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Abstract

The dual-hormone hypothesis proposes that testosterone's relationship with status-seeking behavior is moderated by cortisol. However, research testing this hypothesis has focused on basal cortisol; the potential moderating effect of the acute cortisol response to stress has been largely overlooked. The present research investigated the moderating role of cortisol responses to an acute stressor on basal testosterone's link with dominant, status-relevant decision-making. Also, given the multifaceted nature of the response to acute stress, cardiovascular and affective responses to the stressor were examined as alternative moderators of the testosterone-behavior relationship. Participants (N=112; 56% female) were exposed to a social-evaluative stressor, and their stress responses were measured. Participants subsequently engaged in a one-shot dictator game, wherein they were asked to split money ($10) with a confederate counterpart. The amount of money participants decided to keep for themselves was treated as a metric of dominant status-seeking behavior. For individuals who demonstrated lower cortisol responses to the stressor, basal testosterone was positively associated with more dominant behavior (i.e., keeping more money for oneself), but for those who showed higher cortisol responses, the testosterone-behavior relationship was suppressed. Moreover, other aspects of the stress response (i.e., cardiovascular and affective responses) did not moderate the relationship between basal testosterone and dictator game behavior. These results provide unique support for the dual-hormone hypothesis using markers of stress-induced cortisol change. The findings also suggest that the antagonistic effects of stress on testosterone's role in motivating status-relevant behavior may be specific to cortisol's role in the acute stress response.

Keywords	testosterone; cortisol; dual-hormone hypothesis; stress; dictator game; dominant behavior
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Data set https://osf.io/9zpu3/

OSF: Dataset and Code

Our repository includes data and code (in R) for the analyses that we report in the submitted paper.

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MARSHALL SCHOOL OF BUSINESS

October 4, 2018

To the Editor:

Please find enclosed a **revised version** of the manuscript entitled: "Basal testosterone's relationship with dictator game decision-making depends on cortisol reactivity to acute stress: A dual-hormone perspective on dominant behavior during resource allocation" which we are submitting for your consideration to Psychoneuroendocrinology as an ***Original Research Paper***.

We thank the reviewers for their insightful comments and have made necessary changes to our manuscript. All the changes in our manuscript have been highlighted in yellow. We also provide detailed responses to the comments made by the reviewers and have appended it to the end of our highlighted manuscript.

To carefully address all the comments provided by the reviewers with appropriate and adequate information, we exceeded the word limit stipulated for the manuscript by ~221 words (currently the manuscript is 6221 words long). If exceeding the word limit poses as a matter of concern, we can move some of our discussion points into our supplementary materials by creating a supplementary discussion section.

We thank you for your consideration of this paper.

Sincerely,

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Basal testosterone's relationship with dictator game decision-making depends on cortisol reactivity to acute stress: A dual-hormone perspective on dominant behavior during resource allocation

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Abstract

The dual-hormone hypothesis proposes that testosterone's relationship with status-seeking behavior is moderated by cortisol. However, research testing this hypothesis has focused on basal cortisol; the potential moderating effect of the acute cortisol response to stress has been largely overlooked. The present research investigated the moderating role of cortisol responses to an acute stressor on basal testosterone's link with dominant, status-relevant decision-making. Also, given the multifaceted nature of the response to acute stress, cardiovascular and affective responses to the stressor were examined as alternative moderators of the testosterone-behavior relationship. Participants (N=112; 56% female) were exposed to a social-evaluative stressor, and their stress responses were measured. Participants subsequently engaged in a one-shot dictator game, wherein they were asked to split money ($10) with a confederate counterpart. The amount of money participants decided to keep for themselves was treated as a metric of dominant status-seeking behavior. For individuals who demonstrated lower cortisol responses to the stressor, basal testosterone was positively associated with more dominant behavior (i.e., keeping more money for oneself), but for those who showed higher cortisol responses, the testosterone-behavior relationship was suppressed. Moreover, other aspects of the stress response (i.e., cardiovascular and affective responses) did not moderate the relationship between basal testosterone and dictator game behavior. These results provide unique support for the dual-hormone hypothesis using markers of stress-induced cortisol change. The findings also suggest that the antagonistic effects of stress on testosterone's role in motivating status-relevant behavior may be specific to cortisol's role in the acute stress response.

Keywords: testosterone; cortisol; dual-hormone hypothesis; stress; dictator game; dominant behavior

Basal testosterone's relationship with dictator game decision-making depends on cortisol reactivity to acute stress: A dual-hormone perspective on dominant behavior during resource allocation

1. Introduction

As a species, we have evolved in social hierarchies, and the stratification of individuals within human groups helps organize us and maintain social order (Anderson et al., 2015; Ellis, 1994; Sapolsky, 2005). Within a social hierarchy, having higher status - respect or deference that is based on an individual's perceived social value (Anderson, et al., 2015; Magee and Galinsky, 2008) - grants several benefits, such as access to limited resources and social influence over others (Cheng et al., 2013; Sapolsky, 2005). Given the benefits of having higher status, individuals are often motivated to behave in ways that will aid their ascent in the status hierarchy. One approach to status attainment involves using dominant behavioral strategies - demanding increased respect or deference via assertive or forceful behaviors (Cheng et al., 2013; Mazur and Booth, 1998; Mehta et al., 2017). Further, using dominant behaviors may be evident in the domain of resource allocation where individuals asymmetrically allocate more resources to themselves compared to others as a means to status attainment (Bondarenko and Zakharov, 2018; Sapolsky, 2005). Social endocrine theory posits that testosterone, a steroid hormone released by the hypothalamic-pituitary-gonadal (HPG) axis, underlies dominant behaviors that are related to status seeking (Mazur and Booth, 1998). However, evidence that higher testosterone concentrations directly increase status-seeking behaviors during resource allocations is mixed [for example, testosterone linked to increased dominant decisions: Mehta et al., 2017; null effects of testosterone: Cueva et al., 2017; testosterone linked to increased prosocial behavior: Boksem et al., 2013 (for reciprocity after trust display); see Dreber and Johanneson, *in press*, for review of studies with exogenous hormone administration].

These inconsistent relationships may arise because testosterone's role in status-relevant behaviors may depend on other hormone systems. According to the dual-hormone hypothesis (Mehta and Josephs, 2010), testosterone's influence on status-seeking behavior should depend on cortisol, a hormone released

as part of the hypothalamic-pituitary-adrenal (HPA) axis in response to physical and psychological stress (Dickerson and Kemeny, 2004). More specifically, this hypothesis proposes that higher testosterone concentrations should be related to more status-seeking behaviors when cortisol levels are low but not when cortisol levels are high. Several studies have provided support for the dual-hormone hypothesis across a range of behaviors linked to social status, including dominant behavior (reviewed in Mehta and Prasad, 2015; for other patterns of results, see Welker et al., 2014; for null effects, see Geniole et al., 2013). For example, higher basal testosterone was associated with decisions to allocate more money for oneself in an adapted version of the dictator game when basal cortisol was low, but not when basal cortisol was high (Pfattheicher, 2017).

However, most work on the dual-hormone hypothesis has focused on the moderating role of basal cortisol (Mehta and Prasad, 2015). These studies have tested the dual hormone hypothesis in non-stressful contexts, and therefore have used basal cortisol as a theorized marker of chronic stress exposure (Miller, Chen, and Zhou, 2007). In acutely stressful contexts, cortisol is known to fluctuate (Dickerson and Kemeny, 2004), however, whether the acute cortisol response to a stressor moderates the association between testosterone and status-seeking behavior in acutely stressful contexts remains largely unknown. This gap in the literature remains despite the ubiquity of acute stressors in our social environments and the relative ease with which laboratory stressors produce robust cortisol responses (Dickerson and Kemeny, 2004; Kirschbaum et al., 1993). Recently, one study found that experimentally manipulated acute stress relative to a relaxation condition suppressed the association between basal testosterone and retaliation to unfairness in the ultimatum game (Prasad et al., 2017, *cf* Lozza et al., 2017). Retaliating by rejecting unfair offers is a dominant behavior that is motivated by the desire to protect one's reputation in response to status threats (Raihani and Bshary, 2015; Yamagishi et al., 2012) or punish the proposer in the face of provocation posed by receiving unfair offers (Pillutla and Murnighan, 1996). In line with the dual-hormone hypothesis, Prasad et al. (2017) also found that higher levels of basal testosterone were associated with these retaliatory behaviors but only in individuals with lower cortisol reactivity,

regardless of their experimental condition. However, at higher levels of cortisol reactivity, the testosterone-retaliation relationship was suppressed.

Although the findings in Prasad et al. (2017) provide preliminary evidence that fluctuations in cortisol concentrations modulate testosterone's relationship with status-relevant resource allocations decisions like retaliation in the ultimatum game, this study was not designed to test if individual differences in cortisol responses to an acute stressor *per se* modulate basal testosterone's relationships with dominant behavior[1]. The present research builds upon these initial findings by using a larger, correlational study that specifically focuses on the extent to which individual variability in cortisol responses to an acute stressor moderates the relationship between basal testosterone and dominant status-relevant decisions in the dictator game.

The dual-hormone hypothesis focuses on cortisol, but HPA axis reactivity is only one aspect of the complex, multifaceted response to stress (Sapolsky et al., 2000). Some evidence suggests that other aspects of the response to stress, including the autonomic nervous system and psychosocial responses like one's affective state, may modulate testosterone's relationship with behavior (Chichinadze and Chichinadze, 2008; Liening and Josephs, 2010). Therefore, we explored autonomic nervous system responses (heart rate and heart-rate variability) and positive and negative affect responses as moderators of testosterone's association with dominant status-relevant behavior. Moreover, the acute stress response spans a temporal trajectory that includes both initial reactivity to and recovery from the stressor. We examined the physiological stress measures by calculating area-under-the-curve with respect to increase (AUC_I), an index that captures both the reactivity and recovery to the stressor (Pruessner et al., 2003).

Finally, to measure dominant behavior to signal one's perceived higher status, we used the dictator game, a resource allocation paradigm (Kahneman et al., 1986). In this game, one of the players (the "dictator") unilaterally decides how resources are allocated between herself and another participant.

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[1]Prasad et al. (2017) was designed primarily to examine the causal influence of acute stress (vs. a relaxation control condition) as a moderator of testosterone's role in retaliation. Hence, the study had reduced statistical power for examining individual variability in cortisol responses to acute stress.

Given the zero-sum nature of the game, more resources kept by the dictator results in fewer resources available for the recipient. How the dictator decides to split an endowment with the recipient may therefore evince proactive, dominant status-seeking behaviors (Hoffman et al., 1999), as opposed to reactive dominant behaviors characteristic of ultimatum game responses (Prasad et al., 2017).

2. Methods

2.1. Transparent Reporting

Data and study materials for this report are available on its Open Science Framework website (https://osf.io/jx6fh). These data are part of a broader experimental study; information on sample size, exclusions, and other facets of study design are available in the initial study publication (see Knight and Mehta, 2017).

2.2. Participants

In this study, 110 undergraduate participants successfully completed the broader experimental tasks and had saliva available for assay (as reported in Knight and Mehta, 2017). Of these individuals, 104 participants (57.6% female) also successfully completed the dictator game. Additional participants were missing cardiovascular data due to noise and experimenter error (n = 12 missing heart rate; n = 13 missing heart rate variability), and so were left out of analyses involving heart rate and heart rate variability. The Institutional Review Board at the University of Oregon approved the protocol for this study (Figure 1).

2.3. Acute stressor

All participants completed the Trier Social Stress Task (TSST), a psychological acute stress induction paradigm that reliably increases cortisol concentrations (Dickerson et al., 2008; Kirschbaum et al., 1993). The protocol consisted of a 5-min speech about one's qualification for a job, and a 5-min serial subtraction math task in front of a panel of evaluative observers, who maintained neutral facial and verbal affect throughout the task. All participants were also provided with a 5-min preparation period that was

completed in the presence of a sex-matched confederate with whom they later played an online version the dictator game (see below).

2.4. Dictator Game

Approximately 40 minutes after the TSST, participants were asked to participate in an online, one-shot dictator game. The dictator game paradigm consists of two individuals: a dictator and a recipient. The dictator is endowed with a sum of money and must decide how to split the endowment with the recipient, who must passively accept whatever is offered. Participants were assigned the role of the dictator and were asked how they would split a sum of $10 with the confederate[2] (i.e., the recipient). The amount that participants indicated they would keep for themselves was treated as a measure of dominant behavior.

2.5. Baseline testosterone

Participants were instructed to abstain from eating, drinking, exercising, and smoking for two hours before their scheduled experimental session. To account for diurnal variability in endocrine and autonomic activity, all sessions occurred in the afternoon between 1300 and 1730 hrs. After arriving at the laboratory, participants were seated in an individual testing room where informed consent was obtained to participate in a group activity and perform a speech task. Demographic questionnaires were administered for approximately 10 minutes before a baseline saliva sample was collected via passive drool. The samples were subsequently assayed for testosterone using standard assay protocols (Schultheiss and Stanton, 2009) and commercially available enzyme immunoassay kits (Salimetrics, LLC; State College, PA; see Knight and Mehta, 2017).

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[2] The study (Knight and Mehta, 2017) in which these data were collected experimentally assigned participants to high and low status positions (see section 2.7 and Supplementary Materials). In order to increase the validity of the decision-making task within this experimentally manipulated context, participants saw one of two prompts for the dictator game that were adjusted to match the participant's status assignment. Participants assigned to the high-status position were asked how they would split the money, whereas participant assigned to the low status positions were asked how they would split the money if they were in the high-status position.

2.6. Stress responses

2.6.1. Endocrine Response

Saliva samples were obtained immediately (TSST+0), 20 minutes (TSST+20), and 40 minutes (TSST+40) after the end of the TSST and assayed for testosterone and cortisol in our laboratory. Cortisol and testosterone concentrations were positively skewed and were natural-log transformed.

2.6.2. Positive and Negative Affect

Participants responded to thirteen items related to their momentary positive and negative affect on a 1 to 5 scale, anchored on "Not at all" to "Extremely." These questions were administered just prior to and immediately after the stressor. Positive affect was indexed as the mean of the following items: interested, excited, happy, strong, enthusiastic, proud, self-confident, and in control (*Cronbach's* α = 0.91); negative affect as the mean of the following items: distressed, upset, sad, irritable, ashamed, and nervous (*Cronbach's* α =0.82).

2.6.3. Cardiovascular and Autonomic Nervous System

For a majority of participants (approximately 75%), cardiovascular responses to the stressor were recorded via continuous recording of a modified Lead II electrocardiogram (ECG) from BioPac (BioPac Systems, Inc.), with Ag/AgCl sensors placed at the collarbone, contralateral ribcage, and ipsilateral hip. For the remaining participants, the cardiovascular recording equipment was not available and cardiovascular activity was recorded continuously via a Polar RS800CX watch and chest band (Polar, Inc.). Polar watches have been shown to generally match ECG measurements when analyzed identically (Quintana et al., 2012).

All cardiovascular data were visually inspected and manually corrected for artifacts in Kubios HRV (v.1.0). Heart rate (HR) and heart rate variability (HRV) was derived from interbeat-interval (IBI) timings. Specifically, the power (in $msec^2$) of the high frequency band of heart rate variability (HF HRV; corresponding to frequencies of 0.15 – 0.40 Hz) was determined via the autoregressive method of HRV derivation. HF HRV is often utilized as a relatively clean index of parasympathetic activity, which

generally withdrawals in response to stressors (Thayer and Lane, 2000). Values for HR and HF HRV were averaged within six, five-minute epochs: Baseline, Preparation, two five-minute epochs of the TSST, and two five-minute epochs of a recovery period. HF HRV values were natural-log transformed prior to data analysis to correct a positive skew.

2.7. Other experimental manipulations

The larger study from which these archival data were derived also manipulated social status and stability of the status hierarchy (see Supplementary Materials and Knight and Mehta, 2017). Because the primary interest of this study was to examine the moderating role of stress responses on the testosterone-behavior relationship, we report all statistical analyses controlling for the experimental manipulations in the study (i.e., social status, hierarchy stability, and their interaction).

2.8. Data transformations and analyses

To produce indices of the stress response to the TSST, AUC_I (Pruessner et al., 2003) was calculated across the four epochs of natural-log transformed cortisol data and across the six epochs of HR and HF HRV data. Although not a principle focus of this study, we used the same AUC_I transformations on natural-log transformed testosterone concentrations to explore testosterone reactivity. Affective responses to the TSST were calculated by subtracting the mean pre-stress score from the post-stress score for positive and negative affect.

To test for stress-linked changes in cortisol, affect, and cardiovascular responses, we used multilevel models (MLMs) with time as a polynomial-contrasted, within-subjects measure. Multilevel modeling analyses were conducted in R (v. 3.4.1) using the *lme4* package (Bates et al., 2014). In these models, observations (Level 1) were nested within participants (Level 2), and each model included random intercepts and slopes of time for each participant (coded using polynomial contrasts for the models). Unlike other repeated measures approaches that treat within-subject variance as homogeneous, the random effects in multilevel models account for variation within each subject (Hedeker et al., 2012). For graphing purposes, estimated marginal means and standard errors (SEs) from the models were

determined via the lsmeans package (Lenth, 2016), which takes into account within-subject variances. Further, to test if basal testosterone's association with decision-making in the dictator game depended on stress responses, we used linear regression models in which we examined interactions between basal testosterone and centered indices of the stress response (e.g., cortisol AUC_I). For analyses involving basal measures, testosterone was natural-log transformed (see Knight and Mehta, 2017) then standardized (z-scored) within gender (Mehta et al., 2017; Prasad et al., 2017)[3]. Finally, all models controlled for the experimental manipulations in the study (status, stability, and their interaction).

3. Results

3.1. Dictator game behavioral results

Participants on average chose to keep $5.29 (*SD*= 1.52) for themselves. The amount of money that individuals kept for themselves was not influenced by the other manipulations in the study (status, stability, or their interaction; *ps*>.67). Further, there were no sex differences in dictator game decisions (*p*>.52).

3.2. Stress-induced changes in cortisol

The MLM analysis of cortisol concentrations revealed a significant main effect for time in response to the acute stressor (Time (linear): *B* = 0.037, *95%CI*[-0.04, 0.12], *p* = .374; Time (quadratic): *B* = -0.209, *95%CI*[-0.262, -0.157], *p* <.001; see Figure 2; see also Knight and Mehta (2017) for further analyses of cortisol response). Next, we conducted follow-up analyses that compared baseline hormone concentrations to the measures of cortisol obtained at TSST +0, TSST+20 and TSST+40. We found that compared to baseline hormone concentrations (*M*=0.24 µg/dL, *SD*=0.21)[4], cortisol levels were significantly elevated at TSST+0 (*M*=0.32 µg/dL, *SD*=0.24; *t*(109)=6.29, *p*<.001), and TSST+20 (*M*=0.34 µg/dL, *SD*=0.3; *t*(109)=4.04 *p*<.001), but were not significantly different at TSST+40 (*M* = 0.28 µg/dL,

[3] However, for follow-up analyses involving testosterone responses to the stressor (i.e., AUC_I), testosterone scores were log transformed but not standardized within sex given that AUC_I scores already account for baseline differences in hormones across sexes.

[4] Although analyses were run on natural-log-transformed cortisol concentrations, we report means and SDs for untransformed values.

SD = 0.25; *t*(109) = 1.07, *p* = 0.286). This highlights that our stress manipulation facilitated increases in cortisol levels that then recovered back to baseline. See Tables S1 to S3 for correlations among stress response variables across the entire sample, in males, and in females (Supplementary Materials).

3.3. Basal testosterone × cortisol response

Next, we tested the hypothesis that basal testosterone's role in dictator game decisions depended on the cortisol response to the TSST (i.e., cortisol AUC_I). This analysis revealed no main effect of basal testosterone but did reveal a marginally significant main effect of cortisol AUC_I (see Table 1). Individuals who demonstrated greater cortisol responses to the social stressor kept less money for themselves in the dictator game (i.e., demonstrated less dominant behavior). However, this main effect of cortisol AUC_I was qualified by a statistically significant basal testosterone × cortisol AUC_I interaction (*B* = -0.29, *SE* = 0.13, *95%CI*[-0.55, -0.03], *t*(97) = -2.21, *p* = .029; Figure 3). Simple slope analysis (Preacher et al., 2006) indicated a positive relationship between basal testosterone and the amount of money allocated to oneself in the dictator game among individuals with lower cortisol responses (-1SD: *B* = 0.41, *SE* = 0.21, *t*(97) = 1.97, *p* = 0.052), but not among individuals with relatively greater cortisol responses (+1SD: *B* = -0.30, *SE* = 0.24, *t*(97) = -1.29, *p* = .199). The non-zero interaction term indicates that these slopes were statistically different from each other. In follow-up analyses, this dual-hormone interaction was also robust when analyzing cortisol reactivity (from baseline to immediately after the TSST and 20 minutes after the TSST, Table 1). A similar pattern, albeit somewhat weaker, was also found for cortisol recovery (from baseline to the end of the recovery period; Table 1).

We tested if other manipulations in the study (status, stability, or their interaction) moderated the basal testosterone × cortisol response interaction, but we did not find significant three-or four-way interactions in these analyses (*p*s>.30; Table S4, Supplementary Materials). These results suggest that the basal testosterone × cortisol response interaction did not further depend on these manipulations. Crucially, the basal testosterone × cortisol response interaction on dictator game decisions remained significant in

these analyses, demonstrating the robustness of this dual-hormone interaction effect across multiple statistical models.

3.3.1 Sex differences

Given prior mixed evidence for sex differences in testosterone-behavior relationships (Mehta and Josephs, 2010; Welker et al., 2014) we explored the role of sex as a moderator of the interactive effects of cortisol response and basal testosterone on dictator game decisions. Basal testosterone × cortisol response interactions were not moderated by participant sex (p>.38; see Table S5); both men and women showed similar interaction patterns (Figure S1).

3.4. Other dual-hormone analyses

While we examined the moderating effect of cortisol stress responses on basal testosterone's association with behavior, prior evidence of the dual-hormone hypothesis focused on the moderating effects of basal cortisol (Mehta and Prasad, 2015). However, we did not find support for a basal testosterone × basal cortisol interaction (see Table S6). Moreover, we also did not find a sex × basal testosterone × basal cortisol interaction, indicating that the null effect was not due to weak or opposing effects of basal testosterone × basal cortisol effect in men or women. These findings suggest that in the context of acute stress, cortisol responses to the stressor may moderate the relationship between basal testosterone and dominant behavior, rather than basal levels of cortisol.

The acute stressor also altered testosterone levels (Time (linear): B = -0.03, *95%CI*[-0.06, 0.01], p = .10; Time (quadratic): B = -0.11, *95%CI*[-0.13, -0.09], p <.001), which rose at TSST + 0 and TSST + 20 and then returned to baseline at TSST + 40 (see Knight and Mehta, 2017 for other analysis). Therefore, we also explored the interactive effects of testosterone response with both the cortisol response to the stressor and basal cortisol levels on dictator game decisions. We did not find support for a testosterone response × cortisol response or testosterone response × basal cortisol interaction (Table S6). Neither did we find sex differences in the testosterone response × cortisol response or testosterone response × basal

cortisol interactions. These findings suggest that in an acutely stressful situation, the dual-hormone effects may be specific to the interaction between basal testosterone and the acute cortisol stress response.

We do note a significant, negative zero order correlation between testosterone responses to the stressor and dominant decision-making in the dictator game (Table S1). This relationship between testosterone reactivity and decision-making was weaker and not robust to controlling for testosterone responses × cortisol responses or to the experimental manipulations of social status and hierarchy stability. This effect was also not dependent on sex (B = -1.27, *95%CI* [-2.80, 0.26], p = .10).

3.5. Positive and negative affect responses to stress

To test whether the acute stressor influenced positive or negative affect, we conducted a MLM analysis with time of measurement (pre- vs. post-stress) as a within-subjects factor. We found significant main effects indicating a decline in positive affect (B = -0.205, *95%CI*[-0.30, -0.11], p <.001) but no change in negative affect (B = 0.043, *95%CI* [-0.08, 0.17], p =.508; see Figure 2; see also Knight and Mehta, 2017 for further analyses with affective measures).

3.6. Basal testosterone × affective responses

We tested if basal testosterone's role in dictator game decisions depended on affective responses to the TSST. As a primary metric of affective response, we used affect change from pre- to post-stressor. Our analyses revealed no significant interactions between basal testosterone x affect response scores for either positive or negative affect (*ps*>.95; Table S7).

3.7. Cardiovascular responses to stress

Next, we examined the effects of the acute stressor on cardiovascular responses via MLM analysis. The analysis revealed a significant change in HR (Time (linear): B = -5.43, *95%CI*[-6.58, -4.28], p <.001; Time (quadratic): B = -20.45, *95%CI*[-22.87, -18.03], p <.001) and HF HRV (Time (linear): B = 0.30, *95%CI*[0.19, 0.42], p <.001; Time (quadratic): B = 0.93, *95%CI*[0.74, 1.12], p <.001) over the course of the experiment. Consistent with prior research (Allen et al., 2014), the pattern of activity evident in these models was indicative of increased HR and vagal withdrawal (i.e., reduced HF HRV) during the

preparation period and stressor, with a general return to baseline during the recovery period (*ps*>.37; see Figure 2).

3.8. Basal testosterone × cardiovascular response

Finally, we tested if basal testosterone's role in dictator game decisions depended on cardiovascular responses (HR and HF HRV AUC_I) to the TSST. Our analysis revealed no significant interactions between basal testosterone and cardiovascular responses (*p*s>.38; Table S8).

4. Discussion

Previous research on the dual-hormone hypothesis has focused on basal cortisol in the absence of acute stress. The present study extends this body of work by providing evidence that in the presence of an acute stressor, the acute cortisol response to the stressor moderates basal testosterone's relationship with dominant status-relevant behavior in a dictator game. We found that for individuals with lower cortisol responses to the stressor, basal testosterone was positively associated with keeping more money for oneself in the dictator game (i.e., a dominant status-seeking behavior), but for those with higher cortisol responses, the testosterone-behavior relationship was suppressed. This pattern was found in men and women. These findings are conceptually aligned with the results of a previous study (Prasad et al., 2017), which provided initial evidence that acute cortisol change moderated basal testosterone's association with status-relevant decisions in a different behavioral task (rejecting unfair offers in the ultimatum game).

To a large extent, past research has focused on the HPA-axis as the primary outcome of the acute stress response (Dickerson and Kemeny, 2004). However, the acute stress response is multifaceted, encompassing a wide array of biological and psychological systems that function in concert (Sapolsky et al., 2000). Our findings revealed that despite evidence of parasympathetic nervous system and affective (positive and negative) responses to the stressor, these stress markers did not moderate the relationship between basal testosterone and dictator game decisions. These results suggest that the antagonistic effects of stress on the testosterone-behavior relationship may be specific to cortisol stress responses, a conclusion that further clarifies the dual-hormone hypothesis. Nevertheless, this interpretation is tentative

and must be confirmed in new studies that measure additional stress response systems, including sympathetic nervous system activity, catecholamine levels, and overall cardiac reactivity (Chichinadze and Chichinadze, 2008), as well as other endocrine systems (e.g. DHEAS; Allen et al., 2014) and psychological states (e.g. challenge/threat responses; Mendes et al., 2001). Further, given that our results were correlational, to determine causality future work could administer testosterone and block HPA axis activity prior to a stressor (Andrews et al., 2012). If these two hormone systems do indeed have joint causal influences on behavior, then blocking the HPA axis should facilitate testosterone's effects on dominant decisions after a stressor. Moreover, if other stress responses still do not moderate the testosterone--decision-making relationship under conditions of inhibited HPA axis activity, then these results would implicate the HPA axis specifically, and not the wider stress response, as the moderator of testosterone's association with decision-making.

To determine the robustness of our findings, we tested the extent to which the moderating effect of acute cortisol change on the testosterone-decision relationship was seen across the broader trajectory of the stress response, as well as reactivity to and recovery from the stressor. We found that a composite measure of the cortisol stress response spanning the entire temporal trajectory of the stressor (AUC_I) significantly moderated the relationship between basal testosterone and dictator game decision-making; we found similar effects when examining cortisol reactivity and recovery separately. Exploration of the patterns across different metrics of cortisol stress responses (see Table 1) suggests that the interaction between basal testosterone and acute cortisol responses to the stressor was somewhat stronger for metrics of cortisol reactivity compared to cortisol recovery (similar to Prasad et al., 2017), but any slight differences should be interpreted with caution and must be replicated before firm conclusions are drawn. Further, other areas of stress research have treated reactivity and recovery to a stressor as separate constructs that have differential implications for the downstream effects of stress (i.e., for stress-linked health outcomes; Linden et al., 1997). Therefore, continued research is necessary to examine the time

course of cortisol stress responses and its impact on the testosterone's association with dominant behavior.

It is important to consider possible mechanisms for cortisol's suppressive effects on basal testosterone's link to dominant decision-making that is linked to status seeking. One psychological mechanism may involve cortisol's effects on the approach and avoidance motivational systems (Carver and White, 1994). Higher levels of cortisol have been theorized to decrease motivation to approach and increase motivation to avoid social stimuli (Dickerson and Kemeny, 2004; Roelofs et al., 2009; Tops and Boksem, 2010). Lower cortisol responses to the stressor may propel individuals with higher levels of testosterone to readily approach, and not avoid, status-seeking behavior. In contrast, increased cortisol responses may relate to increased avoidance, thereby blocking testosterone's influence on dominant status-seeking behavior. Measurements of motivational approach and avoidance directly via self-reports and implicit psychological measures (Roelofs et al., 2009) in future research will help elucidate their role as a mechanism of cortisol's inhibitory effects on testosterone and dominant status-seeking behaviors.

Acute cortisol reactivity may also affect associations between testosterone and dominant decision-making via neural systems implicated in reward sensitivity. Testosterone facilitates reward-seeking behavior via activity in the nucleus accumbens in rodents (Packard et al., 1997) and is associated with increased neural activity in the human ventral striatum in anticipation of and when receiving rewards (Hermans et al., 2010). Limited evidence suggests higher cortisol levels relate to down-regulation of activity in reward networks (Kinner et al., 2016; Montoya et al., 2014). Given that reward motivation may partly underlie dominant status-relevant behaviors in the dictator game (Fliessbach et al., 2007), testosterone may result in greater dominant behaviors only when cortisol levels are low; higher levels of cortisol may suppress testosterone's effects on neural reward systems and therefore reduce dominant behaviors. However, other findings link stress and cortisol responses to increased reward-related neural activation and behaviors in humans (Oei et a., 2014) and rodents (Lewis et al., 2014; Rouge-Pont et al.,

1998). Additional research is therefore necessary to elucidate this neural pathway as a mechanism for our results.

At the molecular level, elevated cortisol levels may block the association between testosterone and behavior by suppressing androgen receptors (Tilbrook et al., 2000; Viau, 2002). Given the short duration between the last elevated cortisol sample (TSST + 20) and the measurement of behavior (approximately 25 minutes after the last elevated cortisol sample), it is unlikely that cortisol exerted its effects on behavior via the relatively slow, genomic transcriptional route to suppressing androgenic receptor functioning (Moore and Evans, 1999) seen in studies of chronic cortisol elevation (Tilbrook et al., 2000). Instead, we suspect that elevated levels of cortisol may have altered androgen receptor functioning via rapid, non-genomic pathways (Makara and Haller, 2001; Moore and Evans, 1999) and subsequently altered behavior (Casto and Edwards, 2016). This non-genomic mechanism that explains the moderating effect of an acute cortisol response on the relationship between testosterone and status-relevant behaviors is speculative and in need of further investigation.

We discuss the psychological, neural, and molecular mechanisms of cortisol's moderation of testosterone independently. However, elevated cortisol levels may simultaneously modulate androgen receptor functioning in reward-specific areas of the brain that subsequently changes psychological motivations that drive specific behavior. Future research is necessary to test the role of these mechanisms as independent versus unified responses.

Consistent with prior dual hormone theorizing, the present research provides evidence of endocrine correlates of a dominant route to status attainment in the dictator game (i.e., by keeping more money for oneself). However, research has shown that prosocial tactics may also allow individuals to ascend the status hierarchy (Cheng et al., 2013; Hardy and van Vugt, 2006), and that these prosocial tactics may be especially beneficial for status attainment in specific cooperative contexts (Halevy et al., 2011). For example, it is possible that manipulating the identity of the target in the dictator game - for instance using a charitable organization rather than an unknown confederate in situations in which one's donation

decisions are visible to other group members, may elicit more equitable behavior to gain the respect and admiration of others as a means to ascend the status hierarchy (Eckel and Grossman, 1999). Therefore, we theorize that in this charity version of the dictator game individuals with high basal testosterone and reduced cortisol responses may pursue status by demonstrating prosocial behavior evidenced by being more equitable in their resource allocations. Future research may consider altering specific factors in the social context of the paradigm to investigate dual-hormone effects of basal testosterone and cortisol responses to stressors on both dominant and prosocial routes to status.

In the current research, we provide evidence that individuals with high basal testosterone and a buffered acute cortisol response demonstrated proactive dominant behaviors via asymmetrical resource allocation in the dictator game (Hoffman et al., 1999), but the same endocrine profile facilitated reactive dominant behaviors via greater rejection of unfair offers in the ultimatum game (Prasad et al., 2017). Similar motivations may underlie both patterns of dominant behavior: Taking more money in the dictator game and rejecting unfair offers in the ultimatum game may both represent a heightened concern for one's social status and reputation (Bondarenko and Zakharov, 2018; Raihani and Bshary, 2015).[5] However, it is possible that these emergent dominant behaviors associated with a high basal testosterone and low acute cortisol change may be alternatively motivated by a desire to harm another individual as an

[5] A similar inference about status motivation has also been made in research linking the main effects of testosterone with the proposer decision-making in the ultimatum game. Eisenegger et al. (2010) found that testosterone administration in women increased ultimatum game proposer offers relative to those in the placebo group. The authors argued that due to the explicit threat of having one's offer rejected, individuals administered testosterone made more generous offers because of their concern for status. However, in another study the opposite pattern of effects was found: male proposers who were administered testosterone made less generous offers compared to themselves at baseline (Zak et al., 2009). In this study, the authors argued that individuals administered testosterone were motivated to behave selfishly ostensibly as a means to assert their higher status and therefore made lower offers. Although it is possible that the opposing results may be due to differences in study designs (e.g. sample recruited- females vs. male, nature of hormone administration –crossover vs. between-group design), future research may disentangle these divergent findings and the role of status concern by directly measuring status motivations accompanying ultimatum game proposer behavior. Moreover, given the inconsistent association between testosterone and ultimatum game proposer behavior across both studies, researchers may also consider examining the moderating role of the presence or absence of social stress and subsequent cortisol responses to stressors on the testosterone-behavior relationships, in addition to measuring the underlying status-relevant motivations of the resultant behavior.

ultimatum game respondent (Pillutla and Murnighan, 1996) or by reward maximization as a dictator game proposer (Fliessbach et al., 2007). To clearly delineate the role of status-relevant motivations underlying behaviors in economic decision-making paradigms, future research can modify or develop new economic decision-making paradigms that allow more direct inferences of status-relevance, pit divergent motivations within the same tasks to rule out alternative explanations, or use methodologies that directly measure status motivations and perceptions (for example, measurement of implicit power motivation or social status ratings in groups).

Whereas prior dual-hormone hypothesis research has largely focused on the moderating role of basal cortisol in non-stressful contexts (e.g. Pffatheicher, 2017), this study extends previous work by demonstrating that in acutely stressful contexts, cortisol responses to the stressor moderate basal testosterone's association with dominant status-seeking behavior. Moreover, there was no evidence of basal cortisol moderating the relationship between basal testosterone and dictator game decisions (Table S6). These findings suggest that in contexts involving acute stressors, cortisol responses to a stressor may be a key moderator of basal testosterone's link with status-relevant behaviors such as dictator game decisions and, in the absence of acute stress, basal cortisol may function as a moderator. Future research should directly test this hypothesis by manipulating the presence or absence of acute stress and compare the moderating roles of basal cortisol versus cortisol response on basal testosterone's behavioral effects. To provide rigorous measures of basal hormones and acute hormone changes, future studies should also consider measuring steroid hormones with mass-spectrometry based measures (Welker et al., 2016). Whereas saliva is well suited for measuring hormone responses to acute stressors, future work should consider using hair samples, which may better capture basal hormone concentrations over several months (Grotzinger et al., 2018).

We also did not find evidence of a testosterone response and cortisol response interaction predicting dictator game decisions, but the strong correlation between the hormone reactivity measures (Table S1) may have restricted our ability to detect an interaction. However, we do note that a higher

testosterone response to the stressor was associated less dominant behavior (i.e., keeping less money for oneself in the dictator game), albeit not robustly when controlling for the experimental conditions in this archival data. Moreover, this main effect of testosterone responses on dictator game decisions was in the same direction as the relationship between basal testosterone and dictator game decisions for those who demonstrated greater cortisol reactivity to the stressor, evident as the negative slope between basal testosterone and dominant dictator game decisions at higher levels of acute cortisol change (Figure 3). Cortisol rose on average for this sample (i.e., few people had neutral or withdrawal responses to the stressor), and so this negative, main effect of testosterone stress responses may be illustrative of the relatively restricted range of increased cortisol responses. Although this negative relation between the acute testosterone stress response and dominant decision making was relatively weak, future research should continue to measure testosterone reactivity to social stressors and examine the behavioral consequences of those responses (Knight and Mehta, 2017).

As a limitation, we note the use of archival data (Knight and Mehta, 2017) to conceptually replicate Prasad et al. (2017), and therefore our study included contextual manipulations that may have diminished our effect sizes or acted as contextual moderators. Although we found no evidence of moderation of the basal testosterone and cortisol reactivity interaction by the experimental manipulations, we may have been underpowered to detect those higher-order effects. Similarly, although we found a similar pattern of effects across men and women, we again may not have had sufficient statistical power to detect sex differences. Future research should consider using larger mixed-sex samples to test for contextual moderators of and gender differences in testosterone's relationship with dictator game decisions. This is especially important given that status-relevant features of the social context may modulate both testosterone's independent effects (Eisenegger et al., 2011) and testosterone and cortisol's interactive effects on behavior (Geniole et al., 2011; Mehta and Josephs, 2010).

Furthermore, while we examined cortisol as a moderator of testosterone's association with status-relevant dominant behavior, it is possible that for women, estrogens such as estradiol may bear greater

behavioral consequences than testosterone (Casto and Prasad, 2017). Estradiol has been positively associated with status-seeking behaviors (implicit power motivation: Stanton and Schultheiss, 2007; assertiveness in women: Blake et al., 2017). Moreover, recent evidence suggests that cortisol may also moderate the association between estradiol and dominant behaviors (i.e., externalizing behaviors) in adolescents with higher emotional instability and disagreeableness (Tackett et al., 2015). Future studies should continue to examine estrogens to determine the extent to which they interact with cortisol to direct status-seeking behaviors.

References

Allen, A.P., Kennedy, P.J., Cryan, J.F., Dinan, T.G., Clarke, G., 2014. Biological and psychological markers of stress in humans: Focus on the Trier Social Stress Test. Neurosci. Biobehav. Rev. doi:10.1016/j.neubiorev.2013.11.005

Anderson, C., Hildreth, J. A. D., & Howland, L. (2015). Is the desire for status a fundamental human motive? A review of the empirical literature. Psychological Bulletin, 141(3), 574.

Andrews, J., D'Aguiar, C., Pruessner, J.C., 2012. The combined dexamethasone/TSST paradigm--a new method for psychoneuroendocrinology. PLoS One 7, e38994. doi:10.1371/journal.pone.0038994

Bates, D., Maechler Martin, Walker, S., 2016. Package "lme4". CRAN Repos. doi:10.18637/jss.v067.i01

Blake, K.R., Bastian, B., O'Dean, S.M., Denson, T.F., 2017. High estradiol and low progesterone are associated with high assertiveness in women. Psychoneuroendocrinology 75, 91–99. doi:10.1016/j.psyneuen.2016.10.008

Boksem, M.A.S., Mehta, P.H., Van den Bergh, B., van Son, V., Trautmann, S.T., Roelofs, K., Smidts, A., Sanfey, A.G., 2013. Testosterone Inhibits Trust but Promotes Reciprocity. Psychol. Sci. 24, 2306–2314. doi:10.1177/0956797613495063

Bondarenko, O. & Zakharov, A., 2018. Measurement of Social Status in Experimental Games. Journal of the New Economic Association. 38. 12-47.

Carver, C.S., White, T.L., 1994. Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. J. Pers. Soc. Psychol. 67, 319–333. doi:10.1037/0022-3514.67.2.319

Casto, K. V., Edwards, D.A., 2016. Testosterone, cortisol, and human competition. Horm. Behav. doi:10.1016/j.yhbeh.2016.04.004

Casto, K. V., Prasad, S., 2017. Recommendations for the study of women in hormones and competition research. Horm. Behav. 92, 190–194. doi:10.1016/j.yhbeh.2017.05.009

Cheng, J.T., Tracy, J.L., Foulsham, T., Kingstone, A., Henrich, J., 2013. Two ways to the top: Evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. J. Pers. Soc. Psychol. 104, 103–125. doi:10.1037/a0030398

Chichinadze, K., Chichinadze, N., 2008. Stress-induced increase of testosterone: Contributions of social status and sympathetic reactivity. Physiol. Behav. 94, 595–603. doi:10.1016/j.physbeh.2008.03.020

Cueva, C., Roberts, R.E., Spencer, T.J., Rani, N., Tempest, M., Tobler, P.N., Herbert, J., Rustichini, A., 2017. Testosterone administration does not affect men's rejections of low ultimatum game offers or aggressive mood. Horm. Behav. 87, 1–7. doi:10.1016/j.yhbeh.2016.09.012

Dickerson, S.S., Kemeny, M.E., 2004. Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. Psychol. Bull. 130, 355–91. doi:10.1037/0033-2909.130.3.355

Dickerson, S.S., Mycek, P.J., Zaldivar, F., 2008. Negative Social Evaluation, but Not Mere Social Presence, Elicits Cortisol Responses to a Laboratory Stressor Task. Heal. Psychol. 27, 116–121. doi:10.1037/0278-6133.27.1.116

Dreber, A., Johannesson, M. (in press). Sex hormones and economic decision making in the lab: A review of causal evidence: Past, present, and future, in: O.C. Schultheiss and P.H. Mehta (Eds.), The International Handbook of Social Neuroendocrinology. Routledge Press.

Eckel, C. C., & Grossman, P. J. (1996). Altruism in anonymous dictator games. Games and economic behavior, 16(2), 181-191.

Eisenegger, C., Haushofer, J., Fehr, E., 2011. The role of testosterone in social interaction. Trends Cogn. Sci. doi:10.1016/j.tics.2011.04.008

Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., & Fehr, E. (2010). Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature*, *463*(7279), 356.

Fliessbach, K., Weber, B., Trautner, P., Dohmen, T., Sunde, U., Elger, C.E., Falk, A., 2007. Social comparison affects reward-related brain activity in the human ventral striatum. Science (80-.). 318, 1305–1308. doi:10.1126/science.1145876

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, 1–9. doi:10.1016/j.yhbeh.2013.09.005

Geniole, S.N., Carré, J.M., McCormick, C.M., 2011. State, not trait, neuroendocrine function predicts costly reactive aggression in men after social exclusion and inclusion. Biol. Psychol. 87, 137–145. doi:10.1016/j.biopsycho.2011.02.020

Halevy, N., Chou, E.Y., Cohen, T.R., Livingston, R.W., 2012. Status conferral in intergroup social dilemmas: Behavioral antecedents and consequences of prestige and dominance. J. Pers. Soc. Psychol. https://doi.org/10.1037/a0025515

Hedeker, D., Mermelstein, R.J., Demirtas, H., 2011. Modeling Between- and Within-Subject Variance in Ecological Momentary Assessment (EMA) Data Using Mixed-Effects Location Scale Models. Stat. Med. 1–15. doi:10.1002/sim.0000

Hermans, E.J., Bos, P.A., Ossewaarde, L., Ramsey, N.F., Fernández, G., van Honk, J., 2010. Effects of exogenous testosterone on the ventral striatal BOLD response during reward anticipation in healthy women. Neuroimage 52, 277–283. doi:10.1016/j.neuroimage.2010.04.019

Hoffman, E., McCabe, K., Smith, V.L., 1999. Social distance and other-regarding behavior in dictator games: Reply. Am. Econ. Rev. doi:10.1257/aer.89.1.340

Kahneman, D., Knetsch, J.L., Thaler, R.H., 1986. Fairness and the Assumptions of Economics. J. Bus. 59, S285. doi:10.1086/296367

Kinner, V.L., Wolf, O.T., Merz, C.J., 2016. Cortisol alters reward processing in the human brain. Horm. Behav. 84, 75–83. doi:10.1016/j.yhbeh.2016.05.005

Kirschbaum, C., Pirke, K.M., Hellhammer, D.H., 1993. The "Trier Social Stress Test" - a tool for investigating psychobiological stress responses in a laboratory setting. Neuropsychobioloy 28, 76–81.

Knight, E.L., Mehta, P.H., 2017. Hierarchy stability moderates the effect of status on stress and performance in humans. Proc. Natl. Acad. Sci. 114, 78–83. doi:10.1073/pnas.1609811114

Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, 69(1), 1-33. doi:10.18637/jss.v069.i01

Lewis, A.H., Porcelli, A.J., Delgado, M.R., 2014. The effects of acute stress exposure on striatal activity during Pavlovian conditioning with monetary gains and losses. Front. Behav. Neurosci. 8. doi:10.3389/fnbeh.2014.00179

Liening, S.H., Josephs, R. a, 2010. It is not just about testosterone: Physiological mediators and moderators of testosterone's behavioral effects. Soc. Personal. Psychol. Compass 4, 982–994. doi:10.1111/j.1751-9004.2010.00316.x

Linden, W., Earle, T.L., Gerin, W., Christenfeld, N., 1997. Physiological stress reactivity and recovery: Conceptual siblings separated at birth? J. Psychosom. Res. doi:10.1016/S0022-3999(96)00240-1

Lozza, N., Spoerri, C., Ehlert, U., Hubmann, P., Kesselring, M., Farahmand, F., Sollberger, S., La Marca, R., 2017. Predicting Social Behavior: Basal and Dynamic Joint Effects of Testosterone and Cortisol. Adapt. Hum. Behav. Physiol. 3, 255–274. doi:10.1007/s40750-017-0069-9

Magee, J. C., & Galinsky, A. D. 2008. Social hierarchy: The self-reinforcing nature of power and status. Acad Manag Ann, 2, 351–398. doi:10.1080/19416520802211628

Makara, G.B., Haller, J., 2001. Non-genomic effects of glucocorticoids in the neural system: Evidence, mechanisms and implications. Prog. Neurobiol. 65, 367–390. doi:10.1016/S0301-0082(01)00012-0

Mazur, A., Booth, A. 1998. Testosterone and dominance in men. Behav. Brain Sci. 21, 353–363.

Mehta, P.H., Josephs, R.A., 2010. Testosterone and cortisol jointly regulate dominance: evidence for a dual-hormone hypothesis. Horm. Behav. 58, 898–906. doi:10.1016/j.yhbeh.2010.08.020

Mehta, P.H., Lawless DesJardins, N.M., van Vugt, M., Josephs, R.A., 2017. Hormonal underpinnings of status conflict: Testosterone and cortisol are related to decisions and satisfaction in the hawk-dove game. Horm. Behav. 92, 141–154. doi:10.1016/j.yhbeh.2017.03.009

Mehta, P.H., Prasad, S., 2015. The dual-hormone hypothesis: a brief review and future research agenda. Curr. Opin. Behav. Sci. 3, 163–168.

Mendes, W.B., Blascovich, J., Major, B., Seery, M., 2001. Challenge and threat responses during downward and upward social comparisons. Eur. J. Soc. Psychol. 31, 477–497. doi:10.1002/ejsp.80

Miller, G.E., Chen, E., Zhou, E.S., 2007. If it goes up, must it come down? Chronic stress and the hypothalamic-pituitary-adrenocortical axis in humans. Psychol. Bull. https://doi.org/10.1037/0033-2909.133.1.25

Montoya, E.R., Bos, P.A., Terburg, D., Rosenberger, L.A., van Honk, J., 2014. Cortisol administration induces global down-regulation of the brain's reward circuitry. Psychoneuroendocrinology 47, 31–42. doi:10.1016/j.psyneuen.2014.04.022

Moore, F.L., Evans, S.J., 1999. Steroid hormones use non-genomic mechanisms to control brain functions and behaviors: A review of evidence. Brain. Behav. Evol. 54, 41–50. doi:10.1159/000006610

Packard, M.G., Cornell, A.H., Alexander, G.M., 1997. Rewarding affective properties of intra-nucleus accumbens injections of testosterone. Behav. Neurosci. 111, 219–224. doi:10.1037/0735-7044.111.1.219

Pfattheicher, S. (2017). Illuminating the dual-hormone hypothesis: About chronic dominance and the interaction of cortisol and testosterone. Aggressive behavior, 43(1), 85-92.

Pillutla, M.M., Murnighan, J.K., 1996. Unfairness, anger, and spite: emotional rejections of ultimatum offers. Organ. Behav. Hum. Decis. Process. 68:208–224. http://dx.doi.org/10.1006/obhd.1996.0100.

Ponzi, D., Zilioli, S., Mehta, P.H., Maslov, A., Watson, N. V., 2016. Social network centrality and hormones: The interaction of testosterone and cortisol. Psychoneuroendocrinology 68, 6–13. doi:10.1016/j.psyneuen.2016.02.014

Prasad, S., Narayanan, J., Lim, V.K.G., Koh, G.C.H., Koh, D.S.Q., Mehta, P.H., 2017. Preliminary evidence that acute stress moderates basal testosterone's association with retaliatory behavior. Horm. Behav. 92, 128–140. doi:10.1016/j.yhbeh.2016.10.020

Preacher, K.J., Curran, P.J., Bauer, D.J., 2006. Computational Tools for Probing Interactions in Multiple Linear Regression, Multilevel Modeling, and Latent Curve Analysis. J. Educ. Behav. Stat. 31, 437–448. doi:10.3102/10769986031004437

Quintana, D., Heathers, J., Kemp, A., 2012. On the validity of using the Polar RS800 heart rate monitor for heart rate variability research. Eur. J. Appl. Physiol. 112, 4179–4180. doi:10.1007/s00421-012-2453-2

Raihani, N.J., Bshary, R., 2015. The reputation of punishers. Trends Ecol. Evol. doi:10.1016/j.tree.2014.12.003

Roelofs, K., van Peer, J., Berretty, E., Jong, P. de, Spinhoven, P., Elzinga, B.M., 2009. Hypothalamus-Pituitary-Adrenal Axis Hyperresponsiveness is Associated with Increased Social Avoidance Behavior in Social Phobia. Biol. Psychiatry 65, 336–343. doi:10.1016/j.biopsych.2008.08.022

Sapolsky, R.M., 2000. Stress hormones: Good and bad, in: Neurobiology of Disease. pp. 540–542. doi:10.1006/nbdi.2000.0350

Schultheiss, O.C., Stanton, S.J., 2009. Assessment of salivary hormones. In: Harmon-Jones, E., Beer, J. (Eds.), Methods in Social Neuroscience. The Guilford Press, New York, pp. 17–44.

Stanton, S.J., Schultheiss, O.C., 2007. Basal and dynamic relationships between implicit power motivation and estradiol in women. Horm. Behav. 52, 571–580. doi:10.1016/j.yhbeh.2007.07.002

Tackett, J.L., Reardon, K.W., Herzhoff, K., Page-Gould, E., Harden, K.P., Josephs, R.A., 2015. Estradiol and cortisol interactions in youth externalizing psychopathology. Psychoneuroendocrinology 55, 146–153. doi:10.1016/j.psyneuen.2015.02.014

Thayer, J.F., Lane, R.D., 2000. A model of neurovisceral integration in emotion regulation and dysregulation. J. Affect. Disord. 61, 201–16. doi:10.1016/S0165-0327(00)00338-4

Tilbrook, A.J., Turner, A.I., Clarke, I.J., 2000. Effects of stress on reproduction in non-rodent mammals: the role of glucocorticoids and sex differences. Rev. Reprod. 5, 105–113.

Tops, M., Boksem, M. A. (2011). Cortisol involvement in mechanisms of behavioral inhibition. *Psychophysiology*, *48*(5), 723-732.

Viau, V., 2002. Functional cross-talk between the hypothalamic-pituitary-gonadal and - adrenal axes. J. Neuroendocrinol. 14, 506–513.

Welker, K.M., Lozoya, E., Campbell, J.A., Neumann, C.S., Carré, J.M., 2014. Testosterone, cortisol, and psychopathic traits in men and women. Physiol. Behav. 129, 230–236. doi:10.1016/j.physbeh.2014.02.057

Welker, K.M., Lassetter, B., Brandes, C.M., Prasad, S., Koop, D.R., Mehta, P.H., 2016. A comparison of salivary testosterone measurement using immunoassays and tandem mass spectrometry. Psychoneuroendocrinology 71, 180–188. doi:10.1016/j.psyneuen.2016.05.022

Yamagishi, T., Horita, Y., Mifune, N., Hashimoto, H., Li, Y., Shinada, M., Miura, A., Inukai, K., Takagishi, H., Simunovic, D., 2012. Rejection of unfair offers in the ultimatum game is no evidence of strong reciprocity. Proc. Natl. Acad. Sci. 109, 20364–20368. doi:10.1073/pnas.1212126109

Zak, P.J., Kurzban, R., Ahmadi, S., Swerdloff, R.S., Park, J., Efremidze, L., Redwine, K., Morgan, K., Matzner, W., 2009. Testosterone administration decreases generosity in the ultimatum game. PLoS One. https://doi.org/10.1371/journal.pone.0008330

Zilioli, S., Ponzi, D., Henry, A., Maestripieri, D., 2015. Testosterone, Cortisol and Empathy: Evidence for the Dual-Hormone Hypothesis. Adapt. Hum. Behav. Physiol. 1, 421–433. doi:10.1007/s40750-014-0017-x

Figures

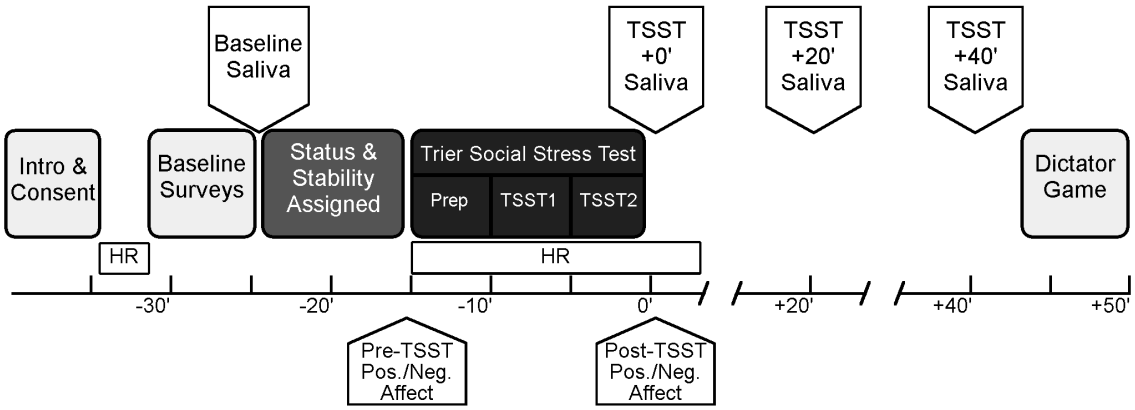

Figure 1. Timeline of the study. Time along the horizontal axis is denoted in minutes from the end of the TSST. "HR" denotes where heart rate was recorded (including a 10-minute recovery period after the TSST).

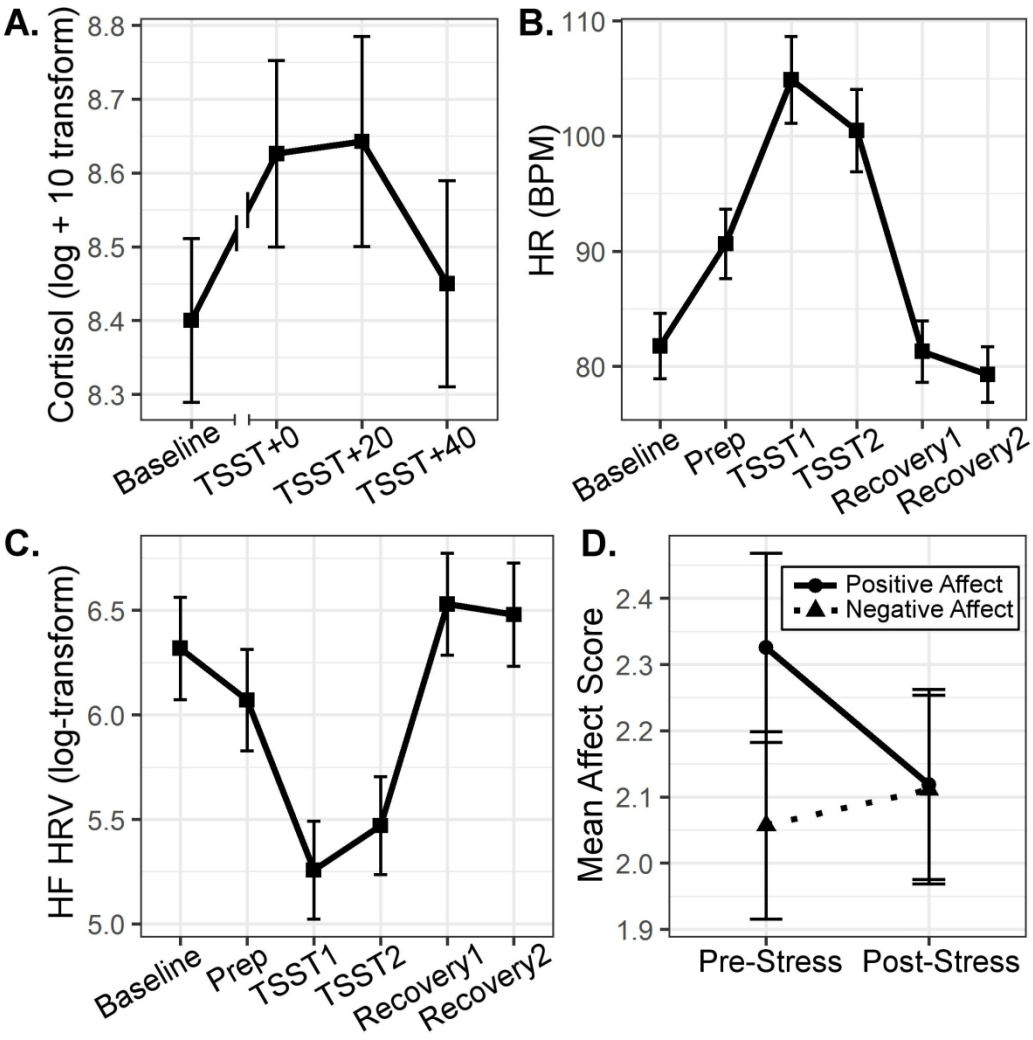

Figure 2. Estimated marginal means of stress responses investigated as potential moderators of testosterone's relationship with dominant behavior. A. Salivary cortisol response (log transformed + 10). B. Heart rate response (in beats per minute). C. Relative power of high-frequency heart rate variability response (log-transformed, ms2). D. Positive and negative affect response from pre- to post-stress.

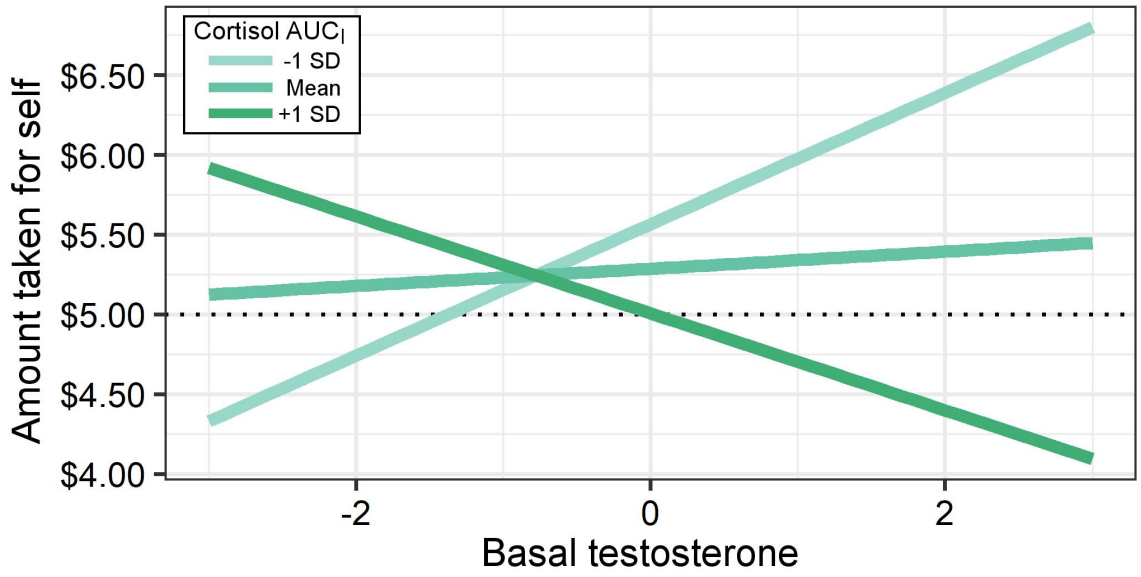

Figure 3. Estimated marginal means of interaction between basal testosterone (log-transformed and standardized within sex) and cortisol responses to the stressor (AUC_I) on the amount of money individuals decided to keep for themselves in the dictator game. Model controls for assignment to experiment conditions.

Tables

Table 1. General Linear Models (GLMs) with reactivity and recovery indices of cortisol response to stressor as moderator of testosterone's effects on dictator game decisions. Each column represents a separate GLM that controls for participant sex and experimental assignment to social status and hierarchy stability conditions.

	AUC_I			**TSST +0**			**TSST +20**			**TSST +40**		
	B	*CI*	*p*	*B*	*CI*	*p*	*B*	*CI*	*p*	*B*	*CI*	*p*
(Intercept)	5.29	4.99 – 5.58	<.001	5.31	5.02 – 5.60	<.001	5.28	4.99 – 5.58	<.001	5.27	4.97 – 5.57	<.001
Basal Testosterone	0.05	-0.25 – 0.36	.725	0.09	-0.21 – 0.39	.567	0.05	-0.26 – 0.35	.750	0.04	-0.27 – 0.35	.811
Cortisol Response	-0.23	-0.47 – 0.02	.071	-0.59	-1.34 – 0.15	.117	-0.46	-0.96 – 0.04	.070	-0.46	-1.00 – 0.09	.099
Testosterone x Cortisol Response	-0.29	-0.55 – -0.03	.029	-1.06	-1.88 – -0.25	.011	-0.54	-1.06 – -0.01	.046	-0.46	-1.03 – 0.10	.108
Social Status	-0.02	-0.32 – 0.27	.873	-0.02	-0.31 – 0.28	.908	-0.02	-0.32 – 0.27	.875	-0.03	-0.33 – 0.27	.840
Hierarchy Stability	-0.03	-0.34 – 0.27	.824	-0.04	-0.35 – 0.26	.779	-0.02	-0.33 – 0.28	.892	-0.02	-0.32 – 0.29	.922
Status x Stability	-0.01	-0.32 – 0.29	.933	-0.01	-0.31 – 0.29	.944	-0.00	-0.30 – 0.30	.988	-0.03	-0.34 – 0.28	.862
Observations		104			104			104			104	
R^2 / adj. R^2		.081 / .024			.092 / .035			.072 / .014			.058 / -.0005	

RESPONSE TO REVIEWERS

Please see our responses to reviewers' comments below in bold.

Note to the editor: To carefully address all the comments of the reviewers with appropriate and adequate information, we exceeded the word limit stipulated for the manuscript by ~221 words (currently the manuscript is 6221 words long). If exceeding the word limit poses as a matter of concern, we can move some of our discussion points into our supplementary materials by creating a supplementary discussion section.

Reviewer 1

This ms. considers the dual hypothesis theory of human dominance and status-seeking which proposes that high T is related to greater dominance in the presence of low cortisol, but not in the presence of high cortisol. More specifically the authors test the possibility that for cortisol, reactivity rather than basal levels, are the key measure. To do this, college students (N= 110 56% female) were subjected to the trier social stress test (TSST) and their salivary cortisol response measured (area under the curve, and individual values at 10, 20, and 40 minutes after the TSST). Measures of heart rate (HR) and heart rate variability (HRV) as well as affectivity were also obtained. Approximately 85 mintues after the start of the TSST (45 minutes after hormone levels were back to baseline) the participants engaged in a single shot dictator game, with the amount of the offer used as the outcome variable. Predictors of interest were basal T, cortisol response and the interaction of the two. Controls included status and stability which had been experimentally manipulated for an earlier study.

We have updated Figure 1 in our paper to reflect greater clarity in the timeline and time markers for our study. Just to clarify, participants played the dictator game approximately 65 minutes (and not 85 minutes) after the start of the TSST.

The results demonstrated a significant interaction between cortisol area under the curve and basal testosterone predicting the size of the offer made. Similar findings were obtained for cortisol at 10 and 20 minutes, but not at return to baseline. No such interaction with baseline testosterone was found for either HR or HRV, or affectivity. The authors suggest that reactivity that is the key measure of cortisol and that additional stress measures be used in future studies to determine whether the moderating effect on testosterone is specific to cortisol or reflect a more general impact of the stress response.

This is a well-done analysis using archival data from a previously done study. As the authors point out cortisol has often been considered to represent the stress response when in fact it is only one part. HR and HRV are not only of interest because they index the sympathetic and parasympathetic system, but because they are accessible to consciousness, making them a potential source of information about bodily status in a stressful situation. Measures of affect are also conscious. Additional elements, including catecholamines and heart rate should be considered as well. Thus this study represents a first step toward clarifying the impact of the stress response on the relationship of testosterone with status-seeking behaviors, including

dominance and aggression. At the same time the study is limited because it does not measure important aspects of the stress response, particularly catecholamines

We have included information about the measurement of additional outcomes of the stress response such as catecholamines and cardiac reactivity (i.e., heart-rate) as possible avenues for future research (p. 15).

Having said that, I think that the authors can do better in situating the study with regard to previous findings. In particular, they do not articulate why considering cortisol reactivity is necessary. Mehta and Prasad (2015; Curr Op Behav Sci 26:866-76) lists 13 studies, including some done by the authors of this ms. that have reported an interaction between basal cortisol and testosterone in predicting status-seeking behavior. If basal cortisol has been a sufficient measure, why did they think they need to study cortisol reactivity?

We now include a more nuanced discussion of our motivation to study cortisol responses in acutely stressful situations, as opposed to basal cortisol (p. 4). A discussion paragraph also helps situate our findings in the context of previous dual hormone hypothesis findings with basal cortisol by arguing that in acutely stressful contexts, cortisol response (and not basal levels) is a more critical moderator of the basal testosterone and behavior relationship (p. 19).

Nor do the authors discuss why the current study did not show a significant interaction between basal cortisol and T. In particular, the authors do not cite Pffatheicher (2017; Aggr Behav 43:85-92) who uses a similar design, but without the TSST, to show an interaction of basal cortisol and T in predicting the outcome of a one shot dictator game, but only with those with chronic dominant personalities. This means that the time between sample collection and the behavior differs from the current study. This might be important in considering possible mechanisms for the interaction of T and cortisol as discussed below.

We thank the reviewer for pointing out the Pffatheicher (2017) paper. It is indeed relevant to our study. We now cite the Pffatheicher (2017) paper in the introduction and in the discussion of the paper.

A related comment concerns the proposed mechanism(s) for how cortisol may impact the effects of T on status-seeking. The authors suggest that the impact of cortisol response on the effects of T might be related to changes in psychological motivation, changes in brain activity related to reward which underlie motivation, or changes in androgen receptors. Of course, these are not three entirely different mechanisms, but rather three different levels of what could be a single mechanism. If hormones are going to change motivation or behavior they presumably do so by acting on specific brain structures. And if the effective level of hormones reaching the neurons in those brain structures changes so will brain activity.

We now include a paragraph after the discussion of our three suggested mechanisms to highlight that these mechanisms may function both independently and/or interdependently (p. 17).

It has been suggested that changes in T with competition might reflect changes in blood volume, adrenal hormones or testicular hormones associated with changes in noradrenaline and adrenaline, as part of the stress response (Carre and Olmstead 2016; Neurosci 286:171-86), which is one reason to study the stress response more broadly than simply cortisol. However in this study T is measured before the TSST and the cortisol response after. So the T value used in the analyses was not subject to the changes in cortisol or other elements of the stress response.

This means that any impact of increased cortisol on the behavioral effect of T presumably works by changing other element(s) of the androgen system. Such an effect would still be evident 65 minutes later (this amount of time between the last elevated cortisol level and the dictator game). The authors are suggesting that cortisol may have an impact on the androgen receptor that would modify the effects of T without changing circulating levels. Another possibility is that the effects of T are modulated through non-genomic actions on other neuronal receptors (Castro & Edwards 2016; Horm & Behav 82:21-37). This seems more likely given the dynamic nature of the interaction between T and cortisol. I realize that there are too many possibilities involved to resolve this issue with the current data, but I think that the authors can be more explicit in relating possible mechanisms to the timing of events in their study.

We thank the reviewer for this comment. As highlighted above, we have updated the document to include information about the measurement of additional outcomes of the stress response that may alter testosterone's link to behaviors (p. 15). We now also include a discussion of rapid non-genomic mechanisms as part of our paragraph discussing molecular mechanisms that may explain the results of our study (p. 17). To help with understanding the timing of these molecular mechanisms, we have also revised Figure 1 to indicate the timeline of our study with more clarity.

My other comments are more minor. The first regards the considering offering less than ½ of the $10 in the single-shot dictator game as a measure of antisocial behavior. I agree that it is egocentric, but is it really antisocial? In a one shot dictator game what would be a prosocial status-seeking behavior, given that you are not going to interact with the other person again. Pfattheicher (2017) provides additional evidence that link the outcome of the ultimatum game in his study to antisocial punishment, strengthening the argument.

We agree that we need to be more careful with our description of the behavior studied. Because of this feedback (and issues discussed below), we have therefore corrected language throughout the document. Within our manuscript, the dictator game decision is now termed a "dominant behavior" that is part of a broader set of status-relevant behaviors previously linked to testosterone. To help with this line of argumentation, we now provide definitions of dominance and status and highlight how the dictator game decision can be construed as a dominant status-relevant behavior (p. 3).

However, we do agree with you that a one-shot dictator game attenuates the likelihood of prosocial responses. To address this point, we now discuss how there may be multiple routes to ascending the status hierarchy - via exerting dominance (keeping more money for oneself) or behaving prosocially (giving more money to others). To measure these prosocial routes to status, we suggest that future research may modify the experimental paradigm of

the dictator game to elicit those behaviors. For example, having participants allocate resources between themselves and a charitable organization may garner more prosocial behaviors as a means to gain status (p.17-18).

The second regards the figures. I realize that there is a lot of room for supplementary material and putting the results from the prior article published out of the larger study is a good use of that space, especially given the overlapping use of variables including status and stability. However, I think that figure S1 showing the time course of different elements of the stress response to the TSST belongs in the main text. Also the placement of the time markers on Figure 1 could be clearer.

Table S1 has now been moved into the main paper (now Figure 2).

Reviewer 2

This is a very well written paper that provides a nice addition to the literature. Here, the authors demonstrate that basal T concentrations predict more selfish behavior in the one-shot dictator game, but only for individuals who demonstrated a relatively smaller increase in cortisol during a stress manipulation task. This relationship was largely non-existent among individual who demonstrated a relatively larger increase in cortisol. I only have some relatively minor suggestions for improving the paper

We thank this reviewer for their enthusiasm.

1 - the authors should avoid using causal language throughout the paper. e.g., the title "Effects of testosterone..." suggest that T was manipulated, but it wasn't. I suggest rewording to "The relationship between testosterone...". Similar language should be modified throughout the paper (including the abstract).

We have updated the title, abstract, and entire body of the document to acknowledge that we are studying non-causal relationships between testosterone and behavior.

2 - Was there any sex difference in dictator decisions? I would expect men to keep more money for themselves. Please report.

We did not find any sex differences in dictator game behavior, and now report this in the paper (p. 10).

3 - Have the authors considered examining basal C x T response interaction predicting DG behavior?

We tested this and did not find a significant interaction. We have included these results in the results section and as part of Table S6 (p. S9 in the supplement).

4 - I'd be interested in the authors thoughts about examining UG proposer behavior and the basal T x cortisol response interaction. If this is all about status concerns, one might predict an even

more robust effect for UG proposer behavior because the threat of rejections might pose an especially big threat to one's status.

We agree this is an interesting future direction for this research to examine. We have added additional information regarding background on testosterone's links to UG proposer behavior and the necessity to test basal testosterone x cortisol response interactions on UG proposer behavior in future research (p. 18; Footnote 5).

5 - regarding reward mechanism.. I think the authors could present a more balanced view of this work. There is some evidence that stress increases activation in reward-related regions, and other studies showing the opposite. So it appears that the story might be much more complicated.

e.g., rodent work indicates that CORT potentiates DA release in reward regions (e.g., nucleus accumbens) and blockade of corticosterone response to stressor blocks DA release.

Rouge-Pont et al., 1998. Individual differences in stress-induced dopamine release in the nucleus accumben s are influenced by corticosterone. Eur J Neurosci, 10(12), 3903-3907.

Moreover, there is evidence that elevated CORT in response to stress is positively correlated with NAcc responses to rewarding stimuli.

Oei et al., 2014. Acute stress-induced cortisol elevations mediate reward system activity during subconscious processing of sexual stimuli. PNEC, 39, 111-120.

*this paper reviews the literature pretty well.

We appreciate this insight and the relevant citations from the reviewer. We now present a more balanced view of the research linking stress and cortisol with reward related neural activity. Further we also recommend that future research must be conducted to clearly delineate the plausibility of this mechanism (p. 16-17).

Reviewer 3

This is an interesting paper. The authors are interested in understanding how variation in cortisol responses to acute stress interacts with testosterone to predict behavior in the dictator game (DG) where the recipient is another person. The results suggest that in their sample of both men and women, testosterone is negatively correlated with DG giving for those with low cortisol responses, while for those with high cortisol responses there was no such relation.

This is an interesting and nice paper. My main comments are regarding the framing of the paper where I am a bit unsure and I would like to see the authors discuss certain things further.

First, it is not clear to me why the paper is about "antisocial behaviors". In the DG the prosocial thing is to give something, whereas the most selfish thing is to keep all. I do not believe that selfish and antisocial are the same thing, so why is this paper not instead about testosterone, cortisol and prosocial or selfish behavior? (And not behaviors.)

We have made several changes across the paper and in the title to be more precise about what we are calling the dictator game decision in our study. As discussed briefly above, we now refer to the dictator's decision of asymmetrically allocating more resources for themselves to fall under the broader suite of dominant, status-relevant behaviors. We argue that allocating more resources to oneself in the dictator game can be construed as a behavior that demands increased respect or deference via assertive or forceful means. Other scholars have referred to these behaviors as "dominant behaviors" that lead to status attainment (p. 3). Moreover, calling dictator game decisions dominant behaviors aligns better with prior theorizing about testosterone and dual hormone relationships these behaviors.

Second, I find it a bit unclear here and in many other papers (including those by Eisenegger and coauthors) what dominance and social status means. In e.g. Eisenegger et al. (2010) the authors were saying that testosterone increases ultimatum game proposals because it is of high status to give high proposals in that game. So that would perhaps predict the opposite behavior here in the DG. But status is of course context dependent – but I guess it is not clear in the current study or in e.g. Eisenegger et al. what participants consider to be of high status. In sum, I find the whole status discussion a bit unclear and imprecise and I think the results are of sufficient interest without this discussion. So I would either tone it down or make it clearer. This should be up to the authors – but to make the whole status argument here and in other papers clearer would be great.

We thank the reviewer for making this rather important comment about our paper and the broader literature. To address the first half of this comment, we now provide definitions of dominance and social status in our introduction (p. 3) and highlight why we think dictator game decisions may be a type of dominant status-relevant behavior. We also agree with the reviewer that behaviors that motivate status-attainment are indeed context dependent. To address this, we now include a revised paragraph in our discussion where we argue that there may be more than one route to status attainment. Specifically, in certain contexts (e.g. if the recipient were a charitable organization) individuals may adopt prosocial (giving more money) rather than dominant (taking more money) strategies to gaining status (p. 17-18). Further, we also highlight that the motivations underlying behaviors in the ultimatum game and dictator game may both be linked to gaining status (i.e., via signaling dominance), but that it is also possible that motivations for these behaviors may also diverge (e.g. reward maximization in the dictator game, and antisocial punishment in the ultimatum) (p. 18-19). To address these conceptual limitations in the broader literature, we recommend researchers design experimental paradigms that allow more direct inferences of status-relevance, pit divergent motivations within the same task, or use methodologies that directly measure status motivations and perceptions.

Third, I think the authors could work a little bit more on motivating why we should test these relations and why we see the results we see.

To address this comment, we provide a discussion of our motivation to study cortisol responses in acutely stressful situations as opposed to basal cortisol (p. 4). We also have a paragraph in our discussion arguing that our results suggest that cortisol responses are a

critical a moderator of basal testosterone effects in stressful contexts, and that basal testosterone and basal cortisol interactions may emerge only in non-stressful contexts (p. 19).

Fourth, the authors perform a large number of tests, and there are even more potential tests than the ones reported here. Given this and the in general weak support for the alternative hypothesis when the p-value is 0.05 (see Benjamin et al. 2018 "Redefine statistical significance"), I think the authors should avoid one-tailed tests and treat all $p>0.05$ as insignificant and not discuss e.g. different effects in men and women when sex is not a significant variable.

It was a mistake on our part to call the analyses in 3.1 "one tailed" and we thank the reviewer for spotting this issue. But these analyses have since been deleted based on your recommendation below. Further, all tests with $p \geq .05$ have been treated as insignificant (e.g. the effects in men and women), and the interpretations have been updated to reflect their statistical insignificance.

These things should all be relatively easy to fix for the authors.

Other comments:

Completely minor point but I also find the discussion about rejecting unfair offers as being about antisocial behavior speculative too. It could also be the opposite – I reject unfair offers because I want to enforce a prosocial or egalitarian norm.

We agree that the behaviors in the ultimatum game could have many motivational factors. We have updated our introduction to clarify our reasoning for explaining why rejections of unfair offers in the ultimatum can be seen as being a dominant status-seeking behavior and include citations for this inference (p. 4).

Study design: Not knowing the other papers by the authors, it is a bit unclear when reading footnote 2 what is going on with the status manipulations and whether this will be relevant in any way for the analysis. Perhaps this could be clarified.

We now include a description of the experimental manipulations in our supplement (p. S2). We further note that none of these manipulations moderated the main results we report in this paper and that all inferential tests controlled for these manipulations.

Section 3.1: This first test is a bit unusual for me, and it looks like people actually are pretty egalitarian. Subjects typically give zero or 50% (and there is some intermediate giving but typically low).

We agree with the reviewer. This analysis has now been removed from the document.

The analysis: As someone who does not do this type of analysis but typically uses other statistical models, I am unsure of how standard errors are treated here when there are repeated observations from the same individuals – perhaps this could be clarified.

We thank the reviewer for this comment. We have updated text in the main document to include the specifications of our models that allow heterogeneity in variances for each participant (p. 9). We have also indicated that our graphs use estimated marginal means and standard errors based on the MLMs that were used for our analysis (p. 9-10). Thus, the standard errors take into account the within-participant variance evident in the analytical models. We have also updated the graph and captions to clarify this point.

Discussion: The results on direct effects of testosterone on prosocial behaviors are not that clear though (see e.g. Zethraeus et al. 2009) so perhaps this could be rewritten to reflect this current state of the literature.

Given that we find evidence for a dual hormone profile of high basal testosterone and low cortisol responses to stress predicting status-relevant behavior, we have now removed the discussion of testosterone's direct effects on prosocial behavior because of its lack of direct relevance to the findings of our paper. Instead, we discuss contexts in which a high basal testosterone and low cortisol response may be linked with prosocial behaviors (p. 17-18).

Finally, the results are of course correlational, which the authors write, but it could be made even clearer early on just to minimize potential confusion (and some parts of the Discussion talk about the effects of testosterone and cortisol).

We agree that our language should be more precise. As above, we have removed all causal language from the title, abstract, and rest of the document.

Highlights

- Cortisol responses to acute stress suppress the testosterone-behavior association
- At low cortisol responses, testosterone positively predicted dominant behavior
- High cortisol responses blocked the testosterone-dominant behavior association
- Other markers of stress did not modulate the testosterone-behavior relationship
- Findings extend prior dual-hormone hypothesis work to acutely stressful contexts

Basal testosterone's relationship with dictator game decision-making depends on cortisol reactivity to acute stress: A dual-hormone perspective on dominant behavior during resource allocation

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Abstract

The dual-hormone hypothesis proposes that testosterone's relationship with status-seeking behavior is moderated by cortisol. However, research testing this hypothesis has focused on basal cortisol; the potential moderating effect of the acute cortisol response to stress has been largely overlooked. The present research investigated the moderating role of cortisol responses to an acute stressor on basal testosterone's link with dominant, status-relevant decision-making. Also, given the multifaceted nature of the response to acute stress, cardiovascular and affective responses to the stressor were examined as alternative moderators of the testosterone-behavior relationship. Participants (N=112; 56% female) were exposed to a social-evaluative stressor, and their stress responses were measured. Participants subsequently engaged in a one-shot dictator game, wherein they were asked to split money ($10) with a confederate counterpart. The amount of money participants decided to keep for themselves was treated as a metric of dominant status-seeking behavior. For individuals who demonstrated lower cortisol responses to the stressor, basal testosterone was positively associated with more dominant behavior (i.e., keeping more money for oneself), but for those who showed higher cortisol responses, the testosterone-behavior relationship was suppressed. Moreover, other aspects of the stress response (i.e., cardiovascular and affective responses) did not moderate the relationship between basal testosterone and dictator game behavior. These results provide unique support for the dual-hormone hypothesis using markers of stress-induced cortisol change. The findings also suggest that the antagonistic effects of stress on testosterone's role in motivating status-relevant behavior may be specific to cortisol's role in the acute stress response.

Keywords: testosterone; cortisol; dual-hormone hypothesis; stress; dictator game; dominant behavior

Basal testosterone's relationship with dictator game decision-making depends on cortisol reactivity to acute stress: A dual-hormone perspective on dominant behavior during resource allocation

1. Introduction

As a species, we have evolved in social hierarchies, and the stratification of individuals within human groups helps organize us and maintain social order (Anderson et al., 2015; Ellis, 1994; Sapolsky, 2005). Within a social hierarchy, having higher status - respect or deference that is based on an individual's perceived social value (Anderson, et al., 2015; Magee and Galinsky, 2008) - grants several benefits, such as access to limited resources and social influence over others (Cheng et al., 2013; Sapolsky, 2005). Given the benefits of having higher status, individuals are often motivated to behave in ways that will aid their ascent in the status hierarchy. One approach to status attainment involves using dominant behavioral strategies - demanding increased respect or deference via assertive or forceful behaviors (Cheng et al., 2013; Mazur and Booth, 1998; Mehta et al., 2017). Further, using dominant behaviors may be evident in the domain of resource allocation where individuals asymmetrically allocate more resources to themselves compared to others as a means to status attainment (Bondarenko and Zakharov, 2018; Sapolsky, 2005). Social endocrine theory posits that testosterone, a steroid hormone released by the hypothalamic-pituitary-gonadal (HPG) axis, underlies dominant behaviors that are related to status seeking (Mazur and Booth, 1998). However, evidence that higher testosterone concentrations directly increase status-seeking behaviors during resource allocations is mixed [for example, testosterone linked to increased dominant decisions: Mehta et al., 2017; null effects of testosterone: Cueva et al., 2017; testosterone linked to increased prosocial behavior: Boksem et al., 2013 (for reciprocity after trust display); see Dreber and Johanneson, *in press*, for review of studies with exogenous hormone administration].

These inconsistent relationships may arise because testosterone's role in status-relevant behaviors may depend on other hormone systems. According to the dual-hormone hypothesis (Mehta and Josephs, 2010), testosterone's influence on status-seeking behavior should depend on cortisol, a hormone released

as part of the hypothalamic-pituitary-adrenal (HPA) axis in response to physical and psychological stress (Dickerson and Kemeny, 2004). More specifically, this hypothesis proposes that higher testosterone concentrations should be related to more status-seeking behaviors when cortisol levels are low but not when cortisol levels are high. Several studies have provided support for the dual-hormone hypothesis across a range of behaviors linked to social status, including dominant behavior (reviewed in Mehta and Prasad, 2015; for other patterns of results, see Welker et al., 2014; for null effects, see Geniole et al., 2013). For example, higher basal testosterone was associated with decisions to allocate more money for oneself in an adapted version of the dictator game when basal cortisol was low, but not when basal cortisol was high (Pfattheicher, 2017).

However, most work on the dual-hormone hypothesis has focused on the moderating role of basal cortisol (Mehta and Prasad, 2015). These studies have tested the dual hormone hypothesis in non-stressful contexts, and therefore have used basal cortisol as a theorized marker of chronic stress exposure (Miller, Chen, and Zhou, 2007). In acutely stressful contexts, cortisol is known to fluctuate (Dickerson and Kemeny, 2004), however, whether the acute cortisol response to a stressor moderates the association between testosterone and status-seeking behavior in acutely stressful contexts remains largely unknown. This gap in the literature remains despite the ubiquity of acute stressors in our social environments and the relative ease with which laboratory stressors produce robust cortisol responses (Dickerson and Kemeny, 2004; Kirschbaum et al., 1993). Recently, one study found that experimentally manipulated acute stress relative to a relaxation condition suppressed the association between basal testosterone and retaliation to unfairness in the ultimatum game (Prasad et al., 2017, *cf* Lozza et al., 2017). Retaliating by rejecting unfair offers is a dominant behavior that is motivated by the desire to protect one's reputation in response to status threats (Raihani and Bshary, 2015; Yamagishi et al., 2012) or punish the proposer in the face of provocation posed by receiving unfair offers (Pillutla and Murnighan, 1996). In line with the dual-hormone hypothesis, Prasad et al. (2017) also found that higher levels of basal testosterone were associated with these retaliatory behaviors but only in individuals with lower cortisol reactivity,

regardless of their experimental condition. However, at higher levels of cortisol reactivity, the testosterone-retaliation relationship was suppressed.

Although the findings in Prasad et al. (2017) provide preliminary evidence that fluctuations in cortisol concentrations modulate testosterone's relationship with status-relevant resource allocations decisions like retaliation in the ultimatum game, this study was not designed to test if individual differences in cortisol responses to an acute stressor *per se* modulate basal testosterone's relationships with dominant behavior[1]. The present research builds upon these initial findings by using a larger, correlational study that specifically focuses on the extent to which individual variability in cortisol responses to an acute stressor moderates the relationship between basal testosterone and dominant status-relevant decisions in the dictator game.

The dual-hormone hypothesis focuses on cortisol, but HPA axis reactivity is only one aspect of the complex, multifaceted response to stress (Sapolsky et al., 2000). Some evidence suggests that other aspects of the response to stress, including the autonomic nervous system and psychosocial responses like one's affective state, may modulate testosterone's relationship with behavior (Chichinadze and Chichinadze, 2008; Liening and Josephs, 2010). Therefore, we explored autonomic nervous system responses (heart rate and heart-rate variability) and positive and negative affect responses as moderators of testosterone's association with dominant status-relevant behavior. Moreover, the acute stress response spans a temporal trajectory that includes both initial reactivity to and recovery from the stressor. We examined the physiological stress measures by calculating area-under-the-curve with respect to increase (AUC_I), an index that captures both the reactivity and recovery to the stressor (Pruessner et al., 2003).

Finally, to measure dominant behavior to signal one's perceived higher status, we used the dictator game, a resource allocation paradigm (Kahneman et al., 1986). In this game, one of the players (the "dictator") unilaterally decides how resources are allocated between herself and another participant.

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[1]Prasad et al. (2017) was designed primarily to examine the causal influence of acute stress (vs. a relaxation control condition) as a moderator of testosterone's role in retaliation. Hence, the study had reduced statistical power for examining individual variability in cortisol responses to acute stress.

Given the zero-sum nature of the game, more resources kept by the dictator results in fewer resources available for the recipient. How the dictator decides to split an endowment with the recipient may therefore evince proactive, dominant status-seeking behaviors (Hoffman et al., 1999), as opposed to reactive dominant behaviors characteristic of ultimatum game responses (Prasad et al., 2017).

2. Methods

2.1. Transparent Reporting

Data and study materials for this report are available on its Open Science Framework website (https://osf.io/jx6fh). These data are part of a broader experimental study; information on sample size, exclusions, and other facets of study design are available in the initial study publication (see Knight and Mehta, 2017).

2.2. Participants

In this study, 110 undergraduate participants successfully completed the broader experimental tasks and had saliva available for assay (as reported in Knight and Mehta, 2017). Of these individuals, 104 participants (57.6% female) also successfully completed the dictator game. Additional participants were missing cardiovascular data due to noise and experimenter error (n = 12 missing heart rate; n = 13 missing heart rate variability), and so were left out of analyses involving heart rate and heart rate variability. The Institutional Review Board at the University of Oregon approved the protocol for this study (Figure 1).

2.3. Acute stressor

All participants completed the Trier Social Stress Task (TSST), a psychological acute stress induction paradigm that reliably increases cortisol concentrations (Dickerson et al., 2008; Kirschbaum et al., 1993). The protocol consisted of a 5-min speech about one's qualification for a job, and a 5-min serial subtraction math task in front of a panel of evaluative observers, who maintained neutral facial and verbal affect throughout the task. All participants were also provided with a 5-min preparation period that was

completed in the presence of a sex-matched confederate with whom they later played an online version the dictator game (see below).

2.4. Dictator Game

Approximately 40 minutes after the TSST, participants were asked to participate in an online, one-shot dictator game. The dictator game paradigm consists of two individuals: a dictator and a recipient. The dictator is endowed with a sum of money and must decide how to split the endowment with the recipient, who must passively accept whatever is offered. Participants were assigned the role of the dictator and were asked how they would split a sum of $10 with the confederate[2] (i.e., the recipient). The amount that participants indicated they would keep for themselves was treated as a measure of dominant behavior.

2.5. Baseline testosterone

Participants were instructed to abstain from eating, drinking, exercising, and smoking for two hours before their scheduled experimental session. To account for diurnal variability in endocrine and autonomic activity, all sessions occurred in the afternoon between 1300 and 1730 hrs. After arriving at the laboratory, participants were seated in an individual testing room where informed consent was obtained to participate in a group activity and perform a speech task. Demographic questionnaires were administered for approximately 10 minutes before a baseline saliva sample was collected via passive drool. The samples were subsequently assayed for testosterone using standard assay protocols (Schultheiss and Stanton, 2009) and commercially available enzyme immunoassay kits (Salimetrics, LLC; State College, PA; see Knight and Mehta, 2017).

[2] The study (Knight and Mehta, 2017) in which these data were collected experimentally assigned participants to high and low status positions (see section 2.7 and Supplementary Materials). In order to increase the validity of the decision-making task within this experimentally manipulated context, participants saw one of two prompts for the dictator game that were adjusted to match the participant's status assignment. Participants assigned to the high-status position were asked how they would split the money, whereas participant assigned to the low status positions were asked how they would split the money if they were in the high-status position.

2.6. Stress responses

2.6.1. Endocrine Response

Saliva samples were obtained immediately (TSST+0), 20 minutes (TSST+20), and 40 minutes (TSST+40) after the end of the TSST and assayed for testosterone and cortisol in our laboratory. Cortisol and testosterone concentrations were positively skewed and were natural-log transformed.

2.6.2. Positive and Negative Affect

Participants responded to thirteen items related to their momentary positive and negative affect on a 1 to 5 scale, anchored on "Not at all" to "Extremely." These questions were administered just prior to and immediately after the stressor. Positive affect was indexed as the mean of the following items: interested, excited, happy, strong, enthusiastic, proud, self-confident, and in control (*Cronbach's* α = 0.91); negative affect as the mean of the following items: distressed, upset, sad, irritable, ashamed, and nervous (*Cronbach's* α =0.82).

2.6.3. Cardiovascular and Autonomic Nervous System

For a majority of participants (approximately 75%), cardiovascular responses to the stressor were recorded via continuous recording of a modified Lead II electrocardiogram (ECG) from BioPac (BioPac Systems, Inc.), with Ag/AgCl sensors placed at the collarbone, contralateral ribcage, and ipsilateral hip. For the remaining participants, the cardiovascular recording equipment was not available and cardiovascular activity was recorded continuously via a Polar RS800CX watch and chest band (Polar, Inc.). Polar watches have been shown to generally match ECG measurements when analyzed identically (Quintana et al., 2012).

All cardiovascular data were visually inspected and manually corrected for artifacts in Kubios HRV (v.1.0). Heart rate (HR) and heart rate variability (HRV) was derived from interbeat-interval (IBI) timings. Specifically, the power (in $msec^2$) of the high frequency band of heart rate variability (HF HRV; corresponding to frequencies of 0.15 – 0.40 Hz) was determined via the autoregressive method of HRV derivation. HF HRV is often utilized as a relatively clean index of parasympathetic activity, which

generally withdrawals in response to stressors (Thayer and Lane, 2000). Values for HR and HF HRV were averaged within six, five-minute epochs: Baseline, Preparation, two five-minute epochs of the TSST, and two five-minute epochs of a recovery period. HF HRV values were natural-log transformed prior to data analysis to correct a positive skew.

2.7. Other experimental manipulations

The larger study from which these archival data were derived also manipulated social status and stability of the status hierarchy (see Supplementary Materials and Knight and Mehta, 2017). Because the primary interest of this study was to examine the moderating role of stress responses on the testosterone-behavior relationship, we report all statistical analyses controlling for the experimental manipulations in the study (i.e., social status, hierarchy stability, and their interaction).

2.8. Data transformations and analyses

To produce indices of the stress response to the TSST, AUC_I (Pruessner et al., 2003) was calculated across the four epochs of natural-log transformed cortisol data and across the six epochs of HR and HF HRV data. Although not a principle focus of this study, we used the same AUC_I transformations on natural-log transformed testosterone concentrations to explore testosterone reactivity. Affective responses to the TSST were calculated by subtracting the mean pre-stress score from the post-stress score for positive and negative affect.

To test for stress-linked changes in cortisol, affect, and cardiovascular responses, we used multilevel models (MLMs) with time as a polynomial-contrasted, within-subjects measure. Multilevel modeling analyses were conducted in R (v. 3.4.1) using the *lme4* package (Bates et al., 2014). In these models, observations (Level 1) were nested within participants (Level 2), and each model included random intercepts and slopes of time for each participant (coded using polynomial contrasts for the models). Unlike other repeated measures approaches that treat within-subject variance as homogeneous, the random effects in multilevel models account for variation within each subject (Hedeker et al., 2012). For graphing purposes, estimated marginal means and standard errors (SEs) from the models were

determined via the lsmeans package (Lenth, 2016), which takes into account within-subject variances. Further, to test if basal testosterone's association with decision-making in the dictator game depended on stress responses, we used linear regression models in which we examined interactions between basal testosterone and centered indices of the stress response (e.g., cortisol AUC_I). For analyses involving basal measures, testosterone was natural-log transformed (see Knight and Mehta, 2017) then standardized (z-scored) within gender (Mehta et al., 2017; Prasad et al., 2017)[3]. Finally, all models controlled for the experimental manipulations in the study (status, stability, and their interaction).

3. Results

3.1. Dictator game behavioral results

Participants on average chose to keep $5.29 (*SD*= 1.52) for themselves. The amount of money that individuals kept for themselves was not influenced by the other manipulations in the study (status, stability, or their interaction; *ps*>.67). Further, there were no sex differences in dictator game decisions (*p*>.52).

3.2. Stress-induced changes in cortisol

The MLM analysis of cortisol concentrations revealed a significant main effect for time in response to the acute stressor (Time (linear): *B* = 0.037, *95%CI*[-0.04, 0.12], *p* = .374; Time (quadratic): *B* = -0.209, *95%CI*[-0.262, -0.157], *p* <.001; see Figure 2; see also Knight and Mehta (2017) for further analyses of cortisol response). Next, we conducted follow-up analyses that compared baseline hormone concentrations to the measures of cortisol obtained at TSST +0, TSST+20 and TSST+40. We found that compared to baseline hormone concentrations (*M*=0.24 μg/dL, *SD*=0.21)[4], cortisol levels were significantly elevated at TSST+0 (*M*=0.32 μg/dL, *SD*=0.24; *t*(109)=6.29, *p*<.001), and TSST+20 (*M*=0.34 μg/dL, *SD*=0.3; *t*(109)=4.04 *p*<.001), but were not significantly different at TSST+40 (*M* = 0.28 μg/dL,

[3] However, for follow-up analyses involving testosterone responses to the stressor (i.e., AUC_I), testosterone scores were log transformed but not standardized within sex given that AUC_I scores already account for baseline differences in hormones across sexes.

[4] Although analyses were run on natural-log-transformed cortisol concentrations, we report means and SDs for untransformed values.

SD = 0.25; *t*(109) = 1.07, *p* = 0.286). This highlights that our stress manipulation facilitated increases in cortisol levels that then recovered back to baseline. See Tables S1 to S3 for correlations among stress response variables across the entire sample, in males, and in females (Supplementary Materials).

3.3. Basal testosterone × cortisol response

Next, we tested the hypothesis that basal testosterone's role in dictator game decisions depended on the cortisol response to the TSST (i.e., cortisol AUC_I). This analysis revealed no main effect of basal testosterone but did reveal a marginally significant main effect of cortisol AUC_I (see Table 1). Individuals who demonstrated greater cortisol responses to the social stressor kept less money for themselves in the dictator game (i.e., demonstrated less dominant behavior). However, this main effect of cortisol AUC_I was qualified by a statistically significant basal testosterone × cortisol AUC_I interaction (*B* = -0.29, *SE* = 0.13, *95%CI*[-0.55, -0.03], *t*(97) = -2.21, *p* = .029; Figure 3). Simple slope analysis (Preacher et al., 2006) indicated a positive relationship between basal testosterone and the amount of money allocated to oneself in the dictator game among individuals with lower cortisol responses (-1SD: *B* = 0.41, *SE* = 0.21, *t*(97) = 1.97, *p* = 0.052), but not among individuals with relatively greater cortisol responses (+1SD: *B* = -0.30, *SE* = 0.24, *t*(97) = -1.29, *p* = .199). The non-zero interaction term indicates that these slopes were statistically different from each other. In follow-up analyses, this dual-hormone interaction was also robust when analyzing cortisol reactivity (from baseline to immediately after the TSST and 20 minutes after the TSST, Table 1). A similar pattern, albeit somewhat weaker, was also found for cortisol recovery (from baseline to the end of the recovery period; Table 1).

We tested if other manipulations in the study (status, stability, or their interaction) moderated the basal testosterone × cortisol response interaction, but we did not find significant three-or four-way interactions in these analyses (*p*s>.30; Table S4, Supplementary Materials). These results suggest that the basal testosterone × cortisol response interaction did not further depend on these manipulations. Crucially, the basal testosterone × cortisol response interaction on dictator game decisions remained significant in

these analyses, demonstrating the robustness of this dual-hormone interaction effect across multiple statistical models.

3.3.1 Sex differences

Given prior mixed evidence for sex differences in testosterone-behavior relationships (Mehta and Josephs, 2010; Welker et al., 2014) we explored the role of sex as a moderator of the interactive effects of cortisol response and basal testosterone on dictator game decisions. Basal testosterone × cortisol response interactions were not moderated by participant sex (p>.38; see Table S5); both men and women showed similar interaction patterns (Figure S1).

3.4. Other dual-hormone analyses

While we examined the moderating effect of cortisol stress responses on basal testosterone's association with behavior, prior evidence of the dual-hormone hypothesis focused on the moderating effects of basal cortisol (Mehta and Prasad, 2015). However, we did not find support for a basal testosterone × basal cortisol interaction (see Table S6). Moreover, we also did not find a sex × basal testosterone × basal cortisol interaction, indicating that the null effect was not due to weak or opposing effects of basal testosterone × basal cortisol effect in men or women. These findings suggest that in the context of acute stress, cortisol responses to the stressor may moderate the relationship between basal testosterone and dominant behavior, rather than basal levels of cortisol.

The acute stressor also altered testosterone levels (Time (linear): B = -0.03, *95%CI*[-0.06, 0.01], p = .10; Time (quadratic): B = -0.11, *95%CI*[-0.13, -0.09], p <.001), which rose at TSST + 0 and TSST + 20 and then returned to baseline at TSST + 40 (see Knight and Mehta, 2017 for other analysis). Therefore, we also explored the interactive effects of testosterone response with both the cortisol response to the stressor and basal cortisol levels on dictator game decisions. We did not find support for a testosterone response × cortisol response or testosterone response × basal cortisol interaction (Table S6). Neither did we find sex differences in the testosterone response × cortisol response or testosterone response × basal

cortisol interactions. These findings suggest that in an acutely stressful situation, the dual-hormone effects may be specific to the interaction between basal testosterone and the acute cortisol stress response.

We do note a significant, negative zero order correlation between testosterone responses to the stressor and dominant decision-making in the dictator game (Table S1). This relationship between testosterone reactivity and decision-making was weaker and not robust to controlling for testosterone responses × cortisol responses or to the experimental manipulations of social status and hierarchy stability. This effect was also not dependent on sex (B = -1.27, *95%CI* [-2.80, 0.26], p = .10).

3.5. Positive and negative affect responses to stress

To test whether the acute stressor influenced positive or negative affect, we conducted a MLM analysis with time of measurement (pre- vs. post-stress) as a within-subjects factor. We found significant main effects indicating a decline in positive affect (B = -0.205, *95%CI*[-0.30, -0.11], p <.001) but no change in negative affect (B = 0.043, *95%CI* [-0.08, 0.17], p =.508; see Figure 2; see also Knight and Mehta, 2017 for further analyses with affective measures).

3.6. Basal testosterone × affective responses

We tested if basal testosterone's role in dictator game decisions depended on affective responses to the TSST. As a primary metric of affective response, we used affect change from pre- to post-stressor. Our analyses revealed no significant interactions between basal testosterone x affect response scores for either positive or negative affect (*ps*>.95; Table S7).

3.7. Cardiovascular responses to stress

Next, we examined the effects of the acute stressor on cardiovascular responses via MLM analysis. The analysis revealed a significant change in HR (Time (linear): B = -5.43, *95%CI*[-6.58, -4.28], p <.001; Time (quadratic): B = -20.45, *95%CI*[-22.87, -18.03], p <.001) and HF HRV (Time (linear): B = 0.30, *95%CI*[0.19, 0.42], p <.001; Time (quadratic): B = 0.93, *95%CI*[0.74, 1.12], p <.001) over the course of the experiment. Consistent with prior research (Allen et al., 2014), the pattern of activity evident in these models was indicative of increased HR and vagal withdrawal (i.e., reduced HF HRV) during the

preparation period and stressor, with a general return to baseline during the recovery period (*ps*>.37; see Figure 2).

3.8. Basal testosterone × cardiovascular response

Finally, we tested if basal testosterone's role in dictator game decisions depended on cardiovascular responses (HR and HF HRV AUC_I) to the TSST. Our analysis revealed no significant interactions between basal testosterone and cardiovascular responses (*p*s>.38; Table S8).

4. Discussion

Previous research on the dual-hormone hypothesis has focused on basal cortisol in the absence of acute stress. The present study extends this body of work by providing evidence that in the presence of an acute stressor, the acute cortisol response to the stressor moderates basal testosterone's relationship with dominant status-relevant behavior in a dictator game. We found that for individuals with lower cortisol responses to the stressor, basal testosterone was positively associated with keeping more money for oneself in the dictator game (i.e., a dominant status-seeking behavior), but for those with higher cortisol responses, the testosterone-behavior relationship was suppressed. This pattern was found in men and women. These findings are conceptually aligned with the results of a previous study (Prasad et al., 2017), which provided initial evidence that acute cortisol change moderated basal testosterone's association with status-relevant decisions in a different behavioral task (rejecting unfair offers in the ultimatum game).

To a large extent, past research has focused on the HPA-axis as the primary outcome of the acute stress response (Dickerson and Kemeny, 2004). However, the acute stress response is multifaceted, encompassing a wide array of biological and psychological systems that function in concert (Sapolsky et al., 2000). Our findings revealed that despite evidence of parasympathetic nervous system and affective (positive and negative) responses to the stressor, these stress markers did not moderate the relationship between basal testosterone and dictator game decisions. These results suggest that the antagonistic effects of stress on the testosterone-behavior relationship may be specific to cortisol stress responses, a conclusion that further clarifies the dual-hormone hypothesis. Nevertheless, this interpretation is tentative

and must be confirmed in new studies that measure additional stress response systems, including sympathetic nervous system activity, catecholamine levels, and overall cardiac reactivity (Chichinadze and Chichinadze, 2008), as well as other endocrine systems (e.g. DHEAS; Allen et al., 2014) and psychological states (e.g. challenge/threat responses; Mendes et al., 2001). Further, given that our results were correlational, to determine causality future work could administer testosterone and block HPA axis activity prior to a stressor (Andrews et al., 2012). If these two hormone systems do indeed have joint causal influences on behavior, then blocking the HPA axis should facilitate testosterone's effects on dominant decisions after a stressor. Moreover, if other stress responses still do not moderate the testosterone--decision-making relationship under conditions of inhibited HPA axis activity, then these results would implicate the HPA axis specifically, and not the wider stress response, as the moderator of testosterone's association with decision-making.

To determine the robustness of our findings, we tested the extent to which the moderating effect of acute cortisol change on the testosterone-decision relationship was seen across the broader trajectory of the stress response, as well as reactivity to and recovery from the stressor. We found that a composite measure of the cortisol stress response spanning the entire temporal trajectory of the stressor (AUC_I) significantly moderated the relationship between basal testosterone and dictator game decision-making; we found similar effects when examining cortisol reactivity and recovery separately. Exploration of the patterns across different metrics of cortisol stress responses (see Table 1) suggests that the interaction between basal testosterone and acute cortisol responses to the stressor was somewhat stronger for metrics of cortisol reactivity compared to cortisol recovery (similar to Prasad et al., 2017), but any slight differences should be interpreted with caution and must be replicated before firm conclusions are drawn. Further, other areas of stress research have treated reactivity and recovery to a stressor as separate constructs that have differential implications for the downstream effects of stress (i.e., for stress-linked health outcomes; Linden et al., 1997). Therefore, continued research is necessary to examine the time

course of cortisol stress responses and its impact on the testosterone's association with dominant behavior.

It is important to consider possible mechanisms for cortisol's suppressive effects on basal testosterone's link to dominant decision-making that is linked to status seeking. One psychological mechanism may involve cortisol's effects on the approach and avoidance motivational systems (Carver and White, 1994). Higher levels of cortisol have been theorized to decrease motivation to approach and increase motivation to avoid social stimuli (Dickerson and Kemeny, 2004; Roelofs et al., 2009; Tops and Boksem, 2010). Lower cortisol responses to the stressor may propel individuals with higher levels of testosterone to readily approach, and not avoid, status-seeking behavior. In contrast, increased cortisol responses may relate to increased avoidance, thereby blocking testosterone's influence on dominant status-seeking behavior. Measurements of motivational approach and avoidance directly via self-reports and implicit psychological measures (Roelofs et al., 2009) in future research will help elucidate their role as a mechanism of cortisol's inhibitory effects on testosterone and dominant status-seeking behaviors.

Acute cortisol reactivity may also affect associations between testosterone and dominant decision-making via neural systems implicated in reward sensitivity. Testosterone facilitates reward-seeking behavior via activity in the nucleus accumbens in rodents (Packard et al., 1997) and is associated with increased neural activity in the human ventral striatum in anticipation of and when receiving rewards (Hermans et al., 2010). Limited evidence suggests higher cortisol levels relate to down-regulation of activity in reward networks (Kinner et al., 2016; Montoya et al., 2014). Given that reward motivation may partly underlie dominant status-relevant behaviors in the dictator game (Fliessbach et al., 2007), testosterone may result in greater dominant behaviors only when cortisol levels are low; higher levels of cortisol may suppress testosterone's effects on neural reward systems and therefore reduce dominant behaviors. However, other findings link stress and cortisol responses to increased reward-related neural activation and behaviors in humans (Oei et a., 2014) and rodents (Lewis et al., 2014; Rouge-Pont et al.,

1998). Additional research is therefore necessary to elucidate this neural pathway as a mechanism for our results.

At the molecular level, elevated cortisol levels may block the association between testosterone and behavior by suppressing androgen receptors (Tilbrook et al., 2000; Viau, 2002). Given the short duration between the last elevated cortisol sample (TSST + 20) and the measurement of behavior (approximately 25 minutes after the last elevated cortisol sample), it is unlikely that cortisol exerted its effects on behavior via the relatively slow, genomic transcriptional route to suppressing androgenic receptor functioning (Moore and Evans, 1999) seen in studies of chronic cortisol elevation (Tilbrook et al., 2000). Instead, we suspect that elevated levels of cortisol may have altered androgen receptor functioning via rapid, non-genomic pathways (Makara and Haller, 2001; Moore and Evans, 1999) and subsequently altered behavior (Casto and Edwards, 2016). This non-genomic mechanism that explains the moderating effect of an acute cortisol response on the relationship between testosterone and status-relevant behaviors is speculative and in need of further investigation.

We discuss the psychological, neural, and molecular mechanisms of cortisol's moderation of testosterone independently. However, elevated cortisol levels may simultaneously modulate androgen receptor functioning in reward-specific areas of the brain that subsequently changes psychological motivations that drive specific behavior. Future research is necessary to test the role of these mechanisms as independent versus unified responses.

Consistent with prior dual hormone theorizing, the present research provides evidence of endocrine correlates of a dominant route to status attainment in the dictator game (i.e., by keeping more money for oneself). However, research has shown that prosocial tactics may also allow individuals to ascend the status hierarchy (Cheng et al., 2013; Hardy and van Vugt, 2006), and that these prosocial tactics may be especially beneficial for status attainment in specific cooperative contexts (Halevy et al., 2011). For example, it is possible that manipulating the identity of the target in the dictator game - for instance using a charitable organization rather than an unknown confederate in situations in which one's donation

decisions are visible to other group members, may elicit more equitable behavior to gain the respect and admiration of others as a means to ascend the status hierarchy (Eckel and Grossman, 1999). Therefore, we theorize that in this charity version of the dictator game individuals with high basal testosterone and reduced cortisol responses may pursue status by demonstrating prosocial behavior evidenced by being more equitable in their resource allocations. Future research may consider altering specific factors in the social context of the paradigm to investigate dual-hormone effects of basal testosterone and cortisol responses to stressors on both dominant and prosocial routes to status.

In the current research, we provide evidence that individuals with high basal testosterone and a buffered acute cortisol response demonstrated proactive dominant behaviors via asymmetrical resource allocation in the dictator game (Hoffman et al., 1999), but the same endocrine profile facilitated reactive dominant behaviors via greater rejection of unfair offers in the ultimatum game (Prasad et al., 2017). Similar motivations may underlie both patterns of dominant behavior: Taking more money in the dictator game and rejecting unfair offers in the ultimatum game may both represent a heightened concern for one's social status and reputation (Bondarenko and Zakharov, 2018; Raihani and Bshary, 2015).[5] However, it is possible that these emergent dominant behaviors associated with a high basal testosterone and low acute cortisol change may be alternatively motivated by a desire to harm another individual as an

[5] A similar inference about status motivation has also been made in research linking the main effects of testosterone with the proposer decision-making in the ultimatum game. Eisenegger et al. (2010) found that testosterone administration in women increased ultimatum game proposer offers relative to those in the placebo group. The authors argued that due to the explicit threat of having one's offer rejected, individuals administered testosterone made more generous offers because of their concern for status. However, in another study the opposite pattern of effects was found: male proposers who were administered testosterone made less generous offers compared to themselves at baseline (Zak et al., 2009). In this study, the authors argued that individuals administered testosterone were motivated to behave selfishly ostensibly as a means to assert their higher status and therefore made lower offers. Although it is possible that the opposing results may be due to differences in study designs (e.g. sample recruited- females vs. male, nature of hormone administration –crossover vs. between-group design), future research may disentangle these divergent findings and the role of status concern by directly measuring status motivations accompanying ultimatum game proposer behavior. Moreover, given the inconsistent association between testosterone and ultimatum game proposer behavior across both studies, researchers may also consider examining the moderating role of the presence or absence of social stress and subsequent cortisol responses to stressors on the testosterone-behavior relationships, in addition to measuring the underlying status-relevant motivations of the resultant behavior.

ultimatum game respondent (Pillutla and Murnighan, 1996) or by reward maximization as a dictator game proposer (Fliessbach et al., 2007). To clearly delineate the role of status-relevant motivations underlying behaviors in economic decision-making paradigms, future research can modify or develop new economic decision-making paradigms that allow more direct inferences of status-relevance, pit divergent motivations within the same tasks to rule out alternative explanations, or use methodologies that directly measure status motivations and perceptions (for example, measurement of implicit power motivation or social status ratings in groups).

Whereas prior dual-hormone hypothesis research has largely focused on the moderating role of basal cortisol in non-stressful contexts (e.g. Pffatheicher, 2017), this study extends previous work by demonstrating that in acutely stressful contexts, cortisol responses to the stressor moderate basal testosterone's association with dominant status-seeking behavior. Moreover, there was no evidence of basal cortisol moderating the relationship between basal testosterone and dictator game decisions (Table S6). These findings suggest that in contexts involving acute stressors, cortisol responses to a stressor may be a key moderator of basal testosterone's link with status-relevant behaviors such as dictator game decisions and, in the absence of acute stress, basal cortisol may function as a moderator. Future research should directly test this hypothesis by manipulating the presence or absence of acute stress and compare the moderating roles of basal cortisol versus cortisol response on basal testosterone's behavioral effects. To provide rigorous measures of basal hormones and acute hormone changes, future studies should also consider measuring steroid hormones with mass-spectrometry based measures (Welker et al., 2016). Whereas saliva is well suited for measuring hormone responses to acute stressors, future work should consider using hair samples, which may better capture basal hormone concentrations over several months (Grotzinger et al., 2018).

We also did not find evidence of a testosterone response and cortisol response interaction predicting dictator game decisions, but the strong correlation between the hormone reactivity measures (Table S1) may have restricted our ability to detect an interaction. However, we do note that a higher

testosterone response to the stressor was associated less dominant behavior (i.e., keeping less money for oneself in the dictator game), albeit not robustly when controlling for the experimental conditions in this archival data. Moreover, this main effect of testosterone responses on dictator game decisions was in the same direction as the relationship between basal testosterone and dictator game decisions for those who demonstrated greater cortisol reactivity to the stressor, evident as the negative slope between basal testosterone and dominant dictator game decisions at higher levels of acute cortisol change (Figure 3). Cortisol rose on average for this sample (i.e., few people had neutral or withdrawal responses to the stressor), and so this negative, main effect of testosterone stress responses may be illustrative of the relatively restricted range of increased cortisol responses. Although this negative relation between the acute testosterone stress response and dominant decision making was relatively weak, future research should continue to measure testosterone reactivity to social stressors and examine the behavioral consequences of those responses (Knight and Mehta, 2017).

As a limitation, we note the use of archival data (Knight and Mehta, 2017) to conceptually replicate Prasad et al. (2017), and therefore our study included contextual manipulations that may have diminished our effect sizes or acted as contextual moderators. Although we found no evidence of moderation of the basal testosterone and cortisol reactivity interaction by the experimental manipulations, we may have been underpowered to detect those higher-order effects. Similarly, although we found a similar pattern of effects across men and women, we again may not have had sufficient statistical power to detect sex differences. Future research should consider using larger mixed-sex samples to test for contextual moderators of and gender differences in testosterone's relationship with dictator game decisions. This is especially important given that status-relevant features of the social context may modulate both testosterone's independent effects (Eisenegger et al., 2011) and testosterone and cortisol's interactive effects on behavior (Geniole et al., 2011; Mehta and Josephs, 2010).

Furthermore, while we examined cortisol as a moderator of testosterone's association with status-relevant dominant behavior, it is possible that for women, estrogens such as estradiol may bear greater

behavioral consequences than testosterone (Casto and Prasad, 2017). Estradiol has been positively associated with status-seeking behaviors (implicit power motivation: Stanton and Schultheiss, 2007; assertiveness in women: Blake et al., 2017). Moreover, recent evidence suggests that cortisol may also moderate the association between estradiol and dominant behaviors (i.e., externalizing behaviors) in adolescents with higher emotional instability and disagreeableness (Tackett et al., 2015). Future studies should continue to examine estrogens to determine the extent to which they interact with cortisol to direct status-seeking behaviors.

References

Allen, A.P., Kennedy, P.J., Cryan, J.F., Dinan, T.G., Clarke, G., 2014. Biological and psychological markers of stress in humans: Focus on the Trier Social Stress Test. Neurosci. Biobehav. Rev. doi:10.1016/j.neubiorev.2013.11.005

Anderson, C., Hildreth, J. A. D., & Howland, L. (2015). Is the desire for status a fundamental human motive? A review of the empirical literature. Psychological Bulletin, 141(3), 574.

Andrews, J., D'Aguiar, C., Pruessner, J.C., 2012. The combined dexamethasone/TSST paradigm--a new method for psychoneuroendocrinology. PLoS One 7, e38994. doi:10.1371/journal.pone.0038994

Bates, D., Maechler Martin, Walker, S., 2016. Package "lme4". CRAN Repos. doi:10.18637/jss.v067.i01

Blake, K.R., Bastian, B., O'Dean, S.M., Denson, T.F., 2017. High estradiol and low progesterone are associated with high assertiveness in women. Psychoneuroendocrinology 75, 91–99. doi:10.1016/j.psyneuen.2016.10.008

Boksem, M.A.S., Mehta, P.H., Van den Bergh, B., van Son, V., Trautmann, S.T., Roelofs, K., Smidts, A., Sanfey, A.G., 2013. Testosterone Inhibits Trust but Promotes Reciprocity. Psychol. Sci. 24, 2306–2314. doi:10.1177/0956797613495063

Bondarenko, O. & Zakharov, A., 2018. Measurement of Social Status in Experimental Games. Journal of the New Economic Association. 38. 12-47.

Carver, C.S., White, T.L., 1994. Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. J. Pers. Soc. Psychol. 67, 319–333. doi:10.1037/0022-3514.67.2.319

Casto, K. V., Edwards, D.A., 2016. Testosterone, cortisol, and human competition. Horm. Behav. doi:10.1016/j.yhbeh.2016.04.004

Casto, K. V., Prasad, S., 2017. Recommendations for the study of women in hormones and competition research. Horm. Behav. 92, 190–194. doi:10.1016/j.yhbeh.2017.05.009

Cheng, J.T., Tracy, J.L., Foulsham, T., Kingstone, A., Henrich, J., 2013. Two ways to the top: Evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. J. Pers. Soc. Psychol. 104, 103–125. doi:10.1037/a0030398

Chichinadze, K., Chichinadze, N., 2008. Stress-induced increase of testosterone: Contributions of social status and sympathetic reactivity. Physiol. Behav. 94, 595–603. doi:10.1016/j.physbeh.2008.03.020

Cueva, C., Roberts, R.E., Spencer, T.J., Rani, N., Tempest, M., Tobler, P.N., Herbert, J., Rustichini, A., 2017. Testosterone administration does not affect men's rejections of low ultimatum game offers or aggressive mood. Horm. Behav. 87, 1–7. doi:10.1016/j.yhbeh.2016.09.012

Dickerson, S.S., Kemeny, M.E., 2004. Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. Psychol. Bull. 130, 355–91. doi:10.1037/0033-2909.130.3.355

Dickerson, S.S., Mycek, P.J., Zaldivar, F., 2008. Negative Social Evaluation, but Not Mere Social Presence, Elicits Cortisol Responses to a Laboratory Stressor Task. Heal. Psychol. 27, 116–121. doi:10.1037/0278-6133.27.1.116

Dreber, A., Johannesson, M. (in press). Sex hormones and economic decision making in the lab: A review of causal evidence: Past, present, and future, in: O.C. Schultheiss and P.H. Mehta (Eds.), The International Handbook of Social Neuroendocrinology. Routledge Press.

Eckel, C. C., & Grossman, P. J. (1996). Altruism in anonymous dictator games. Games and economic behavior, 16(2), 181-191.

Eisenegger, C., Haushofer, J., Fehr, E., 2011. The role of testosterone in social interaction. Trends Cogn. Sci. doi:10.1016/j.tics.2011.04.008

Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., & Fehr, E. (2010). Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature*, *463*(7279), 356.

Fliessbach, K., Weber, B., Trautner, P., Dohmen, T., Sunde, U., Elger, C.E., Falk, A., 2007. Social comparison affects reward-related brain activity in the human ventral striatum. Science (80-.). 318, 1305–1308. doi:10.1126/science.1145876

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, 1–9. doi:10.1016/j.yhbeh.2013.09.005

Geniole, S.N., Carré, J.M., McCormick, C.M., 2011. State, not trait, neuroendocrine function predicts costly reactive aggression in men after social exclusion and inclusion. Biol. Psychol. 87, 137–145. doi:10.1016/j.biopsycho.2011.02.020

Halevy, N., Chou, E.Y., Cohen, T.R., Livingston, R.W., 2012. Status conferral in intergroup social dilemmas: Behavioral antecedents and consequences of prestige and dominance. J. Pers. Soc. Psychol. https://doi.org/10.1037/a0025515

Hedeker, D., Mermelstein, R.J., Demirtas, H., 2011. Modeling Between- and Within-Subject Variance in Ecological Momentary Assessment (EMA) Data Using Mixed-Effects Location Scale Models. Stat. Med. 1–15. doi:10.1002/sim.0000

Hermans, E.J., Bos, P.A., Ossewaarde, L., Ramsey, N.F., Fernández, G., van Honk, J., 2010. Effects of exogenous testosterone on the ventral striatal BOLD response during reward anticipation in healthy women. Neuroimage 52, 277–283. doi:10.1016/j.neuroimage.2010.04.019

Hoffman, E., McCabe, K., Smith, V.L., 1999. Social distance and other-regarding behavior in dictator games: Reply. Am. Econ. Rev. doi:10.1257/aer.89.1.340

Kahneman, D., Knetsch, J.L., Thaler, R.H., 1986. Fairness and the Assumptions of Economics. J. Bus. 59, S285. doi:10.1086/296367

Kinner, V.L., Wolf, O.T., Merz, C.J., 2016. Cortisol alters reward processing in the human brain. Horm. Behav. 84, 75–83. doi:10.1016/j.yhbeh.2016.05.005

Kirschbaum, C., Pirke, K.M., Hellhammer, D.H., 1993. The "Trier Social Stress Test" - a tool for investigating psychobiological stress responses in a laboratory setting. Neuropsychobioloy 28, 76–81.

Knight, E.L., Mehta, P.H., 2017. Hierarchy stability moderates the effect of status on stress and performance in humans. Proc. Natl. Acad. Sci. 114, 78–83. doi:10.1073/pnas.1609811114

Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, 69(1), 1-33. doi:10.18637/jss.v069.i01

Lewis, A.H., Porcelli, A.J., Delgado, M.R., 2014. The effects of acute stress exposure on striatal activity during Pavlovian conditioning with monetary gains and losses. Front. Behav. Neurosci. 8. doi:10.3389/fnbeh.2014.00179

Liening, S.H., Josephs, R. a, 2010. It is not just about testosterone: Physiological mediators and moderators of testosterone's behavioral effects. Soc. Personal. Psychol. Compass 4, 982–994. doi:10.1111/j.1751-9004.2010.00316.x

Linden, W., Earle, T.L., Gerin, W., Christenfeld, N., 1997. Physiological stress reactivity and recovery: Conceptual siblings separated at birth? J. Psychosom. Res. doi:10.1016/S0022-3999(96)00240-1

Lozza, N., Spoerri, C., Ehlert, U., Hubmann, P., Kesselring, M., Farahmand, F., Sollberger, S., La Marca, R., 2017. Predicting Social Behavior: Basal and Dynamic Joint Effects of Testosterone and Cortisol. Adapt. Hum. Behav. Physiol. 3, 255–274. doi:10.1007/s40750-017-0069-9

Magee, J. C., & Galinsky, A. D. 2008. Social hierarchy: The self-reinforcing nature of power and status. Acad Manag Ann, 2, 351–398. doi:10.1080/19416520802211628

Makara, G.B., Haller, J., 2001. Non-genomic effects of glucocorticoids in the neural system: Evidence, mechanisms and implications. Prog. Neurobiol. 65, 367–390. doi:10.1016/S0301-0082(01)00012-0

Mazur, A., Booth, A. 1998. Testosterone and dominance in men. Behav. Brain Sci. 21, 353–363.

Mehta, P.H., Josephs, R.A., 2010. Testosterone and cortisol jointly regulate dominance: evidence for a dual-hormone hypothesis. Horm. Behav. 58, 898–906. doi:10.1016/j.yhbeh.2010.08.020

Mehta, P.H., Lawless DesJardins, N.M., van Vugt, M., Josephs, R.A., 2017. Hormonal underpinnings of status conflict: Testosterone and cortisol are related to decisions and satisfaction in the hawk-dove game. Horm. Behav. 92, 141–154. doi:10.1016/j.yhbeh.2017.03.009

Mehta, P.H., Prasad, S., 2015. The dual-hormone hypothesis: a brief review and future research agenda. Curr. Opin. Behav. Sci. 3, 163–168.

Mendes, W.B., Blascovich, J., Major, B., Seery, M., 2001. Challenge and threat responses during downward and upward social comparisons. Eur. J. Soc. Psychol. 31, 477–497. doi:10.1002/ejsp.80

Miller, G.E., Chen, E., Zhou, E.S., 2007. If it goes up, must it come down? Chronic stress and the hypothalamic-pituitary-adrenocortical axis in humans. Psychol. Bull. https://doi.org/10.1037/0033-2909.133.1.25

Montoya, E.R., Bos, P.A., Terburg, D., Rosenberger, L.A., van Honk, J., 2014. Cortisol administration induces global down-regulation of the brain's reward circuitry. Psychoneuroendocrinology 47, 31–42. doi:10.1016/j.psyneuen.2014.04.022

Moore, F.L., Evans, S.J., 1999. Steroid hormones use non-genomic mechanisms to control brain functions and behaviors: A review of evidence. Brain. Behav. Evol. 54, 41–50. doi:10.1159/000006610

Packard, M.G., Cornell, A.H., Alexander, G.M., 1997. Rewarding affective properties of intra-nucleus accumbens injections of testosterone. Behav. Neurosci. 111, 219–224. doi:10.1037/0735-7044.111.1.219

Pfattheicher, S. (2017). Illuminating the dual-hormone hypothesis: About chronic dominance and the interaction of cortisol and testosterone. Aggressive behavior, 43(1), 85-92.

Pillutla, M.M., Murnighan, J.K., 1996. Unfairness, anger, and spite: emotional rejections of ultimatum offers. Organ. Behav. Hum. Decis. Process. 68:208–224. http://dx.doi.org/10.1006/obhd.1996.0100.

Ponzi, D., Zilioli, S., Mehta, P.H., Maslov, A., Watson, N. V., 2016. Social network centrality and hormones: The interaction of testosterone and cortisol. Psychoneuroendocrinology 68, 6–13. doi:10.1016/j.psyneuen.2016.02.014

Prasad, S., Narayanan, J., Lim, V.K.G., Koh, G.C.H., Koh, D.S.Q., Mehta, P.H., 2017. Preliminary evidence that acute stress moderates basal testosterone's association with retaliatory behavior. Horm. Behav. 92, 128–140. doi:10.1016/j.yhbeh.2016.10.020

Preacher, K.J., Curran, P.J., Bauer, D.J., 2006. Computational Tools for Probing Interactions in Multiple Linear Regression, Multilevel Modeling, and Latent Curve Analysis. J. Educ. Behav. Stat. 31, 437–448. doi:10.3102/10769986031004437

Quintana, D., Heathers, J., Kemp, A., 2012. On the validity of using the Polar RS800 heart rate monitor for heart rate variability research. Eur. J. Appl. Physiol. 112, 4179–4180. doi:10.1007/s00421-012-2453-2

Raihani, N.J., Bshary, R., 2015. The reputation of punishers. Trends Ecol. Evol. doi:10.1016/j.tree.2014.12.003

Roelofs, K., van Peer, J., Berretty, E., Jong, P. de, Spinhoven, P., Elzinga, B.M., 2009. Hypothalamus-Pituitary-Adrenal Axis Hyperresponsiveness is Associated with Increased Social Avoidance Behavior in Social Phobia. Biol. Psychiatry 65, 336–343. doi:10.1016/j.biopsych.2008.08.022

Sapolsky, R.M., 2000. Stress hormones: Good and bad, in: Neurobiology of Disease. pp. 540–542. doi:10.1006/nbdi.2000.0350

Schultheiss, O.C., Stanton, S.J., 2009. Assessment of salivary hormones. In: Harmon-Jones, E., Beer, J. (Eds.), Methods in Social Neuroscience. The Guilford Press, New York, pp. 17–44.

Stanton, S.J., Schultheiss, O.C., 2007. Basal and dynamic relationships between implicit power motivation and estradiol in women. Horm. Behav. 52, 571–580. doi:10.1016/j.yhbeh.2007.07.002

Tackett, J.L., Reardon, K.W., Herzhoff, K., Page-Gould, E., Harden, K.P., Josephs, R.A., 2015. Estradiol and cortisol interactions in youth externalizing psychopathology. Psychoneuroendocrinology 55, 146–153. doi:10.1016/j.psyneuen.2015.02.014

Thayer, J.F., Lane, R.D., 2000. A model of neurovisceral integration in emotion regulation and dysregulation. J. Affect. Disord. 61, 201–16. doi:10.1016/S0165-0327(00)00338-4

Tilbrook, A.J., Turner, A.I., Clarke, I.J., 2000. Effects of stress on reproduction in non-rodent mammals: the role of glucocorticoids and sex differences. Rev. Reprod. 5, 105–113.

Tops, M., Boksem, M. A. (2011). Cortisol involvement in mechanisms of behavioral inhibition. *Psychophysiology*, *48*(5), 723-732.

Viau, V., 2002. Functional cross-talk between the hypothalamic-pituitary-gonadal and - adrenal axes. J. Neuroendocrinol. 14, 506–513.

Welker, K.M., Lozoya, E., Campbell, J.A., Neumann, C.S., Carré, J.M., 2014. Testosterone, cortisol, and psychopathic traits in men and women. Physiol. Behav. 129, 230–236. doi:10.1016/j.physbeh.2014.02.057

Welker, K.M., Lassetter, B., Brandes, C.M., Prasad, S., Koop, D.R., Mehta, P.H., 2016. A comparison of salivary testosterone measurement using immunoassays and tandem mass spectrometry. Psychoneuroendocrinology 71, 180–188. doi:10.1016/j.psyneuen.2016.05.022

Yamagishi, T., Horita, Y., Mifune, N., Hashimoto, H., Li, Y., Shinada, M., Miura, A., Inukai, K., Takagishi, H., Simunovic, D., 2012. Rejection of unfair offers in the ultimatum game is no evidence of strong reciprocity. Proc. Natl. Acad. Sci. 109, 20364–20368. doi:10.1073/pnas.1212126109

Zak, P.J., Kurzban, R., Ahmadi, S., Swerdloff, R.S., Park, J., Efremidze, L., Redwine, K., Morgan, K., Matzner, W., 2009. Testosterone administration decreases generosity in the ultimatum game. PLoS One. https://doi.org/10.1371/journal.pone.0008330

Zilioli, S., Ponzi, D., Henry, A., Maestripieri, D., 2015. Testosterone, Cortisol and Empathy: Evidence for the Dual-Hormone Hypothesis. Adapt. Hum. Behav. Physiol. 1, 421–433. doi:10.1007/s40750-014-0017-x

Figures

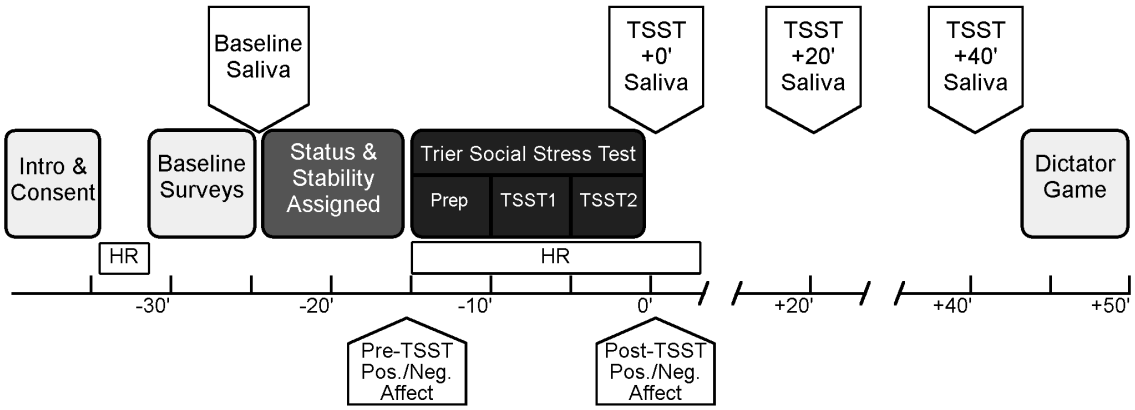


Figure 1. Timeline of the study. Time along the horizontal axis is denoted in minutes from the end of the TSST. "HR" denotes where heart rate was recorded (including a 10-minute recovery period after the TSST).

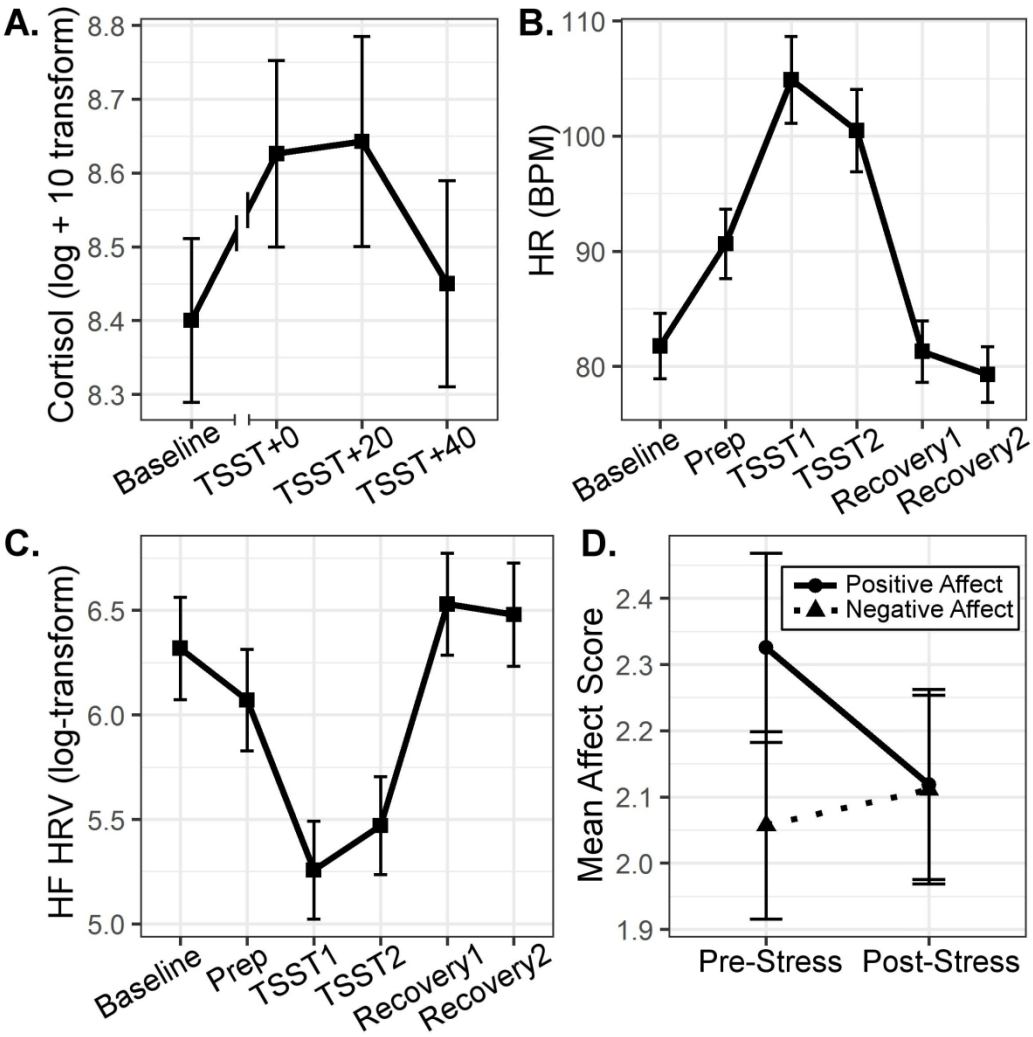


Figure 2. Estimated marginal means of stress responses investigated as potential moderators of testosterone's relationship with dominant behavior. A. Salivary cortisol response (log transformed + 10). B. Heart rate response (in beats per minute). C. Relative power of high-frequency heart rate variability response (log-transformed, ms2). D. Positive and negative affect response from pre- to post-stress.

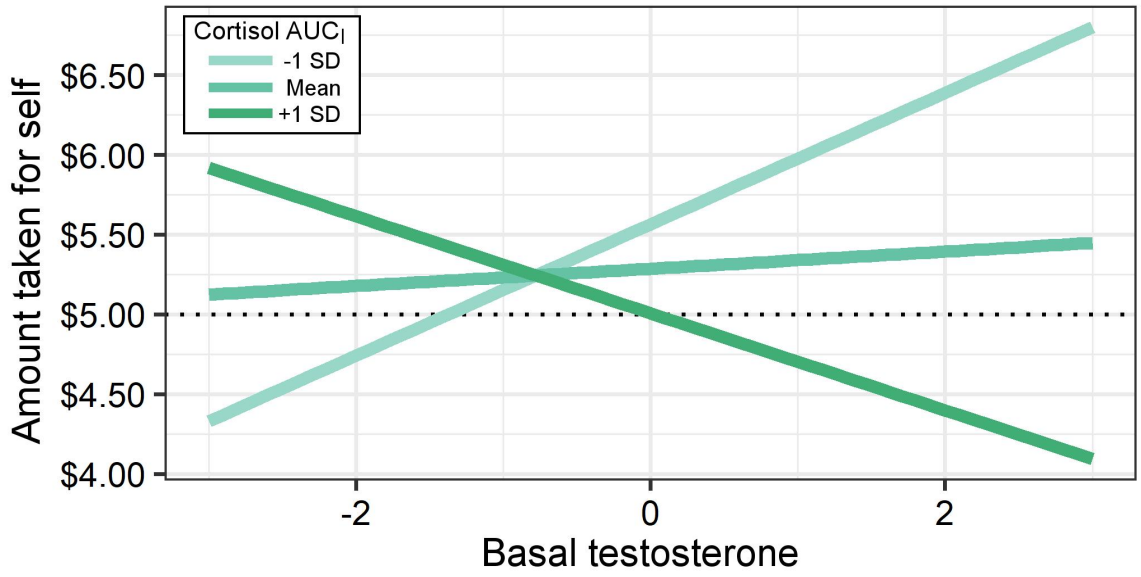
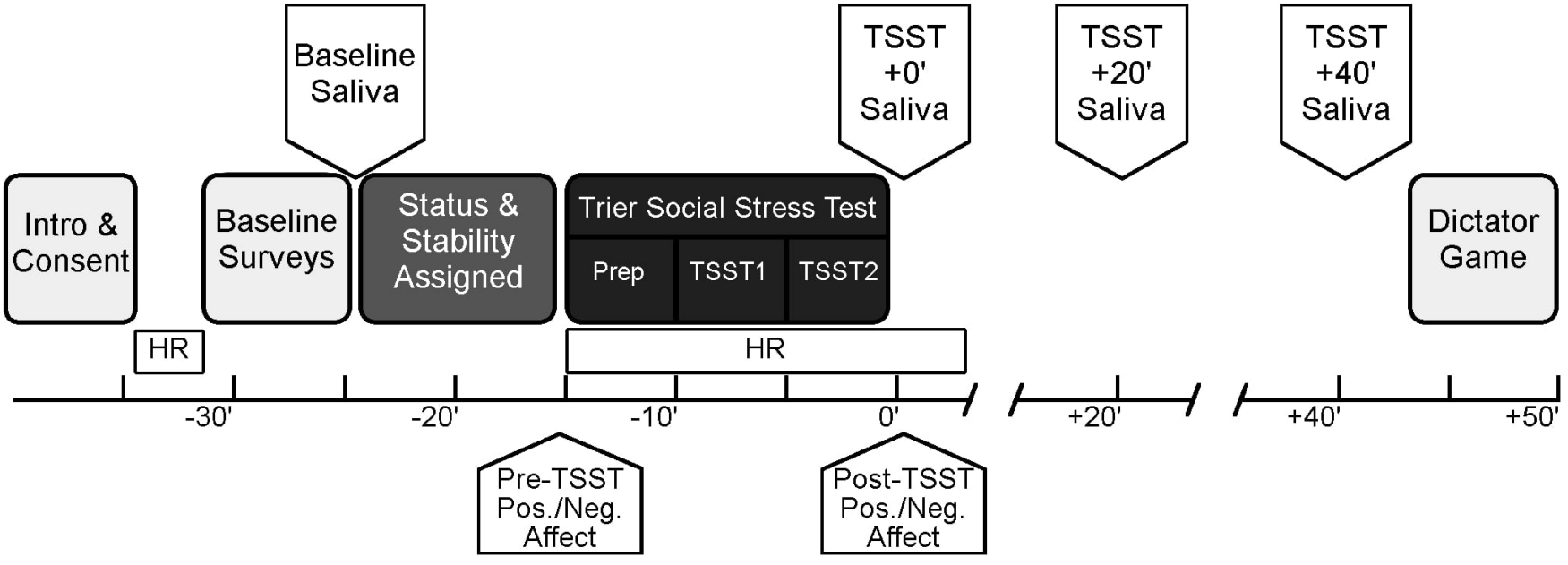


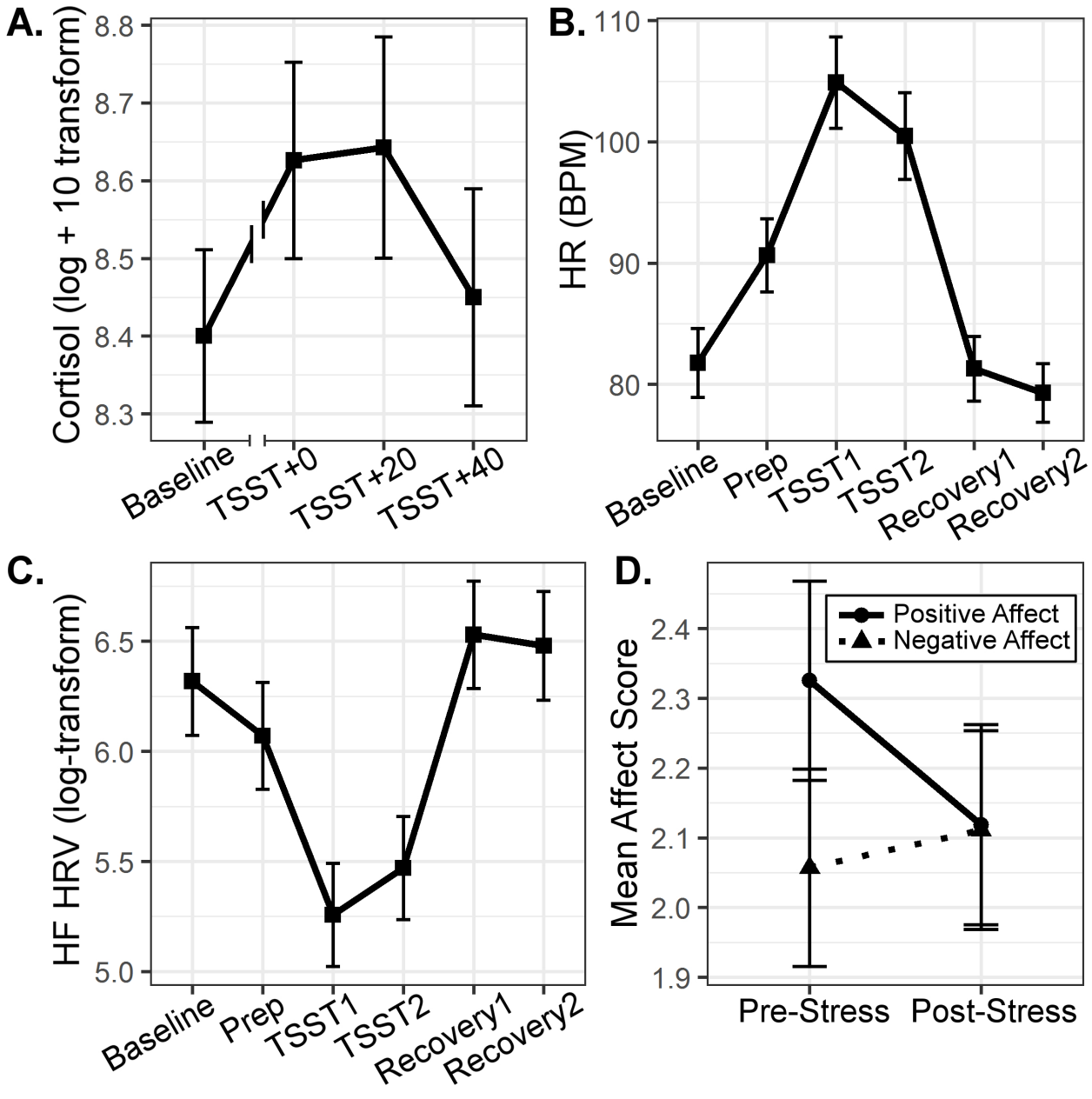
Figure 3. Estimated marginal means of interaction between basal testosterone (log-transformed and standardized within sex) and cortisol responses to the stressor (AUC_I) on the amount of money individuals decided to keep for themselves in the dictator game. Model controls for assignment to experiment conditions.

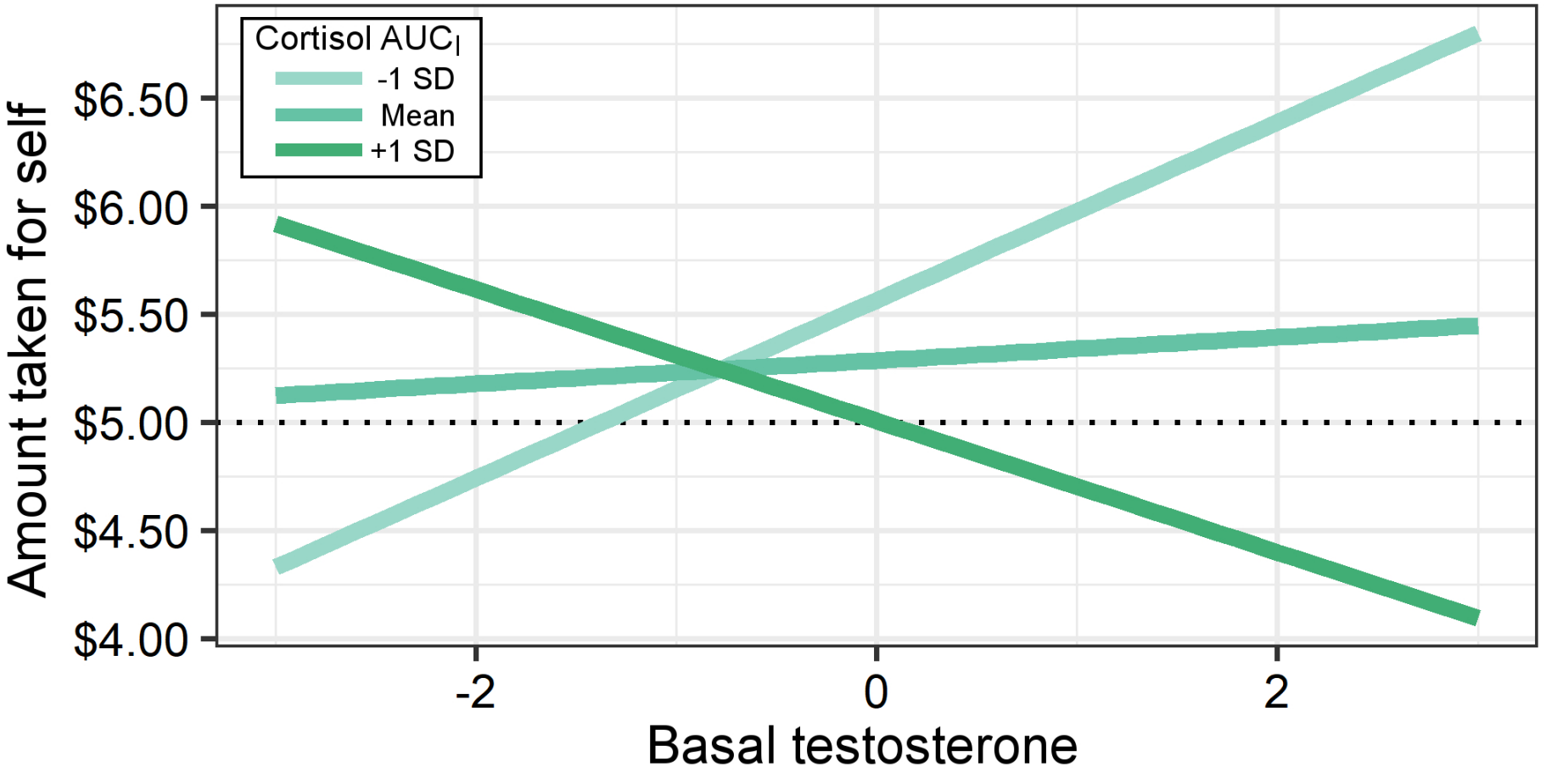
Tables

Table 1. General Linear Models (GLMs) with reactivity and recovery indices of cortisol response to stressor as moderator of testosterone's effects on dictator game decisions. Each column represents a separate GLM that controls for participant sex and experimental assignment to social status and hierarchy stability conditions.

	AUC_I			**TSST +0**			**TSST +20**			**TSST +40**		
	B	*CI*	*p*	*B*	*CI*	*p*	*B*	*CI*	*p*	*B*	*CI*	*p*
(Intercept)	5.29	4.99 – 5.58	<.001	5.31	5.02 – 5.60	<.001	5.28	4.99 – 5.58	<.001	5.27	4.97 – 5.57	<.001
Basal Testosterone	0.05	-0.25 – 0.36	.725	0.09	-0.21 – 0.39	.567	0.05	-0.26 – 0.35	.750	0.04	-0.27 – 0.35	.811
Cortisol Response	-0.23	-0.47 – 0.02	.071	-0.59	-1.34 – 0.15	.117	-0.46	-0.96 – 0.04	.070	-0.46	-1.00 – 0.09	.099
Testosterone x Cortisol Response	-0.29	-0.55 – -0.03	.029	-1.06	-1.88 – -0.25	.011	-0.54	-1.06 – -0.01	.046	-0.46	-1.03 – 0.10	.108
Social Status	-0.02	-0.32 – 0.27	.873	-0.02	-0.31 – 0.28	.908	-0.02	-0.32 – 0.27	.875	-0.03	-0.33 – 0.27	.840
Hierarchy Stability	-0.03	-0.34 – 0.27	.824	-0.04	-0.35 – 0.26	.779	-0.02	-0.33 – 0.28	.892	-0.02	-0.32 – 0.29	.922
Status x Stability	-0.01	-0.32 – 0.29	.933	-0.01	-0.31 – 0.29	.944	-0.00	-0.30 – 0.30	.988	-0.03	-0.34 – 0.28	.862
Observations		104			104			104			104	


Baseline Saliva
TSST +0' Saliva
TSST +20' Saliva
TSST +40' Saliva
Intro & Consent
Baseline Surveys
Status & Stability Assigned
Trier Social Stress Test
Prep
TSST1
TSST2
Dictator Game
HR
HR
-30'
-20'
-10'
0'
+20'
+40'
+50'
Pre-TSST Pos./Neg. Affect
Post-TSST Pos./Neg. Affect


A.
Cortisol (log + 10 transform)
8.8
8.7
8.6
8.5
8.4
8.3
Baseline
TSST+0
TSST+20
TSST+40
B.
HR (BPM)
110
100
90
80
Baseline
Prep
TSST1
TSST2
Recovery1
Recovery2
C.
HF HRV (log-transform)
6.5
6.0
5.5
5.0
Baseline
Prep
TSST1
TSST2
Recovery1
Recovery2
D.
Mean Affect Score
2.4
2.3
2.2
2.1
2.0
1.9
Positive Affect
Negative Affect
Pre-Stress
Post-Stress


Cortisol AUCI
-1 SD
Mean
+1 SD
Amount taken for self
$6.50
$6.00
$5.50
$5.00
$4.50
$4.00
-2
0
2
Basal testosterone

CONFLICT OF INTEREST DECLARATION FORM

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

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Supplementary Materials for:

Basal testosterone's relationship with dictator game decision-making depends on cortisol reactivity to acute stress: A dual-hormone perspective on dominant behavior during resource allocation

Supplementary Methods

Status and stability manipulations

The larger study from which the present data were derived manipulated social status and hierarchy stability (Knight and Mehta, 2017). A computer program informed participants that they had been assigned to complete an upcoming puzzle-building task as either a "manager" (high status) or "builder" (low status) based on their responses to questionnaires (Jordan, et al., 2011; Fast et al., 2009). Participants were also informed that another participant (a confederate) would perform the unassigned role. In reality, the roles were randomly assigned and there was no puzzle task. The program further stated that the manager would be in charge of directing subordinates in the building process and would evaluate the "builder" at the end of the task to determine how to split bonus money.

Following the status manipulation, participants were given information about the Trier Social Stress Test (see main document for details). Participants were then informed that their role (manager/builder) could change based on their performance in the TSST (unstable hierarchy) or that their performance on the task would not affect their role assignment (stable hierarchy). Panelists and confederates were blind to participants' randomly assigned conditions.

As noted in the main manuscript, all our analyses were robust to the status and stability manipulations. Further, our manipulations did not moderate the main results reported in this paper.

AUC_I Calculation for Cardiovascular Measures

For 84% (n = 93) of the participants with all epochs of cardiovascular data available, AUC_I was calculated as proscribed for time invariant data (i.e., each epoch was approximately 5 minutes in length and so was treated as invariant; Pruessner et al., 2003). For participants missing epochs of data (n = 5, 4.8%), an adjusted AUC_I was calculated if the following criteria were met:

1. Baseline data present.
2. At least 1 TSST epoch present.
3. At least 1 recovery epoch present.

Using these parameters, a response could be calculated from baseline, through the TSST and recovery periods using the Pruessner et al. (2003) time-variant method of AUC_I that could account for the missing data but still closely approximate the shape of the response had all data been available. For example, among participants with full data, an AUC_I calculated after removing one epoch each from the TSST and recovery epochs correlated highly with the full AUC_I score that did not arbitrarily remove epochs ($r = 0.98$, $p < .001$); similarly AUC_I calculated after removing the preparation epoch correlated strongly with the full AUC_I value ($r = 0.93$, $p < .001$). Using this adjusted AUC_I allowed for the sample size reported in the main document (n = 92 for cardiovascular analyses).

Supplementary Results

Table S1. Correlations among baseline and stress-linked change in study variables.

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
1. Basal Cortisol												
2. Cortisol AUC_I	-0.158											
3. Pre-Stress Negative Affect	0.128	-0.030										
4. Negative Affect Reactivity	-0.247*	-0.006	-0.298**									
5. Pre-Stress Positive Affect	-0.133	0.065	-0.316***	0.211*								
6. Positive Affect Reactivity	0.013	-0.119	0.095	-0.437***	-0.380***							
7. Baseline HR	0.113	0.074	0.103	0.142	-0.201*	-0.051						
8. HR AUC_I	0.207*	0.381***	-0.044	-0.102	0.129	-0.022	-0.342***					
9. Baseline HF HRV	-0.128	-0.090	-0.050	-0.023	0.142	0.069	-0.652***	0.093				
10. HF HRV AUC_I	-0.085	-0.163	-0.003	0.065	-0.041	-0.083	0.187+	-0.394***	-0.555***			
11. Basal T	0.308**	-0.004	0.007	-0.251**	0.015	-0.037	-0.087	0.201+	0.076	-0.061		
12. T AUC_I	-0.067	0.573***	0.144	-0.028	-0.030	-0.084	0.096	0.122	-0.063	-0.174	-0.187	
13. Dictator Game, Amount to self	-0.015	-0.174	-0.207*	-0.018	0.215*	0.034	-0.067	-0.024	-0.016	-0.003	0.061	-0.218*

Note: Cortisol and testosterone values are natural-log transformed. The log transformed basal testosterone scores were also standardized within sex. + < .10, * < .05, **<.01, ***<.001

Table S2. Correlations among baseline and stress-linked change in study variables in females.

Females	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
1. Basal Cortisol												
2. Cortisol AUC_I	-0.134											
3. Pre-Stress Negative Affect	0.041	-0.014										
4. Negative Affect Reactivity	-0.249	-0.113	-0.362**									
5. Pre-Stress Positive Affect	-0.13	0.142	-0.331**	0.301*								
6. Positive Affect Reactivity	0.055	-0.188	0.272*	-0.435***	-0.463***							
7. Baseline HR	0.21	0.106	0.128	0.129	-0.168	-0.012						
8. HR AUC_I	0.15	0.438***	-0.043	-0.191	0.173	-0.022	-0.319*					
9. Baseline HF HRV	-0.221	-0.104	-0.027	0.009	0.211	0.00	-0.745***	0.259				
10. HF HRV AUC_I	-0.044	-0.225	-0.09	0.012	-0.179	-0.017	0.319*	-0.656***	-0.561***			
11. Basal T	0.375**	-0.007	0.003	-0.400**	-0.094	0.129	-0.147	0.211	0.04	-0.146		
12. T AUC_I	-0.065	0.629***	0.222	-0.125	-0.056	0.001	0.168	0.236	-0.173	-0.206	-0.235	
13. Dictator Game, Amount to self	0.027	-0.081	-0.284*	-0.073	0.256*	-0.045	-0.207	0.038	0.127	-0.09	0.16	-0.168

Note: Cortisol and testosterone values are natural-log transformed. The log transformed basal testosterone scores were also standardized within sex.
+ < .10, * < .05, **<.01, ***<.001.

Table S3. Correlations among baseline and stress-linked change in study variables in males.

Males	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*
1. Basal Cortisol												
2. Cortisol AUC_I	-0.202											
3. Pre-Stress Negative Affect	0.254	-0.023										
4. Negative Affect Reactivity	-0.245	0.171	-0.219									
5. Pre-Stress Positive Affect	-0.142	-0.215	-0.308*	0.133								
6. Positive Affect Reactivity	-0.049	-0.028	-0.102	-0.449**	-0.315*							
7. Baseline HR	-0.026	0.161	0.054	0.163	-0.128	-0.127						
8. HR AUC_I	0.295	0.269	-0.005	0.029	-0.036	-0.018	-0.327*					
9. Baseline HF HRV	0.012	-0.121	-0.071	-0.074	0.034	0.168	-0.535***	-0.122				
10. HF HRV AUC_I	-0.155	-0.16	0.146	0.194	0.058	-0.182	0.024	-0.162	-0.580***			
11. Basal T	0.207	-0.001	0.009	-0.006	0.167	-0.255	0.004	0.19	0.125	0.088		
12. T AUC_I	-0.073	0.490***	0.032	0.192	-0.103	-0.227	0.061	-0.126	0.128	-0.173	-0.105	
13. Dictator Game, Amount to self	-0.066	-0.308*	-0.122	0.055	0.156	0.115	0.091	-0.088	-0.171	0.088	-0.043	-0.342*

Note: Cortisol and testosterone values are natural-log transformed. The log transformed basal testosterone scores were also standardized within sex.
$^{+}$< .10, * < .05, **<.01, ***<.001.

Basal testosterone × cortisol response effects are robust to experimental manipulation

The archival data available to test the present hypotheses were part of a larger study of the effects of social status and hierarchy stability on responses to stress (Knight & Mehta, 2017). Analyses contained in the main document controlled for the individual and interactive effects of these experimental assignments. Here we demonstrate weak moderation by social status, hierarchy stability, and their interaction on the testosterone × cortisol effects reported in the main document (Table S2). In each model, the new interaction term from the testosterone × cortisol × experimental assignment is null and the basal testosterone × cortisol response interaction remains relatively unchanged.

Table S4. Testosterone x Cortisol x Status x Stability. Test for moderation effects of experimental manipulations on the basal testosterone and cortisol AUC_I interaction.

	Basal T x C AUC_I x Status			Basal T x C AUC_I x Stability			Basal T x C AUC_I x Status x Stability		
	B	*CI*	*p*	*B*	*CI*	*p*	*B*	*CI*	*p*
(Intercept)	5.31	5.01 – 5.60	<.001	5.30	4.99 – 5.61	<.001	5.28	4.95 – 5.60	<.001
Testosterone (T)	0.02	-0.29 – 0.34	.883	0.10	-0.22 – 0.42	.524	0.07	-0.28 – 0.43	.679
Cortisol AUCI (C)	-0.23	-0.47 – 0.02	.066	-0.27	-0.53 – -0.02	.036	-0.26	-0.53 – 0.00	.052
Social Status	-0.03	-0.32 – 0.27	.851	-0.06	-0.37 – 0.25	.698	-0.06	-0.38 – 0.27	.724
Hierarchy Stability	-0.07	-0.38 – 0.24	.650	-0.05	-0.36 – 0.25	.727	-0.08	-0.40 – 0.25	.644
Status x Stability	-0.05	-0.36 – 0.26	.757	-0.00	-0.31 – 0.31	.993	-0.06	-0.39 – 0.26	.704
T x C	-0.33	-0.60 – -0.06	.017	-0.32	-0.60 – -0.04	.024	-0.34	-0.65 – -0.03	.034
T x Status	-0.19	-0.50 – 0.12	.235				-0.13	-0.49 – 0.22	.460
C x Status	-0.23	-0.47 – 0.01	.064				-0.27	-0.53 – -0.01	.046
T x C x Status	-0.09	-0.36 – 0.18	.525				-0.10	-0.41 – 0.21	.525
T x Stability				-0.11	-0.43 – 0.21	.497	-0.07	-0.42 – 0.29	.713
C x Stability				-0.09	-0.34 – 0.17	.510	-0.09	-0.36 – 0.17	.478
T x C x Stability				0.14	-0.14 – 0.42	.315	0.10	-0.22 – 0.41	.543
T x Status x Stability							-0.12	-0.47 – 0.24	.518
C x Status x Stability							-0.09	-0.36 – 0.17	.491
T x C x Status x Stability							0.08	-0.23 – 0.39	.601
Observations	104			104			104		
R^2 / adj. R^2	.129 / .046			.101 / .015			.158 / .015		

Sex differences in interactive effects of basal testosterone and cortisol response.

In the main document, we standardized testosterone within sex to control for sex differences. Here, we examine whether participant sex moderates the interactive effects of basal testosterone and cortisol responses on dictator game decisions. Sex was not found to moderate the basal testosterone × cortisol response interaction (Table S3). Visual inspection of the testosterone × cortisol effects on dictator game decisions revealed largely similar patterns across male and female participants, with some evidence for the interaction being stronger in men compared to women (Fig. S2).

Table S5. Test for sex-moderated effects of basal testosterone and cortisol AUC_I.

	Sex differences: Basal T x C AUC_I		
	B	*CI*	*p*
(Intercept)	5.18	4.78 – 5.57	<.001
Basal Testosterone (T)	0.17	-0.22 – 0.57	.388
Cortisol AUC_I (C)	-0.08	-0.43 – 0.26	.634
T x C	-0.18	-0.57 – 0.21	.358
Sex	0.40	-0.21 – 1.02	.197
T x Sex	-0.22	-0.83 – 0.39	.468
C x Sex	-0.41	-0.90 – 0.08	.098
T x C x Sex	-0.24	-0.77 – 0.30	.383
Social Status	-0.05	-0.35 – 0.25	.747
Hierarchy Stability	-0.03	-0.34 – 0.29	.866
Status x Stability	-0.03	-0.34 – 0.27	.836
Observations		104	
R^2 / adj. R^2		.132 / .038	

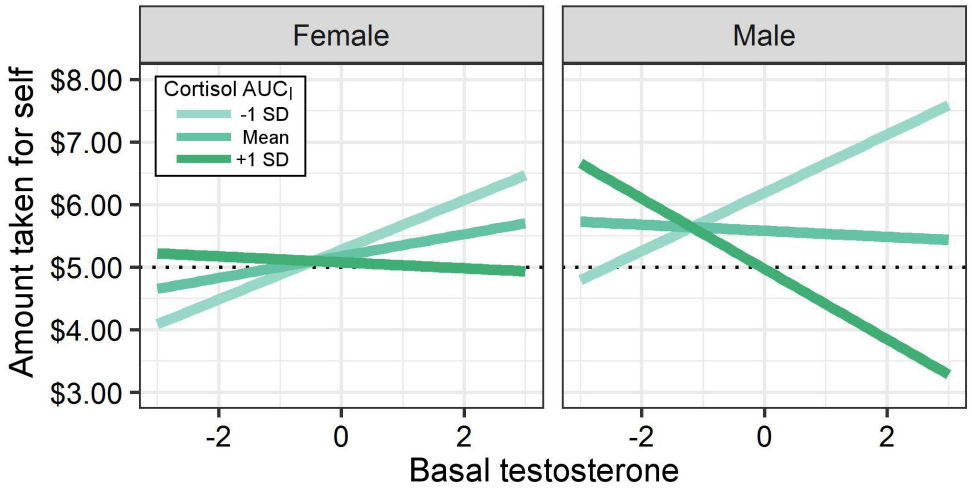

Figure S1. Patterns of effects of basal testosterone x cortisol responses on dictator game decisions in men and women.

Alternative testosterone × cortisol models

While the current study focused on the interactive effects of basal testosterone and cortisol reactivity to an acute stressor, prior dual-hormone work has also investigated basal testosterone x basal cortisol and testosterone reactivity x cortisol reactivity (Mehta & Prasad, 2015). We therefore followed-up our primary analyses with exploratory models of these alternative testosterone × cortisol dual-hormone hypothesis models. No other iteration of testosterone and cortisol interaction was found.

Table S6. Testosterone x cortisol effects using other indices testosterone and cortisol.

	Basal T × Basal C			T AUC_I × C AUC_I			T AUC_I × Basal C		
	B	*CI*	*p*	*B*	*CI*	*p*	*B*	*CI*	*p*
(Intercept)	5.34	5.02 – 5.65	<.001	5.30	4.95 – 5.64	<.001	5.46	5.12 – 5.79	<.001
Testosterone	0.08	-0.24 – 0.41	.607	-0.69	-1.59 – 0.22	.138	-0.85	-1.59 – -0.10	.026
Cortisol	-0.09	-0.66 – 0.47	.740	-0.09	-0.43 – 0.24	.529	-0.13	-0.80 – 0.55	.711
Testosterone × Cortisol	-0.27	-0.84 – 0.30	.352	-0.01	-0.59 – 0.58	.982	-0.09	-0.40 – 0.22	.566
Social Status	-0.01	-0.32 – 0.30	.943	0.01	-0.29 – 0.31	.937	0.02	-0.29 – 0.32	.919
Hierarchy Stability	0.07	-0.24 – 0.38	.669	-0.01	-0.32 – 0.29	.925	0.01	-0.30 – 0.31	.968
Status × Stability	0.02	-0.29 – 0.32	.919	-0.09	-0.40 – 0.22	.564	0.06	-1.24 – 1.36	.928
Observations	104			104			104		
R^2 / adj. R^2	.015 / -.046			.071 / .013			.052/-.006		

Moderation of testosterone's effects by other stress responses

The main document focused primarily on cortisol responses to stress. Here we present models in which we explored whether other stress response systems similarly moderated testosterone's effects on dictator game decisions. As reported in the main text, positive and negative affect responses to the stressor (Table S5), and heart rate (HR) and high-frequency heart rate variability (HF HRV) responses to the stressor (Table S6) did not moderate basal testosterone's effects on dictator game decisions.

Table S7. Interactive effects of basal testosterone and affective responses to stress do not predict dictator game decisions. Each column represents a separate GLM for either positive or negative affect as moderators of basal testosterone's effects on dictator game decisions.

	Basal T x Positive Affect			Basal T x Negative Affect		
	B	*CI*	*p*	*B*	*CI*	*p*
(Intercept)	5.30	4.99 – 5.60	<.001	5.27	4.95 – 5.58	<.001
Affect	0.12	-0.51 – 0.76	.696	-0.001	-0.47 – 0.47	.996
Basal Testosterone	0.09	-0.23 – 0.41	.578	0.09	-0.24 – 0.41	.592
Testosterone x Affect	-0.02	-0.60 – 0.57	.956	0.01	-0.39 – 0.42	.951
Social Status	-0.03	-0.34 – 0.29	.876	0.01	-0.30 – 0.32	.942
Hierarchy Stability	0.06	-0.26 – 0.37	.712	0.02	-0.29 – 0.33	.900
Status x Stability	-0.005	-0.32 – 0.31	.976	0.04	-0.27 – 0.35	.807
Observations		103			102	
R^2 / adj. R^2		.006 / -.056			.005 / -.058	

Table S8. Interactive effects of basal testosterone and cardiovascular responses to stress do not predict dictator game decisions. Each column represents a separate GLM for HR or HF HRV as moderators of basal testosterone's effects on dictator game decisions.

	Basal T x HR AUC_I			Basal T x HF HRV AUC_I		
	B	*CI*	*p*	*B*	*CI*	*p*
(Intercept)	5.32	4.974 – 5.666	<.001	5.31	4.961 – 5.653	<.001
Basal Testosterone	0.19	-0.190 – 0.562	0.33	0.21	-0.176 – 0.601	0.28
HR AUC_I	0.00	-0.007 – 0.008	0.92			
T x HR AUC_I	0.00	-0.009 – 0.003	0.32			
HF HRV AUC_I				0.00	-0.096 – 0.088	0.93
T x HF HRV AUC_I				0.04	-0.053 – 0.137	0.38
Social Status	-0.06	-0.407 – 0.279	0.71	-0.09	-0.440 – 0.262	0.61
Hierarchy Stability	0.02	-0.328 – 0.368	0.91	0.05	-0.298 – 0.405	0.76
Status x Stability	-0.03	-0.380 – 0.318	0.86	-0.02	-0.368 – 0.334	0.92
Observations	92			91		
R^2 / adj. R^2	.024 / -.045			.022 / -.048		

Supplementary References

Fast, N. J., Gruenfeld, D. H., Sivanathan, N., & Galinsky, A. D. (2009). Illusory control: A generative force behind power's far-reaching effects. *Psychological Science*, *20*(4), 502-508.

Jordan, J., Sivanathan, N., & Galinsky, A. D. (2011). Something to lose and nothing to gain: The role of stress in the interactive effect of power and stability on risk taking. *Administrative Science Quarterly*, *56*(4), 530-558.

Knight, E. L., & Mehta, P. H. (2017). Hierarchy stability moderates the effect of status on stress and performance in humans. *Proceedings of the National Academy of Sciences*, *114*(1), 78-83.

Pruessner, J. C., Kirschbaum, C., Meinlschmid, G., & Hellhammer, D. H. (2003). Two formulas for computation of the area under the curve represent measures of total hormone concentration versus time-dependent change. *Psychoneuroendocrinology*, *28*(7), 916-931.