxation tasks) may reveal a positive association between basal testosterone and reactive aggression in the PSAP, whereas increasing acute stress may inhibit the association between basal testosterone and reactive aggression in the PSAP. There is some indirect evidence in the PSAP that is consistent with this hypothesis[5] (see footnote 5), but direct evidence for the causal impact of acute stress in influencing basal testosterone's association with aggressive behavior in these alternative paradigms will require additional studies.

[5] Geniole et al., 2011 recruited male participants, experimentally manipulated social inclusion versus social exclusion, and measured aggressive behavior in the PSAP. This manipulation did not increase cortisol concentrations, but it is likely that social exclusion was perceived as more stressful than social inclusion. Although not reported in their paper, personal communication with the second author (JC) indicates that there was a positive relationship between basal testosterone and aggressive behavior when controlling for condition (partial r = .26, p = .045). In line with our theorizing that acute stress should block testosterone's behavioral effects, this association between basal testosterone and aggression was stronger in the social inclusion condition (r = .34, p = .053) and was non-significant in the social exclusion condition (r = .15, p = .43). Geniole et al., 2011 also found that there was a positive association between acute testosterone reactivity and aggressive behavior (ΔR^2 = 6.5%, p = .04), but this effect was statistically significant only in the social inclusion condition (ΔR^2 = 13.3%, r = .36, p = .03) and was non-significant in the social exclusion condition (ΔR^2 = 1.8%, r = .13, p = .49). Collectively, these results from Geniole et al., 2011 suggest that one form of acute stress (social exclusion) may inhibit effects of both basal testosterone and acute testosterone reactivity on aggressive behavior in the PSAP. Future research that adopts standard stress manipulations such as the Trier Social Stress Test prior to the PSAP can test this hypothesis directly.

Sixth, we found that acute stress inhibited the association between basal testosterone and retaliation, but acute stress did not moderate the relationship between acute testosterone reactivity and retaliatory behavior. As mentioned earlier, there was likely insufficient statistical power to detect three-way interactions between participant sex, the stress condition, and acute testosterone reactivity in the present study. Future studies with greater statistical power should test these interactions. Indeed, there is indirect evidence in other behavioral paradigms suggesting that markers of stress may inhibit the association between testosterone change and aggressive behavior in men (e.g., dispositional anxiety, Norman et al., 2014; social exclusion, see see footnote 5 for a discussion of Geniole et al., 2011). Additional research should provide clear tests of this hypothesis in larger samples.

Finally, our study found that an experimental manipulation of stress causally inhibited the association between *endogenous* testosterone and retaliatory behavior. Another important direction for future research will be to experimentally manipulate both stress and testosterone (with exogenous hormone administration) in the same study. Our theorizing and initial results suggest that exogenous testosterone will enhance aggressive and dominant behaviors compared to placebo only in low-stress environments, whereas exogenous testosterone will inhibit aggressive and dominant behaviors compared to placebo in high-stress environments. We look forward to future behavioral pharmacology studies that adopt such designs to test the interactive effects of testosterone and stress on numerous status-relevant behaviors, including dominant leadership behavior (Mehta and Josephs, 2010), trust and empathy (Boksem et al., 2013; Zilioli et al., 2014), competitive decisions (Mehta and Josephs, 2010), risk-taking (Mehta et al., 2015b), overbidding in auctions (van den Bos et al., 2013), and social status (Edwards and Casto, 2013).

Acknowledgements

We thank Shereen Fatimah, Jared Nai, and Zheng Xue for help with data collection; Kai Wai and Vivian Ng for assistance with hormone assays; and Cassandra Brandes, Bethany Lassetter, Erik L. Knight and Jeffrey D. Whitaker for feedback on the manuscript. This work was supported by Academic Research Funds provided to JN from the National University of Singapore, and a National Science Foundation (NSF) grant awarded to PHM.

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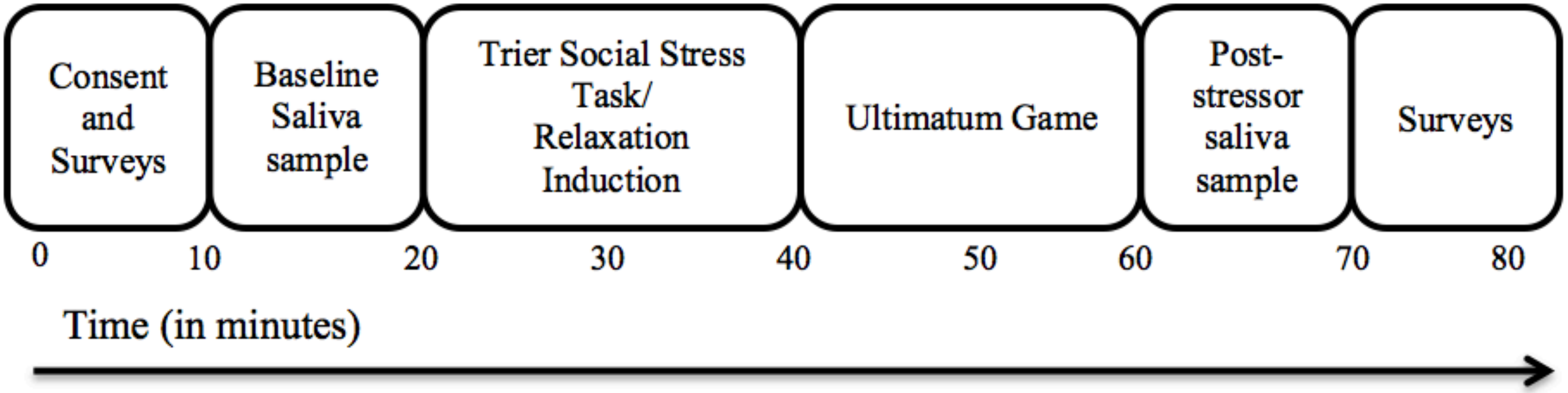
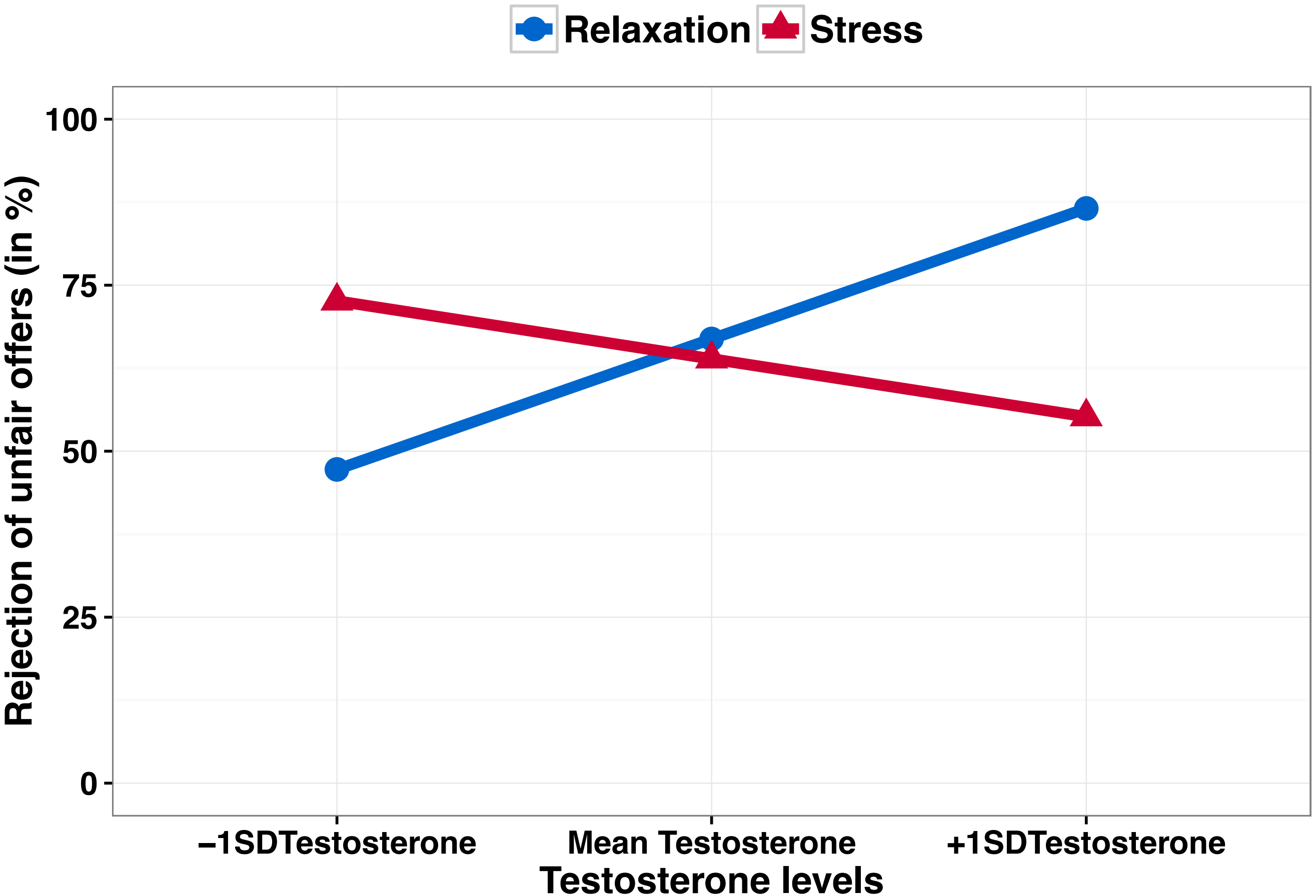
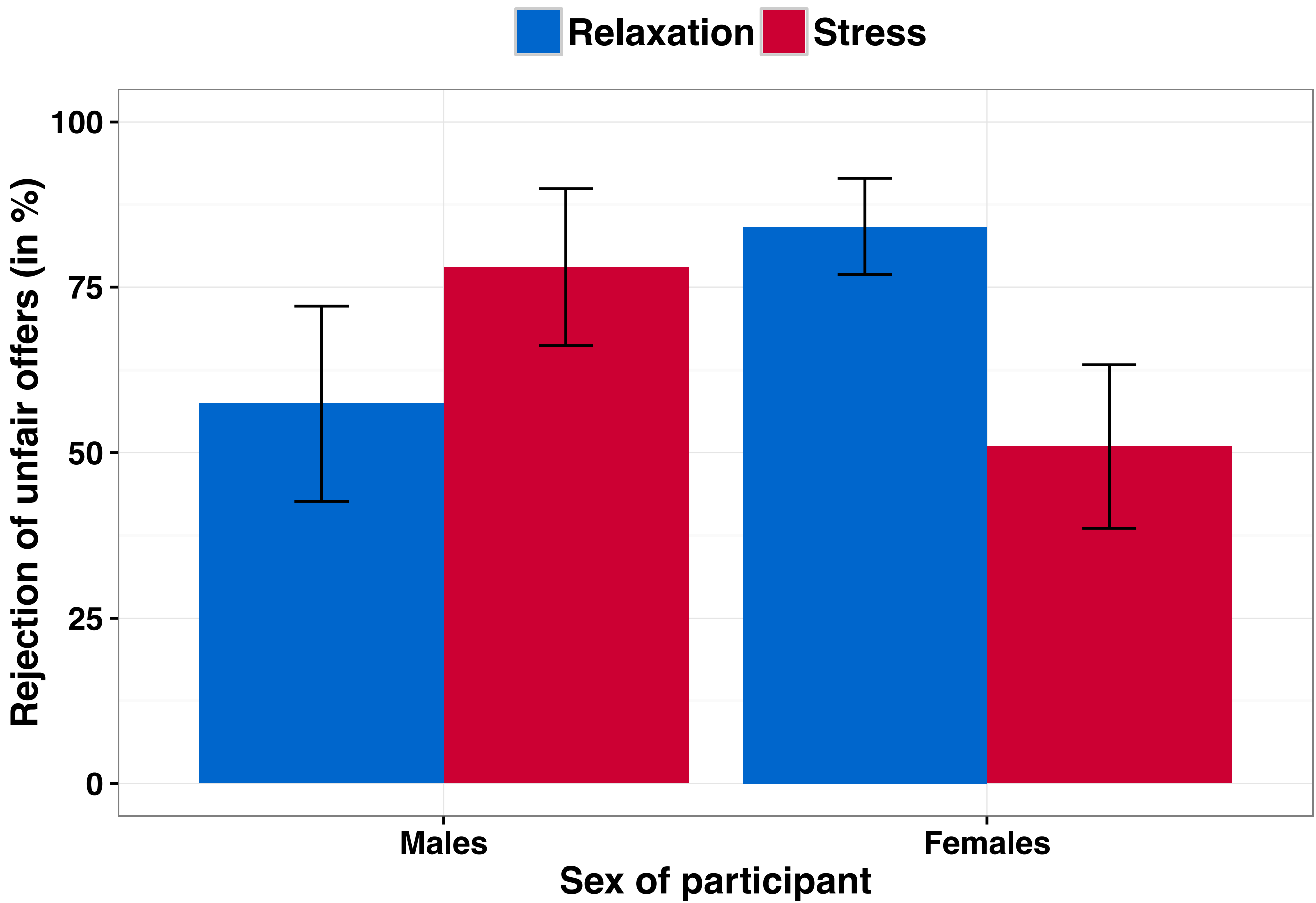
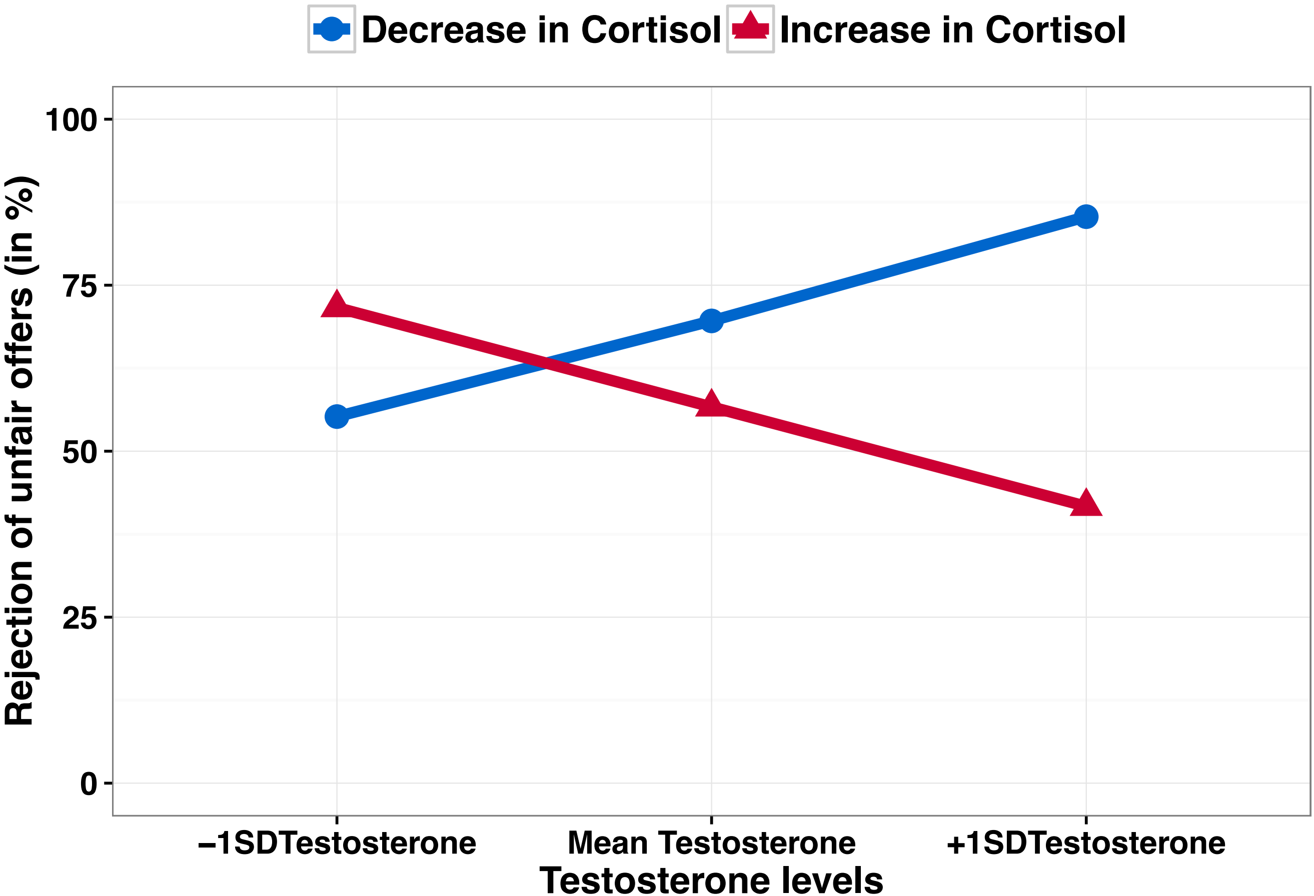

Consent and Surveys
Baseline Saliva sample
Trier Social Stress Task/ Relaxation Induction
Ultimatum Game
Post-stressor saliva sample
Surveys
0
10
20
30
40
50
60
70
80
Time (in minutes)

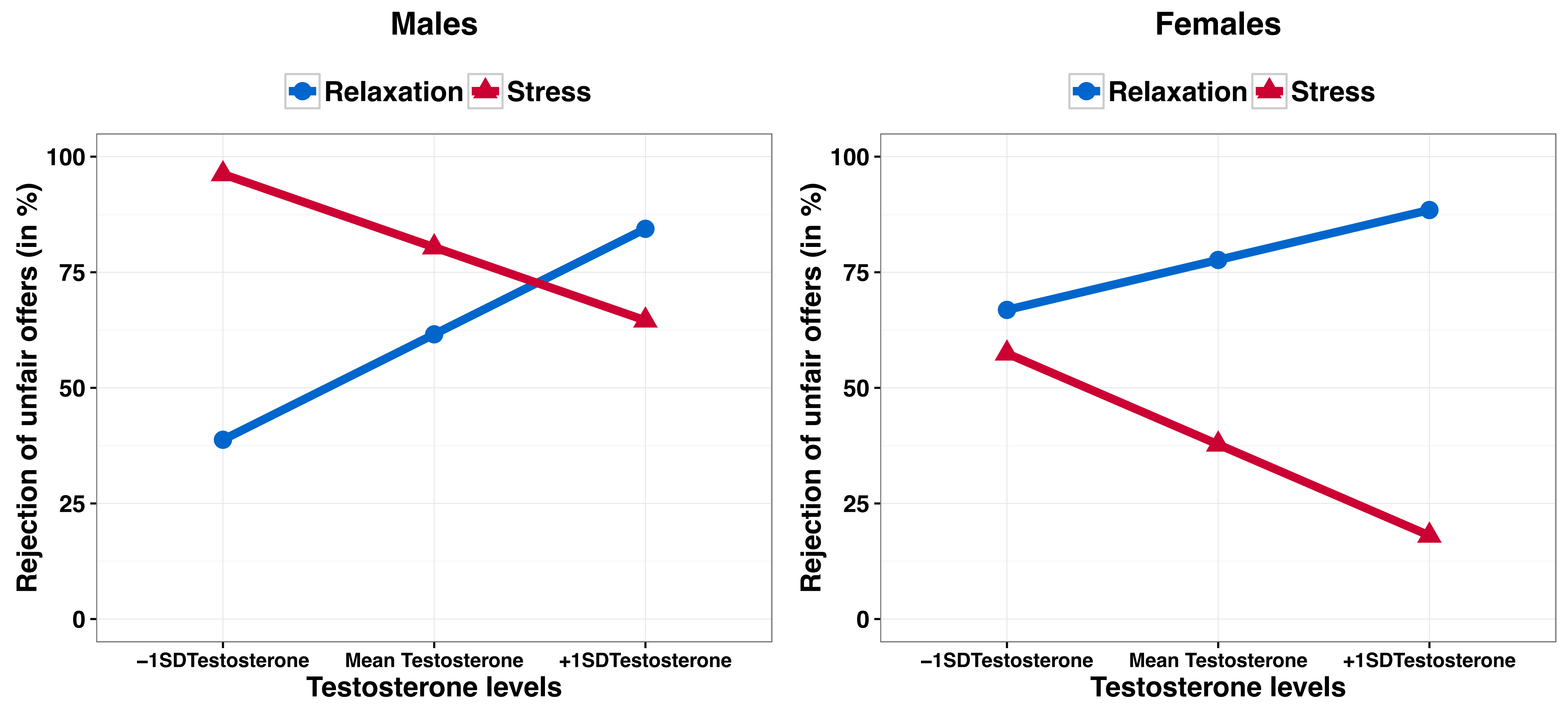

Relaxation
Stress
Rejection of unfair offers (in %)
100
75
50
25
0
−1SDTestosterone
Mean Testosterone
+1SDTestosterone
Testosterone levels



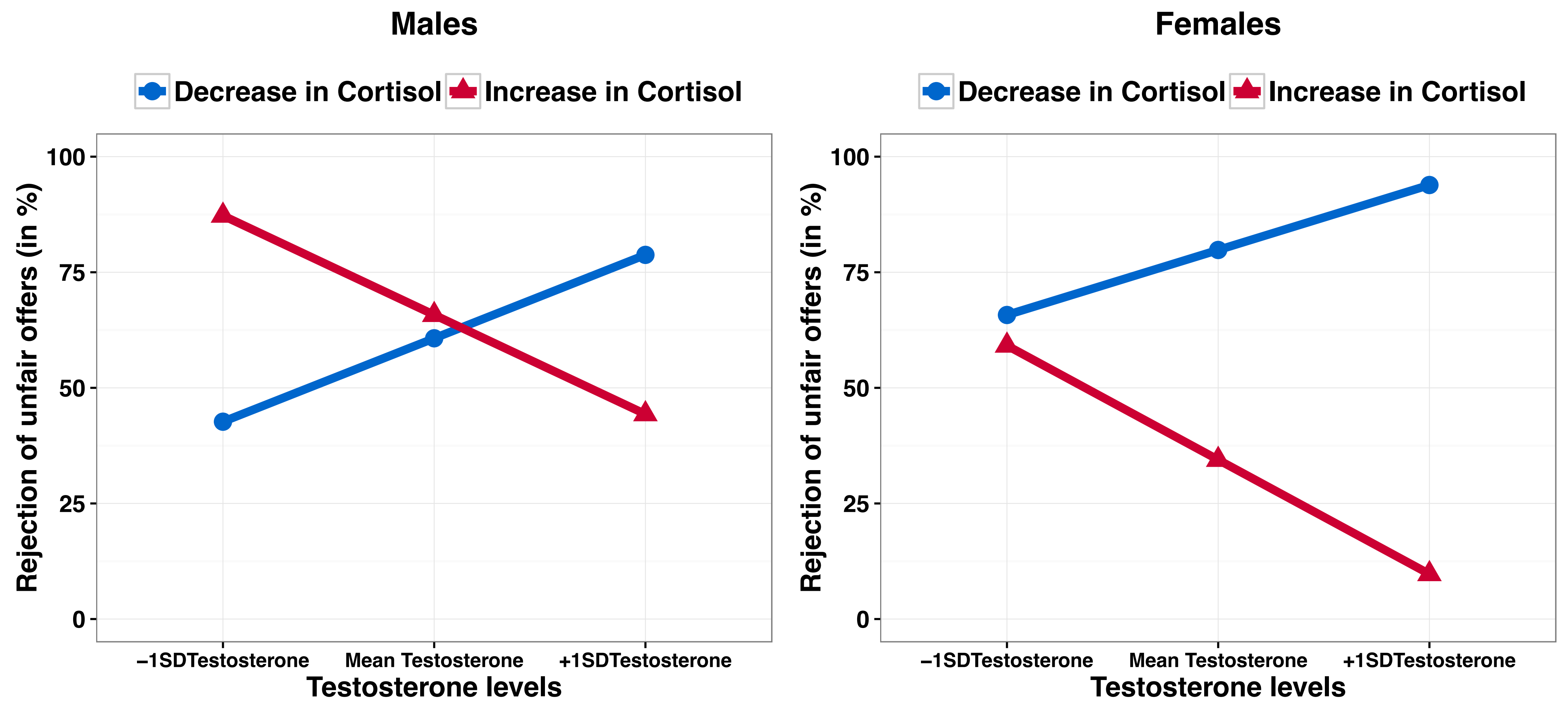
Relaxation
Stress
100
75
50
25
0
Rejection of unfair offers (in %)
Males
Females
Sex of participant



Decrease in Cortisol
Increase in Cortisol
100
75
50
25
0
Rejection of unfair offers (in %)
−1SDTestosterone
Mean Testosterone
+1SDTestosterone
Testosterone levels



Males
Relaxation
Stress
Rejection of unfair offers (in %)
100
75
50
25
0
–1SDTestosterone
Mean Testosterone
+1SDTestosterone
Testosterone levels
Females
Relaxation
Stress
Rejection of unfair offers (in %)
100
75
50
25
0
–1SDTestosterone
Mean Testosterone
+1SDTestosterone
Testosterone levels



Males
Decrease in Cortisol
Increase in Cortisol
Rejection of unfair offers (in %)
100
75
50
25
0
−1SDTestosterone
Mean Testosterone
+1SDTestosterone
Testosterone levels
Females
Decrease in Cortisol
Increase in Cortisol
Rejection of unfair offers (in %)
100
75
50
25
0
−1SDTestosterone
Mean Testosterone
+1SDTestosterone
Testosterone levels

Highlights

- Examined the role of stress moderating the testosterone-retaliation relationship
- Under conditions of low stress, basal testosterone positively predicted retaliation
- Experimentally induced stress blocked the testosterone-retaliation relationship
- Stress-induced cortisol reactivity was a likely mechanism of this effect

Supplementary Results

Stress-induced changes in testosterone and cortisol

We conducted confirmatory analyses to examine differences in cortisol and testosterone levels across time using repeated measures GLM. For cortisol, we found that raw cortisol levels did indeed change across time as a function of the condition that participants had been assigned (time X stress condition: $F(1, 37)= 11.74$, $p= .002$, $\eta^2=.24$). Follow-up analyses indicated that the low-stress condition decreased cortisol levels ($t(18)=3.11$, $p=.006$), whereas the high-stress condition marginally increased cortisol levels ($t(19)=-1.75$, $p=.096$) (see Table S1 for Means and SDs). The significant time x stress interaction indicates that the cortisol changes in the high-stress condition significantly differed from the cortisol change in the low-stress condition, which provides strong evidence that our experimental manipulation was successful in eliciting different patterns of cortisol changes in the two experimental groups. For testosterone, we only found a trend level time X stress condition interaction (while treating sex as a covariate) ($F(1, 36)= 2.96$, $p=.09$), thereby supporting the analyses reported in the main paper.

Basal testosterone, basal cortisol, and unfair offer rejections

We also conducted analyses that examined whether basal testosterone and basal cortisol interactions predicted unfair offer rejections. However, we did not find evidence for basal cortisol interacting with basal testosterone in predicting unfair offers (while controlling for the stress condition) ($\beta= .25$, $p=.15$), and this is consistent with some prior research that also failed to find basal testosterone x basal cortisol interaction on measures of ultimatum game decision making and reactive aggression (Geniole et al., 2013; Mehta et al., 2015). We also did not find support for a three-way stress x basal testosterone x basal cortisol interaction ($\beta= .46$, $p=.19$). Even though these analyses revealed non-significant effects, we recommend testing for similar interactions in larger samples to boost statistical power, and we also recommend that future studies consider the moderating effects of personality traits and context factors. Indeed, there is preliminary evidence that basal testosterone and basal cortisol interact with one another, with personality traits, and with the social context to predict aggressive behavior (personality traits: Tackett et al., 2014; social context: Denson et al., 2013; Geniole, et al., 2013). Finally, we recommend that future studies consider the moderating effects of *acute* stress. After all, the present study provides preliminary evidence suggesting that acute stress — compared to markers of chronic stress such as basal cortisol — may more robustly impact testosterone's association with aggressive and retaliatory behaviors.

Supplementary Results: Tables

			Basal Cortisol		Post-stress Cortisol		Basal Testosterone		Post-stress Testosterone	
		N	M	SD	M	SD	M	SD	M	SD
Low-stress	Male	10.00	3.98	2.76	2.64	1.01	151.23	26.36	148.36	21.49
	Female	9.00	5.97	4.94	3.19	1.69	126.50	20.78	114.01	32.59
	Total	19.00	5.03	4.08	2.93	1.40	138.22	26.18	130.28	32.36
High-stress	Male	9.00	3.55	1.83	5.38	4.68	162.25	38.31	173.69	35.68
	Female	11.00	3.22	1.30	3.65	1.39	94.53	18.22	94.43	17.18
	Total	20.00	3.40	1.58	4.60	3.62	131.79	45.90	138.02	49.31

Table S1. Means and SDs of the untransformed testosterone (in pg/mL) and cortisol levels (in nmol/L) – at baseline and post-manipulation, split by sex and condition.

Supplementary Results: Figures

<<Insert Fig. S1>>

Fig. S1. The interaction between testosterone and stress condition in predicting the rejection of unfair offers, across men and women.

<<Insert Fig. S2>>

Fig. S2. The interaction between basal testosterone and cortisol change in predicting the rejection of unfair offers, across men and women

Supplementary References

Denson, T.F., Mehta, P.H., Ho Tan, D., 2013. Endogenous testosterone and cortisol jointly influence reactive aggression in women. Psychoneuroendocrinology 38, 416–424. doi:10.1016/j.psyneuen.2012.07.003

Geniole, S.N., Busseri, M.A., McCormick, C.M., 2013. Testosterone dynamics and psychopathic personality traits independently predict antagonistic behavior towards the perceived loser of a competitive interaction. Horm. Behav. 64, 790–798. doi:10.1016/j.yhbeh.2013.09.005

Mehta, P.H., Mor, S., Yap, A.J., Prasad, S., 2015. Dual-Hormone Changes Are Related to Bargaining Performance. Psychol. Sci. 26, 866–876. doi:10.1177/0956797615572905

Tackett, J.L., Herzhoff, K., Harden, K.P., Page-Gould, E., Josephs, R.A., 2014. Personality × hormone interactions in adolescent externalizing psychopathology. Personal. Disord. 5, 235–46. doi:10.1037/per0000075