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Beyond the Challenge Hypothesis: The Emergence of the Dual-Hormone Hypothesis and Recommendations for Future Research

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Abstract

The challenge hypothesis makes specific predictions about the association between testosterone and status-seeking behaviors, but the findings linking testosterone to these behaviors are inconsistent. The dual-hormone hypothesis was developed to help explain these inconsistencies. Specifically, according to this hypothesis, testosterone's association with status-seeking behavior depends on levels of cortisol. Here, we (1) describe the dual-hormone hypothesis in relation to the challenge hypothesis; (2) review recent studies that tested the dual-hormone hypothesis as well as meta-scientific evidence of heterogeneous dual-hormone findings across studies; (3) discuss potential explanations for this heterogeneity, including methodological considerations, contextual factors, and individual differences; and (4) provide recommendations for new work aimed at testing and extending the dual-hormone hypothesis.

Introduction

The challenge hypothesis was originally developed to explain the relationship between testosterone and aggression in seasonally breeding birds (Wingfield et al., 1990). The authors proposed a multifaceted role for testosterone, where baseline testosterone levels are involved in the development and maintenance of reproductive systems. Within the challenge hypothesis framework, competitive interactions during the breeding season induce surges in testosterone levels above this baseline, which in turn direct territorial aggression and inter-male competitive behavior for access to receptive females and territory. The challenge hypothesis authors also posited that elevated testosterone levels reduced expression of paternal care.

The challenge hypothesis was later adapted to explain testosterone's association with status-seeking behaviors more broadly in primates (including humans; Archer, 2006; Muller & Wrangham, 2004). However, evidence of a direct association between testosterone and status-relevant behavior in humans is often inconsistent: While testosterone correlates positively with status-seeking behaviors such as aggression (Archer, 2006) and competitiveness (Eisenegger et al., 2017) in some reports, there have also been several observations of weak or null associations (Archer et al., 2005; Apicella et al., 2011).

The dual-hormone hypothesis sprang from these inconsistent associations between testosterone and social behavior (Mehta & Josephs, 2010; Mehta & Prasad, 2015; Sarkar, Mehta, & Josephs, 2018). Specifically, this hypothesis provided a framework for interpreting the relatively mixed findings on testosterone-behavior links in terms of a physiological moderator, the glucocorticoid steroid cortisol. Cortisol is a

product of the hypothalamic-pituitary-adrenal (HPA) axis that is released in response to physical and psychological stress (Dickerson & Kemeny, 2004) and mediates an array of metabolic and physiological responses to stress (McEwen, 2019). Stress plays a fundamental role in animal competition and mating, which are relevant to social status (Sapolsky, 2005). Further, the HPA and HPG axes influence each other at multiple levels (Viau, 2002; Burnstein et al., 1995; Chen et al. 1997; Johnson et al., 1992; Smith et al., 1985; Tilbrook et al., 2000; see also Mehta & Josephs, 2010, and Grebe et al., 2019a for discussion of putative mechanisms), suggesting that testosterone and cortisol may interact to affect behavior. Theoretical frameworks that link endocrine activity to status seeking, such as the challenge hypothesis, should therefore also account for cortisol levels. However, the challenge hypothesis focuses entirely on testosterone and does not emphasize a role for cortisol. Thus, previous studies that tested the challenge hypothesis may have found weak or null results because they did not consider cortisol as a potential moderator of testosterone's association with behaviors linked to status.

According to the dual-hormone hypothesis, testosterone's association with status-relevant behavior depends on cortisol levels, specifically that the positive association between testosterone and status-seeking behavior is more robust when cortisol levels are low[1] (Mehta & Josephs, 2010), while this association is attenuated when cortisol levels are high. The statistical prediction of this hypothesis is a negative

[1] Throughout this manuscript, we use "high" and "low" levels of hormones to refer to relative levels within a given study. High and low are often represented statistically by examining patterns one standard deviation above and below a hormone's mean, respectively (see Aiken & West, 1991 for discussion of this approach; see also Mehta & Josephs, 2010). This terminology does not refer to an individual's absolute hormone levels, but future studies may able to quantify absolute levels accurately with mass-spectrometry based techniques (see section on validity of hormone measurement).

testosterone × cortisol interaction term, when higher scores on the outcome measure indicate increases in behaviors related to the pursuit of high status.

The Dual-hormone Hypothesis

Mehta and Josephs (2010) formally proposed the dual-hormone hypothesis. Across two studies, testosterone and cortisol were measured in afternoon saliva samples in undergraduate students. In Study 1, men and women participated in a leadership task. Seven judges rated video recordings of these social interactions on dominant leadership behaviors, defined as an assertive and self-assured behavioral style (Anderson & Kilduff, 2009). The rated variables included assertiveness, confidence, decisiveness, anxiety (reverse scored), and being perceived as "leader-like". Ratings of these dominance-related variables based on behavioral observations predict the attainment of higher status in social groups (Anderson & Kilduff, 2009). In Study 2 (males only), participants chose whether or not to re-enter a competition against the same opponent after winning or losing. Choosing to challenge an opponent to a re-match after losing can be considered a status-seeking behavior because it may enable upward advancement in the social hierarchy (Mehta & Josephs, 2006). Both studies found testosterone × cortisol interactions consistent with the dual-hormone hypothesis: Higher basal testosterone levels were related to more dominant leadership behaviors (e.g. assertiveness, confidence, being perceived as leader-like) and decisions to re-enter competitions against the same opponent after defeat, but only when cortisol levels were low. When cortisol levels were high, higher testosterone levels were unrelated to dominant leadership behaviors (Study 1) and were negatively related to decisions to re-enter competitions against the same opponent after defeat (Study 2).

Although Mehta and Josephs (2010) first named and delineated the dual-hormone hypothesis, testosterone × cortisol interactions had been observed earlier, in research on aggression and criminal violence in male delinquent adolescents (Dabbs et al., 1991; Popma et al., 2007); basal testosterone correlated positively with aggression and violence among low-cortisol individuals but not among high-cortisol individuals. In groups of delinquent adolescents, anti-social behaviors like aggression and violence may be effective in increasing one's status by inducing fear and submissive behaviors in other group members (Daly & Wilson, 1988).

Since these initial observations, testosterone × cortisol interactions consistent with the dual-hormone hypothesis have been found to predict a wide array of behaviors humans may employ in the acquisition or maintenance of social status (reviewed in Mehta & Prasad, 2015; Sarkar et al., 2019). Moreover, new evidence suggests that this dual-hormone interaction is related to the actual attainment of higher status in real-world hierarchies.

For example, in studies of collegiate and Olympic female athletes, higher basal testosterone levels were related to higher social status, including teammate perceptions of leadership, but only when cortisol levels were low; higher testosterone levels were either unrelated or negatively related to social status when cortisol levels were high (Edwards & Casto, 2013; Casto et al., 2019). In another study of male rugby players, a social network analysis showed a similar pattern of results: Higher basal testosterone levels were related to higher status in the social network (e.g. higher popularity scores) only among players with low-cortisol levels but not among players with high-cortisol levels (Ponzi et al., 2016). A fourth study recruited male executives who held leadership

positions in the public sector, including federal government officials, senior military officers, and some private-sector managers whose work was tied to the public sector (Sherman et al., 2016). Social status was indexed by the number of subordinates over which the individual had authority (Sherman et al., 2016). In line with the dual hormone hypothesis, basal testosterone was positively related to social status (a higher number of subordinates) among individuals with low cortisol but not among individuals with high cortisol.

Taken together, these studies suggest that the interaction between testosterone and cortisol is related to behaviors implicated in the pursuit of status (e.g. assertive and confident behaviors; re-challenging an opponent to a re-match after facing a defeat) as well as actual attainment of higher status in social groups (e.g. being perceived as a leader and having authority over larger groups of subordinates; but see also Mazur et al., 2015).

Meta-analysis and "File-drawer" Studies

Recently, a meta-analysis was conducted to estimate the effect size of testosterone × cortisol interactions across studies and test for potential moderators of the effect (Dekkers et al., 2019). This meta-analysis included thirty-three studies with forty-nine effects[2], and found evidence of a small but significant testosterone × cortisol interaction consistent with the dual-hormone hypothesis, but with substantial heterogeneity in the direction and magnitude of effect sizes (Dekkers et al., 2019). Upon examining individual categories of behaviors, this meta-analysis found that the evidence in support of the dual-hormone hypothesis was stronger for explicit indices of status

[2] Effects from each study were split by gender and by any additional conditions analyzed and reported as a moderator within each study.

(e.g., actual status rankings within hierarchies) compared to specific categories of behaviors (e.g. aggression, psychopathy). There was also stronger support for the dual-hormone hypothesis in males than females. However, it is important to note that these were only directional patterns; as the authors point out, there was limited statistical power to detect statistically significant differences in the moderator analyses.

Another recent article examined the dual-hormone hypothesis in a set of unpublished "file-drawer" studies that primarily utilized self-reported measures of status-striving personality features (e.g., a self-reported scale of competitiveness; Grebe et al., 2019a). The results did not provide strong evidence for a testosterone × cortisol interaction in line with the dual-hormone hypothesis. The authors argued that this result, in conjunction with a *p*-curve analysis, suggests that the published literature is characterized by low statistical power. However, Bayesian analyses did not reveal strong evidence in favor of the null hypothesis either. Thus, the results do not clearly favor the interpretation that testosterone × cortisol interactions are unrelated to self-reported status-striving personality traits. Grebe and colleagues also highlight a pattern of imprecision regarding behaviors that are categorized as "status seeking," as well as inconsistency in which hormone measures show significant T x C interactions (e.g., basal versus dynamic change measures). Each of these scenarios could reasonably lead to wide-ranging and subjectively interpreted outcomes.

Based on the findings from this recent meta-analysis and "file drawer" study (Dekkers et al., 2018; Grebe et al., 2019a), we draw the interim conclusion that although there is some promising support for the dual-hormone hypothesis, the evidence is somewhat tepid and inconsistent across studies. How should researchers approach

these inconsistent results? There are several plausible explanations for the heterogeneous results across studies. As such, there are new opportunities for discovery on associations between these dual-hormone interactions, status-seeking behaviors and actual status attainment, as well as better understanding the causal pathways that explain these associations. In the subsequent sections, we build on these recent papers to discuss potential explanations for the heterogeneous results across studies and we offer recommendations for future research aimed at testing and extending the dual-hormone hypothesis in light of these explanations.

Possible Drivers of Heterogeneity in Dual-Hormone Interactions

Methodological Explanations

The combination of low statistical power (Button et al., 2013), publication bias (i.e. the tendency for scientific journals to publish studies that produce novel and statistically significant results and undervalue direct replication studies), and the consequences of this bias for researcher practices (e.g. undisclosed flexibility in analyses, lack of direct replications; Wicherts et al., 2016; Maxwell, 2004), have led to what some researchers are calling a “reproducibility crisis” across many scientific fields (Schultheiss & Mehta, 2019; Maxwell et al., 2015). A “credibility revolution” has begun in fields such as psychology, neuroscience, and behavioral neuroendocrinology, which aims to improve research methods and reduce publication bias (Shrout & Rodgers, 2018). Here we discuss methodological limitations that may explain heterogenous dual-hormone findings. Although some of the recommendations we provide are not specific to research on the dual-hormone hypothesis and could improve methods in any

research domain, future research on the dual-hormone hypothesis would benefit from careful attention to these issues.

Statistical Power. The recent meta-analysis of the dual-hormone hypothesis (Dekkers et al., 2019) indicates that studies testing the hypothesis had relatively low power and excess significance, or too many significant results given the estimated meta-effect and the corresponding sample sizes of the studies analyzed. The median sample size of the effects examined (i.e., testosterone × cortisol effect in each gender and experimental condition) was $n = 64$, with a low of $n = 15$. Low-powered samples are also evident in p-curve analyses provided by Grebe and colleagues (2019a) with the results suggesting the published literature had 16% power to detect real, non-zero effects. Based on an 80% power to detect the meta-estimate of direct measures of status reported in Dekkers ($r = -0.16$), sample sizes of approximately $n = 300$ would yield 80% power to detect an endogenous dual-hormone interaction on direct measures of social status[3]. We recommend that future research on the dual hormone hypothesis aim to achieve this sample size or even larger samples. For studies that have lower sample sizes, we recommend that researchers discuss low power as a potential limitation of the research. Relatedly, we recommend that researchers report and discuss the uncertainty in their estimates of dual-hormone findings (e.g. confidence intervals) rather than only focusing solely on binary significance/non-significance.

Flexibility in Analyses. Researchers are susceptible to making *ad hoc* methodological decisions that alter approaches and outcomes of analyses, often unintentionally (Simons et al., 2011). For example, researchers may make choices

[3] These values will likely differ if using other methodology, such as hormone administration, or running simpler studies that lack multiple conditions.

about which analyses to conduct and report in a particular study based in part on the results observed in that same study. This data-dependent flexibility in analyses has been conceptualized as a “garden of forking paths” in which analytical choices are made implicitly without predetermination (Gelman & Loken, 2013). It is possible that prior dual-hormone research may have inflated effect sizes or produced false positive results due to data-dependent flexibility in analyses (Dekkers et al., 2019; Grebe et al., 2019a). One solution to counter this flexibility is to preregister hypotheses and analytical approaches. Prior to data analysis (and preferably, prior to data collection), researchers should describe their intended analytical approach for hormones – e.g., using basal or dynamic measures, defining outliers, exclusion criteria for participation, and so on. For example, two recent studies preregistered hypotheses and analytical plans, and subsequently tested and found support for testosterone × cortisol interactions associated with behavioral measures of risk taking in men (Ronay et al., 2018) and with changes in self-reported competitiveness and dominance (Kordsmeyer & Penke, 2019). Moreover, if studies and findings are published as registered reports – i.e., preregistrations that are peer-reviewed and provisionally accepted prior to data collection – then these practices should also help to reduce publication bias (Nosek & Lakens, 2014). We recommend that researchers adopt pre-registration or registered reports in new studies that are being planned to test the dual hormone hypothesis. These approaches can also be employed when analyzing archival datasets (Mertens & Krypotos, 2019). When a dual-hormone interaction is found through exploratory analyses, we recommend that researchers be explicit that the analyses that produced the result were exploratory in nature.

Validity of hormone measurement techniques. Commercially available testosterone immunoassays – a widely used method for quantifying hormone concentrations - may have unstable validity, particularly in samples with intrinsically low levels of hormones (Prasad et al. 2019; Welker et al., 2017). This could produce heterogeneous results and undermine reproducibility (Schultheiss, Dlugash, & Mehta, 2019). The increased instability at lower concentrations makes accurate measurement of testosterone in women more difficult, which may also explain why the meta-analysis found slightly stronger support for the dual-hormone hypothesis in males than females. Researchers should consider using liquid chromatography tandem mass spectrometry (LC-MS/MS) to improve the accuracy of hormone measurement. Two recent studies have provided evidence for testosterone × cortisol interactions using LC-MS/MS to measure hormone concentrations in hair: High testosterone and low cortisol levels were associated with increased externalizing behaviors (Grotinzger et al., 2018) and increased risked taking among men (Ronay et al., 2018).

Replications. Studies included in the Dekkers et al. (2019) meta-analysis used a variety of methods to test the dual-hormone hypothesis across a range of outcomes. Even for studies within the same categories of behavior, the outcome measures varied. Thus, it is not surprising that the meta-analysis found substantial heterogeneity both between and within categories of behavior. To provide more certainty as to whether a specific dual-hormone finding is reproducible, we recommend that researchers conduct high-powered pre-registered replication studies that examine associations between dual-hormone interactions and the same behavioral outcome measure used in a previous study. Given the limitations of immunoassays for testosterone measurement

that we described earlier, we recommend that these replication studies adopt mass-spectrometry based methods for testosterone measurement. Further, we recommend that researchers publish such studies, regardless of outcome (e.g., as a registered report). Two recent studies that adopted mass-spectrometry based testosterone measurement and used the same outcome measure as previous studies found some evidence for reproducible dual-hormone interactions (e.g. Ronay et al., 2018; Roy et al., 2019).

Variations in Outcomes that may contribute to Heterogeneity

Direct measures of status versus other outcome measures. The most basic prediction inherent to the dual-hormone hypothesis is that the testosterone × cortisol interaction is associated with behaviors meant to earn status. Although the connection between specific behaviors and perceptions of social status were clear in some dual-hormone studies (e.g. ratings of “leader-like” were correlated with observed behaviors such as assertiveness, confidence, and decisiveness in Mehta & Josephs, 2010), in other studies it remains unclear whether the behavioral outcome measure was relevant to status. Studies that measure social status directly do not suffer from such interpretation problems and thus may provide clearer support for the dual-hormone hypothesis. In line with this reasoning, the testosterone × cortisol interaction in Dekker and colleagues’ meta-analysis was more strongly related to direct measures of status (r = -0.16) than to other outcomes (meta-effect sizes ranged from r = -0.04 to 0.02). Nevertheless, this was only a directional pattern; as the authors mention, the meta-analysis had limited power to detect statistically significant differences in the moderator analyses.

This pattern suggests that future dual-hormone research should target the most direct measures of status possible – e.g., status conferred in naturally occurring groups (Edwards & Casto, 2013; Casto et al., 2019). Work that examines behaviors that are thought to represent status seeking should preregister their expectations in terms of what outcome would be considered a status-seeking behavior *a priori*, in addition to preregistering other analytical and methodological choices.

Behavioral measures of social status versus self-reported personality traits. Grebe and colleagues' (2019a) analysis of testosterone × cortisol interactions focused on self-reported indices of status-striving personality. However, prior work suggests that testosterone is more robustly linked to implicit or behavioral measures of status motivation than to self-reported measures (Van Honk et al., 1999; Stanton & Schultheiss, 2009). Akinola and colleagues (2016) demonstrated that behavioral outcomes were associated with testosterone × cortisol interactions[4] when controlling for self-reported personality traits conceptually related to testosterone and cortisol (e.g., dominance and anxiety). This result suggests that hormonal interactions on behavior cannot be easily explained by variation in explicitly measured psychological factors (see also Mehta, 2007). Hence, the psychological effects of hormones may occur outside of conscious awareness to influence status-seeking behaviors.

Grebe and colleagues (2019a) report dual-hormone comparisons of self-reported personality traits and behavioral outcome measures and find a pattern that is directionally consistent with this explanation. However, there was limited power for detecting statistically significant differences in their moderator analyses given the small

[4] This article used a novel measure of group-level hormone concentrations and examined groups' behavioral performance in a business simulation decision-making task.

number studies, thereby making interpretation of these results difficult. We recommend that future studies test for testosterone × cortisol associations on behavioral or implicit measures of status-seeking motives (e.g. the picture story exercise; Stanton & Schultheiss, 2007), or on direct measures of status attainment.

Self-reported psychological states versus trait constructs. Another consideration for self-report measures that likely introduces heterogeneity to testosterone × cortisol interactions is the measurement of state versus trait psychological constructs. Specifically, testosterone × cortisol may more strongly associate with measures of psychological states in response to status-relevant social interactions compared to measures of trait constructs. For example, Kordsmeyer and Penke (2019) report associations of a testosterone reactivity × basal cortisol interaction with changes in self-reported personality states of the interpersonal circumplex (i.e., dominance and competitiveness). Testosterone × cortisol interactions were not evident for baseline (trait) measures of these psychological variables. In other work, the testosterone × cortisol interaction was associated with satisfaction with a status-relevant economic game (hawk-dove game; Mehta et al., 2017). Similar effects have been reported for the causal effects of testosterone treatment on feelings of pleasure derived from an aggression paradigm (Geniole et al., 2019). Hence, if self-reported measures are relied upon in a dual-hormone study, consideration should be given for measuring state versus trait indices of the psychological construct of interest.

Sex and Gender Differences

Some evidence suggests that the association between the testosterone × cortisol interaction and behavior is stronger in males than females (Dekkers et al., 2019).

Whereas testosterone is the primary reproductive hormone in males, estradiol (an estrogen) is the predominant estrogen found in pre-menopausal females and may have greater consequences for status seeking in females. Estradiol has been associated with implicit measures of status seeking (i.e., implicit power motivation; Stanton & Edelstein, 2009; Stanton & Schultheiss, 2007) and assertiveness in females (Blake et al., 2017). Moreover, one study has found that estradiol's association with antisocial, aggressive behavior in adolescents was more robust when cortisol levels were low and when individual difference traits related to personality disorders were high (disagreeableness and emotional instability; Tackett et al., 2015). However, this pattern was observed in both male and female adolescents, and thus it remains unclear whether the estradiol × cortisol interaction is indeed a stronger predictor of status-seeking behavior in females compared to males. New work will be needed that directly compares testosterone x cortisol and estradiol x cortisol interaction effects in both males and females.

A further consideration for examining gender differences and similarities in the dual-hormone association with status seeking behavior is the extent to which male and female status hierarchies differ. Male status hierarchies and behavior may not be good analogues for female status seeking among nonhuman primates (Lewis, 2018; Foerster et al., 2016). This rationale has also been clearly delineated for human gender differences in status seeking behavior, particularly with regard to competitiveness, for which sociocultural influences may dictate the nature and timing of competitive, status-seeking behaviors (Casto & Prasad, 2017). Social expectations of female behavior may result in affiliative behaviors being more strongly associated with obtaining status for females compared to males (Cashdan, 1996; Hays, 2013; Casto & Prasad, 2017).

Hence, hypotheses focused on hormones and behavior informed by theories of male hierarchies may obscure or misguide research on the endocrine underpinnings of status seeking in females.

Despite these arguments for possible gender differences in the dual-hormone interactions, alternative arguments suggest gender differences may not be robust or may be influenced by methodological issues in measuring hormone concentration. Several studies have found testosterone × cortisol associations with status-seeking behavior in both males and females (e.g., Mehta & Joseph, 2010). Other work has focused solely on females and has reported robust testosterone × cortisol associations with direct measures of social status (Edwards & Casto, 2013; Casto et al., 2019). Finally, as discussed above, testosterone immunoassays seem to be less reliable at lower concentrations, and in particular, for females (Prasad et al., 2019; Welker et al., 2016). This would suggest that weaker testosterone × cortisol effects may be due to less reliable measures of testosterone in females rather than a lack of a true association between hormones and behavior. Overall, meaningful investigations of possible gender differences in dual-hormone research will require future work to consider a wider range of hormones, rely on more inclusive theoretical frameworks of status-seeking, employ more inclusive sampling strategies (i.e., study large samples of males and females), and assay sex hormones with more reliable methods, such as LC-MS/MS.

Individual differences in personality and trait-level constructs

Other factors that may introduce heterogeneity in testosterone × cortisol interactions on status-seeking behavior are self-reported trait personality constructs. Prior work in personality psychology has shown that implicit and explicit forms of a given

construct (e.g., trait dominance) may interactively determine behavior (reviewed in Slatcher et al., 2011). Testosterone – considered an implicit, or subconscious determinant of status-seeking behavior – coupled with high levels of self-reported personality constructs related to status seeking may heighten status-seeking behaviors. Here we review initial evidence suggesting that individual differences in self-reported trait dominance and traits related to some aspects of personality disorder (specifically, disagreeableness and emotional instability) may moderate the testosterone × cortisol interaction on status-seeking behavior.

Trait Dominance. Trait dominance is a personality construct that reflects an individual's self-reported motivation to gain status, typically via assertive, forceful, or intimidating behaviors (Mehta et al., 2015b; Anderson & Kilduff, 2009; Cheng et al., 2013). Prior work has shown that the causal effects of testosterone treatment on female competitive behavior (Mehta et al., 2015b) and male aggressive behavior (Carré et al. 2017) are stronger for individuals high in self-reported trait dominance. Other correlational studies have found similar effects for trait dominance moderating associations among endogenous testosterone and aggressive behavior (Carré et al., 2009) and mating behaviors (Slatcher et al., 2011). In these studies, those who had high testosterone and explicitly viewed themselves as dominant (i.e., high self-reported trait dominance) were more likely to display these behaviors.

These studies suggest that trait dominance strengthens the association between testosterone and behavior. Limited evidence suggests trait dominance may also moderate testosterone × cortisol associations with status-seeking behavior. For example, a testosterone × cortisol interaction was marginally moderated by trait

dominance such that the dual-hormone pattern – i.e., testosterone concentrations were associated with taking money from opponents amongst participants with low, but not high, cortisol concentrations – was more robust among males with higher trait dominance (Pfattheicher, 2017). However, as the author notes, these effects were weak and the study was likely underpowered to detect a three-way interaction. A recent testosterone administration study provides a contrasting perspective as well: Self-reported trait dominance did not moderate testosterone treatment × endogenous cortisol effects on male competitive behavior (Knight et al., 2019). This inconsistency may be attributable to differences between exogenous and endogenous testosterone or from the varying measures of trait dominance and status-seeking behaviors used. Recent evidence suggests trait dominance may be part of a personality profile (including trait dominance, impulsivity, and independent self-construal) that moderates testosterone's causal effects on aggressive behavior. Specifically, testosterone treatment given to men with higher levels of this dominant-related personality profile demonstrated increased aggressive behavior due to increased enjoyment of behaving in an aggressive fashion (Geniole et al., 2019). Future work may benefit from taking a wider view of dominant-related traits in larger samples to determine the exact aspects of trait dominance and related constructs that modulate testosterone's effects on aggression, competitive decisions, and status-seeking behaviors.

Traits related to Personality Disorders. Dual-hormone associations with externalizing behavior have also been shown to depend on personality traits such as disagreeableness and emotional instability in one study of adolescents (Tackett et al., 2014). Disagreeableness and emotional instability are higher-order facets of personality

disorder that were hypothesized to enable antisocial, aggressive behaviors associated with externalizing among adolescents. High basal testosterone and low basal cortisol concentrations were associated with externalizing behaviors among participants with high levels of parent-reported disagreeableness and emotional instability. Participants with lower levels of these personality traits did not demonstrate robust testosterone × cortisol associations with externalizing behaviors. Thus, like trait dominance, these personality disorder traits may represent explicit factors that heighten testosterone's and cortisol's implicit influences on status-seeking behavior (Slatcher et al., 2011).

Factors that may Reverse the Typical Dual-Hormone Hypothesis Pattern

We have reviewed factors that may contribute to heterogeneity in testosterone × cortisol associations with status-seeking behaviors by accentuating or attenuating the magnitude of the dual-hormone effect. However, these factors seem unlikely to explain reversals of the dual-hormone pattern that have been observed in some work. Specifically, a few studies have now reported that anti-social behaviors such as increased aggression, cheating behavior, and higher levels of psychopathic traits were positively associated with high testosterone when cortisol levels were *high* but not when cortisol levels were low (Denson, Mehta, & Tan, 2013; Welker et al., 2014; Roy et al., 2019). Some evidence suggests this 'reverse' profile of high testosterone and high cortisol has been associated with stimuli related to social or status threat, which tend to co-activate testosterone and cortisol responses (Turan et al., 2015; Dismukes et al., 2015; Scheepers & Knight, 2020; Knight & Mehta, 2017; Knight et al., 2017). Here we propose putative explanations for when testosterone × cortisol will link with status-seeking behavior in the traditional dual-hormone hypothesis pattern (high testosterone,

low cortisol), and when a behavioral association with a “reversed” pattern (high testosterone, high cortisol) may be more likely.

Social Contextual Cues to an Opponent’s Status

Divergent behaviors toward low- and high-status opponents may explain some of the heterogeneity in dual-hormone interactions. High concern for status (high testosterone) and low stress (low cortisol) may specifically direct behaviors targeted towards challenging higher-status opponents as a means to rise in the hierarchy. Competing against a lower-status opponent does not facilitate an increase in one’s own social status. In contrast, the pairing of high concern for status (high testosterone) with high stress (high cortisol) may be related to enhanced social threat, resulting in avoiding higher-status opponents and engaging in competitive behavior with lower-status opponents instead. This argument suggests that elevated testosterone should be related to increased status-seeking behavior against high-status opponents, but only when cortisol levels are low; in a reversal of this pattern, elevated testosterone should be related to increased status-seeking behavior against lower-status opponents when cortisol levels are high.

Within a competitive setting, a prior victory or defeat against an opponent is an objective indicator of one’s status compared to that opponent. Thus, winning or losing is a social cue to an opponent’s status relative to one’s own status that may alter testosterone × cortisol associations with competitive behavior. One correlational study reported that the association of the testosterone × cortisol interaction with decisions to re-enter a competition was dependent on prior victory or defeat (study 2; Mehta & Josephs, 2010). Males with high testosterone and low cortisol concentrations were

more likely to seek a rematch against the same opponent after losing compared to after winning. Males with high testosterone and high cortisol concentrations displayed a reversed pattern, avoiding rematches against the same opponent after losing (i.e., a higher-status opponent) but competing against the same opponent after winning (a lower-status opponent).

A testosterone administration experiment conceptually replicated this context-dependent dual-hormone hypothesis and extended the effects to implicit cues of an opponent's social status. Whereas winning or losing provides explicit information about an opponent's status, gender stereotypes or other stereotypes may provide implicit indicators of perceived opponent status in a competition. For example, females are often stereotyped as weak competitors in areas such as mathematics and science (Fiske et al., 2002; Spencer, Steele, & Quinn, 1999). In one study of a math-based competition, males administered testosterone who had low (endogenous) cortisol were more likely to choose to compete against male opponents (perceived to be higher-status opponent) and tended to avoid competition against female opponents (perceived to be lower-status). In contrast, males administered testosterone who had high cortisol levels competed against female opponents (perceived to be lower-status opponents) and avoided competitions against male opponents (perceived to be higher-status opponents; Knight et al., 2019).

In this same experiment, after providing feedback on whether the participant had won or lost against the same series of opponents, testosterone treatment in males who had low endogenous cortisol concentrations resulted in more competitive behavior against prior winners (higher-status opponents) and avoidance of prior losers (lower-

status opponents). Testosterone treatment in males who had high (endogenous) cortisol levels resulted in more competitive behavior against prior losers (lower-status opponents) and avoided prior winners (higher-status opponents). The testosterone treatment × cortisol interaction was not moderated by opponent gender in these later rounds. Thus, an opponent's gender seemed to operate as a subjective indicator of opponent status based on gender stereotypes in the absence of objective status cues based on winning or losing.

These two studies suggest that cues to an opponent's status may be critical moderators of the testosterone × cortisol interaction and may explain some of the heterogeneity in previous dual-hormone findings. These initial studies examined previous wins and losses and gender stereotypes as cues to an opponent's status, but other cues may exert similar moderating effects, depending on the nature of the competition or social hierarchy. For example, physical formidability or dominant nonverbal behavior may operate as cues to opponent status in a physical contest, but may not matter to the same extent for a nonphysical contest (Kordsmeyer et al., 2019a). Future work should examine cues to opponent status both more explicitly – i.e., by experimentally manipulating cues to opponent status – and more broadly by examining larger, more diverse samples in a wider array of competitions and social hierarchies.

Context-Dependence Based on How Social Status may be Earned. This subsection has focused on context-dependence determined by cues to an opponent's status, but context-dependence may also emanate from differences in how social status is earned within a group (de Waal-Andrews et al., 2016). For example, aggressive or violent behaviors may be a viable means to gain social status in groups that encourage

or rely on antisocial behavior. Hence, high testosterone and low cortisol are associated with increased aggressive and violent behaviors among groups of juvenile offenders (Dabbs et al., 1991; Popma et al., 2007). Among other groups, such as non-institutionalized undergraduate students, anti-social behaviors may not be effective for gaining social status. Testosterone × cortisol interactions may be reversed for antisocial behaviors among these groups, such that high testosterone and low cortisol may be associated with lower levels of aggressive or anti-social behavior (Denson et al., 2013; Welker et al. 2014; Roy et al., 2019; Lee et al. 2015). Future research should examine this explicitly by conducting naturalistic studies that observe different styles of social hierarchies or via experimental work in which context-dependence is manipulated.

Neural Responses to Reward and Threat

The dual-hormone profiles of high testosterone levels coupled with lower or higher cortisol levels may be related to status-seeking behavior via different mechanisms. In particular, mechanisms involving neural responses to reward and threat may help explain inconsistent testosterone × cortisol associations with behavior. We review evidence indicating that reward and threat may link to divergent patterns of behavior for individuals with high testosterone and low versus high cortisol levels, with a particular emphasis on neural pathways that underlie these processes.

Reward. Behavioral, psychological, and neural systems associated with reward have been focal points of mechanistic hypotheses in the literature on testosterone as well as the dual-hormone hypothesis literature (Welker et al., 2015). Extensive work in rodents provides robust evidence of testosterone's intrinsically rewarding properties vis-á-vis addictive-like self-administration and conditioned place preference (Johnson &

Wood, 2001; Wood et al., 2004; Wood, 2002; Peters & Wood, 2005; Arnedo et al., 2000; Packard et al., 1997). In humans, testosterone has been associated with state psychological measures of reward processes, such as increased enjoyment of aggressive behavior or enjoyment of a decisive victory within a laboratory competition task (Geniole et al., 2019; Mehta et al., 2015c). This positive association between testosterone and reward extends to the neural substrates of reward perception, including increased activity in mesolimbic reward areas such as the ventral striatum, nucleus accumbens, and ventral tegmentum (Hermans et al., 2010; Op de Macks et al., 2011).

Conversely, higher cortisol levels have been associated with reductions in activity in reward-processing areas, including the basolateral amygdala and striatum in some research (Kinner et al., 2016; Montoya et al., 2014). Given evidence that the HPA axis may inhibit the action of testosterone (Viau, 2002), high testosterone levels may be associated with increased focus on reward or reward-sensitivity only when cortisol levels are low. High cortisol levels may block this reward-focusing effect of testosterone. In line with this reasoning, one recent study found that high basal testosterone was positively related to a psychological measure of reward (enjoyment of a status-relevant economic game, the hawk-dove game), but only among low-cortisol but not high-cortisol individuals (Mehta et al., 2017). The increased reward-seeking tendency of individuals with high testosterone and low cortisol levels may explain their tendency to selectively compete against high-status opponents (Mehta & Josephs, 2010; Knight et al., 2019): After all, competing against a higher status opponent offers the potential for the reward of earning higher status. However, some research has also found that cortisol may

increase activity in some well-studied reward systems, such as dopaminergic signaling in the nucleus accumbens (Oswald et al., 2005; Pruessner et al., 2004). These results suggest that cortisol alters neural responses to reward, but that it may exert both anti-rewarding and rewarding effects, which future research must clarify via empirical testing.

Threat. Threat is another possible mechanism underlying divergent patterns in dual-hormone interactions. Testosterone and cortisol are both individually associated with heightened responses to threat. Experimental research indicates that testosterone enhances responses to socially threatening stimuli in males and females in the medial amygdala (Goetz et al., 2014; Hermans et al., 2008), a brain region classically associated with threat salience. Other investigations have qualified these effects by revealing that testosterone increases activation only during trials in which a social threat was approached, not when a threat was avoided (Radke et al., 2015). These results suggest that testosterone's association with threat may be predicated on the approach of potentially threatening targets. Cortisol has also been associated with heightened neural responses to threatening stimuli (Montoya et al., 2015).

Whereas high testosterone coupled with low testosterone may be more associated with reward pathways, the research reviewed in this subsection suggests that high testosterone and high cortisol levels may be associated with neural responses to threatening stimuli that subsequently link to a reversed pattern in the dual-hormone interaction. For example, the coupling of high testosterone with high cortisol levels may accentuate the threat of high-status opponents, which may lead high testosterone-high cortisol individuals to avoid competition against them (Mehta & Josephs, 2010; Knight et

al., 2019). For an individual with high testosterone and low cortisol levels, the threat inherent to a higher-status opponent may not be as salient and, as discussed above, the potential reward from competing with a higher-status opponent perhaps is more persuasive. Overall, this work suggests testosterone may heighten the rewarding or threatening properties of a given status-relevant situation, dependent on cortisol levels. These heightened threat or reward responses may then explain the traditional and reversed dual-hormone patterns evident in the published literature.

Future Directions for the Dual-hormone Hypothesis

The explanations and recommendations discussed above specifically aimed to account for heterogeneity in previous dual-hormone findings. Here we discuss key directions that are important for testing and extending the dual-hormone hypothesis.

Testing Causality in the Dual-hormone Hypothesis

Although a significant body of research has examined the effects of exogenously administered testosterone or cortisol on social behavior, to date no study has reported the behavioral effects of simultaneous pharmacological manipulation of both hormones. Some prior work has administered testosterone and measured endogenous cortisol (Knight et al., 2019), or experimentally manipulated stress levels while measuring endogenous testosterone (Prasad et al., 2017). Pharmacological experiments in general tend to provide stronger evidence of causality, because they allow for experimental control over hormone levels. A more robust causal test of the dual-hormone hypothesis consisting of double-blind, placebo-controlled, crossover design involving both testosterone and cortisol is therefore needed.

One challenge in determining causality in the dual-hormone effect is the multitude of stress systems with which cortisol is associated, each of which could be altered by elevated cortisol levels and could in turn affect gonadal functioning. For example, a given stressor or chronic stress can simultaneously impact autonomic, immune, and adrenal responses in addition to or in coordination with the HPA-axis (Juster et al., 2010). The HPA-axis also has bidirectional connections to each of these stress response systems. Causal testing of cortisol's role in the dual-hormone hypothesis must therefore proceed with an eye toward the potentially confounding roles of other stress response systems. One recent report has highlighted the specificity of endogenous cortisol's moderating influence - and not cardiovascular indices of stress responses - on the link between testosterone and status seeking (Prasad, Knight, and Mehta, 2019). This evidence is consistent with the dual-hormone hypothesis, in which cortisol levels specifically, rather than other stress response systems, are proposed to moderate testosterone's effect on status-seeking behavior. In order to provide more rigorous tests of the dual-hormone hypothesis, future work should continue to examine the involvement of parallel stress systems that have been linked to cortisol and/or testosterone, including sympathetic nervous system activity (Chichinadze & Chichinadze, 2008; Leining & Josephs, 2010) and acute inflammatory responses (Steptoe, Hamer, & Chida, 2007; Muehlenbein, 2006).

Basal versus Dynamic Endocrine Responses

Most of the research on the dual-hormone hypothesis has focused on baseline hormone levels. Yet some work has extended the dual-hormone hypothesis to levels of acute hormone change. An important direction for future dual-hormone research will be

to more explicitly determine when testosterone × cortisol interaction effects may be seen with baseline hormone levels versus dynamic hormonal responses. For example, under acute stress, cortisol fluctuates by several orders of magnitude (Dickerson & Kemeny, 2004), and as such, acute cortisol responses may be a stronger moderator of testosterone's association with status seeking behavior under acute stress.

A few recent studies support this suggestion. In one study, baseline testosterone was positively related to retaliation in the ultimatum game (i.e., rejection of unfair offers, which may be considered a status-seeking behavior)[5] in a relaxation condition in which cortisol levels acutely declined. This testosterone-behavior association was suppressed in an experimentally-induced social stressor condition during which cortisol levels rose (Prasad et al., 2017). A similar pattern was reported in another study, in which a stress condition blocked an association between higher levels of testosterone and lower levels of a behavioral index of empathic accuracy that was seen in a control (non-stress) condition (a link between testosterone levels and self-reported empathy was not found; Nitschke & Bartz, *in press*). Lower empathic accuracy has been linked to earning status in a competition (Vongas & Al Hajj, 2014) and fluctuations in this cognitive process may support status seeking. Elsewhere, basal testosterone's relation with status seeking was also found to depend on cortisol responses to an acute social stressor: Basal testosterone was positively related to keeping more money for oneself in a dictator game (considered a status-seeking behavior) only among participants who showed relatively low cortisol responses to the stressor, but this testosterone-behavior relationship was suppressed among participants who showed relatively increased

[5] But *cf.* Grebe and colleagues' (2019a) criticism of labeling rejections in the ultimatum game as a status-seeking behavior.

cortisol responses to the stressor (Prasad et al., 2019). Basal cortisol did not moderate testosterone's association with status-seeking behavior in either study.

We tentatively propose that in situations in which there is little to no expectation that participants experience cortisol changes prior to measuring status-seeking behavior (e.g. no acute stressor), basal cortisol will moderate testosterone's association with status-seeking behavior. But when acute cortisol changes are expected prior to the measurement of status-seeking behavior, acute cortisol responses to the stressor may be a stronger moderator of testosterone's behavioral effects compared to basal cortisol. This hypothesis should be tested directly in new studies.

Within the challenge hypothesis, *fluctuations* in testosterone drive behavior in contexts of inter-male challenges relevant to reproduction (Archer, 2006), suggesting dynamic measures of testosterone may more strongly associate with behavior than basal measures within competitive or other status-challenging contexts. Limited work has examined this possibility. For example, Kordsmeyer and Penke (2019) manipulated testosterone levels via an inter-male competition that was directed by an attractive female experimenter; a control condition consisted of watching a documentary movie in a lab session led by a male experimenter. In the competition condition, dynamic measures of testosterone were related to changes competitiveness and dominance, as was the change in testosterone × basal cortisol interaction (changes in testosterone relating to changes in status-relevant personality states were not tested in the control condition in this manuscript; follow-up analyses with data available online suggest they are unrelated). Future work must empirically determine the conditions under which

basal or dynamic measures of testosterone and cortisol will more strongly relate to status-seeking behavior.

Lifespan Perspectives

The majority of work on the dual-hormone hypothesis has focused on young adults and has tested the hypothesis by comparing hormone profiles across individuals. However, levels of these hormones naturally fluctuate across the lifespan. Testosterone and other sex hormones substantially increase in adolescence (Sisk & Zehr, 2005). Later in life, male testosterone levels decline with increasing age, falling approximately 1% per year starting in the early midlife period (i.e., 30-40 years of age; Matsumoto, 2002) and women's sex hormone levels plummet at menopause (Longcope et al., 1986). The HPA axis also undergoes age-related changes in both males and females, resulting in generally increased cortisol levels with increasing age (Yiallourous et al., 2019).

Alongside these biological changes, older adults' social environments and behaviors change as well. Older adults prune social networks to close, familial ties and exclude lesser known or novel social partners (Fredrickson & Carstensen, 1990; Fung, Carstensen, & Lutz, 1999). Older adults are also motivated by emotional well-being goals that can be achieved in their (seemingly limited) lifetime, rather than the acquisition of resources that may relate to social status (Carstensen, 1992). These developmental trajectories contrast with young adulthood, which is characterized as a peak time for mating, reproductive, and status-seeking behaviors.

A key extension of the dual-hormone hypothesis would be to test whether within-person changes in testosterone and cortisol predict within-person changes in status-

seeking behavior. A longitudinal approach focused on key developmental periods would help determine whether developmental changes in testosterone – i.e., increases at puberty, or reductions in later life – and cortisol are associated with intra-individual change in status-seeking behaviors.

One theory that unites hormones and behavior within a developmental perspective is life history theory. This framework suggests that testosterone may mediate motivational and metabolic trade-offs between seeking and competing for sexual partners (high testosterone levels) and caring for offspring (lower testosterone levels; Hau, 2007; Grebe et al., 2019b). Life history theory takes a *life-course* perspective (i.e., focusing on certain milestones in life such as parturition) and only limited work has focused on testosterone × cortisol in this context. For example, a testosterone × cortisol interaction was associated with parenting quality among fathers (but not mothers), such that higher testosterone levels were more negatively associated with postnatal parenting quality among men with higher cortisol levels (Bos et al., 2018). Future work should continue to examine whether cortisol modulates testosterone's associations with life-course dependent behaviors as another possible developmental examination of the dual-hormone hypothesis.

The Dual-Hormone Hypothesis and Health

Another future direction dual-hormone hypothesis research could pursue is examining the joint effects of testosterone and cortisol on immune functioning and health. Extensive work has linked testosterone and cortisol individually to a wide array of health outcomes including metabolic disorder, cardiovascular disease, mental health outcomes, and diseases of aging, such as Alzheimer's Disease (Yeap, 2009; Pike et al.,

2009; Adam et al., 2017; Ennis et al., 2017), but few studies have examined the testosterone × cortisol interaction on immune functioning or health outcomes. A line of research related to the dual-hormone hypothesis – called the stress-linked immunocompetence handicap hypothesis (SL-ICHH; Rantala et al., 2012) – outlines testosterone and cortisol's joint role in regulating immune functioning and their effects on social signaling. Specifically, the SL-ICHH posits that testosterone reduces the immune system's effectiveness in responding to certain challenges *and* produces secondary sex characteristics (e.g., plumage in birds, facial morphology in humans), but only when cortisol levels are low. Consequently, testosterone may generate honest signals of immune functioning and fitness when coupled with lower cortisol levels: A secondary-sex characteristic produced by testosterone signals the ability to withstand immune system challenges despite testosterone's immunosuppressive effects.

In research with humans, Kordsmeyer and colleagues (2019b) provided limited evidence that testosterone (reactivity) × basal cortisol interactions were associated with facial cues to dominance (but not facial cues of healthiness; see also Kandrik et al., 2017, which reports inconsistent testosterone × cortisol associations with facial cues to dominance, and no associations with healthiness of attractiveness). Other work has shown that testosterone × cortisol interactions were associated with both facial attractiveness and immune responses to vaccine (Rantala et al., 2012). In broader human health research, testosterone and cortisol have also been jointly linked to health outcomes, such as hippocampal volume and cognitive functioning in middle-aged men (Panizzon et al., 2018). Panizzon and colleagues' results indicate a "reversed" dual-hormone pattern in which high testosterone and high cortisol were associated with

larger hippocampal volume and better cognitive functioning. More research is necessary at the intersection of hormones, immune functioning, and status-relevant behavior to determine the dual-hormone hypothesis' implications for health.

Extending the dual hormone hypothesis

Another key step for future scientific inquiry is to extend the dual-hormone hypothesis by integrating empirical results across multiple fields of research that study the endocrine system. Although research on the dual-hormone hypothesis has focused on behaviors linked to status, interactions between the HPG and HPA axes have now been observed on a variety of outcomes, including biological processes such as hormone receptor expression, neural activity, immune function and health, physical athletic performance, cognition, as well as outcomes linked to reproduction (e.g. sexual desire) and parental care (Bos et al., 2018; Burnstein et al., 1995; Chen et al. 1997; Crewther et al., 2018; Denson et al., 2013; Johnson et al., 1992; Raisanen et al. 2018; Rantala et al., 2012; Panizzon et al., 2018; Smith et al., 1985; Tilbrook et al., 2000; Viau, 2002). These results suggest that the HPG and HPA axes may be interacting with each other to influence a range of hormone-dependent processes throughout the body.

Extensions of the dual-hormone hypothesis will also have to account for the reciprocal nature of hormones and behavior. The challenge hypothesis conceptualizes causal effects of hormones on behaviors, as well as causal effects of behaviors and social contexts (e.g., competitive vs. non-competitive context) on hormone levels. This reciprocity is evident in some dual-hormone manuscripts already, in which researchers manipulated social contexts as a means to manipulate hormone levels (Kordsmeyer & Penke, 2019; Prasad et al., 2017). These studies are based on the assumption of a

direct, causal association between social contexts and hormone levels, consistent with the challenge hypothesis. These assumptions of reciprocal hormone-behavior relationships should be explored further.

Conclusion

The influence of the endocrine system on animal social behavior is complex and multifaceted, and a number of theories have been developed in the last several decades to explain these associations. The challenge hypothesis has played a central role in predicting the nature of testosterone's relationships with status seeking in a variety of animals. The dual-hormone hypothesis expands the scope of this relationship by explicitly considering how cortisol interacts with testosterone to predict status-seeking behaviors. This approach enables the generation of specific predictions about which individuals are likely to express testosterone-associated status seeking (i.e., those with low cortisol). Nevertheless, as noted here, the dual-hormone hypothesis has been beset by its own share of methodological and interpretational concerns, which mirror those noted elsewhere in experimental psychology (e.g., low statistical power, flexibility in analysis and interpretation; Open Science Collaboration, 2015; Simmons, Nelson, & Simonsohn, 2011). We offer a number of recommendations to guide progress in this field (Table 1). Ultimately, a fuller understanding of the endocrine bases of status seeking will require the integration of the effects of other relevant hormones and consider meaningful social-contextual and individual differences that would interact with the endocrine system in the regulation of social behavior.

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Table 1. Overview and Recommendations for Research on the Dual-Hormone Hypothesis

Overview

- The dual-hormone hypothesis extends the challenge hypothesis by focusing on interactions between testosterone and cortisol as predictor of status-seeking behavior.
- This hypothesis predicts that high testosterone is linked to status-seeking behavior more strongly when cortisol levels are low; testosterone's link to status-seeking behavior is expected to weaken or reverse when cortisol levels are high.

Statistical and Methodological Recommendations

- Based on a published meta-analysis, 80% power is accomplished with approximately *n* = 300 participants for testosterone × cortisol interaction predicting direct measures of social status attainment (ignoring covariates, other moderators, etc.).
- Liquid chromatography tandem mass spectrometry (LC-MS/MS) measurement is suggested for testosterone assays, especially among lower-concentration samples. Immunoassays may be sufficient for cortisol.
- Eliminate flexibility in analyses and improve reproducibility by preregistering and systematically replicating.
- Remove publication bias by publishing studies based on methodological rigor, independent of outcome, such as with registered reports.
- Behavioral outcomes should focus on direct measures of status; other status-relevant behaviors may be explored but preregistration will help reduce flexibility in analyses.

Future Directions

- Examining social contextual and individual difference factors may help clarify the heterogeneity in dual-hormone interactions, including evidence of 'reversed' dual-hormone patterns.
- Testing causal effects of testosterone and cortisol – by pharmacologically attenuating and enhancing hormone levels – on status-seeking behavior and social status is a critical next step for the dual-hormone hypothesis.
- Acute fluctuations in hormones (e.g., in response to stress), long-term changes in hormones and behavior at key developmental stages (e.g., puberty or later adulthood), and immune and health outcomes should be examined within the dual-hormone hypothesis framework.
- Integrating empirical results across multiple fields of research that study the endocrine system and accounting for reciprocal effects of hormones and behavior will be key to developing a formal dual-hormone theory.

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