



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.

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, 2000). 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, 2000). 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, 2000). 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

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[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 Johannesson, 2018 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 et al., 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 behavior². 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

² 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.

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. 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 (Fig. 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 min after the TSST, participants were asked to participate in an online, one-shot dictator game. The dictator game

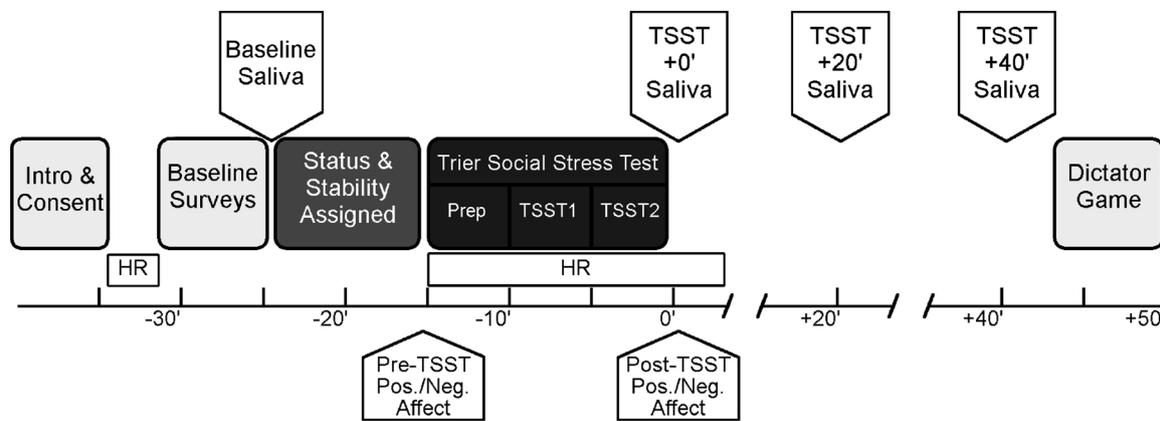


Fig. 1. Timeline of the study. Time along the horizontal axis is denoted in minutes from the end of the TSST. “HR” denotes where heart rate was recorded (including a 10-minute recovery period after the TSST).

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 confederate³ (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 h. 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 min 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).

2.6. Stress responses

2.6.1. Endocrine response

Saliva samples were obtained immediately (TSST + 0), 20 min (TSST + 20), and 40 min (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 1–5 scale, anchored on “Not at all” to “Extremely.” These questions were administered just prior to and

³ 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.

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* $\alpha = 0.91$); negative affect as the mean of the following items: distressed, upset, sad, irritable, ashamed, and nervous (*Cronbach’s* $\alpha = 0.82$).

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 msec²) 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 withdraws 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_1 (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., 2016). 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., 2011). 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)⁴. 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 Fig. 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 ($M = 0.24 \mu\text{g/dL}$, $SD = 0.21$)⁵, cortisol levels were significantly elevated at TSST + 0 ($M = 0.32 \mu\text{g/dL}$, $SD = 0.24$; $t(109) = 6.29$, $p < .001$), and TSST + 20 ($M = 0.34 \mu\text{g/dL}$, $SD = 0.3$; $t(109) = 4.04$, $p < .001$), but were not significantly different at TSST + 40 ($M = 0.28 \mu\text{g/dL}$, $SD = 0.25$; $t(109) = 1.07$, $p = 0.286$). 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).

⁴ 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.

⁵ Although analyses were run on natural-log-transformed cortisol concentrations, we report means and SDs for untransformed values.

3.3. Basal testosterone \times 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 \times cortisol AUC_i interaction ($B = -0.29$, $SE = 0.13$, $95\%CI[-0.55, -0.03]$, $t(97) = -2.21$, $p = .029$; Fig. 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 ($+1SD$: $B = -0.30$, $SE = 0.24$, $t(97) = -1.29$, $p = 0.199$). 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 min 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 \times cortisol response interaction, but we did not find significant three- or four-way interactions in these analyses ($ps > .30$; Table S4, Supplementary Materials). These results suggest that the basal testosterone \times cortisol response interaction did not further depend on these manipulations. Crucially, the basal testosterone \times 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 \times 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 \times basal cortisol interaction (see Table S6). Moreover, we also did not find a sex \times basal testosterone \times basal cortisol interaction, indicating that the null effect was not due to weak or opposing effects of basal testosterone \times 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

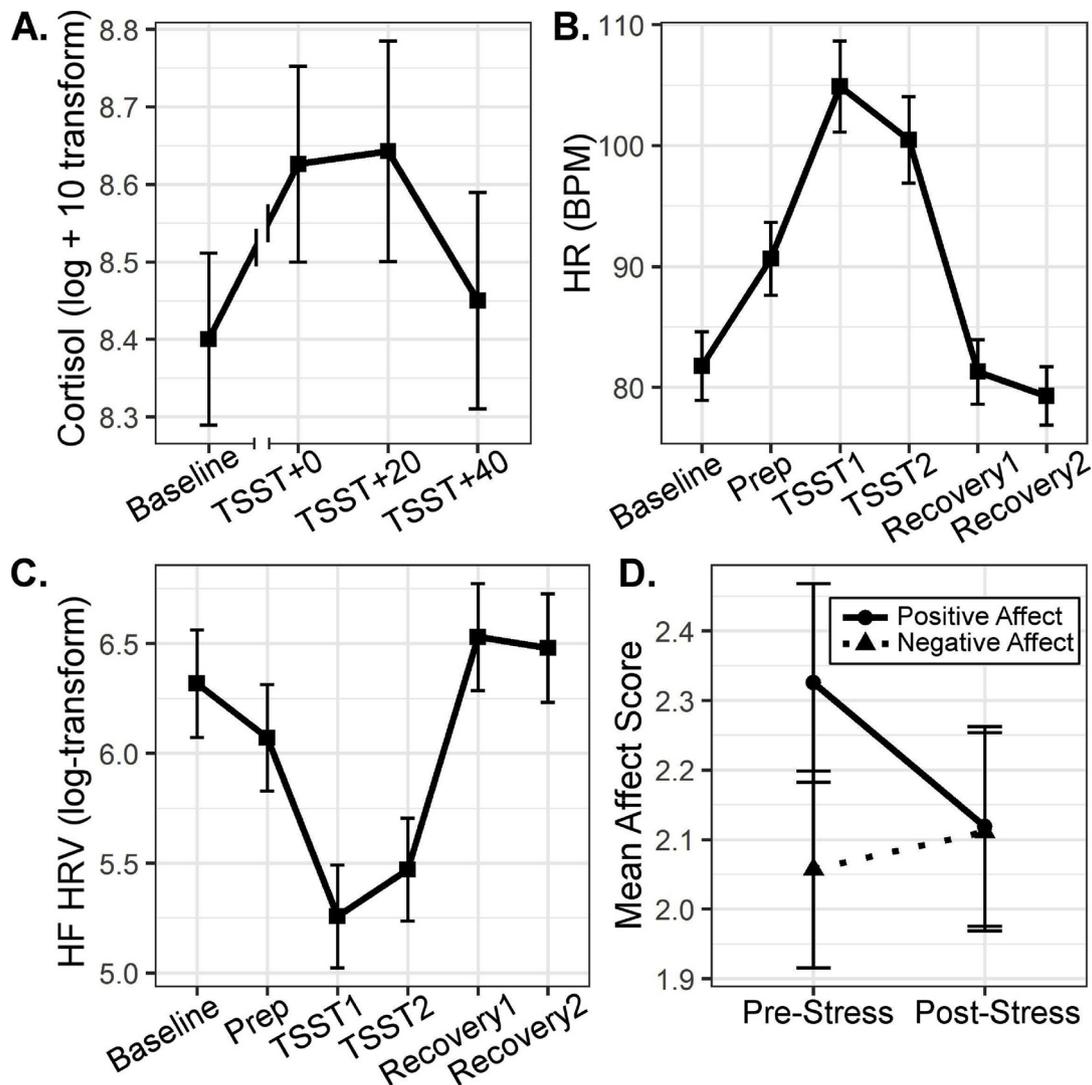


Fig. 2. Estimated marginal means of stress responses investigated as potential moderators of testosterone's relationship with dominant behavior. A. Salivary cortisol response (log transformed + 10). B. Heart rate response (in beats per minute). C. Relative power of high-frequency heart rate variability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

find support for a testosterone response \times cortisol response or testosterone response \times basal cortisol interaction (Table S6). Neither did we find sex differences in the testosterone response \times cortisol response or testosterone response \times 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 \times 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 Fig. 2; see also Knight and Mehta, 2017 for further analyses with affective measures).

3.6. Basal testosterone \times 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 \times affect response scores for either positive or negative affect (p s $> .95$; 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)

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

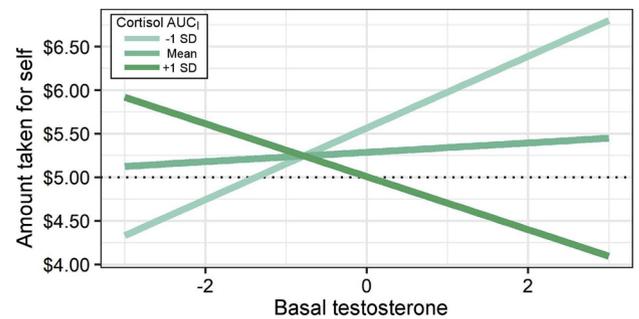


Fig. 3. Estimated marginal means of interaction between basal testosterone (log-transformed and standardized within sex) and cortisol responses to the stressor (AUC_i) on the amount of money individuals decided to keep for themselves in the dictator game. Model controls for assignment to experiment conditions.

during the preparation period and stressor, with a general return to baseline during the recovery period ($ps > .37$; see Fig. 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 ($ps > .38$; 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_c) 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, 2011). 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 al., 2014) and rodents (Lewis et al., 2014; Rougé-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 min 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 androgen 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., 2012). 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, 1996). 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).⁶ However, it is possible that these emergent

⁶ 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. It is however important to note some limitations in the Zak et al. study, including a small sample

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 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. Pfattheicher, 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 with 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 (Fig. 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

(footnote continued)

size and problematic statistical analysis (see Dreber and Johannesson, 2018 for more discussion). Although it is also 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.

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.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.psyneuen.2018.11.012>.

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