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Testosterone and cortisol jointly regulate dominance: Evidence for a dual-hormone hypothesis

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ABSTRACT

Traditional theories propose that testosterone should increase dominance and other status-seeking behaviors, but empirical support has been inconsistent. The present research tested the hypothesis that testosterone's effect on dominance depends on cortisol, a glucocorticoid hormone implicated in psychological stress and social avoidance. In the domains of leadership (Study 1, mixed-sex sample) and competition (Study 2, male-only sample), testosterone was positively related to dominance, but *only* in individuals with low cortisol. In individuals with high cortisol, the relation between testosterone and dominance was blocked (Study 1) or *reversed* (Study 2). Study 2 further showed that these hormonal effects on dominance were especially likely to occur after social threat (social defeat). The present studies provide the first empirical support for the claim that the neuroendocrine reproductive (HPG) and stress (HPA) axes interact to regulate dominance. Because dominance is related to gaining and maintaining high status positions in social hierarchies, the findings suggest that only when cortisol is low should higher testosterone encourage higher status. When cortisol is high, higher testosterone may actually *decrease* dominance and in turn motivate lower status.

Social groups are often organized into status hierarchies. Higher status within a hierarchy comes with important benefits, including increased access to resources and greater influence over subordinates (Magee and Galinsky, 2008). It is not surprising, then, that low-ranking individuals are often motivated to rise in the hierarchy whereas high-ranking individuals are often motivated to maintain their status. One behavioral strategy that can be adopted to gain or maintain high status is to display dominance: a behavioral style that is assertive and self-assured (Anderson and Kilduff, 2009). Indeed, dominance behavior is associated with higher status across animal and human groups (Anderson and Kilduff, 2009; Saposky, 2005). Given the importance of dominance in hierarchical interactions, a large body of research has been devoted to understanding the biological factors that influence dominance behavior. In the current research we examine neuroendocrine influences on dominance in humans. We test the hypothesis that two hormones – testosterone and cortisol – jointly regulate dominance.

A large literature indicates that dominance behavior is influenced by testosterone (T), a steroid hormone regulated by the hypothalamic-pituitary-gonadal (HPG) axis. Naturally occurring and experimentally elevated T levels are positively related to aggressive and dominant behaviors in a variety of animal species, especially when social status is threatened (Anestis, 2006; Archer, 2006; Beehner et al., 2006; Giammanco et al., 2005; Gould and Ziegler, 2007; Wingfield et al., 1990). Consistent with these animal studies, there are human studies indicating that T is linked to dominance under conditions of status threat or challenge (Archer, 2006; Josephs et al., 2003, 2006; Jones and Josephs, 2006; Mazur and Booth, 1998; Mehta and Beer, 2010; Mehta et al., 2008, 2009; Newman et al., 2005; Wirth and Schultheiss, 2007; Zyphur et al., 2009). Other studies, however, have found weak or null results. For example, some recent human studies show little to no relation between circulating T and a variety of indices of dominance (toughness, leadership, van Bokhoven et al., 2006; competitive behavior, Mehta and Josephs, 2006; Carré and McCormick, 2008; self-reported dominance, Johnson et al., 2007; Josephs et al., 2006). Overall, the evidence suggests that higher T is related to social dominance, but some inconsistencies have emerged in this literature.

One possible explanation for the inconsistent findings is that the HPG axis may act in concert with other neuroendocrine systems to regulate behavior. If that is the case, then measurement of other hormones along with T might reveal hormone–behavior associations where none (or weak associations) had been observed previously. Although it has been speculated that interactions between hormone systems may be an important mechanism for social behavior (Terburg et al., 2009), this approach has received scant attention in empirical research. In fact, to date no research has explored whether T works together with other hormones to drive dominance behavior. Here we propose that T may interact with cortisol to regulate dominance.

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Cortisol (C) is a glucocorticoid hormone that is released by the hypothalamic-pituitary-adrenal (HPA) axis in response to physical and psychological stress (Dickerson and Kemeny, 2004; McEwen, 1998; Taylor et al., 2000). High C levels are linked to anxiety and social avoidance, whereas low C levels are linked to decreased stress and social approach (Brown et al., 1996; Dickerson and Kemeny, 2004; McEwen, 1998; Roelofs et al., 2009; Taylor et al., 2000). Most research has investigated T and C independently, but neurobiological studies hint at the possibility that C may antagonize the relation between T and behavior. For example, C suppresses the activity of the HPG axis, C inhibits the action of T on target tissues, and C downregulates androgen receptors (Burnstein et al., 1995; Chen et al., 1997; Johnson et al., 1992; Smith et al., 1985; Tilbrook et al., 2000). These studies demonstrate that C inhibits the pathway from T to behavior at multiple levels, bringing up the possibility that high C levels may block the influence of T on dominance.

Consistent with the hypothesis that C alters the effect of T on behavior, two studies in male clinical populations found that T interacts with C to predict physical aggression (Dabbs et al., 1991; Popma et al., 2007). In both studies, T levels were positively related to aggression, but only in individuals with low C. These previous studies imply that T may interact with C to influence dominance behavior. However, no empirical studies to date have tested this possibility.

The present research examined whether T and C jointly regulate dominance. We tested this *dual-hormone hypothesis* in the domains of leadership (Study 1) and competition (Study 2). Leadership is arguably one of the most important domains in which to study status and dominance, but there is surprisingly little research on hormones and leadership in humans (but see Rowe et al., 2004 for a study of T and leadership in male adolescents). Furthermore, even though most research on T and behavior has been conducted in males, there is growing evidence that T also plays a role in female social behavior (Josephs et al., 2003, 2006; Mehta et al., 2008, 2009; Newman et al., 2005; Wirth and Schultheiss, 2007; Zyphur et al., 2009). Therefore in Study 1 we obtained a large mixed-sex sample and tested our hypothesis across men and women. All participants provided a saliva sample for T and C measurements and were then videotaped in a position of leadership. Observers later watched the videos and rated leaders on dominance.

In Study 2 we tested the generalizability of our hypothesis by examining dominance in a head-to-head competition. Pairs of men reported to the laboratory and provided a saliva sample for T and C measurements. Then the participants competed against each other on a cognitive task in which victory and defeat were experimentally manipulated. After the competition, we measured dominance by asking individuals whether they wanted to re-challenge their opponent to a second competition (Carré and McCormick, 2008; Mehta et al., 2008; Mehta and Josephs, 2006). According to traditional theories (Archer, 2006; Mazur and Booth, 1998; Wingfield et al., 1990), T should be related to increased dominance in both studies. However, according to the dual-hormone hypothesis, T and C should jointly regulate behavior such that higher T should be positively related to dominance *only* when C is low.

Study 1: Dual-hormone regulation of dominance in leaders

Method

Participants

One hundred students (50% women) enrolled in an introductory psychology course at the University of Texas-Austin participated in the study in exchange for research credit. All procedures were approved by the University of Texas at Austin Institutional Review Board. Six participants were excluded because they could not be analyzed for hormone levels. The final analysis included 94 participants (45 men).

Procedure

Participants reported to the lab in same-sex pairs. All participants were instructed to sign up for an experimental session with a person that they did not know. Experimental sessions were conducted between 11:30 A.M. and 4:30 P.M. to minimize the effects of circadian fluctuations in T and C levels (Touitou and Haus, 2000). The experimenter led each participant to a separate lab room, obtained informed consent, and collected a saliva sample for T and C measurements. Standard salivary hormone collection procedures were used (Schultheiss and Stanton, 2009).

Leadership task. Participants were randomly assigned to the position of leader or follower (Newman et al., 2005) and then completed the leadership task while being videotaped (the WAIS-III Block Design Task, Wechsler, 1997). Participants were explicitly told that they were either "leader" or "follower" on the task and were given clear instructions for their role. The leader stood behind the follower, who was seated in front of a series of blocks. The experimenter handed the first block design picture to the leader. Leaders directed followers using verbal commands only on how to move the blocks in order to make the design of interest. Followers did not see a picture of the design. Once the design was complete, the leader indicated to the follower to stop the timer. The experimenter recorded the time and handed the leader the next design until nine designs were completed. Participants were then informed that they would switch leader and follower roles. This role switch was done so that all participants could be observed in a leadership position. Leaders and followers switched positions and repeated the block design task for nine new block design puzzles.

Observers' ratings of dominance in leaders

Once data collection in all pairs was complete, a scale was developed to assess dominance in leaders. The scale was inspired by previous psychological theory and research on dominance (Anderson and Kilduff, 2009; Buss and Craik, 1980). Previous research suggests that dominance is characterized by a constellation of global behavioral styles linked to a motivation to gain high status (Anderson and Kilduff, 2009; Mazur and Booth, 1998), including assertiveness and confidence; energetic, enthusiastic, and extraverted behaviors; verbal fluency; leader-like behavior; directive behavior and decisiveness; masculinity; and an expansive posture (Anderson and Kilduff, 2009; Buss, 1981; Buss and Craik, 1980; Rueb et al., 2008). Our final measure included 19 items that tap into dominance: engaged, bored (reverse-scored), leader-like, energetic, confident, shy/timid (reverse-scored), gave clear instructions, comfortable, assertive, directive, indecisive (reverse-scored), dominant, comfortable giving instructions, nervous (reverse-scored), stumbled over words (reverse-scored), masculine, anxious (reverse-scored), strong posture, and hesitant (reverse-scored). Seven independent observers (4 women, 3 men) watched the videotaped interactions and rated leaders on these 19 items using a 7-point Likert scale. These observers were research assistants who were not familiar with the participants in the study and were unaware of the study hypotheses. Inter-rater reliability for the 19 items was reasonable (average Cronbach's alpha was .80 across the 19 items). We aggregated across the 19 items to create an overall index of dominance in leaders. First, we took the average rating for each item across the seven observers. Then we reverse coded seven of the items: bored, shy/timid, indecisive, nervous, stumbled over words, anxious, and hesitant. Then we averaged across these seven reversed items along with the remaining 12 items to create an overall index of dominance. Scores on this dominance index ranged from 2.59 to 6.37, with a mean of 4.71. As part of the study, participants filled out a self-report measure of trait dominance prior to completion of the leadership task (Helmes and Jackson, 1977). As expected, self-reported trait dominance was moderately positively correlated with this index of observed dominance in leaders ($r = .31$, $p < .05$).

Hormone assays

The saliva samples were shipped on dry ice to Yerkes Biomarkers Laboratory (Emory University, Atlanta, GA). The samples were analyzed for T and C concentrations (Diagnostic Systems Laboratories, Webster, TX). All samples were assayed in duplicate. Intra-assay coefficient of variation (CV) for each sample was less than 20% for both T and C, and inter-assay CVs averaged across high and low controls were 3.65% for C and 10.67% for T. T and C levels were in the normal ranges (T in men: M = 99.93 pg/mL, SD = 44.45; T in women: 21.66 pg/mL, SD = 11.80; C in men: M = 0.94 μg/dL, SD = .58; C in women: M = 0.81 μg/dL, SD = .49).

Data analysis strategy

Our dual-hormone hypothesis posits that the relationship between T and dominance depends on C. In statistical terms, this hypothesis translates into a statistical interaction between T and C. An interaction term in statistics indicates that the relationship between variable X (e.g., T levels) and variable Y (e.g., dominance) depends on a third variable (C levels) (Aiken and West, 1991). Thus, a statistically significant interaction between T and C would provide robust evidence in support of the dual-hormone hypothesis. When there are multiple continuous variables (T and C levels) being used to predict a continuous dependent variable (dominance in leaders), the appropriate statistical approach is multiple regression (Aiken and West, 1991). Although researchers who are not familiar with regression sometimes test similar hypotheses by converting continuous variables into categories (median splits, upper and lower tertiles), this technique has significant drawbacks and therefore is not recommended by statisticians. One drawback is that the researcher loses information when grouping continuous variables into categories. For example, if a median split is performed on T levels, then an individual just above the median on T is considered the same as an individual at the very end of the T distribution. A second drawback is that there is a loss of statistical power with this approach, relative to a regression approach (Aiken and West, 1991). To interpret significant T × C interactions in regression, we employed the Aiken and West (1991) approach in which we used the regression model intercepts and slopes to graph dominance scores one standard deviation above and below the means for T and C levels. We also conducted simple slopes analyses for the relationship between T and dominance one standard deviation above and below the mean for C to test whether these simple slopes statistically differed from zero (Aiken and West, 1991). For an overview of multiple regression and interpreting interactions in multiple regression, see Aiken and West (1991).

Consistent with previous research (Mehta and Josephs, 2006; Mehta et al., 2008; Wirth et al., 2006), the C distribution was skewed in the present study so we log-transformed the distribution to approximate a normal distribution. T scores were standardized separately for men and women by converting the raw scores for every participant to z-scores (Josephs et al., 2006; Mehta and Beer, 2010; Mehta et al., 2009; Newman et al., 2005; Zyphur et al., 2009). High scores on this distribution indicate high T levels relative to other individuals of the same sex. Consistent with previous papers (Josephs et al., 2006; Mehta et al., 2008, 2009; Mehta and Beer, 2010; Newman et al., 2005; Zyphur et al., 2009; Wirth and Schultheiss, 2007), our main analysis combined men and women. There are two important benefits to combining men and women in the same analysis. First, statistical power is increased in a combined analysis. Second, patterns of hormone–behavior relationships can be examined for statistically significant sex differences in a combined analysis. In addition to our main multiple regression model that included both men and women, we also conducted follow-up simple slopes analyses in which we examined men and women separately. Finally, we included secondary analyses in which we conducted median splits on T and C levels. As reviewed above this approach is less robust than multiple regression, but we included these analyses because we reasoned they may be easier to interpret for readers unfamiliar with regression.

Results

Preliminary analyses

Consistent with prior research (Mehta et al., 2008; Popma et al., 2007), T and C levels were modestly positively correlated (analysis with men and women combined: $r = .28$, $p < .05$; men only: $r = .19$, $p = .21$; women only: $r = .36$, $p < .05$). Time of day was negatively correlated with C levels ($r = -.28$, $p < .05$) and cognitive performance was correlated with dominance scores (leaders who performed the block design leadership task more quickly were seen as more dominant, $r = -.35$, $p < .05$), so we included time of day and cognitive performance as covariates in our main analysis below.

Dual-hormone hypothesis

We hypothesized that the interaction between T and C would predict dominance in leaders such that T would be positively related to dominance only when C is low. To test this hypothesis and to test for sex differences, we conducted a hierarchical multiple regression analysis (see Data analysis strategy section above for justification and additional information on our statistical approach). In this analysis we entered dominance as the dependent variable and the following variables as predictors: time of day and cognitive performance as covariates in Step 1, gender, T, and C in Step 2, the T × C interaction in Step 3, and the gender × T × C interaction in Step 4. In support of the dual-hormone hypothesis, a statistically significant T × C interaction emerged, $\Delta R^2 = 4.8\%$, $F(1, 82) = 4.96$, $p < .05$.[1] There were no main effects of T or C (p's > .10). There was a marginally significant main effect of gender on dominance scores such that male leaders ($M = 4.87$, $SE = .12$) were rated marginally higher on dominance than female leaders ($M = 4.55$, $SE = .12$, $p < .10$), but there was a non-significant gender × T × C interaction (p's > .10) which indicates that the pattern of the T × C interaction was statistically equivalent across men and women.

To interpret the significant T × C interaction, we used the multiple regression model to graph dominance scores one standard deviation above and below the means for T and C (Aiken and West, 1991) (see Fig. 1). Simple slopes were also computed for the relation between T and behavior one standard deviation above and below the C mean, and these slopes were tested for statistical significance from zero (Aiken and West, 1991). In support of the hypothesis that high C blocks the effect of T on dominance, T was positively related to dominance in individuals low in C ($\beta = .34$, $p < .05$, see Fig. 1, solid line), but T and dominance were unrelated in individuals high in C ($\beta = -.08$, $p = .55$, see Fig. 1, striped line).

The non-significant gender × T × C interaction indicates that the T × C interaction pattern was statistically equivalent in men and women. We repeated the simple slopes analyses separately in men and women to confirm that the pattern of the interaction was indeed similar across the sexes. Consistent with the main analysis, T was

[1] The T × C interaction remained statistically significant when the covariates of time of day and cognitive performance were excluded from the regression model (p's < .05), but we decided to report the analysis with the covariates included because we believe it is a better estimate of the pattern of the interaction. Additional analyses found that T, C, and the T × C interaction were unrelated to cognitive performance in leaders (p's > .10). We also verified that the order of leadership (being the leader first or being the leader second) did not interact with hormones to predict dominance behavior (p's > .05). Finally, we confirmed that the T × C interaction was still statistically significant when we averaged across observers' ratings only for the one item "dominant" and ignored the other 18 items on the scale ($p < .05$), providing converging support for our hypothesis that T and C interact to predict dominance in leaders.

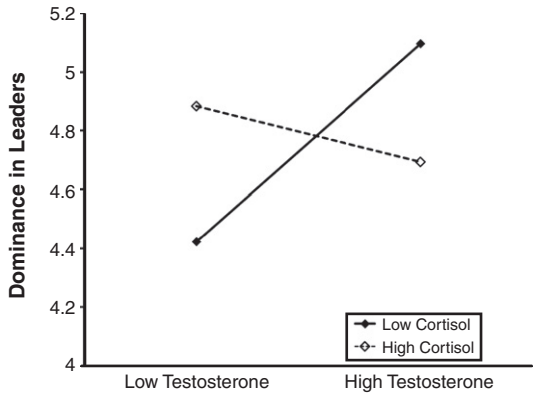

Fig. 1. Study 1: dominance in leaders (average of observers' ratings on a 7-point scale) as a function of testosterone and cortisol levels. Hormone levels were measured at the beginning of the experiment. Low = 1 standard deviation below mean; high = 1 standard deviation above mean. The intercept and slopes from the multiple regression model were used to plot dominance scores one standard deviation above and below the means for testosterone and cortisol.

positively related to dominance among men low in C ($\beta = .40$, $p < .05$), but T and dominance were unrelated among men high in C ($\beta = -.06$, $p > .70$). A similar pattern emerged in women. There was a positive slope between T and dominance only among women low in C ($\beta = .26$, $p = .14$), not among women high in C ($\beta = -.08$, $p > .60$). The similar patterns of simple slopes coupled with a non-significant gender × T × C interaction suggest that dual-hormone regulation of dominance generalizes to both men and women.

As an additional approach to understand the pattern of the T × C interaction, we created low and high T and C groups by conducting median splits on the T and C distributions. Individuals in the high T group included men and women in the upper median of T relative to other individuals of the same sex, and individuals in the low T group included men and women in the lower median of T relative to other individuals of the same sex (Josephs et al., 2006; Newman et al., 2005). As mentioned above in the Data analysis strategy section, median split analyses have significant drawbacks compared to multiple regression (loss of information and significant loss of statistical power), but we reasoned that this approach may be more understandable to readers unfamiliar with multiple regression. We conducted an analysis of covariance (ANCOVA) in which we entered dominance as the dependent variable, the median split T and C variables as predictors, and gender, performance, and time of day as covariates. Consistent with the main regression analysis, there was a statistically significant T × C interaction, $F(1, 82) = 4.43$, $p < .05$, and a non-significant T × C × gender interaction, $p > .90$. We then conducted follow-up analyses to examine the relationship between T and dominance in individuals with low and high C. In strong support of the claim that T increases dominance when C is low and consistent with the solid line in Fig. 1, individuals in the high T, low C group ($M = 5.04$, $SE = .21$) showed statistically higher dominance scores than individuals in the low T, low C group ($M = 4.47$, $SE = .17$), $F(1, 41) = 4.41$, $p < .05$. But consistent with the claim that high C blocks the effect of T on dominance and consistent with the striped line in Fig. 1, there was no statistically significant difference in dominance scores between the high T, high C group ($M = 4.61$, $SE = .14$) and the low T, high C group ($M = 4.82$, $SE = .16$), $F(1, 38) = .39$, $p > .30$. We then looked separately at men and women to verify that the patterns were similar in men and women. We did not expect statistically significant effects because of the dramatic reduction in statistical power associated with splitting our sample in half. These follow-up ANCOVA analyses revealed marginally significant T × C interactions in men ($F(1, 39) = 2.86$, $p < .10$) and in women ($F(1,40) = 2.78$, $p = .10$). The pattern of dominance scores across the low and high T and C groups was striking similar in men and women and was highly consistent with the dual-hormone hypothesis (men in the high T, low C group: $M = 5.28$, $SE = .31$; men in the low T, low C group, $M = 4.63$, $SE = .23$; men in the high T, high C group: $M = 4.72$, $SE = .23$; men in the low T, high C group, $M = 4.95$, $SE = .25$; women in the high T, low C group: $M = 4.83$, $SE = .22$; women in the low T, low C group: $M = 4.36$, $SE = .20$; women in the high T, high C group: $M = 4.45$, $SE = .23$; women in the low T, high C group, $M = 4.73$, $SE = .27$). Overall then, these median split analyses are consistent with the main regression analysis and provide convergent support for our hypothesis.

The results of Study 1 provide the first empirical support for dual-hormone regulation of dominance in showing that T interacts with C to predict dominance in leaders. The primary goal of Study 2 was to test the generality of the dual-hormone hypothesis by examining hormones and dominance in a different status-relevant domain: head-to-head competition. Another goal of Study 2 was to test whether dual-hormone regulation of dominance depends on the social context. A growing literature demonstrates that hormonal effects on dominance are especially likely to occur under conditions of status threat (e.g., social defeat, Carré and McCormick, 2008; Mehta et al., 2008; Jones and Josephs, 2006). Thus, in Study 2 we experimentally manipulated the social context by randomly assigning individuals to social defeat (status threat) or victory (no threat). We hypothesized that T and C should jointly predict dominance, but only after status is threatened.

Study 2: Dual-hormone regulation of dominance in competition

Method

Participants

Sixty-four males enrolled in an introductory psychology course at the UT-Austin participated in the study in exchange for research credit. All procedures were approved by the University of Texas at Austin Institutional Review Board. Hormone data were not available for seven participants, leaving 57 participants with complete data. Results from this dataset on independent effects of T and C were published in a previous paper (Mehta and Josephs, 2006), but analyses for interactions between T and C had not been conducted previously. For the purposes of the present research, we went back to this archival dataset and conducted analyses for pre-competition T × pre-competition C interactions.

Procedure

Pre-competition phase. Participants reported to the lab in pairs. All participants were instructed to sign up for an experimental session with a person that they did not know. Experimental sessions were conducted between 12:00 P.M. and 3:30 P.M. to minimize the effects of circadian fluctuations in T and C (Touitou and Haus, 2000). The experimenter then led each participant to a separate lab room, obtained informed consent, and collected a saliva sample to assess pre-competition T and C levels (Schultheiss and Stanton, 2009). To rule out possible changes in hormone levels due to anticipation of competition, participants were unaware that they would be competing at the time of saliva collection.

Competition task. After saliva collection, both participants were escorted into the same room and seated at two desks facing opposite walls. The experimenter announced to the participants that they would be competing against each other on a test of an important type of intelligence called “spatial processing speed”. The task used for the competition was the Number Tracking Task which consists of several puzzles (Josephs et al., 2006; Mehta et al., 2008). Participants thought they were competing on the same puzzles, but the competition was rigged. The participant randomly assigned to

win was given easier puzzles than the participant assigned to lose. Participants completed six puzzles, saying "done" after completing each one. The average duration of the competition was seven and a half minutes.

Post-competition hormone levels. Participants were escorted to separate rooms after the competition and worked on a filler task (a word search). Fifteen minutes after the end of the competition (approximately 30 to 35 min after the first saliva sample), participants provided a second saliva sample. This second saliva sample was included to examine acute fluctuations in hormone levels from before to after the competition. We waited 15 min after the end of the competition to collect this second saliva sample because it takes a few minutes for hormone levels in blood to reach saliva (cf. Riad-Fahmy et al., 1987). Our statistical analyses focused primarily on hormone concentrations from the first (pre-competition) saliva sample because our primary hypothesis concerned interactions between pre-competition T and C levels, but we also conducted follow-up analyses with dynamic hormone changes to examine secondary research questions of relevance in the present paper (see Results section).

Dominance. Following the second saliva sample participants completed a measure of dominance, a decision-making questionnaire in which participants were asked to choose the next experimental task (Carré and McCormick, 2008; Mehta et al., 2008). This questionnaire asked participants to choose one of two options: (a) compete again on six new puzzles of the Number Tracking Task against the same participant or (b) complete a questionnaire on food and entertainment preferences. The choice questionnaire indicated that option (b) would take about as long to complete as the Number Tracking Task. Participants made their choice by circling (a) or (b). This choice measure has been used in previous research on hormones and dominance and has high degree of ecological validity in that it measures an actual decision to enter into or avoid a second dominance battle against the same opponent (Carré and McCormick, 2008; Mehta et al., 2008).

Hormone assays and data analysis strategy. The saliva samples were analyzed for T and C concentrations (Salimetrics kits, State College, PA, USA). Intra-assay coefficient of variation (CV) averaged across all 57 participants was 4.7% for T and 3.1% for C. Inter-assay CVs for assays conducted in our lab average 8.7% for T and 2.8% for cortisol. T and C levels in the pre-competition saliva sample were in the normal ranges (T: $M = 159.50$ pg/mL, $SD = 70.31$, C: $M = 0.31$ μg/dL, $SD = .26$).

We hypothesized that T would interact with C to predict dominance, but only under conditions of status threat (social defeat). In statistical terms, this hypothesis translates into a three-way statistical interaction between T, C, and the experimental condition (victory or defeat). When there is a combination of categorical variables (experimental condition) and continuous variables (T and C levels) being used to predict a binary dependent variable (compete again versus complete alternative non-competitive task), the appropriate statistical approach is binary logistic regression. Although researchers sometimes test similar hypotheses by converting continuous variables into categories (median splits, upper and lower tertiles), this technique has significant drawbacks (loss of information, loss of statistical power) and therefore is not recommended by statisticians (Aiken and West, 1991). To interpret significant interactions in binary logistic regression, we employed the Aiken and West (1991) approach in which we used the binary regression model intercepts and slopes to graph dominance (probability of choosing to compete again) one standard deviation above and below the means for pre-competition T and C levels. We also conducted simple slopes analyses based on Aiken and West (1991) for the relationship between T and dominance one standard deviation above and below the mean for C. Finally, we included secondary analyses in which we conducted median splits on T and C levels. As reviewed above this approach is less robust than regression, but we included these analyses because we reasoned they may be easier to interpret for readers unfamiliar with logistic regression.

Results

Consistent with Study 1, we log-transformed the pre-competition C distribution because it was positively skewed. Pre-competition T and C levels were marginally positively correlated in the current study ($r = .25$, $p = .06$), which is in line with findings from Study 1 and prior studies (Mehta et al., 2008; Popma et al., 2007). Previous research on hormones and competition indicates that neuroendocrine systems are most strongly related to dominance when status is threatened (e.g., after social defeat but not after victory, Carré and McCormick, 2008; Mehta et al., 2008; Jones and Josephs, 2006). Therefore, we expected that the interaction between pre-competition T and pre-competition C would predict dominance following social defeat (status threat), but not following victory (no threat). To test this prediction, we conducted a hierarchical binary logistic regression analysis with the decision to re-challenge one's opponent to a second competition as the dependent variable (1 = re-challenge opponent, 0 = complete alternative non-competitive task) and the following variables as predictors: victory/defeat condition, pre-competition T, and pre-competition C as predictors in Step 1, the three two-way interactions in Step 2, and the victory/defeat × pre-competition T × pre-competition C three-way interaction in Step 3. Consistent with our hypothesis, there was a statistically significant three-way interaction ($\chi^2 = 6.30$, $p < .05$), indicating that hormones were differentially related to dominance in the victory and defeat conditions. To interpret this three-way interaction, we conducted separate binary logistic regression analyses in the victory and defeat conditions. In support of the hypothesis that T and C jointly influence dominance in response to a status threat, there was a statistically significant pre-competition T × pre-competition C interaction in the defeat condition ($\chi^2 = 6.58$, $p < .05$), but not in the victory condition ($p > .10$). For both defeat and victory conditions, there were no main effects of pre-competition T or pre-competition C (p's $> .10$).

To interpret the significant T × C interaction after defeat, we used the binary logistic regression model to graph the probability of

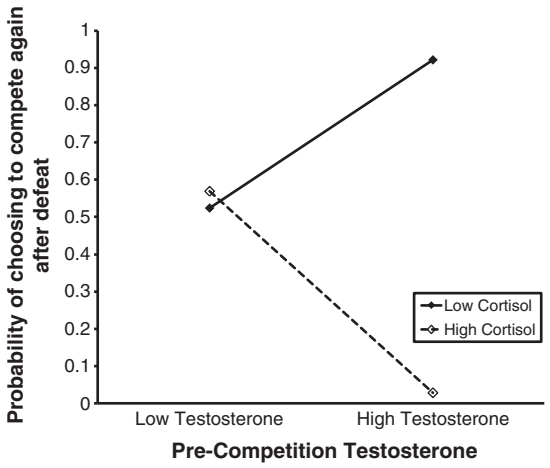

Fig. 2. Study 2: dominance after social defeat (probability of choosing to compete again) as a function of pre-competition testosterone and cortisol levels. Low = 1 standard deviation below mean; high = 1 standard deviation above mean. The intercept and slopes from the binary logistic regression model in the defeat condition were used to plot the probability of choosing to compete again one standard deviation above and below the means for pre-competition testosterone and cortisol.

choosing to compete again one standard deviation above and below the means for T and C (see Fig. 2) (Aiken and West, 1991). Simple slopes were also computed for the relation between T and dominance one standard deviation above and below the C mean (Aiken and West, 1991). Consistent with the claim that C alters the relation between T and dominance, there was a positive relationship between pre-competition T and dominance when pre-competition C was low ($B = 1.36$; see Fig. 2, solid line), but this relationship completely *reversed* when pre-competition C was high; that is, there was a *negative* association between pre-competition T and dominance in individuals with high pre-competition C ($B = -1.72$; see Fig. 2, striped line). The significant interaction term indicates that these slopes statistically differed from each other.

As an additional approach to understand the pattern of the T×C interaction after defeat, we conducted median split analyses. As mentioned above in the Data analysis strategy section, median split analyses have significant drawbacks compared to regression (loss of information and significant loss of statistical power), but this approach may be more understandable to some readers who are less familiar with interpreting interactions in regression. We created two groups – a low pre-competition C group and a high pre-competition C group – by conducting a median split on pre-competition C in the defeat condition. We used binary logistic regression to examine the slope of the relationship between pre-competition T and dominance in the low and high C groups. Consistent with the analyses reported above and with Fig. 2, there was a statistically significant positive relationship between pre-competition T and dominance in the low pre-competition C group ($B = 1.39$; $\chi^2 = 4.38$, $p < .05$), but there was a statistically significant negative relationship between pre-competition T and dominance in the high pre-competition C group ($B = -2.39$; $\chi^2 = 9.67$, $p < .05$). In other words, higher pre-competition T was associated with increased dominance after defeat in individuals low in pre-competition C, but higher pre-competition T was associated with *decreased* dominance after defeat in individuals high in pre-competition C.

Next we conducted a median split on the pre-competition T distribution and created four groups: a high pre-competition T, low pre-competition C group; a low pre-competition T, low pre-competition C group ; a high pre-competition T, high pre-competition C group; and a low pre-competition T, high pre-competition C group. We examined the percentage of participants who chose to re-challenge their opponent to a second competition after defeat in each of these four hormone groups. The pattern of percentages mimicked the pattern observed in Fig. 2. Eighty-three percent of the high T, low C group; 42% of the low T, low C group; 0% of the high T, high C group; and 67% of the low T, high C group chose to re-challenge their opponent to a second competition after defeat. Taken together, these median split analyses converge with the main binary logistic regression analyses to support the claim that pre-competition T interacts with pre-competition C to predict dominance after social defeat.

Dual-hormone regulation of dynamic T changes

Previously we reported that a dynamic drop in T from before to after the competition was related to decreased dominance after defeat in this sample (Mehta and Josephs, 2006), and an independent group replicated this finding (Carré and McCormick, 2008). These results bring up the possibility that an acute decrease in T may be a mechanism for the negative relationship between pre-competition T and dominance in individuals with high pre-competition C (Fig. 2, striped line). To test this possibility, first we conducted multiple regression analyses with pre-competition T, pre-competition C, and the pre-competition T×pre-competition C interaction as predictors of post-competition T. These analyses revealed a statistically significant pre-competition T×pre-competition C interaction in the defeat condition, $\Delta R^2 = 7.5\%$, $F(1, 27) = 7.27$, $p < .05$, but not in the victory condition ($p > .10$). To interpret the significant interaction, we graphed the simple change in T scores one standard deviation above and below the means for pre-competition T and pre-competition C, and we conducted simple slopes analyses (Aiken and West, 1991) (see Fig. 3). These analyses revealed that when pre-competition C was high, higher pre-competition T was associated with a *decrease* in T after defeat ($\beta = -.40$, $p < .01$, see Fig. 3, striped line). When pre-competition C was low, however, pre-competition T was *unrelated* to T changes after defeat ($\beta = .10$, $p = .51$, see Fig. 3, solid line). We next conducted mediation analyses based on procedures outlined by Nathaniel Herr (http://www.nrherr.bol.ucla.edu/Mediation/logmed.html) to determine whether the significant pre-competition T×pre-competition C interaction on dominance was mediated by acute changes in T. Although these analyses failed to show robust evidence for mediation (Sobel test: $Z = 1.14$, $p = .25$), they were in the predicted direction. The lack of statistical significance was likely due to insufficient statistical power given that the present study was not designed specifically to test for statistical mediation. Together, these analyses provide preliminary evidence that a dynamic T drop after social defeat in part explains the reversed relationship between pre-competition T and dominance when pre-competition C is high, but studies with larger sample sizes and with T and C measurements across multiple time points should be conducted to test this mechanism more rigorously.

T/C ratio

Recently it has been proposed that the T/C ratio should predict aggressive and dominant behaviors (Terburg et al., 2009), so we also examined whether this ratio was related to dominance behavior in our two studies. However, this ratio was only marginally related to dominance behavior in Study 1 ($\beta = .18$, $p = .08$) and failed to predict dominance behavior in Study 2 (across the two experimental conditions, or when we looked at the victory and defeat conditions separately, p's>.10). Overall then, the findings across the two studies demonstrate that the interaction between T and C significantly predicts dominance behavior, but the T/C ratio does not.

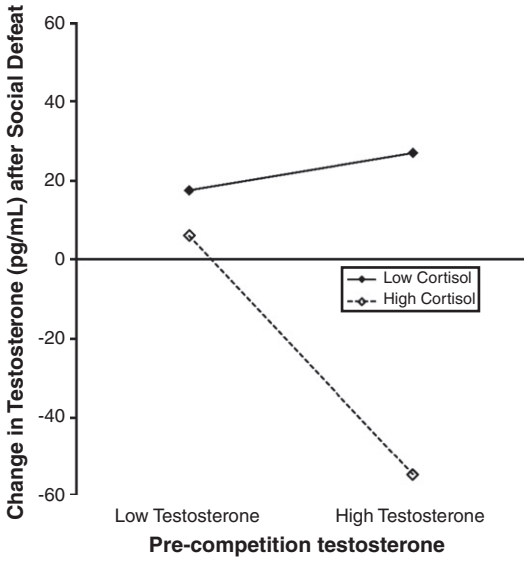

Fig. 3. Study 2: acute changes in testosterone after social defeat (post-competition testosterone minus pre-competition testosterone) as a function of pre-competition testosterone and cortisol levels. Low = 1 standard deviation below mean; high = 1 standard deviation above mean. The intercept and slopes from the multiple regression model in the defeat condition were used to plot testosterone change scores one standard deviation above and below the means for pre-competition testosterone and cortisol.

General discussion

Two studies provide compelling support for the claim that T and C jointly regulate dominance. In individuals with low C, higher T was related to increased dominance (Studies 1 and 2). But in individuals with high C, the relation between T and dominance was either blocked (Study 1) or *reversed* (Study 2). The findings generalized across different status-relevant domains (competition and leadership), across multiple measures of dominance, and across men and women. These results point to a new direction for research on the neuroendocrinology of dominance. Traditional theories posit that T and C should influence behavior independent of each other (Archer, 2006; Mazur and Booth, 1998; Wingfield et al., 1990), but research to date has failed to provide consistent support for these theories. Consistent with some previous null findings, T and C alone were unrelated to dominance in our studies. The T/C ratio was not a significant predictor of dominance either. Only when the interaction between T and C was taken into account was there strong evidence for neuroendocrine regulation of behavior. In future studies, we suggest that researchers consider using a dual-hormone approach instead of traditional single-hormone approaches when investigating the neuroendocrinology of dominance and other status-seeking behaviors.

One possible mechanism for dual-hormone regulation of dominance is through the inhibitory effects of C on the gonadal axis. C suppresses HPG axis function at multiple levels, C inhibits the effects of T on target tissues, and C downregulates androgen receptor levels (Burnstein et al., 1995; Chen et al., 1997; Johnson et al., 1992; Smith et al., 1985; Tilbrook et al., 2000). Thus, when output in the stress axis is low (low C), higher T may increase dominance because the pathway between T and behavior functions efficiently. When output in the stress axis is high (high C), the relation between T and dominance may be blocked due to C suppression of the T-behavior pathway. This explanation fits with the results from Study 1 showing that T and dominance behavior in leaders were unrelated when C was high (Fig. 1, striped line). But unexpectedly, in Study 2 there was actually a *reversed* (negative) relationship between T and dominance under conditions of high C (Fig. 2, striped line).

Further analyses in Study 2 indicate that an acute T drop in response to status threat may drive this novel reversal effect. As shown in Fig. 3, pre-competition T and C had synergistic effects on T changes following social defeat such that a combination of high pre-competition T and high pre-competition C was associated with a decrease in T after social defeat (Fig. 3, striped line), and this decrease in T was associated with decreased dominance behavior (Mehta and Josephs, 2006). Thus, it seems that pre-competition T was *negatively* related to dominance when pre-competition C was high due in part to a dynamic drop in T in response to social threat. This pattern of results fits roughly with some previous findings showing effects of T and C on HPG axis function, including the release of gnRH from the hypothalamus, LH and FSH from the pituitary gland, and subsequent T release in the gonads (Johnson et al., 1992; Terburg et al., 2009; Tilbrook et al., 2000). Interactions between hormone levels before and after status-relevant social events as a mechanism for dominance are an important avenue for future research.

Another mechanism for dual-hormone regulation of dominance may be through hormonal effects on neural activity in the limbic regions and the frontal lobes. T and C modulate neural activity in the amygdala and the orbitofrontal cortex (Derntl et al., 2009; Hermans et al., 2008; Manuck et al., 2010; Mehta and Beer, 2010; Stanton et al., 2009; van Wingen et al., 2009, 2010), and these changes in neural activity may explain hormone–behavior relations (e.g., Mehta and Beer, 2010). Most relevant to the current research, a recent study showed that an endocrine profile of high T and low C predicted increased activity in the amygdala in response to social threat cues (Hermans et al., 2008). It is possible that interactive effects of T and C on activity in the amygdala, orbitofrontal cortex, or functional connectivity between these regions may be a mechanism for dominance behavior. Future studies that combine measures of hormones, neural activity, and behavior in the same study hold great promise for identifying the neural mechanisms for interactions between T and C on behavior.

A broader psychological explanation for our results may be through C's associations with stress and social avoidance (Brown et al., 1996; Dickerson and Kemeny, 2004; Popma et al., 2007; Roelofs et al., 2009; Taylor et al., 2000). It is plausible that higher T is positively related to dominance when C is low because low C facilitates social approach and thus allows for the overt expression of dominant behaviors. However, higher T may in fact decrease dominance behavior when C is high due to C's effects on stress and social inhibition. Future research that incorporates measures of stress/anxiety, approach, or inhibition can test this explanation.

Throughout this paper we have argued that C alters the effect of T and dominance, but an alternative interpretation of the present findings is that the causal direction may go the other way — that T moderates the relation between C and dominance. Indeed, there is evidence that T can directly inhibit HPA axis function (Viau, 2002). However, two issues make this alternative interpretation less likely. First, the current findings suggest that higher T *strengthens* the negative relationship between C and dominance (e.g., see Fig. 2), but the extant neurobiological evidence would suggest just the opposite — that T *suppresses* the effects of C at multiple levels (Viau, 2002), and therefore that high T levels should block (not strengthen) the negative association between C and dominance. Second, the findings from Study 2 show that T and C levels prior to a dominance contest jointly modulate T changes after defeat (see Fig. 3), a finding that is highly consistent with C directly altering HPG axis function but not with T influencing HPA axis function. Overall then, the findings from the current research together with previous studies favor the explanation that C alters the effect of T on dominance rather than the other way around. Nevertheless, additional studies are needed to better understand the mechanisms that guide dual-hormone effects on dominance.

The current research also contributes to a growing literature on hormone × environment interactions. Most behavioral endocrinology studies examine hormone–behavior relations collapsed across multiple situations or under neutral conditions. Our findings are consistent with recent experimental studies in showing that social threat is an important environmental "trigger" for hormonal influences on dominance (Carré and McCormick, 2008; Jones and Josephs, 2006; Josephs et al., 2003, 2006; Mehta et al., 2008; Newman et al., 2005; Zyphur et al., 2009) and mirror the literature on gene association studies which show that environmental stressors such as social threats moderate the relationship between genetic variants and psychological outcomes (Caspi et al., 2010). Indeed, in Study 2 we found that only after status was threatened (after social defeat in a competitive interaction) did T and C levels predict dominance. On the basis of this growing literature on context-dependent effects of hormones, we suggest strongly that future research continue to manipulate or measure key aspects of the social environment to provide further insights into connections between hormones and dominance.

The current research had some methodological limitations that should be addressed in future studies. First, we measured afternoon hormone levels at the beginning of our experiments to assess T and C levels, and we used these hormone measures to predict dominance behavior. Previous research suggests that T and C levels measured at the same time of day are stable across several weeks (Liening et al., 2010), suggesting these hormone measures are tapping into stable individual differences (basal T and basal C). However, T and C levels fluctuate throughout the day and respond to environmental factors, so it is still possible that a portion of the variance in T and C may

have been due to individual differences in circadian rhythms or environmental factors. Future studies that measure T and C in multiple saliva samples across several days and throughout the day can provide greater insights into interactions between the HPA and HPG axes as a mechanism for dominance. Second, we cannot be sure that T and C directly caused dominance and submission because we measured naturally occurring T and C. Experimental studies that exogenously alter steroid hormone concentrations (e.g., Eisenegger et al., 2010; Hermans et al., 2008) are necessary to determine whether interactions between T and C do indeed cause behavioral variation in dominance. Although some of these hormone administration studies have shown behavioral effects with a single-hormone approach (e.g., T administration and status-related behaviors in women, Eisenegger et al., 2010), a dual-hormone approach may account for an even greater proportion of the variance in behavior.

The current research examined the neuroendocrinology of dominance, but the findings also have implications for the emergence of status hierarchies in social groups. Dominance behavior is associated with gaining and maintaining high status within hierarchical organizations (Anderson and Kilduff, 2009; Saposky, 2005). The HPG and HPA axes have been studied in the context of social hierarchy, but the effects of these systems on social status remain unclear. Although speculative, the evidence presented in this article suggests that only when C levels are low should higher T promote attaining positions of leadership/power and maintaining these positions over time. When C levels are high, higher T may actually *decrease* dominance and in turn motivate lower status.

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