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

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33 Abstract

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

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

55

56

Introduction

57 Provocation that threatens one's social status can lead to retaliation. For example, an
58 employee who is denied a promotion that is long overdue may react aggressively towards
59 coworkers. Neuroendocrine theories have posited that in the face of threats to status, testosterone
60 should be associated with greater retaliatory behavior as a means to restore lost status (Mazur
61 and Booth, 1998; Archer, 2006). In support of this theory, studies have found a positive
62 relationship between testosterone and status-seeking behaviors such as aggression, competitive
63 behavior, and dominance, especially when status is threatened (Archer, 2006; Carré et al., 2011).
64 However, several other studies have only found weak or null effects (Archer, 2006; Archer et al.,
65 2005; Carré et al., 2011). For example, meta-analyses reveal only a weak positive association
66 between basal testosterone and human aggression ($r = .08$ in Archer, et al., 2005). Although there
67 is some evidence that testosterone is related to increased retaliation in response to social
68 provocation, findings across studies are mixed.

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

79 Josephs, 2010; reviewed in Mehta and Prasad, 2015). The dual hormone hypothesis proposes that
80 testosterone's role in status-relevant social behavior should depend on cortisol — a hormone
81 released as part of the hypothalamic-pituitary-adrenal (HPA) axis response to physical and
82 psychological stress (Dickerson and Kemeny, 2004). Specifically, the dual hormone hypothesis
83 predicts that higher concentrations of cortisol should inhibit testosterone's positive impact on
84 status-seeking behaviors. In support of this hypothesis, several studies have demonstrated that
85 basal testosterone is positively related to measures of aggression, dominance, and social status
86 when basal cortisol is low but not when basal cortisol is high (aggression: Dabbs et al., 1991;
87 Popma et al., 2007; Tackett, et al., 2014; see also social inclusion condition of Geniole, et al.,
88 2011; dominance: Mehta and Josephs, 2010; social status: Edwards and Casto, 2013; Ponzi, et
89 al., 2016; Sherman, et al., 2016; group performance: Akinola, et al., in press; for a recent review,
90 see Mehta and Prasad, 2015). However, other research revealed non-significant dual-hormone
91 interaction effects on aggressive behavior (Geniole, et al., 2013; Mazur and Booth, 2014).

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

101 The ultimatum game is a laboratory decision-making paradigm that assesses retaliatory
102 behavioral responses to social provocation (Güth, 1995; Wang et al., 2011). This game involves
103 two players: a proposer and a responder. The proposer decides how to split a sum of money (e.g.,
104 \$10) with the responder. The responder then decides whether to accept or reject the proposer's
105 offer. If the responder accepts the offer, the money is split as proposed. If the responder rejects
106 the offer, both players receive \$0. A round concludes once the responder makes a decision to
107 accept or reject. Responders generally accept fair offers (e.g., \$5: \$5 split), but they often reject
108 unfair offers (e.g., \$8: \$2 split) even though accepting these unequal offers guarantees financial
109 reward. These unfair offer rejections — a retaliatory behavioral response designed to punish the
110 proposer in the face of perceived provocation (unfair treatment) — can be considered a measure
111 of aggressive behavior. Indeed, receiving an unfair offer increases feelings of anger and spite,
112 emotions strongly related to aggressive motivation (Brañas-Garza et al., 2014; Espín et al., 2015;
113 Pillutla and Murnighan, 1996; Raihani and Bshary, 2015). In addition, evidence from social
114 neuroscience suggests that several brain regions linked to impulsive aggression — such as the
115 insula, amygdala, and ventromedial prefrontal cortex — are related to rejection of unfair offers
116 (Gospic et al., 2011; Koenigs and Tranel, 2007; Mehta and Beer, 2010; Moretti, et al., 2008;
117 Sanfey et al., 2003). Further, experimental depletion of serotonin, which has been linked to
118 impulsive aggression in prior research, increases rejections of unfair offers (Crockett et al.,
119 2008). Finally, personality traits that are related to aggressive behavior — high trait aggression
120 and low trait agreeableness — also predict increased unfair offer rejections (Mehta, 2008; Mehta,
121 et al., 2015a; Nguyen et al., 2011). Together, these studies provide convergent evidence
122 supporting the construct validity of the ultimatum game as a paradigm to investigate aggressive
123 behavioral responses to unfair treatment.

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

140 As reviewed earlier, there is mixed evidence regarding the direct association between
141 testosterone and status-relevant social behaviors. Consistent with this broader literature on
142 testosterone and human social behavior, studies that examined the association between
143 testosterone and unfair offer rejections in the ultimatum game also yielded mixed results
144 (positive associations in studies with basal testosterone: male-only sample - Burnham, 2007;
145 mixed-sex sample - Mehta and Beer, 2010; positive association with basal testosterone in
146 intergroup competition setting: male-only sample - Diekhof et al., 2014; null effect with basal

147 testosterone: Mehta, et al., 2015a; positive effect of exogenous testosterone in males - Zak et al.,
148 2009; trend-level negative effect of exogenous testosterone in a mixed-sex sample: Kopsida, et
149 al., 2016; non-significant effects of exogenous testosterone in females - Eisenegger et al., 2010;
150 Zethraeus et al., 2009). These equivocal results, combined with correlational evidence suggesting
151 that markers of stress moderate testosterone's behavioral effects, led to our hypothesis that acute
152 stress would causally inhibit basal testosterone's association with unfair offer rejections. We
153 tested this key hypothesis by measuring basal testosterone, experimentally manipulating levels of
154 acute stress using standard methods (Kirschbaum et al., 1993; Ventura et al., 2012), and then
155 measuring retaliatory behavioral responses to unfair treatment in the ultimatum game. We
156 hypothesized that basal testosterone would be positively related to unfair offer rejections at lower
157 levels of stress, but not at higher levels of stress. In other words, we expected that acute stress
158 would block testosterone's behavioral effects.

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

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

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

179 Finally, we conducted exploratory analyses that tested for sex differences. Prior research
180 has found mixed evidence for sex differences in testosterone's behavioral effects (Carré et al.,
181 2011; Mehta and Josephs, 2010), and there is initial evidence for sex differences in behavioral
182 responses to acute stress (Lighthall, et al., 2009; van den Bos, et al., 2009). Therefore, we
183 explored the role of sex as a moderator of the effects of acute stress and testosterone on
184 retaliatory behavior in the ultimatum game.

185

186 **Materials and Methods**

187 **Participants**

188 Thirty-nine (20 males and 19 females¹; $M_{age} = 21.69$ years, $SD = 1.96$) undergraduate
189 students enrolled for an introductory management course at a large Singaporean University
190 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 ($p=.97$).

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

193 **Ethics Statement**

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

196 **Procedure**

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

201 **Baseline saliva sample**

202 A baseline saliva sample was collected once participants completed the initial survey,
203 approximately 10 minutes after arrival to the laboratory. Before providing the sample
204 participants were asked to rinse their mouths with water to remove any remnant food particles.
205 To further avoid contamination of the saliva samples, prior to the actual day of the experiment
206 participants were requested to refrain from eating, drinking and brushing their teeth at least an
207 hour before their timeslot. Participants were also asked to refrain from consuming any
208 caffeinated products like coffee, tea and cocoa. Saliva samples were collected using an oral swab
209 (Salivette®) that was placed under the tongue for 1.5 minutes to allow sufficient saliva to
210 accumulate² (see footnote 1 for validation studies that demonstrate strong correlations between

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

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

223 **Stress Manipulation**

224 After completing the baseline saliva sample participants were randomly assigned to either
225 a high- or low-stress condition. The high-stress condition consisted of the Trier Social Stress
226 Task, a psychological stress induction paradigm involving performance of a speech and
227 completion of challenging math problems in front of an evaluative audience (Dickerson et al.,
228 2008; Kirschbaum et al., 1993; Kudielka et al., 2007). This paradigm has been shown to reliably
229 increase cortisol concentrations approximately 20-30 minutes after the manipulation (Dickerson

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.

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

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

249 After the preparatory period, the experimenter led the participant back to the interview
250 room. During the course of the entire interview, the participant stood at a marked spot
251 approximately 2 meters from where the interviewers were seated. Before the interview began,
252 one of the interviewers stood up to switch on a camera so that the participant believed the speech

253 was being video-recorded (in reality, the participants were not being recorded). The interviewers
254 then reiterated the instructions; they specifically went over the timeline of the interview and
255 subsequently asked the participants to begin their speech. If the participants ran out of things to
256 say, they were prompted to keep going until 3 minutes were up. The interviewers followed this
257 up with three prepared questions: (i) what are your greatest strengths? (ii) what would you
258 consider your weaknesses? and (iii) what makes you special? Finally, during the last 5 minutes
259 of the interview, participants were asked to perform a complex mathematical task in which they
260 counted down prime numbers starting with 300. If they provided an incorrect response, they
261 interviewer stopped them saying: “Wrong. Start again!”, and were asked to start from the
262 beginning. Over the course of the interview, the panel maintained neutral affect and did provide
263 any verbal or non-verbal feedback when the participant was talking. The entire task including the
264 time taken to provide instructions lasted approximately 20 minutes.

265 The low-stress condition consisted of a relaxation task in which participants listened to
266 instrumental music and read travel magazines. The experimenter provided the participants with a
267 set of travel magazines, turned on the music, and left the room. Participants stayed in the room
268 alone for the entire duration of the relaxation condition. This condition also lasted for 20
269 minutes, which was approximately the same overall duration as the high-stress condition. We
270 modeled the low-stress condition on relaxation-induction interventions that have been previously
271 used in alternative medicine research to alleviate anxiety and lower cortisol levels (Khalifa et al.,
272 2003; Ventura et al., 2012). Ventura et al. (2012) had participants either read a magazine or listen
273 to music to induce relaxation, but we combined the two conditions to maximize the effect of this
274 intervention on reduced cortisol concentrations. This design in which we compared a **social**

275 stress to a relaxation condition allowed us to maximize differences in cortisol, a theorized
276 mechanism for the impact of stress on the testosterone-behavior association.

277 **Ultimatum game**

278 Immediately after the social stress or relaxation manipulation, participants were escorted
279 to another room, where they played a computerized version of the ultimatum game (Güth, 1995;
280 Koenigs and Tranel, 2007; Sanfey et al., 2003). Participants believed that that they would play
281 the ultimatum game with 20 players in one-shot interactions but in reality they were playing with
282 the computer. At the start of the game, all participants were assigned to the role of a responder
283 and were made to believe their assignment to this role was completely random. In each of the 20
284 rounds that the participant played, they were required to split S\$10 (~8USD) with another
285 individual (the fictitious proposer). At the start of each round, participant first saw the proposer's
286 unique user id, followed by the offer they made. Proposers made offers of a pre-determined offer
287 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
288 across the 20 rounds that the participant played, and was randomized across each participant.
289 After the offer was made, participants were asked if they would like to accept or reject the offer.
290 If they accepted the offer, the \$10 would be split in the manner proposed. If they rejected the
291 offer, both players would receive \$0. Every round concluded once the responder made the
292 decision to accept or reject the proposed offer. At the end of the 20 rounds, a random trial was
293 selected, and participants were compensated for that trial based on their decision to reject or
294 accept the offer in that round. Prior to playing the game, participants were informed their
295 compensation would be based on their decision to accept or reject offers in a randomly selected
296 trial. The ultimatum game took about 20 minutes to complete.

297

298 Post-stress saliva sample

299 At the end of the ultimatum game, a second saliva sample was taken. The timing of this
300 second sample was approximately 20 minutes after the completion of the high- or low-stress
301 manipulations, and served to measure acute cortisol fluctuations from before to after the **social**
302 **stress** or relaxation tasks. We waited for 20 minutes after the end of **social stress**/relaxation tasks
303 to collect the second saliva sample because it takes several minutes for hormones in serum to
304 reach saliva (Riad-Fahmy et al., 1987) and because cortisol levels tend peak approximately 15-
305 20 minutes after laboratory stressors (Kirschbaum et al., 1993; Wirth et al., 2006).

306 Self-reported fairness and anger ratings

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

316 <<Insert Figure 1>>

317 Fig. 1. Timeline for the study**318 Hormone Assays**

319 The samples that were collected in the laboratory were transported to an in-house
320 biomarker lab where they were analyzed for testosterone and cortisol concentrations using

321 salivary enzyme immunoassay (EIA) kits purchased from Salimetrics (Salimetrics LLC, State
322 College, PA, USA). Standard procedures and protocol were followed during the assay process
323 (Schultheiss and Stanton, 2009). All the standards and controls were assayed in duplicate, and
324 30% of the samples on that plate were randomly chosen and assayed in duplicates. Both the
325 average intra-assay coefficient of variation (CV) and inter-assay CV for testosterone and cortisol
326 were below 10%.

327 **Statistical Analyses**

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

343 mean for cortisol reactivity scores. The simple slopes of the relationship between testosterone
344 unfair offer rejection rate were also tested using standard procedures (see Aiken et al., 1991).

345 **Results**

346 **Preliminary analyses**

347 First we conducted analyses to verify that there were no differences in baseline hormone
348 levels as a function of the stress manipulation. As expected, participants did not differ in their
349 basal cortisol levels across the low and high stress conditions ($F(1, 37)=2.74, p=.11$). We also
350 did not find sex differences in basal levels of cortisol across all participants ($F(1, 37)=.85,$
351 $p=.36$). As expected, there was a sex difference in basal testosterone concentrations
352 ($F(1,37)=23.60, p<.001$). When controlling for participant sex, there were non-significant
353 differences in basal testosterone between the low and high stress conditions ($F(1,36)=1.12,$
354 $p=.30$). See Table S1 for means and SDs of untransformed testosterone and cortisol
355 concentrations before and after the stress manipulation, and across sexes.

356 Next we examined associations between testosterone and cortisol. Our standardized basal
357 testosterone and basal cortisol scores were positively correlated ($r=0.46, p=.003$), which is
358 consistent with previous research (Mehta and Josephs, 2010; Mehta et al., 2008.; Popma et al.,
359 2007). Additionally, the standardized cortisol reactivity and testosterone reactivity scores were
360 also positively correlated ($r=0.44, p=.005$), which is also consistent with prior research
361 (correlation between hormone change scores: Mehta & Josephs, 2006; Mehta, et al., 2015;
362 evidence of positive co-variation between HPA-HPG axes: Dismukes, et al., 2015; Marceau et
363 al., 2014).

364

365

366 Stress-induced changes in cortisol and testosterone

367 To ascertain if the experimental manipulation of stress influenced cortisol or testosterone
368 changes, we computed percent changes in raw cortisol and testosterone. The change in cortisol
369 for participants in the high stress condition differed from the change in cortisol for participants in
370 the low-stress condition ($t(27.28)=-3.23, p=.003, d=1.02, 95\% CI: -111.40, -25.01$). Comparing
371 the means of cortisol change revealed that the individuals in the high-stress condition
372 demonstrated greater increases in cortisol ($M=43.40, SD=84.87, 95\% CI: 3.68, 83.12$) relative to
373 those in the low-stress condition ($M=-24.80, SD= 39.80, 95\%CI: -43.99, -5.62$). Follow-up one-
374 sample t-tests revealed that the cortisol increase in the high-stress condition and the cortisol
375 decrease in the low-stress condition were both significantly different from zero (high stress:
376 $t(19)=2.29, p=.03$; low stress: $t(18)=-2.72, p=.01$). These findings indicate that our stress and
377 relaxation manipulations successfully altered cortisol levels in the expected direction consistent
378 with prior research (Kudielka et al., 2007; Ventura et al., 2012). Supplementary analyses using
379 repeated measures GLM analyses showed the same pattern of cortisol changes (see
380 Supplementary Results and Table S1).

381 We also found that changes in testosterone in the high-stress condition only marginally
382 differed from the low-stress condition ($t(36.98)=-1.91, p=.06, 95\% CI: -23.24, .71$). Comparing
383 the means of testosterone change indicated that those in the high-stress condition ($M= 5.93, SD=$
384 $19.14, 95\% CI: -3.02, 14.90$) marginally rose in testosterone relative to the low-stress condition
385 ($M= -5.32, SD= 17.76, 95\% CI: -13.88, 3.23$). Supplementary analyses using repeated measures
386 GLM also showed marginally significant results (see Supplementary Results and Table S1). The
387 simultaneous activation of both the HPA and HPG axis is consistent with prior research that

388 provides evidence their co-activation, especially in stressful contexts (Dismukes, et al., 2015;
389 Lemarie et al., 1997).

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

392 **Ultimatum game preliminary analyses**

393 The average rejection rates in the present study (\$5 offers: $M = 7.05\%$, $SD = 21.42$; \$4
394 offers: $M = 21.79\%$, $SD = 38.55$; \$3 offers: $M = 55.77\%$, $SD = 46.40$; \$2 offers: $M = 69.87\%$, SD
395 $= 42.21$; \$1 offers: $M = 80.13\%$, $SD = 35.90$) were similar to behavioral results found prior
396 research on the ultimatum game (Koenigs and Tranel, 2007; Mehta and Josephs, 2010; Sanfey et
397 al., 2003). To test our main hypotheses, we categorized \$3, \$2 and \$1 offers as *unfair offers*, and
398 we averaged across these offer types to create an overall index of the percentage of unfair offers
399 rejected ($M = 68.59\%$, $SD = 37.7$). This classification was done for two reasons. Firstly, previous
400 research used the same grouping (see Koenigs and Tranel, 2007; Mehta and Josephs, 2010).
401 Therefore, this classification allows us to compare the present results to prior studies. Secondly,
402 self-reported fairness perceptions were consistent with this classification. Specifically, the \$4 and
403 \$5 offer values received fairness ratings above the mid-point of the 7-point scale (\$5 offer: 6.5
404 ($SD = .88$); \$4 offer: 4.9 ($SD = 1.56$)), whereas the \$3, \$2, and \$1 offers received fairness ratings
405 below the midpoint indicating that these offers were indeed perceived as unfair (\$3 offer: $M =$
406 3.2 ($SD = 1.61$); \$2 offer: $M = 2.1$ ($SD = 1.39$); \$1 offer: $M = 1.69$ ($SD = 1.36$)).

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

411 -15.51, $p < .001$, 95% CI: -3.84, -2.95), unfair offers elicited more anger ($M = 2.72$, $SD = 1.16$) than
412 fair offers ($M = 1.24$, $SD = .39$ ($t(38) = 9.31$, $p < .001$, 95% CI: 1.15, 1.79), and unfair offers were
413 more likely to be rejected ($M = 68.59\%$, $SD = 37.7$) than fair offers ($M = 14.51\%$, $SD = 26.57$)
414 ($t(38) = 9.25$, $p < .001$, 95% CI: 42.31, 65.02).

415 **Basal testosterone, stress, and unfair offer rejections**

416 We tested the hypothesis that basal testosterone's role in unfair offer rejections would
417 depend on environmental stress. Specifically, we expected that testosterone would be positively
418 associated with unfair offer rejections in the low-stress condition, but in the high-stress
419 condition, this relationship between testosterone and unfair offer rejections would be suppressed.
420 To test this hypothesis, we conducted a hierarchical multiple regression in which we entered the
421 stress condition (dummy coded: 1 as high-stress and 0 as low-stress condition) and basal
422 testosterone in Step 1, and the basal testosterone x stress condition interaction in Step 2 (Aiken et
423 al., 1991). This analysis revealed no main effects in Step 1, but there was a statistically
424 significant basal testosterone x stress interaction in Step 2 ($\Delta R^2 = .13$, $\beta = -.57$, $b = -28.75$, $t(35) = -$
425 2.28 , $p = .028$, 95% CIs: -54.28, -3.22). Fig. 2 demonstrates the pattern of this interaction. An
426 analysis of simple slopes (Aiken & West, 1991) revealed that the relationship between
427 testosterone and unfair offer rejection rate was positive in the low-stress condition ($b = 19.92$,
428 $t(35) = 2.05$, $p = .05$, 95% CI: .20, 39.64). In support for the hypothesis that stress blocks
429 testosterone's behavioral effects, there was a non-significant association between basal
430 testosterone and unfair offer rejection rate in the high-stress condition ($b = -8.83$, $t(35) = -1.12$,
431 $p = .28$, 95% CI: -25.05, 7.39). Follow-up analyses revealed that this effect was robust when
432 controlling for relevant covariates; the basal testosterone x stress interaction remained
433 statistically significant when controlling for participant sex ($\Delta R^2 = .16$, $\beta = -.71$, $b = -35.52$, $t(34) = -$

434 2.57, $p=.015$, 95% CI: -63.65, 7.39), the time of the basal hormone sample ($\Delta R^2=.16$, $\beta=-.65$,
435 $b=-32.47$, $t(34)=-2.67$, $p=.012$, 95% CI: -57.24, -7.71), wake-up time ($\Delta R^2=.096$, $\beta=-.51$, $b=-$
436 25.74, $t(34)=-1.20$, $p=.057$, 95% CI: -52.24, .76), and time from awakening (in minutes
437 calculated by subtracting the time of the baseline saliva sample from the time the participant
438 woke up) ($\Delta R^2=.097$, $\beta=-.51$, $b=-25.44$, $t(34)=-2.01$, $p=.05$, 95% CI: -51.14, .26)³.

439 <<Insert Figure 2>>

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

442 *Participant sex moderation analyses*

443 Follow-up regression analysis explored if sex moderated the basal testosterone x stress
444 condition interaction on unfair offer rejections. There was a non-significant sex x basal
445 testosterone x stress condition interaction ($\beta=-.09$, $b= 8.14$, $t(31)=.28$, $p=.78$, 95% CI: -50.85,
446 67.14). Despite not finding a significant sex x basal testosterone x condition interaction, we
447 conducted additional analyses to confirm that the interaction pattern was similar across both
448 sexes. We did not expect to find significant results because of reduced statistical power in these
449 analyses. Separate analyses for each sex confirmed a similar basal testosterone x stress condition
450 interaction pattern in males ($\beta = -.78$, $p = .08$) and females ($\beta = -.53$, $p = .13$) (see Fig. S1 for the
451 basal testosterone x stress condition interaction patterns in males and females separately; in both
452 men and women, there were positive slopes between basal T and unfair offer rejection rates in
453 the low-stress condition but not in the high-stress condition). These analyses suggest that there
454 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.

455 Even though we did not find a significant sex x basal testosterone x stress interaction, our
456 analyses did reveal a sex x stress condition interaction ($F(1, 35)= 5.24, p=.03, \eta_p^2=.13$). As
457 shown in Fig. 3, post-hoc analyses indicated that females rejected more unfair offers in the low-
458 stress condition ($M= 84.17, SD=23.06$) compared to the high-stress condition ($M= 50.93,$
459 $SD=37.14$) ($t(17)= 2.37, p=.03, d= 1.07, 95\% CI: 3.67, 62.81$). The opposite pattern was found in
460 males, although these behavioral differences in males were non-significant (high-stress
461 condition: $M= 78.03, SD= 39.31$; low-stress condition: $M= 57.41, SD=44.18; t(18)= -1.10,$
462 $p=.28, d= .49, 95\% CI: -59.86, 18.61$). This pattern of results conceptually replicates and extends
463 previous work that has examined sex differences in the impact of stress on risky decision-making
464 (Lighthall, et al., 2009; van den Bos et al., 2009).

465 <<Insert Figure 3>>

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

468 **Basal testosterone, cortisol reactivity, and unfair offer rejections**

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

478 The pattern of this interaction was similar to the interaction between testosterone and stress
479 condition (see Fig. 4). An analysis of simple slopes indicated a positive relationship between
480 basal testosterone and rejection of unfair offers only among individuals who decreased in cortisol
481 (-1SD: $b = 15.40$, $t(35) = -1.98$, $p = .056$, 95% CIs: -.41, 31.21), but not among individuals who
482 increased in cortisol (+1SD: $b = -15.17$, $t(35) = -1.56$, $p = .13$, 95% CIs: -34.93, 4.60). The
483 statistically significant interaction term indicates that these slopes statistically differed from each
484 other.

485 Further, we found that the basal testosterone x cortisol reactivity interaction remained
486 statistically significant even when controlling for the stress condition ($\Delta R^2 = .15$, $\beta = -.44$, $b = -$
487 15.50 , $t(34) = -2.48$, $p = .018$, 95% CIs: -28.19, -2.81), the sex of the participant ($\Delta R^2 = .16$, $\beta = -.45$,
488 $b = -15.92$, $t(34) = -2.57$, $p = .015$, 95% CIs: -28.51, -3.32) and when controlling for the stress
489 condition and participant sex in the same analysis ($\Delta R^2 = .16$, $\beta = -.45$, $b = -15.88$, $t(33) = -2.48$,
490 $p = .02$, 95% CIs: -28.91, -2.86). In other follow-up analyses, the basal testosterone x cortisol
491 reactivity interaction remained significant when controlling for time of the basal hormone sample
492 ($\Delta R^2 = .17$, $\beta = -.47$, $b = -16.37$, $t(34) = -2.80$, $p = .008$, 95% CIs: -28.27, -4.48), wake-up time
493 ($\Delta R^2 = .15$, $\beta = -.44$, $b = -15.40$, $t(34) = -2.58$, $p = .01$, 95% CIs: -27.52, -3.28), and time from
494 awakening ($\Delta R^2 = .16$, $\beta = -.45$, $b = -15.72$, $t(34) = -2.69$, $p = .01$, 95% CIs: -27.59, -3.85). We also
495 conducted analyses using an alternate metric of cortisol reactivity — residualized cortisol change
496 — and found a similar interaction pattern to the one noted above ($\Delta R^2 = .06$, $\beta = -.28$, $b = -.14$,
497 $t(34) = -1.59$, $p = .12$, 95% CIs: -.32-.039).

498 <<Insert Figure 4>>

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

501 *Participant sex moderation analyses*

502 We again tested for sex differences in the basal testosterone x cortisol reactivity interaction
503 and again found a non-significant sex X basal testosterone x cortisol reactivity interaction ($\beta =$
504 $.04, b = -1.95, t(31) = -.13, p = .90, 95\% CIs: -31.90, 27, 99$). There were also non-significant sex x
505 basal T and sex x cortisol reactivity interactions in this analysis. Despite not finding a significant
506 sex x basal testosterone x cortisol reactivity interaction, we conducted additional analyses to
507 confirm that the basal testosterone x cortisol reactivity interaction pattern was similar across both
508 sexes. Subsequent analyses confirmed that the this interaction term showed a similar pattern
509 across males ($\beta = -.47, p = .054$) and females ($\beta = -.73, p = .058$) (see Fig. S2 for the basal
510 testosterone x cortisol reactivity interaction patterns in males and females separately). These
511 analyses indicate that there were no sex differences in the pattern of the basal T x cortisol
512 reactivity interaction.

513 *Moderated Mediation Analyses*

514 We conducted moderation mediation analyses to explore whether cortisol reactivity was a
515 potential mechanism through which acute stress causally inhibited basal testosterone's
516 association with rejection of unfair offers. Using the PROCESS macro (v 2.12.1), Model 15
517 template in SPSS (v21, IBM Corp), we tested a moderated mediation model with stress condition
518 as the independent variable, cortisol reactivity as the mediator, basal testosterone as the
519 moderator of both the stress condition and cortisol reactivity, and rejection of unfair offers as the
520 dependent variable. This analysis revealed non-significant moderated mediation ($\omega = -10.32, SE =$
521 $8.64, 95\% CI: -26.12, 5.40$). Because this study was not designed to test moderated mediation,
522 the lack of statistical significance in these analyses was likely due to insufficient statistical
523 power. Given that the basal testosterone x cortisol reactivity interaction remained significant

524 even after controlling for the stress condition, we conclude that the present study provides
525 preliminary evidence that cortisol reactivity may be a potential mechanisms through which
526 heightened stress causally inhibits basal testosterone's association with unfair offer rejections.
527 Future studies with larger sample sizes should be conducted to test for moderated mediation
528 more rigorously.

529 **Self-reported anger and fairness**

530 Although unfair offer rejection rates were positively correlated with perceptions of anger
531 ($r(39) = .39, p = .014$) and negatively correlated with perceptions of fairness ($r(39) = -.61, p < .001$)
532 multiple-regression analyses indicated that basal testosterone and the stress manipulation did not
533 predict perceptions of anger or fairness (no main effects or interactions, all $ps > .10$). These results
534 are consistent with prior research that also found null associations between testosterone and self-
535 reported psychological measures (Eisenegger et al., 2010; Kopsida, et al., 2016; Zak et al., 2009).
536 Further, these findings provide additional support for the claim that testosterone's behavioral
537 effects likely operate outside of conscious awareness (Josephs, et al., 2006; Schultheiss et al.,
538 2005; Terburg, et al., 2012).

539 **Testosterone reactivity and unfair offer rejections**

540 Our primary analyses focused on basal testosterone to be consistent with most prior
541 research on endogenous hormone concentrations in the ultimatum game (Burnham, 2007;
542 Diekhof et al., 2014; Mehta and Josephs, 2010; but see also Mehta, et al., 2015a). However,
543 other research that used different behavioral paradigms found that acute fluctuations in
544 testosterone are related to subsequent aggressive behavior especially in men (Carré et al., 2011).
545 Thus, we conducted follow-up analyses in which we examined associations between acute
546 fluctuations in testosterone from before to after the stress manipulation and ultimatum game

547 decision-making. While testosterone marginally rose in the stress condition compared to the
 548 relaxation condition (reported above), there were non-significant associations between acute
 549 fluctuations in testosterone and unfair offer rejections ($r = .07, p = .65$), fairness perceptions ($r =$
 550 $.19, p = .24$), and anger ($r = .09, p = .60$), and acute testosterone fluctuations did not significantly
 551 interact with the stress condition or cortisol reactivity to predict unfair offer rejections, fairness,
 552 perceptions, or anger (all p 's > .10).

553 While we did not find statistically significant testosterone reactivity x stress or
 554 testosterone reactivity x cortisol reactivity interactions, we found that the testosterone reactivity
 555 x sex interaction significantly predicted anger reported in response to receiving unfair offers
 556 ($\Delta R^2 = .10, \beta = -.44, b = -.75, t(34) = -2.31, p = .028, 95\% CIs: -1.41, -.09$) and marginally predicted
 557 unfair offer rejections ($\Delta R^2 = .09, \beta = -.43, b = -23.50, t(34) = -1.89, p = .067, 95\% CIs: -48.70,$
 558 1.71), while controlling for the stress condition⁴. Analyses of simple slopes indicated that
 559 testosterone increases in men were associated with greater anger ($b = 15.32, t(34) = 1.74, p = .09,$
 560 $95\% CI: -2.56, 33.20$) and higher rates of unfair offer rejections ($b = 19.92, t(35) = 2.05, p = .05,$
 561 $95\% CI: .20, 39.64$). In women, there were non-significant associations between testosterone
 562 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 ($\Delta R^2 = .10, \beta = -.44, b = -.74, t(34) = -2.31, p = .027, 95\% CIs: -1.39, -.09$), and was marginally significant for unfair offer rejections ($\Delta R^2 = .10, \beta = -.43, b = -23.77, t(35) = -1.94, p = .06, 95\% CIs: -48.68, 1.15$). The analyses were also robust to other covariates for both anger experienced towards unfair offers: time of the basal hormone sample ($\Delta R^2 = .09, \beta = -.42, b = -.71, t(34) = -2.19, p = .036, 95\% CIs: -1.36, -.05$), wake-up time ($\Delta R^2 = .10, \beta = -.44, b = -.75, t(34) = -2.31, p = .027, 95\% CIs: -1.41, -.09$), and time from awakening ($\Delta R^2 = .10, \beta = -.44, b = -.75, t(34) = -2.29, p = .028, 95\% CIs: -1.41, -.09$), and rejection of unfair offers: time of the basal hormone sample ($\Delta R^2 = .08, \beta = -.40, b = -21.98, t(34) = -1.81, p = .08, 95\% CI: -46.71, 2.75$), wake-up time ($\Delta R^2 = .09, \beta = -.42, b = -23.05, t(34) = -1.88, p = .068, 95\% CI: -47.92, 1.82$), and time from awakening ($\Delta R^2 = .084, \beta = -.41, b = -22.33, t(34) = -1.84, p = .075, 95\% CI: -47.02, 2.36$).

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

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

570 Discussion

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

582 Additional analyses suggest that an acute stress-induced cortisol increase might be one
583 likely mechanism through which stress blocks testosterone's behavioral effects. In support of this
584 hypothesis, we found that the social stress condition increased cortisol concentrations compared
585 to the relaxation condition. Further analyses revealed that basal testosterone interacted with these

586 cortisol changes to predict unfair offer rejections, even when controlling for the stress condition.
587 Previous studies on the dual hormone hypothesis found that basal cortisol inhibits the association
588 between basal testosterone and behaviors such as aggression and dominance (Dabbs et al., 1991;
589 Edwards and Casto, 2013; Mehta and Josephs, 2010; Popma et al., 2007; Tackett et al., 2014, see
590 also social inclusion condition in [Geniole et al., 2011](#)). The present study advances this body of
591 research by demonstrating that **acute stress** causally suppresses the association between basal
592 testosterone and retaliatory behavior, and that this effect may be driven by **acute stress**-induced
593 activation of the HPA axis (increased cortisol). **Although we found some initial support for acute**
594 **cortisol change as a plausible mechanism, our study did not find clear evidence for mediation.**
595 **Evidence for mediation will require additional studies with greater statistical power.**

596 **At the molecular level, high levels of cortisol have the capability of inhibiting the**
597 **pathways between testosterone and behavior at multiple levels, an effect that may be**
598 **accomplished via reduction in androgen receptors and the suppression of testosterone's effects**
599 **on target tissues (Burnstein et al., 1995; Chen et al., 1997; Johnson et al., 1992; Smith et al.,**
600 **1985; Tilbrook et al., 2000; Viau, 2002). While the effects of chronic stressors suppressing**
601 **testosterone's functioning are well documented, there is variability surrounding the effects of**
602 **acute stressors on HPG-axis activity (Tilbrook et al., 2000). It is possible that acute stress may**
603 **inhibit testosterone's impact on retaliation via cortisol suppression of the HPG axis at the**
604 **molecular level. However, this hypothesis remains highly speculative, and direct tests of it will**
605 **require additional research.**

606 **Although we found preliminary evidence for acute cortisol change as a possible**
607 **mechanism for the moderating effects of stress on testosterone's role in social behavior, there are**
608 **other related mechanisms that should be investigated in future research. Neuroimaging studies**

609 have revealed that activation in the amygdala — a region implicated in aggressive motivation in
610 response to social provocation — is positively related to unfair offer rejections (Gospic et al.,
611 2011), whereas activation in the ventromedial prefrontal cortex (vmPFC) — a region implicated
612 in self-regulation and impulse control — is negatively related to unfair offer rejections (Koenigs
613 and Tranel, 2007; Mehta and Beer, 2010). Further research suggests that testosterone enhances
614 amygdala reactivity to social threat cues (e.g., angry faces- Gospic et al., 2011; Hermans et al.,
615 2008) and inhibits vmPFC activity when receiving an unfair offer in the ultimatum game (Mehta
616 and Beer, 2010). Most relevant to the present research are two neuroimaging studies that
617 examined basal profiles of testosterone and cortisol. A profile of high testosterone and low
618 cortisol was associated with enhanced amygdala activity to angry faces in one study (Hermans et
619 al., 2008). In another study, the high testosterone low cortisol profile was associated with
620 increased connectivity between the amygdala and vmPFC in response to social provocation (a
621 verbal insult - Denson, Ronay, von Hippel & Schira, 2013). Thus, it is possible that acute stress
622 may block testosterone's effect on unfair offer rejections in the ultimatum game through
623 interactions between testosterone and cortisol in these subcortical and prefrontal regions (for a
624 related theory that predicts testosterone/cortisol ratio effects instead of statistical interaction
625 effects, see Montoya et al., 2012; Terburg et al., 2009).

626 A broader psychological mechanism for the present findings may involve interactions
627 between approach and avoidance motivational systems. Testosterone has been associated with
628 approach motivation (e.g., dominance motivation- Mazur and Booth, 1998), whereas social stress
629 and acute cortisol increases enhance threat vigilance and are associated with behavioral
630 inhibition as well as avoidant behaviors (Dickerson and Kemeny, 2004; Gray and McNaughton,
631 2003; Roelofs et al., 2009). A combination of high approach motivation (high testosterone) and

632 low behavioral inhibition (low-stress social context) may encourage status-seeking behaviors
633 such as aggression, whereas the increased avoidance tendencies in high-stress contexts may
634 counteract the influence of high approach motivation (high testosterone), resulting in the
635 inhibition of aggression (Dabbs et al., 1991; for similar arguments, see Carré et al., 2011; Maner
636 et al., 2012; Mehta and Josephs, 2010; Montoya et al., 2012; Popma et al., 2007; Terburg et al.,
637 2009). More broadly, it may be evolutionarily adaptive for high environmental stress to block the
638 effects of increased testosterone activity on approach-oriented status-seeking behaviors such as
639 retaliation because such behaviors are metabolically costly and potentially dangerous (Buchanan
640 et al., 2003; Carré and Mehta, 2011; Haselton and Buss, 2000; Maner et al., 2012). And only
641 when environmental stress is low may it be beneficial for a high-testosterone individual to adopt
642 retaliatory behaviors in pursuit of status.

643 Another related psychological mechanism may involve cognitive appraisals of unfair
644 offers as posing either a challenge or a threat (Mendes et al., 2001; Seery, 2011). Challenge
645 appraisals are defined as perceptions that available resources outweigh situational demands and
646 are associated with approach-oriented behavioral responses to social stress (Blascovich et al.,
647 2004; Blascovich, 2013). Threat appraisals are defined as perceptions that situational demands
648 outweigh available resources and are associated with avoidant behavioral responses to stress
649 (Mendes et al., 2007). It is plausible that a high-testosterone individual in a low-stress
650 environment may appraise unfair offers as being a challenge: that there are adequate resources to
651 deal with the situational demands of the social provocation. This challenge appraisal may lead to
652 retaliatory behaviors (i.e., rejection of unfair offers). However, a high-testosterone individual in a
653 high-stress environment may perceive the unfair offer as being a threat: that the social
654 provocation poses greater demands relative to available resources. This threat appraisal may lead

655 to conciliatory behaviors (i.e., acceptance of unfair offers). Follow-up research should test these
656 psychological mechanisms directly by measuring challenge versus threat appraisals (Mendes et
657 al., 2001; Mendes, et al., 2007; Skinner and Brewer, 2002) and approach-avoidance motivation
658 (Craver and White, 1994) in the ultimatum game.

659 **Sex Differences**

660 There were no sex differences for our primary results. In both men and women, there
661 were positive associations between basal testosterone and unfair offer rejection rates in the low-
662 stress condition but not in the high-stress condition. These non-significant sex differences for
663 basal testosterone's association with behavior in our study aligns well with prior research, which
664 also found similar basal T-behavior associations in men and women (Josephs et al., 2006;
665 Newman et al., 2005, Mehta & Josephs, 2010). However, we did find a sex difference in
666 ultimatum game decision making under varying levels of stress that was independent of basal
667 testosterone. Women engaged in less retaliation (reduced rejection of unfair offers) in the high-
668 stress condition compared to the low-stress condition, whereas men showed the opposite pattern
669 (increased rejection of unfair offers in the high stress-condition compared to the low-stress
670 condition, though these differences in men were not statistically significant). According to the
671 tend-and-befriend theory, stressful contexts should encourage women to inhibit behaviors such
672 as aggression and risk-taking and instead engage in affiliative and conciliatory behaviors (e.g.
673 accept unfair offers). In contrast, stressful contexts should prompt men to engage in fight-or-
674 flight behaviors such risk taking and social aggression (e.g., reject unfair offers) (Taylor, 2006;
675 Taylor et al., 2000). Previous studies have provided initial support for the tend-and-befriend
676 theory on measures of risk-taking. Women showed reduced risk-taking in the stress condition
677 compared to the control condition, whereas men showed increased risk-taking in the stress

678 condition compared to the control condition (Lighthall, et al., 2009; van den Bos, et al., 2009; see
679 also footnote 4 of Mehta, et al., 2015b). The current findings provide additional support for the
680 tend-and-befriend theory by revealing a previously unknown sex difference in the impact of
681 stress on behavioral responses to social provocation in the ultimatum game.

682 Our primary analyses focused on basal testosterone's association with retaliatory behaviors
683 under varying levels of stress, but we also measured acute testosterone reactivity in our study. In
684 doing so, we uncovered a sex difference in the association between testosterone reactivity and
685 behavior in both the low- and high-stress conditions, with a pattern that aligns well with previous
686 research. Specifically, men who rose in testosterone reported greater anger after receiving unfair
687 offers and rejected these offers at higher rates. Women, on the other hand, did not demonstrate
688 these associations. These sex differences in the relationship between testosterone reactivity and
689 behavioral responses to social provocation are consistent with prior research, which found that
690 increased testosterone reactivity in competitive contexts predicts men's - but not women's -
691 status-relevant behaviors in other behavioral paradigms besides the ultimatum game (mixed-sex
692 sample: Carré et al., 2009, 2013; male only sample: Apicella, et al., 2014; Carré & McCormick,
693 2008; Mehta and Josephs, 2006). These new findings on retaliatory behavior in the ultimatum
694 game provide further support for the claim that acute testosterone increases are related to
695 aggressive, competitive, and dominant behaviors following social provocation in men but not in
696 women.

697 **Limitations and Future Directions**

698 Despite the contribution that these findings make, there are some limitations of the present
699 study that should be addressed in future research. Firstly, in the present study we manipulated
700 stress by randomly assigning participants to a relaxation condition in which cortisol dropped or a

701 stress condition in which cortisol increased. This manipulation was employed in order to
702 maximize differences in cortisol concentrations between the two conditions. However, it remains
703 unclear to what extent the moderating effect of this stress manipulation was driven by the social
704 stress condition, the relaxation condition, or both. Future research should include additional
705 control conditions in order to better understand the mechanisms for the impact of stress and
706 relaxation on the relationship between testosterone and behavior (e.g., a non-evaluative control
707 condition that can be compared to the socially evaluative stress condition- Het et al., 2009; a
708 control condition in which participants sit alone that can be compared to the relaxation condition-
709 Ventura et al., 2012). Relatedly, to elicit a cortisol response we employed a social evaluative
710 stress paradigm that is designed to create a context of uncontrollability and increase threats to the
711 self (Dickerson et al., 2008; Kirschbaum et al., 1993; Kudielka et al., 2007). It is not clear
712 whether the behaviors we observed in the ultimatum game were a product of the interpersonally
713 threatening nature of the stressor, or other aspects of the stressor. Additional studies comparing
714 social and non-social stressors (e.g., the standard cold pressor task- Hines and Brown, 1932) can
715 help further elucidate the mechanisms underlying the impact of causal stress manipulations on
716 the association between basal testosterone and aggression.

717 Secondly, the present study included 39 participants (20 men, 19 men) who were randomly
718 assigned to a low- or high-stress condition prior to the ultimatum game. In line with our
719 theorizing, we found that acute stress moderates the association between basal testosterone
720 retaliatory behavior in both men and women. However, there may not have been sufficient
721 statistical power to detect three-way interactions between participant sex, the stress condition,
722 and testosterone, and direct tests of moderated-mediation models will also require greater

723 statistical power. Therefore, the present study must be directly and conceptually replicated with
724 larger mixed-sex samples before firm conclusions are drawn.

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

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

745 conditions, and hormonal medication in their examination of the relationship between basal
746 testosterone and retaliatory behaviors.

747 Fifth, in this study we used rejection of unfair offers in the ultimatum game as a measure
748 of retaliatory aggression. Future research can employ well-validated metrics of retaliation and
749 aggression from other related paradigms - for example, the Point Subtraction Aggression
750 Paradigm (PSAP). Past research has generally revealed null effects of basal testosterone on
751 reactive aggression in the PSAP (Carré et al., 2011), but these studies did not examine the
752 moderating role of acute environmental stress. The results of the present study suggest that
753 reducing acute environmental stress (e.g., with relaxation tasks) may reveal a positive association
754 between basal testosterone and reactive aggression in the PSAP, whereas increasing acute stress
755 may inhibit the association between basal testosterone and reactive aggression in the PSAP.
756 There is some indirect evidence in the PSAP that is consistent with this hypothesis⁵ (see footnote
757 5), but direct evidence for the causal impact of acute stress in influencing basal testosterone's
758 association with aggressive behavior in these alternative paradigms will require additional
759 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 ($\Delta R^2 = 6.5\%$, $p = .04$), but this effect was statistically significant only in the social inclusion condition ($\Delta R^2 = 13.3\%$, $r = .36$, $p = .03$) and was non-significant in the social exclusion condition ($\Delta R^2 = 1.8\%$, $r = .13$, $p = .49$). 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.

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

770 Finally, our study found that an experimental manipulation of stress causally inhibited the
771 association between *endogenous* testosterone and retaliatory behavior. Another important
772 direction for future research will be to experimentally manipulate both stress and testosterone
773 (with exogenous hormone administration) in the same study. Our theorizing and initial results
774 suggest that exogenous testosterone will enhance aggressive and dominant behaviors compared
775 to placebo only in low-stress environments, whereas exogenous testosterone will inhibit
776 aggressive and dominant behaviors compared to placebo in high-stress environments. We look
777 forward to future behavioral pharmacology studies that adopt such designs to test the interactive
778 effects of testosterone and stress on numerous status-relevant behaviors, including dominant
779 leadership behavior (Mehta and Josephs, 2010), trust and empathy (Boksem et al., 2013; Zilioli
780 et al., 2014), competitive decisions (Mehta and Josephs, 2010), risk-taking (Mehta et al., 2015b),
781 overbidding in auctions (van den Bos et al., 2013), and social status (Edwards and Casto, 2013).
782

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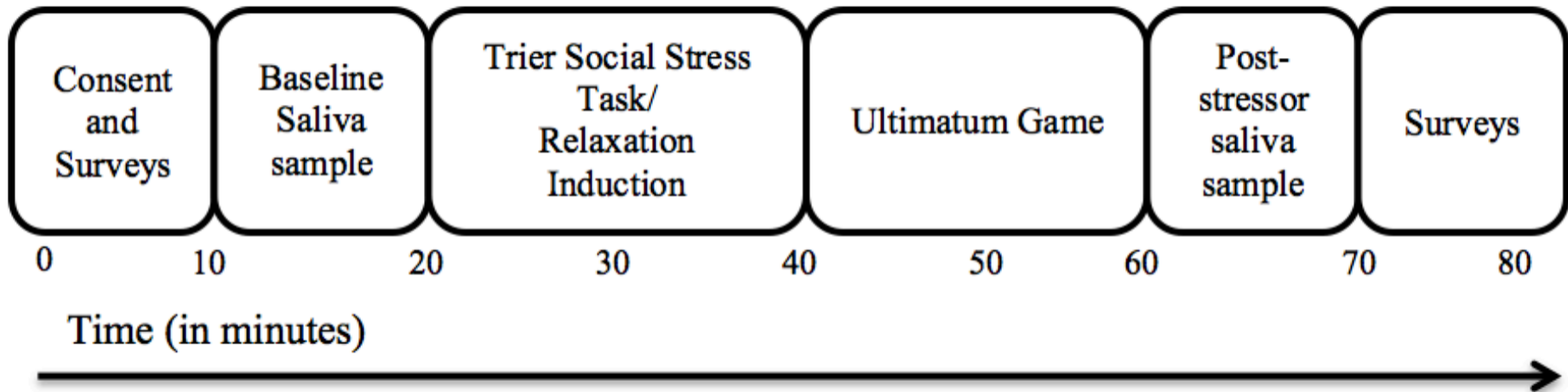
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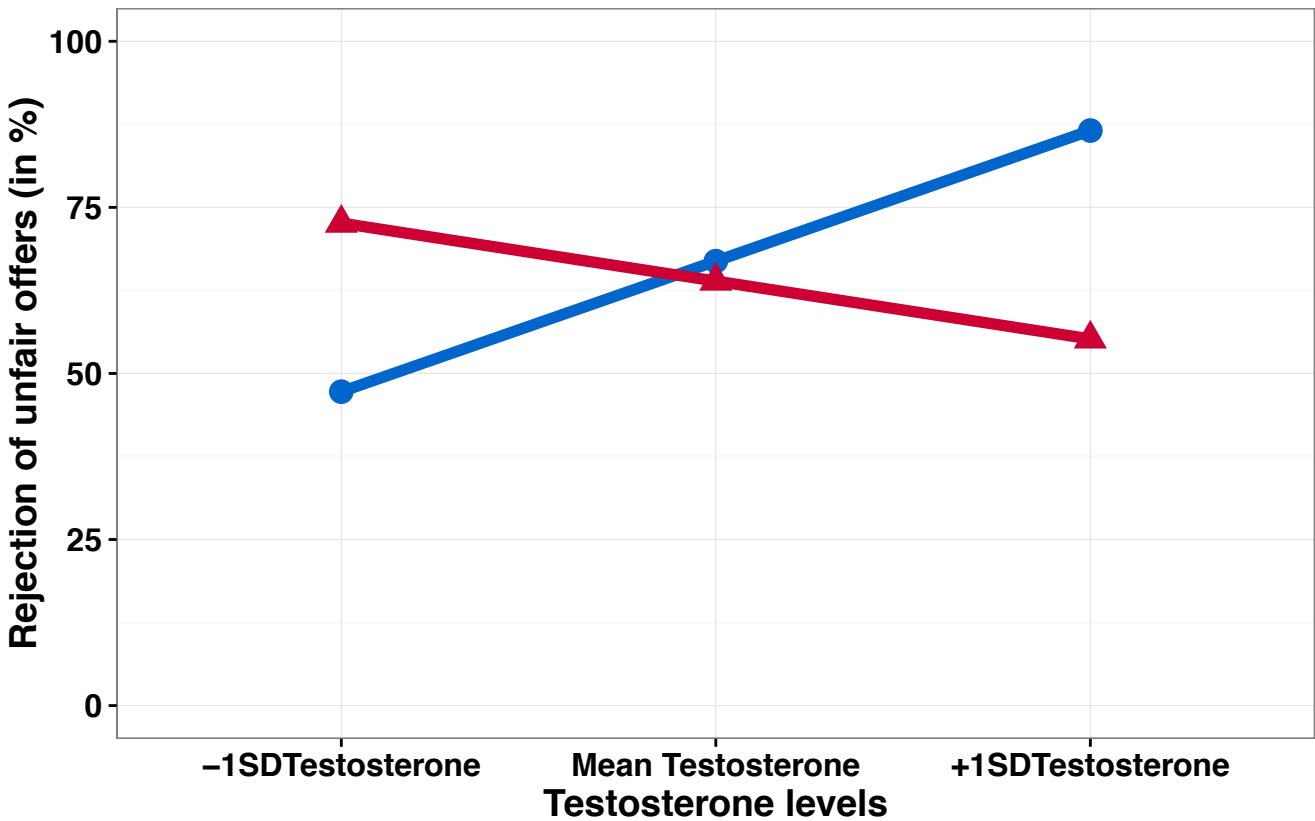
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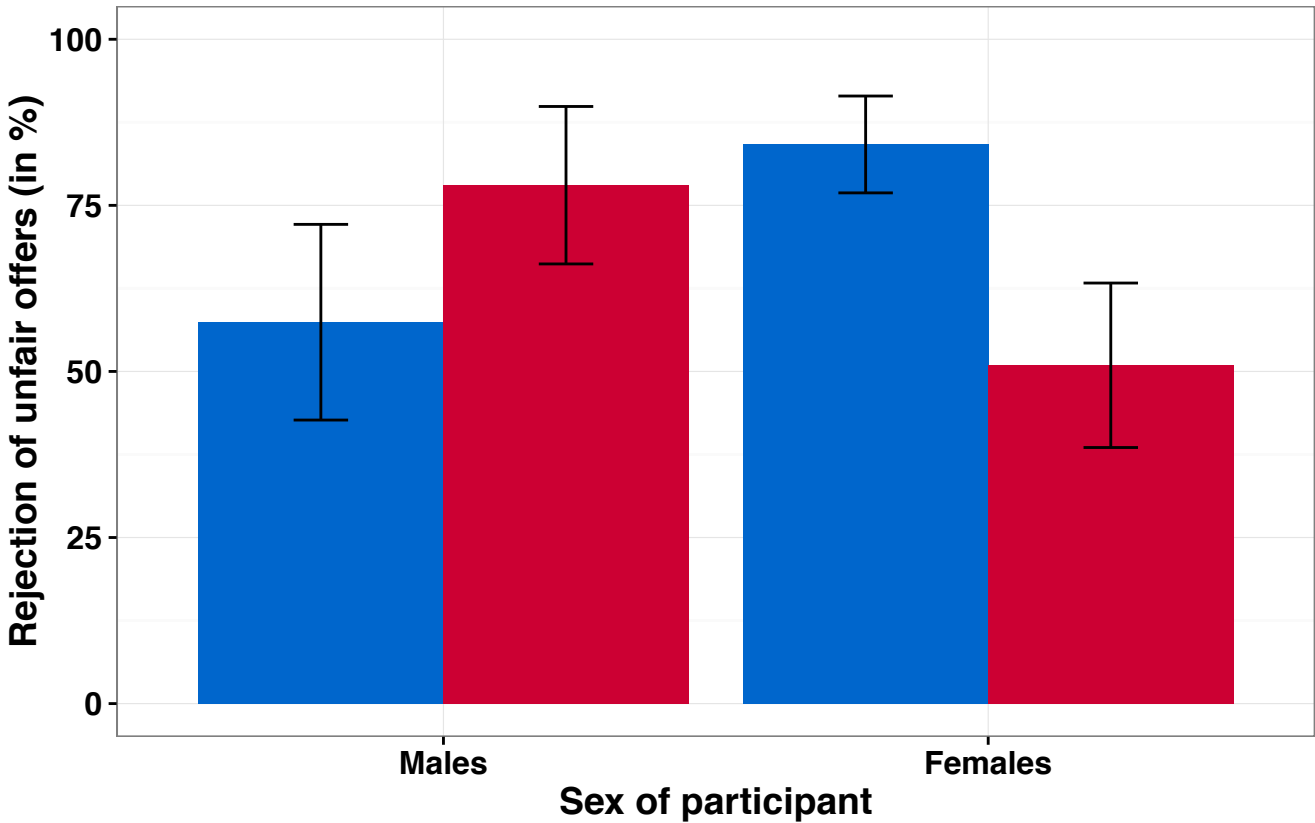
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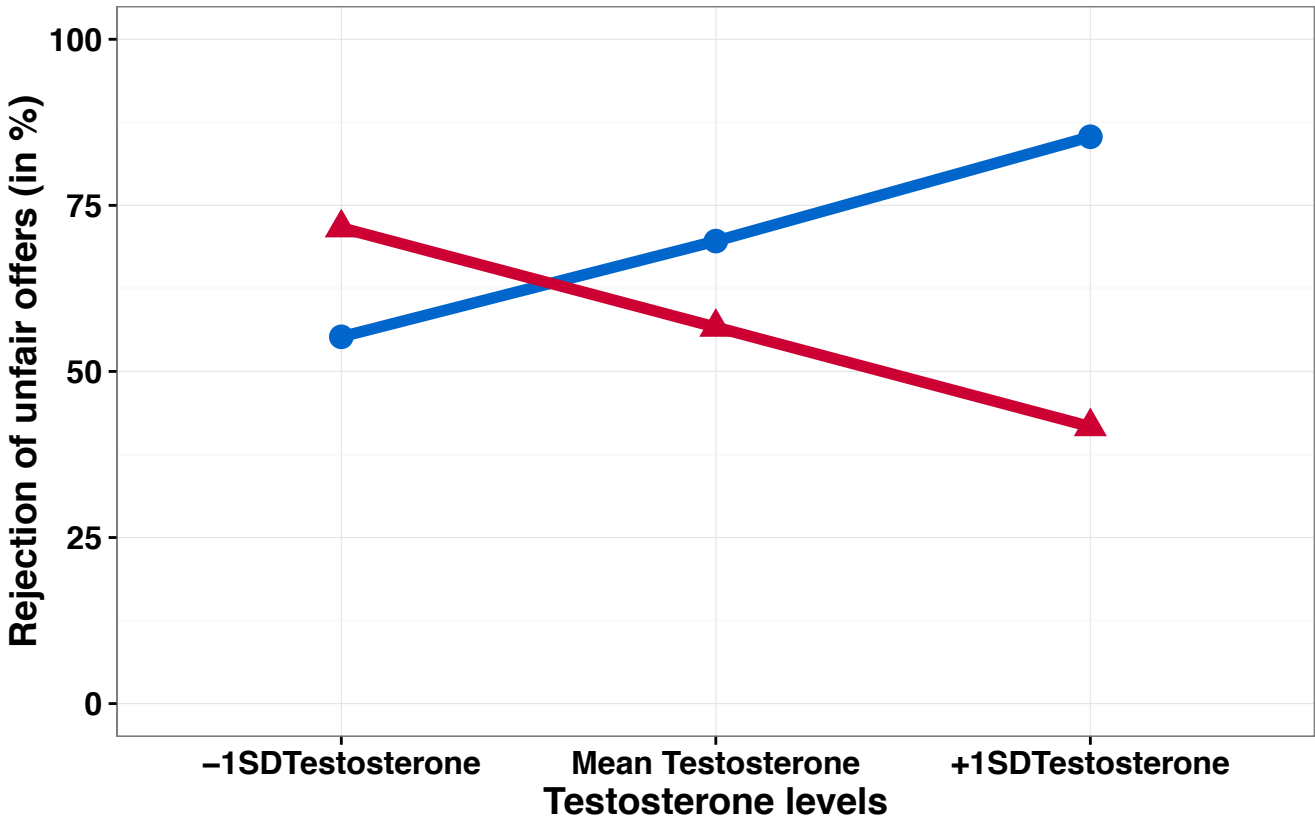
Relaxation Stress



Relaxation **Stress**

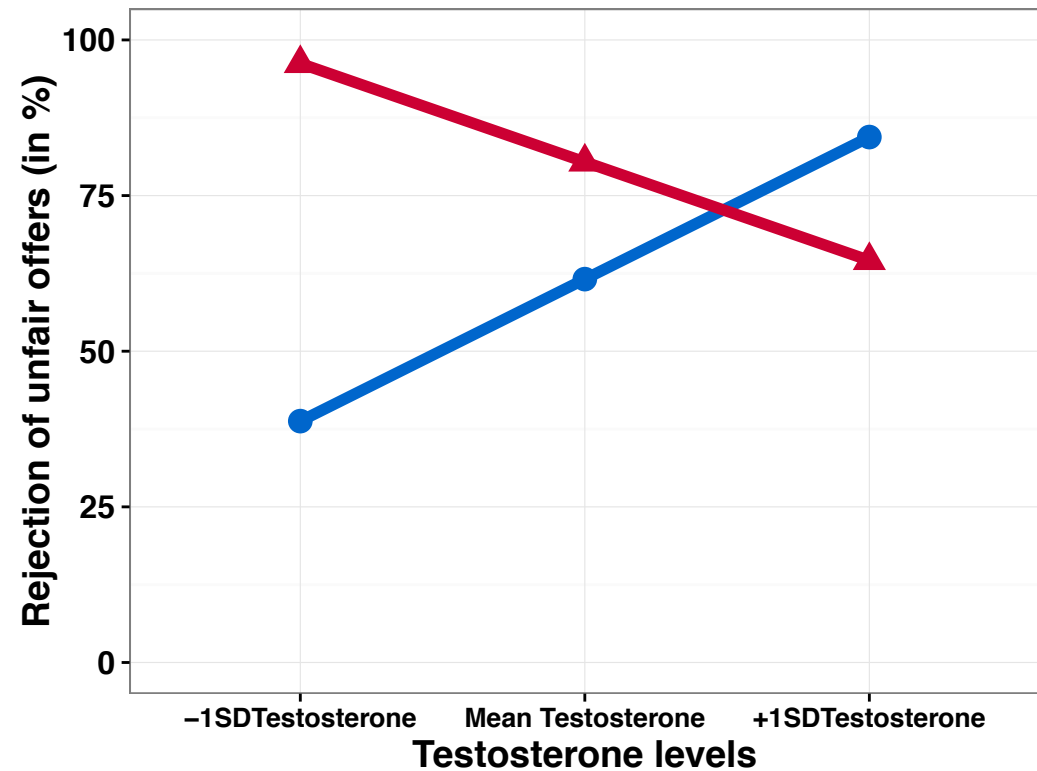


Decrease in Cortisol Increase in Cortisol



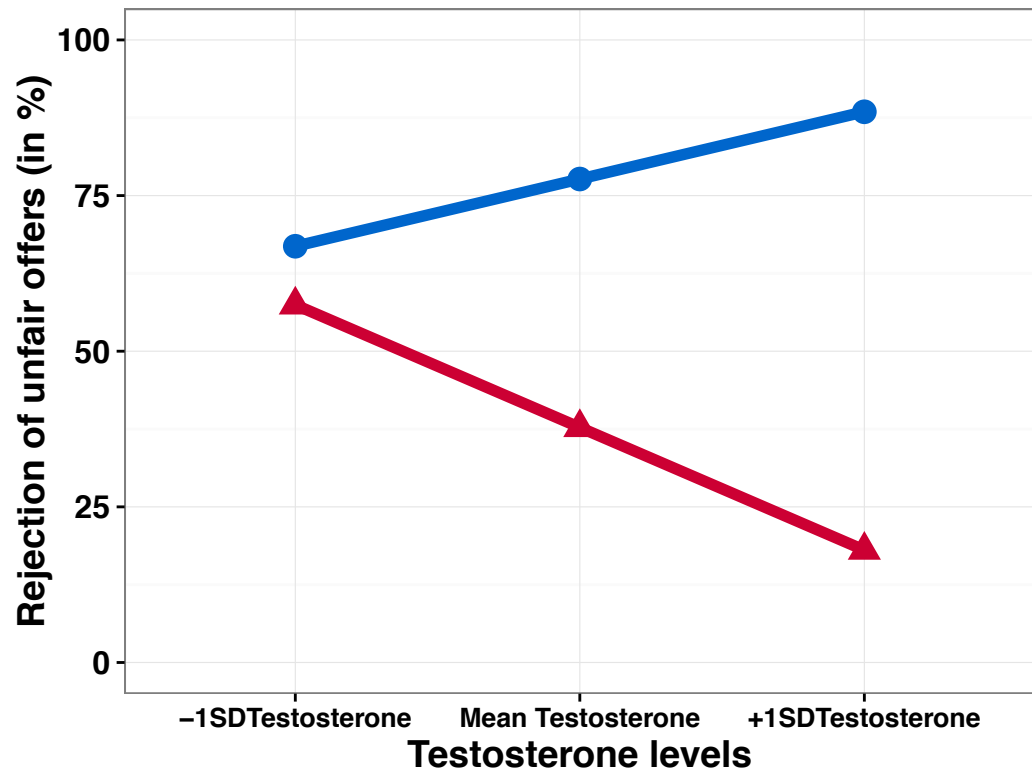
Males

Relaxation Stress



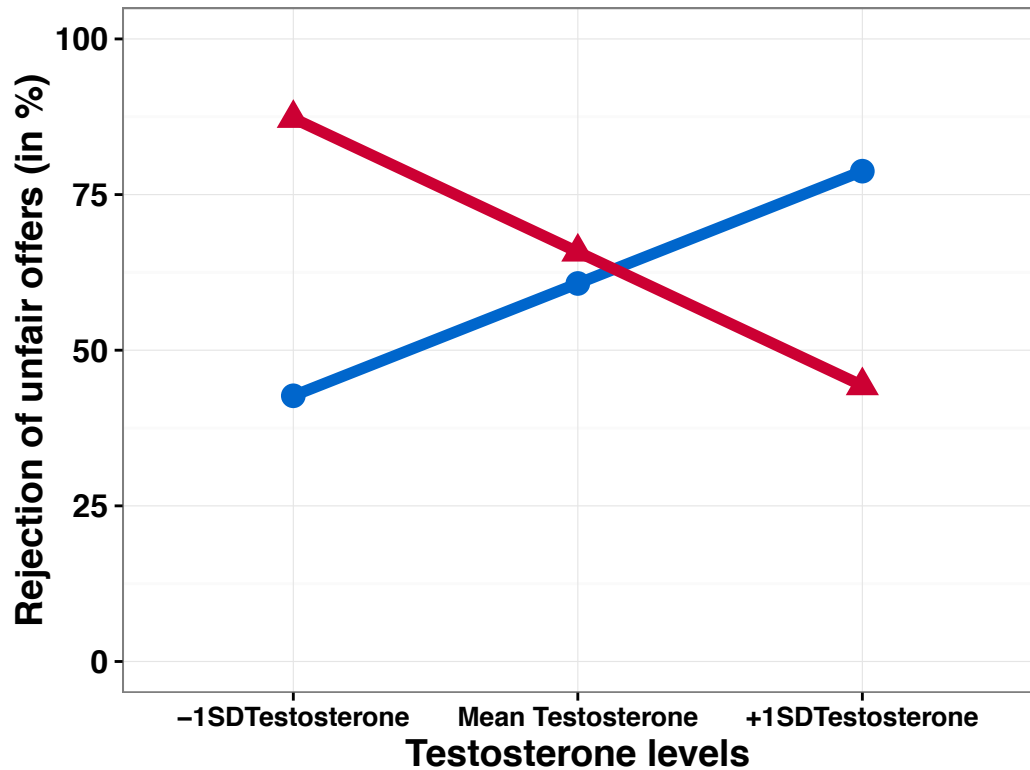
Females

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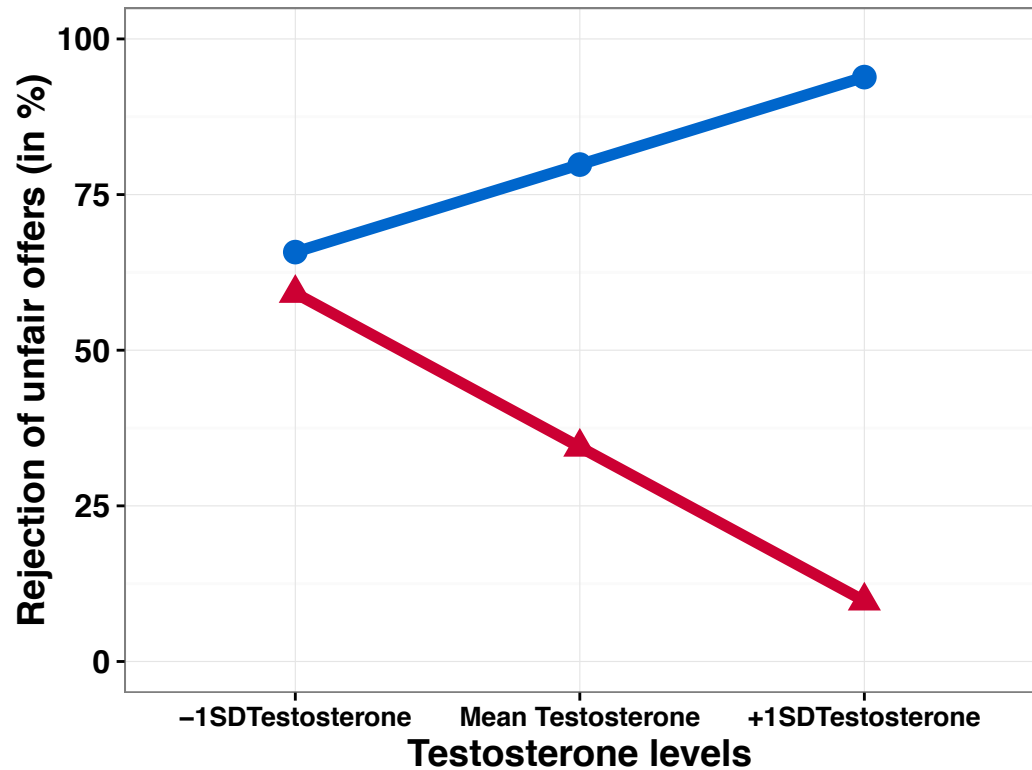
Males

Decrease in Cortisol Increase in Cortisol



Females

Decrease in Cortisol Increase in Cortisol



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

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