

Social Neuroendocrinology of Status: A Review and Future Directions

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Abstract Status hierarchies are universal across human and non-human animal social groups. Hormones and status interact with one another in a reciprocal manner. The present paper reviews the current literature on the interaction between testosterone (T), cortisol (C) and status in humans, with reference to non-human animal research. We discuss the complexity of the social neuroendocrinology of status with a focus on stable status, competitions for status, and the effects of severe social subjugation. Importantly, we conclude that the relationship between these hormones and status is not direct. We address moderators of the relationship between hormones and status, such as sex, individual differences, context, and T x C interactions, to get a more nuanced understanding of this relationship. Future directions include suggestions for examining this relationship longitudinally, including more females in status research, additional focus on social context and hormonal interactions, as well as non-competitive routes to status.

Keywords Competition · Testosterone · Cortisol · Dominance · Status hierarchy · Social neuroendocrinology

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Testosterone (T), dominance, and, by association, masculinity, are often positively associated in the scientific literature and in popular media. Of course, like all hormone-behavior interactions, the interaction between social status and hormones is more complicated than a simplistic understanding of this relationship. It has been argued that much of the research on T, masculinity, dominance, and other associated factors is driven by pre-theory assumptions (van Anders 2013). Several important components of the T-status relationship often get lost in the narrative around dominance and T, including the bidirectional (or reciprocal) relationship between hormones and the social environment; the role of other, non-androgenic hormones; and whether hormone-behavior relationships are similar or different in males and females. The goal of the present paper is to highlight the research on hormones and status while emphasizing the complexity inherent in these systems. This complexity necessitates the incorporation of moderators such as sex, social context, and hormonal interactions to provide a more complete picture of the interrelations between hormones and status and their relationship with behavioral outcomes.

Higher status within social hierarchies provides advantages that promote survival and reproduction, such as privileged access to limited resources (money, food, sexual partners), greater power over subordinates, and good health (Ellis 1994). Because of these many benefits, individuals are often motivated to gain and maintain higher social rank over others. In fact, theorists note that the drive for status is one of the most fundamental social motives (Mazur and Booth 1998). However, high status is not always linked with good health; it can also be high stress (e.g., Sapolsky 2005). Additionally, humans have very complex social systems, and one person can hold different social ranks in different social hierarchies. Although the added complexity of human social interactions may make the links between hormones and status less clear than in non-human animals, hormones do play a role in establishing and maintaining status. Studying hormone-status relationships is an important component in understanding the complexity of status in both humans and non-human animals.

Social neuroendocrinology is a burgeoning field that focuses on the reciprocal interactions between hormones and the social environment. There has been a rapid increase in human hormonal research in psychology, largely due to the ease with which hormones can be collected from saliva and the availability of reliable assays to quantify individual variability in salivary hormones. There is an extensive literature on the neuroendocrinology of status in non-human mammals (and other species), but research on humans has only really begun to accelerate within the last decade.

Much of the research on status examines T in those seeking to attain high status, with the assumption that high status and higher T are always preferable. However, this perspective fails to acknowledge that not all people are motivated to seek high status (e.g., Anderson et al. 2012) or that there are benefits of low T (Aucoin and Wassersug 2006; Mehta et al. 2009; van Anders 2013). There has also been little attention paid to sex differences and similarities in the literature on dominance, competition, and status. In fact, a large percentage of studies, particularly on competitive outcomes, have been conducted exclusively with male participants or have not considered sex as a variable (cf. Cashdan 2003). Reasons for this bias toward research on men may include the assumption that T (the most studied hormone related to status) is only important for males, a lack of significant effects observed in females, the overt dominance displays by males of many species (e.g., battling for territory), the difficulty reliably measuring T in women due to assay sensitivity, and the changes in female hormonal and

behavioral responses that vary with the estrus or menstrual cycle. Theories for sex differences and similarities are needed in this research area.

In this paper, we review research on the neuroendocrine systems that influence and respond to behaviors implicated in social status. We focus on hormones and status processes in human hierarchies, but we rely on non-human animal work to inform our discussion. In the first section we review research on basal hormone concentrations and status-seeking behaviors with a focus on recent studies that have examined interactions between T and cortisol (C). We then discuss research on rapid changes in hormone concentrations – especially T changes – in status-relevant contexts and the functional effects of these changes. Next we turn our attention to bullying/social defeat as important status-relevant contexts with potential psychological and physical health implications. Finally, we conclude the paper by discussing future directions for research on hormones and human hierarchies.

Testosterone and Cortisol are Primary Hormones Involved in Status

We chose to limit this review to the hormones T and C because they are the primary hormones assessed in human studies of status. T is an anabolic sex steroid and the most commonly studied status-related hormone in both humans and non-human animals. T is an end product of the hypothalamic-pituitary-gonadal (HPG) axis, and male T is predominantly secreted by the testes. Women also produce T in smaller quantities, with only about 25 % secreted from the ovaries. Other sources include 25 % from the adrenal glands, and the remaining 50 % is converted from prohormones (Greenspan and Gardner 2001).

C is from the class of steroid hormones known as glucocorticoids and is an end product of the hypothalamic-pituitary-adrenal axis (HPA). Its primary role is metabolic, but it also serves additional functions, such as suppressing inflammation and altering immune responses. It is released from the adrenal glands in response to physical and psychosocial stressors (among other functions), and it is a catabolic hormone that helps provide glucose to muscles that need energy when in a state of “fight or flight” (Sapolsky 2002). Many aspects of status can be physically or psychologically stressful. These include competing for status, maintaining high status, or being very low in status. As such, C is involved in all of these components of status, which will be reviewed below.

Basal Hormones and Status

Basal Testosterone and Status

T plays an important role in reproductive development and behavior. Since reproduction opportunities are linked with status, in turn, T also influences and is influenced by status-seeking behaviors. T has a circadian rhythm; concentrations are highest in the morning and drop throughout the day. But T concentrations measured at the same time of day are temporally stable over time (Granger et al. 2004; Liening et al. 2010; Sellers et al. 2007). For example, in one study male and female participants provided saliva samples between noon and 4 PM over 5 days (Study 1, Sellers et al. 2007). The intraclass correlation for T concentrations across the five days was $r=0.94$ for males

and $r=0.81$ for females. Thus, T measured at the same time of day across multiple days may function as a personality trait that shows stable associations with social behavior (Sellers et al. 2007).¹ In this section, we review studies examining effects of stable endogenous T concentrations (i.e., basal T).

It has long been hypothesized that T should be related to status-seeking behaviors and in turn higher social status (Mazur and Booth 1998). For social status within a hierarchy, there is some empirical research to support this theory. Studies of non-human animals, in particular, have found significant relationships between T and higher social status in wild dogs (Johnston et al. 2007), baboons (Gesquiere et al. 2011), and wolves (van Kesteren et al. 2012), among other species (See below for exceptions to this finding). It is more difficult to study hierarchies and hormones in humans, and the few studies that have examined this relationship have been equivocal. One study of 9–15 year old boys found that T was a predictor of parental reports of leadership (one item) in their sons (Rowe et al. 2004). Another study of men in college did not find any relationship between T and rankings of status by their suitemates (McIntyre et al. 2011). A study of female college students living together in groups of 10 showed that T was related to dominance behaviors, such as reduced smiling, but was inversely correlated with status rankings by their housemates (Cashdan 1995). The discrepancies in these findings can potentially be explained by social context and variations in C levels, which are discussed below.

On a broader, societal level, if we look at the relationship between T and markers related to socioeconomic status (SES), there is still no clear link between status and T. One early study did find a relationship between T and occupation with athletes and actors (high status occupations) showing higher levels of T than ministers (lower status occupation) (Dabbs et al. 1990). A study of male Vietnam veterans compared male lawyers, other white collar workers, and blue collar workers and found that the lower SES group of blue collar workers had the highest level of T. A study of the same Vietnam veterans directly compared high SES and low SES men and found that men who were lower in SES had higher levels of testosterone. There was also an interaction showing that higher T was linked to antisocial behavior in low, but not high SES men (Dabbs and Morris 1990).

Although there is not a clear relationship between status and T, there is an abundance of evidence that, across a variety of animal species, endogenous T concentrations are positively related to socially dominant *behaviors* – defined as behaviors to attain or maintain high status (e.g., male chimpanzees, Muller and Wrangham 2004; male and female baboons, Beehner et al. 2005, 2006; Sapolsky 1991; male fish, Oliveira et al. 1996; male & female lemurs Cavigelli and Pereira 2000; von Engelhard et al. 2000). Most social neuroendocrinology research on T's role in social behavior studies males, but similar effects of T on dominance have also been reported in females of some species, as noted above.

There is evidence that T is associated with psychological markers of dominance and status-seeking motivation in humans as well, for both males and females (reviewed in Archer 2006; Carré et al. 2011; Eisenegger et al. 2011; Mazur and Booth 1998). As

¹ Related studies with C have found that several averaged daily measurements of C may be necessary to accurately assess the individual rise of C (Hellhammer et al. 2007). Thus, averaging T levels over multiple days is also likely to improve reliability when measuring basal T.

previously noted, Cashdan (1995) found that dominance-related behaviors were positively correlated with T in female college students, even while T was negatively correlated with peer-rankings of status. So, subtle dominant behaviors the women were possibly unconsciously engaging in resulted in being disliked by other group members, perhaps due to social expectations of women's behavior as non-dominant. Basal T predicts increased attention and approach orientation toward dominance cues such as angry faces in both males and females (van Honk et al. 1999; Wirth and Schultheiss 2007). T's role in threat vigilance is thought to be unconscious, as T's effects on attention to angry faces are strongest when faces are presented outside of conscious awareness (Terburg et al. 2012; Wirth and Schultheiss 2007). These results suggest that T is an *implicit* marker of dominance that motivates individuals to gain and maintain their social status. Since T is an implicit marker of dominance with modest effects, we would expect that the implicit motivations could be overridden by competing conscious/explicit motivations.

Basal T is also related to reduced cooperative motivation in males and females (Mehta et al. 2009), lower empathy in workplace hierarchies (Ronay and Carney 2013), and an increased likelihood of making utilitarian decisions when faced with a moral dilemma (which requires inhibiting negative social emotions such as guilt; Carney and Mason 2010). These studies suggest that males and females high in basal T adopt a social cognitive profile that may be adaptive in competitive interactions because hyper-benevolent behavior may leave one vulnerable to exploitation or injury in a threatening environment. However, as discussed below, findings from exogenous T administration studies suggest that in a nonthreatening environment, T may also be related to prosocial ways to attain status (e.g., van Honk et al. 2012)

By increasing dominance motivation and reducing cooperation in situations in which status may be threatened or challenged (e.g., situations in which betrayal is possible, competitive social interactions), higher T may prepare individuals to vie for or defend their status in competitive or socially threatening interactions. The benefits of high T in times of competition or threat are predicted by the *challenge hypothesis* (Wingfield et al. 1990; described below). In line with this reasoning, high T individuals perform better on cognitive tasks (logic questions taken from the Graduate Record Examination) when they are told they are competing against another player as opposed to cooperating with another player (Mehta et al. 2009), further supporting a role of T in the motivation to gain or maintain high status. These data paint a picture of a high T individual as one who is motivated to gain or protect social status.

In summary, basal T and an individual's status within a group are often not directly related. This is likely because varying social contexts may have different rules for what determines status (e.g., men vs. women, social group vs. work colleagues.) The strongest correlate of T seems to be specific behaviors that are related to dominance. Depending on the context, these behaviors may be linked to status, but in other contexts they may not.

Basal Cortisol and Status

C levels have also been shown to be related to status and dominance in several non-human animal species. Like T, C has a diurnal rhythm. It shows a sharp increase first thing in the morning, declines rapidly at first and then more slowly over the course of

the day. The C increase in the morning (averaged over 2–6 days) and the C response to stressors (averaged over 4 days) also appears to be relatively stable and linked to personality traits, such as dominance (Hellhammer et al. 2007; Pruessner et al. 1997). In most species studied, there is a negative relationship between dominance and C with high-ranking animals having the lowest levels of C (Sapolsky 2005). The high C (or corticosterone) often seen in low-ranking group members is thought to be related to the stress of being low status. This finding has been demonstrated in rodent and primate studies in which groups of animals are observed in semi-natural housing and social groups (Sapolsky 2005; Tamashiro et al. 2005). However, there are many exceptions to this average finding (Abbott et al. 2003; Creel 2001). C levels and their relationship with status may depend on the stability of the hierarchy; unstable hierarchies can result in dominant animals with higher C because they have to defend their position. Unstable hierarchies could also result in no relationship between C and status since all members of the social group may find the instability to be stressful. It can also depend on the type of social group and whether cooperation or aggression is more prevalent, group size, and other factors related to the level of stress one's role confers.

As noted previously, in humans, it is more difficult to observe social hierarchies within established groups, but there has been some research looking at the relationship between C and SES. SES is a measure of individual or familial wealth and education within society or a community (Adler and Ostrove 1999), but it is operationalized differently across studies. Measures of C also vary with studies examining the C awakening response (CAR), morning C, average C across the day (area under the curve), and/or slope of the decline across the day. The relationship between SES and C is unclear, likely because both SES and C are measured differently across studies, but the most common finding is that aspects of the diurnal response are attenuated. This includes a less strong CAR (Hajat et al. 2010), lower levels of morning C, and a less steep decline in C across the day (Agbedia et al. 2011; Kumari et al. 2010) in those low in SES. These differences often result in higher levels of C throughout the day (e.g., with less decline over the day), but some only show differences in the morning. Additionally, many studies have found no differences in C secretion related to SES (reviewed by Dowd et al. 2009; Kristenson et al. 2004). The evidence does seem to suggest that the higher levels of stress experienced by those lower in SES generally result in diurnal C patterns that differ compared to those higher in SES. There are factors such as social support and sense of control that can ameliorate the effects of a stressful environment, and these moderators can also affect the relationship between status and C (see Dickerson and Kemeny 2004; Uchino 2006).

When examining the relationship between status and C in a hierarchical organization, as opposed to looking at broad measures of SES, a recent study found that leaders had lower afternoon C relative to non-leaders in a community sample of military and business personnel (mixed-sex sample, Sherman et al. 2012). (C is most stable in the afternoons, so it is often used as the measure for basal C.) The leaders in the study reported a greater sense of control, which is one explanation for the lower C levels. Lack of control for those lower in status can be related to greater psychological and physical stressors in their environments, resulting in hyper-activity of the HPA axis (Sapolsky 2005). Another possibility is that low-C individuals may behave in ways to attain higher rank in social hierarchies such as through displays of dominance, a hypothesis consistent with exogenous glucocorticoid administration in non-human

animals (e.g., rainbow trout, DiBattista et al. 2005). Future research is needed to test the mechanisms through which C and status influence one another. Although the study of status in humans did indeed demonstrate an inverse association between higher status and basal C, there have also been studies showing that there was no such effect, and that the stressfulness of a particular job is an important factor to consider (e.g., Gadinger et al. 2011).

Overall, the evidence does seem to point to a link between status and C, although the direction and strength of the relationship varies. As demonstrated in non-human primate studies, the relationship between status and C changes depending on the social dynamics of the group and other contextual factors. Although there have only been a few studies assessing C and status in controlled environments, there is a need to examine moderators of this relationship to get a clearer picture.

Moderators of Relationships Between Basal Hormones and Status

Broadly, high T is associated with dominance behaviors and potentially higher status, while high C tends to be associated with lower status and greater exposure to stressors. However, as reviewed above, there are inconsistencies in the literature. These inconsistencies point to the importance of studying individual, situational, and group differences that may account for the variability seen in the relationship between hormones and status. Sex is likely a moderator of this relationship, but research on women is limited, so we have little empirical work to draw on. Below we discuss additional moderators that have been shown to affect the relationship between status and basal hormones.

Stability of the Hierarchy The association between T and dominance is strongest within unstable hierarchies. In wild baboons, for example, T is related to dominant behaviors when the alpha position is up for grabs, such as after the alpha male is injured (Sapolsky 1991). But T is unrelated to dominance when the hierarchy is stable. Similar results emerge in other species as well, such in fish (Oliveira et al. 1996) and birds (Wingfield et al. 1990). Wingfield et al. (1990) defined the challenge hypothesis, which predicts that T will be elevated in times of challenge. The challenge hypothesis states that in species (of birds) with parental males, T will show large increases in times of threat or other competitive interaction. The increase in T in response to competitive situations is hypothesized to facilitate behaviors that will enhance the likelihood of success in the face of challenge, such as increased aggression. Unstable status hierarchies would be a type of context described by the challenge hypothesis that would result in higher levels of T. Data from the non-human animal literature thus suggest that high T levels are linked to dominant behaviors when the status hierarchy is in flux in males, and possibly in females. To our knowledge, the hormonal effects of unstable hierarchies in groups of humans have not been tested, although research on competitive encounters (discussed below) are related to this phenomenon.

C levels are also likely related to the stability of the hierarchy because an unstable hierarchy can be stressful (e.g., Sapolsky 1992). Associated factors include individual variables, such as sense of control (Sherman et al. 2012), which would vary depending on the stability of the hierarchy. Additionally, the type of social hierarchy, whether

cooperative or competitive affects C levels in non-human primates (Abbott et al. 2003), and likely also affect humans.

The Dual-hormone Hypothesis: Testosterone x Cortisol Interactions and Status-Seeking Behaviors One explanation for the mixed results related to hormones and status is that T and C may interact to predict status-seeking behaviors. According to the *dual-hormone hypothesis* (Mehta and Josephs 2010), T should be positively related to status-seeking behaviors and higher status when C concentrations are low, but T's effect on status-seeking behaviors should be blocked when C concentrations are high. Several studies provide empirical support for the dual-hormone hypothesis (e.g., Dabbs et al. 1991; Edwards and Casto 2013; Mehta and Josephs 2010; Pfattheicher et al. 2014; Popma et al. 2007). See Table 1 for a list of published studies that have reported basal T x C interactions. Examples include lab-based studies of leadership in which basal T was found to be positively related to dominance only among leaders with low basal C, but basal T was unrelated to dominance in leaders high in basal C for both men and women (Mehta and Josephs 2010). Similar findings have emerged in real-life situations, such as in a study of team status in collegiate female athletes on soccer, softball, volleyball, and tennis teams. This study found that higher T was related to higher social status in female athletes with low basal C, but basal T and status were unrelated in athletes with high basal C (Edwards and Casto 2013). Overall, these studies suggest that T and C interactively predict the attainment of status through dominant behaviors.

Although the precise mechanisms for dual-hormone effects on dominance and status remain unclear, several lines of evidence across disparate fields provide plausible mechanisms. First, C has the capability of interfering with the effects of T on behavior on a physiological level; for example, C suppresses the activity of the HPG axis, inhibits the action of T on target tissues, and downregulates androgen receptor expression (e.g., Burnstein et al. 1995; Chen et al. 1997; Tilbrook et al. 2000; Viau 2002), which all may lead to an inhibitory effect of C on T's behavioral effects. Second, the influence of T on the neural systems implicated in status threat depends on C concentrations (e.g., amygdala activation and prefrontal cortex-amygdala connectivity in response to status threat, Denson et al. 2013b; Hermans et al. 2008), and these dual-hormone influences on neural circuitry may have downstream consequences for status-seeking behavior. Third, T and C may interact on a psychological level. T is implicated in an implicit desire for status (Stanton and Schultheiss 2009; Terburg et al. 2012), and C is associated with behavioral inhibition (Roelofs et al. 2009). A combination of high status-seeking motivation (high T) and behavioral approach (low C) may encourage status-seeking and risk taking behaviors such as dominance, whereas the behavioral inhibition tendencies associated with high C may block the influence of high status-seeking motivation (high T) on dominance and status. More broadly, high C may be an evolutionary mechanism to block the effects of elevated reproductive axis activity in the pursuit of status during periods of heightened environmental stress because such behaviors may be metabolically costly and potentially dangerous (Carré and Mehta 2011; Maner et al. 2012). Only when environmental stress is low may it be beneficial and adaptive for a high T individual to adopt behaviors in pursuit of status.

Despite this evidence in support of the dual-hormone hypothesis on markers of dominance and status, studies that examined basal T x C interactions on measures of aggressive and anti-social behavior have yielded mixed results (see Table 1). Although

Table 1 Review of basal T × C on dominance/competition/aggression in published literature

Year	Reference	Sample size	Hormone parameters	Dependent variable	Result of testosterone X cortisol interaction
1991	Dabbs et al.	113 M	1 Morning	Real Life Crime	T (+) DV at low C, but not at high C.
2013	Edwards & Casto	74 F	1 Afternoon/Evening	Teammate Status	T (+) DV at low C, but not at mean or high C.
2011	Geniole et al.	74 M	1 Afternoon/Evening	Aggression	T (+) DV at low C (inclusion group). ^a
2010	Mehta & Josephs	45 M 49 F	1 Afternoon	Dominance	T (+) DV at low C, but not at high C.
2010	Mehta & Josephs	57 M	1 Afternoon	Compete Again	T (+) DV at low C, T (-) DV at high C (defeat condition).
2010	Mehta & Josephs	57 M	1 Afternoon	T Change	T (-) DV at high C, but not at low C (defeat condition).
2013	Pfättheicher et al.	72 M	2 Afternoon, AVG	Aggression	T (+) DV at low C, but not at high C.
2007	Popma et al.	103 M	3 Afternoon, AVG	Aggression	T (+) DV at low C, but not at high C.
2014	Tackett et al.	47 M 57 F	1 Afternoon	Psychopathy	T (+) DV at low C, but not at high C (high PD trait).
2013	van den Bos et al.	26 M	2 Afternoon, AVG	Overbidding	T (+) DV at low C, but not at high C.
2012	Zilioli & Watson	70 M	1 Afternoon/Evening	T Change	T (+) DV at low C, T (-) DV at high C.
2012	Cote et al.	24 M 25 F	3 Days Diurnal	Aggression	Not Significant. ^d
2011	Geniole et al.	74 M	1 Afternoon/Evening	Aggression	Not Significant (exclusion group).
2013	Geniole et al.	104 M 97 F	1 Afternoon/Evening	Aggression	Not Significant.
2014	Mazur & Booth	4462 M	1 Blood Serum	Aggression	Not Significant.
1999	Salvador et al.	28 M	1 Blood Serum	Competition	Not Significant.
1994	Scerbo & Kolko	37 M 3 F	1 Morning	Aggression	Not Significant.
2011	Victoroff et al. ^b	41 M	4 Morning, AVG	Aggression	Not Significant (see Carré and Mehta 2011).
2013	Denson et al.	53 F	1 Afternoon	Aggression	T (+) DV at high C, but not at mean or low C.

Table 1 (continued)

Year	Reference	Sample size	Hormone parameters	Dependent variable	Result of testosterone X cortisol interaction
2014	Welker et al.	114 M 123 F	1 Early Afternoon	Psychopathy	T (+) DV at high C, T (-) DV at low C (in men).

Studies are sorted to first list findings supporting the Dual Hormone Hypothesis, followed by non-significant findings, and ending with examples of the reverse trend. All samples are salivary unless otherwise stated. Hormone Parameters reflect the number of basal samples that were collected and the approximate time said samples were collected. A (+) denotes a positive prediction, while a (-) denotes a negative prediction

T Testosterone, C Cortisol, DV Dependent Variable, M Male, F Female, AVG some or all samples were averaged

^a Results trending in right direction, but $p = .14$

^b Reported in Carré and Mehta (2011)

^c Effect size of $T \times C \times \text{Inclusion/Exclusion}$

^d Reported in Gentile et al. 2011

some studies show dual-hormone interactions on aggression that resemble patterns described above (Dabbs et al. 1991; Popma et al. 2007), other studies show dual-hormone interactions with a different pattern, such as a positive association between T and aggression among individuals *high* in C, but not low in C (Denson et al. 2013a; social exclusion condition of Geniole et al. 2011; Welker et al. 2014), and yet other studies have found non-significant interactions between basal T and C (e.g., Geniole et al. 2013; Mazur and Booth 2014). These inconsistent results for dual-hormone interactions on aggression and anti-social behavior mirror the larger literature on basal hormones and aggression in humans, which by and large have shown weak or mixed results.

One possibility for these inconsistencies is that the high basal T low basal C profile may lead to aggressive behavior only in populations in which aggression is beneficial to status (e.g., male prisoners or male delinquent adolescents, Dabbs et al. 1991; Popma et al. 2007). A second possibility is that basal T x C effects on aggression may depend on contextual factors such as the presence or absence of social provocation (Geniole et al. 2011; Denson et al. 2013a) or other personality traits (Tackett et al. 2014). Moderators for T x C effects on aggression and anti-social behaviors should be examined in future research.

Changes in Status: Effects on Hormones and Behavior

Thus far we have outlined the relationship between status and basal T and C. Much of the research done in this area focuses on a single time point. It is difficult, especially in humans, to identify how a person develops high or low status and how hormones become chronically high or low relative to others in a group. Throughout daily interactions, hormones influence behavior and, in turn, behavior influences hormones. Competition, both formal and informal, overt and subtle, plays a large role in establishing dominance hierarchies and altering hormonal outputs in human and nonhuman species. There is a large amount of research on competition and endogenous T changes in humans, so we will focus on human research for this section of the paper. However, there are several excellent non-human animal experimental studies that demonstrate effects of exogenous T behavior that will be discussed below.

Testosterone Responses to Competition: Effects of Winning vs. Losing

The *biosocial model of status* (Mazur 1985) is a key theoretical model guiding current research on the relationship between hormones and human competitive behavior. This model posits that T concentrations change in response to human competition and that the outcome of competition influences the pattern of T release. Specifically, drawing on research in non-human primates, Mazur (1985) hypothesized that T levels would increase in response to a victory and decrease in response to a defeat. Mazur (1985) hypothesized that winners of competitive interactions may face additional challenges for status and that the increase in T may serve to promote competitive and aggressive behaviors aimed at defending one's status. In contrast, the decrease in T in response to defeat may serve to promote submissive behaviors aimed at avoiding further loss of

status and/or physical injury. This reciprocal component of the model suggests that changes in T during competition may enable organisms to adaptively adjust future social behavior according to changes in the social environment. The biosocial model is contrasted with the challenge hypothesis (Wingfield et al. 1990), which predicts that competition increases T for all competitors.

While status may be gained or lost in numerous ways, the vast majority of human studies have used acute competitive interactions to examine the effects on T release, and thus, we focus on this literature in this section (see Archer 2006; Oliveira and Oliveira 2014; van Anders and Watson 2006 for reviews). Although a number of studies have found that male winners have elevated T concentrations relative to losers (47 % of published studies; $n=45$ studies), there have also been an equal number of studies reporting no significant difference in T reactivity patterns between male winners and losers (49 % of published studies). Notably, only three studies reported that losers have elevated T concentrations relative to winners (Filaire et al. 2001; Oliveira et al. 2014; Parmigiani et al. 2006). The effect of winning versus losing on T reactivity (win > loss) has also been documented in spectators watching their favorite team (Bernhardt et al. 1998), among voters of political elections (Stanton et al. 2009) and among athletes watching themselves compete on a video recording (Carré and Putnam 2010). In a review of this literature, Archer (2006) found that despite heterogeneity of findings, male winners do demonstrate increased T concentrations relative to losers. See Supplementary Table 1 for a summary of studies on T and competition outcome.

A smaller number of studies have investigated the relationship between competition outcome and T release in women. Although the majority of these studies (53 % of published studies; $n=15$ studies) have not found significant differences in T responses between winners and losers, some studies (27 % of published studies) have found that winners have elevated T concentrations relative to losers. Three studies (20 % of published studies) found that female losers had elevated T concentrations relative to winners (Oliveira et al. 2014; Zilioli et al. 2014 [2 studies]). See Supplementary Table 1 for a summary of studies on T and competition outcome. More studies involving women are needed to get a better picture of the effects of competition on T responses.

Cortisol Responses to Competition

Although Mazur's (1985) biosocial model of status made no specific mention of C, a number of studies have now investigated the effect of competition outcome on C concentrations. In men, there has only been one study showing a decrease in C in response to winning a competition (Mehta et al. 2008), while many others have failed to detect differences in C response as a function of competition outcome (see Supplementary Table 2). In contrast to the studies in males, there is some evidence that female losers have higher C concentrations relative to winners (see Supplementary Table 2). Nevertheless, these findings are based on a small sample of studies ($n=10$ studies with women; $n=24$ studies with men), and thus, future work will be needed to determine the extent to which competition outcome has any impact on acute fluctuations in C concentrations. C changes may depend on moderators related to individual differences, the closeness of the match, or other contextual variables. It is important to note the

difference between chronically elevated or suppressed C, which is unhealthy, versus acute C responses to competition, which is an adaptive response (e.g., Sapolsky 2005).

Moderators of Testosterone Responses to Competition

Although meta-analytic evidence supports the idea that winners have elevated T concentrations relative to losers (Archer 2006), there is a large amount of variability in T responses to victory and defeat. Thus, it is important to identify that factors that give rise to such variability.

Sex In the few studies that have included both men and women the increased T concentrations in winners relative to losers occurs in men, but not women (Carré et al. 2013; Stanton et al. 2009; van Anders and Watson 2007). Nevertheless, one study did report similar findings (winners>losers) in both sexes (Jiménez et al. 2012), and as discussed above, some studies have reported that female winners have elevated T concentrations relative to losers. Thus, it remains to be determined whether effects of competition outcome on T release are more or less robust in men compared to women.

Males and females engage in competition-like behaviors in a variety of contexts, such as competing for resources and for mates, protecting young, etc. Thus, it is possible that they may have similar T responses to competition. However, men have much higher levels of T than women, so the effects may be more robust and/or easier to detect in men. The context of the competition is also important to consider in relation to the gendered nature of some types of competitions. In one recent study, a video game competition (boxing & volleyball) was used to elicit competition in the laboratory and found that the increase in T in winners vs. losers was found in men, but not women (Carré et al. 2013). Notably, men are much more inclined to play video games that involve some form of physical competition (e.g., sports, racing games), whereas women are more likely to engage in puzzle-solving, fantasy games and/or adventure games (Greenberg et al. 2010). Therefore, future competition studies will need to consider differences in the extent to which certain games are appealing to women versus men – as this may impact how T responds to competitive interactions.

Individual Differences in Motivation Several investigators have identified individual difference factors that moderate the relationship between competition outcome and T release. For instance, Schultheiss and colleagues (e.g., Schultheiss et al. 2005) have found that winners have elevated T concentrations compared to losers, but only to the extent that they have a personality style characterized by an implicit need for power and dominance. Similarly, Wirth and colleagues have found that power motivation moderates the effect of competition outcome on C release. In this work, the authors reported that losing was associated with increased C reactivity – but only among individuals high in power motivation. Interestingly, winning was associated with increased C reactivity among individuals low in power motivation (Wirth et al. 2006). Collectively, these findings indicate that an individual's implicit need for dominance and power plays an important role in shaping variability in neuroendocrine responses to human competition.

Situational Factors In addition to individual differences, there are many situational factors that can affect the relationship between T and competition. An individual's personal contribution to the outcome may play an important role in modulating T release (Gonzalez-Bono et al. 1999; Trumble et al. 2012). Some studies have found that winner/loser effects only occur in the context of competition when people compete with the 'outgroup' but not when competing with one's 'ingroup' (Flinn et al. 2012; Oxford et al. 2010). Finally, the location of a competitive interaction can influence the magnitude of the T response to competition. For example, male hockey players showed greater increased in T after wins that occurred on home ice compared to an opponent's venue (Carré 2009). A strikingly similar finding has been observed in male California mice in which T concentrations rise after winning in one's home cage, but not in a neutral cage (Fuxjager et al. 2009).

Basal Hormones In addition to these social/psychological factors, some work suggests that baseline neuroendocrine function may modulate hormonal responses to victory and defeat. For instance, in two studies, Mehta et al. (2008) demonstrated that baseline T concentrations moderated the effect of competition outcome on C reactivity. Here, men (study 1) and women (study 2) demonstrated an increase in C after defeat, and decrease in C after victory, but only to the extent that they had relatively elevated baseline T concentrations. Similarly, Zilioli and Watson (2012) have reported that losers experience elevated C concentrations relative to winners, but only to the extent that they have elevated baseline T concentrations. These findings fit nicely with evidence that people with elevated baseline T concentrations experience negative affect when assigned to low status (Josephs et al. 2006).

Functional Effects of Testosterone Changes on Behavior

Endogenous Testosterone As suggested by Mazur (1985) and others (e.g., Oliveira and Oliveira 2014; Wingfield et al. 1990; Gleason et al. 2009), T responses to competitive interactions may function to modulate one's social behavior according to changes in the environment. There is now a growing body of evidence in humans examining the extent to which acute changes in T during competition map onto future dominance-related behaviors. In two studies, men demonstrating a rise in T during competition were more willing to approach a subsequent competitive interaction relative to men demonstrating a decrease in T (Carré and McCormick 2008; Mehta and Josephs 2006). An increase in T was also shown to predict subsequent aggression in men, but not women (Carré et al. 2009, 2013). Aggressive behavior in this work was assessed using the Point Subtraction Aggression Paradigm, a well-validated behavioral measure of reactive aggression (Cherek et al. 2006). Moreover, the effect of winning on subsequent aggressive behavior was mediated by heightened T concentrations after the victory (Carré et al. 2013). The latter findings provide the first complete support for the biosocial model of status as originally proposed by Mazur (1985).

Other work of practical significance has been conducted with elite-level athletes. In one study, Cook and Crewther (2012a) investigated the extent to which acute changes in T during a sport motivational intervention would influence subsequent athletic

performance and physical strength in male rugby players. The authors reported that athletes receiving positive feedback from their coaches prior to a competitive interaction demonstrated both a rise in T concentrations and better athletic performance. In a subsequent study, the authors reported that watching motivational and aggressive video clips increased T concentrations and improved subsequent physical strength as indexed by squat performance (Cook and Crewther 2012b).

Recent work has also demonstrated that a long-term intervention program designed to curtail antisocial behavior in ‘at-risk’ youth was associated with hormonal and behavioral differences in adulthood. This intervention was implemented in kindergarten; when tested 20 years later, the intervention group demonstrated less aggressive behavior and decreased T reactivity to social provocation compared to the control group. Notably, the association between assignment to the intervention condition and decreased aggression was statistically mediated by decreased T reactivity to provocation (Carré et al. 2014).

The above studies indicate that acute changes in T during competition or in response to provocation predict competitive and aggressive behaviors measured shortly after the rise in T is measured. There is also evidence from non-human animal models suggesting these effects are long lasting (Gleason et al. 2009; Trainor et al. 2004). T responses to victory may serve to reinforce learning processes associated with winning competition (Gleason et al. 2009). Recent work in humans also indicates that T responses to competition modulate behavior measured long after the change in T occurs. In their work, Zilioli and Watson (2014) found that male winners and losers demonstrating an increase in T during an initial Tetris competition performed better on the same task 24 h later compared to individuals demonstrating either a decrease, or no change in T.

Collectively, these findings are consistent with the idea that acute fluctuations in T within the context of human competition may have important effects on current and/or future social behavior. Only a few studies have examined the functional role of T dynamics in males and females in the same study. Here, the effects of T dynamics on aggressive behavior were found exclusively in men (Carré et al. 2009, 2013), and thus, it remains unclear whether acute changes in T during competition exert effects on competitive and aggressive behaviors in women. One clear limitation to this body of research is that it is correlational. Without manipulation of T concentrations, it is not possible to make causal claims concerning T’s role in modulating competitive and aggressive behavior. To demonstrate a causal link between T and behavior, experiments in which T is manipulated through exogenous supplementation or inhibition of T is necessary.

Acute Exogenous Testosterone Manipulations Non-human animal research is particularly useful for testing causal mechanisms shaping complex social behavior. In recent experiments, administration of T to male California mice after winning a competitive interaction increased aggressive behavior (Fuxjager et al. 2010; Gleason et al. 2009; Trainor et al. 2004) and the probability of winning subsequent interactions (Gleason et al. 2009). In addition, Oliveira et al. (2009) examined the role of T in mediating the ‘winner’ and ‘loser’ effects in male tilapia. In control fish, winners of a first aggressive interaction were more likely to win a subsequent aggressive interaction (88 % won second fight), whereas losers were more likely to lose subsequent interactions (87 % lost second fight). Winners treated with an anti-androgen drug, which

prevented the normal increase in T in response to competitive interactions, were less likely to win a subsequent aggressive interaction (44 % won second fight). In contrast, losers treated with an androgen (11-ketotestosterone) were not more likely to win a subsequent aggressive interaction (81 % lost second fight). These findings indicate that the winner effect (an ability to increase winning behavior in response to previous victories) is in part mediated by T, but that the negative effects of losing cannot be altered by T administration.

T administration studies in women reveal that even a single administration of T modulates behavioral and physiological processes of relevance to human dominance behavior. Specifically, a single administration of T decreases fear potentiated startle (Hermans et al. 2006), increases attention toward angry faces (Terburg et al. 2012), decreases empathic behavior (e.g., Hermans et al. 2006), and decreases interpersonal trust (e.g., Boksem et al. 2013). However, T administration has also been shown to increase prosocial behavior, perhaps through its effects on status concerns, in behavioral economics tasks (Eisenegger et al. 2010; van Honk et al. 2012). In contrast, exogenous T administration in men decreases prosocial behavior on similar tasks (Zak et al. 2009). Although most of the T administration results in women resulted in anti-social effects, there were prosocial effects in some situations. Boksem et al. (2013) theorized that in threat situations, T may lead to antisocial behavior to defend status, while in non-threatening contexts, status may be better maintained through prosocial acts. These divergent findings may also in part be explained by potential sex differences in the effects of T on social behavior, but there have been too few studies conducted with male participants to say conclusively. Collectively, these experiments provide compelling support for the role of competition-induced T dynamics in mediating ongoing and/or future social behavior.

Chronic Social Defeat

At the extreme end of the status spectrum are those who are chronically socially subjugated (also called social defeat or bullying in humans). Being low status does not always have to be stressful, as demonstrated by different species of non-human primates with differing levels of stress and social support (Abbott et al. 2003), but non-human animals and humans who experience chronic social defeat through both physical and psychological aggression have been shown to have altered HPA responses compared to those who are not chronically defeated (e.g., Virgin and Sapolsky 1997; Wommack and Delville 2003). Most of the research reviewed above, particularly in humans, focuses on those who are high or low status within a normal range, but those who are chronically socially defeated may experience more problematic effects than just being on the lower end of the status spectrum. Because of the stress inherent in social defeat, the majority of the research focuses on glucocorticoids (C and corticosterone), as opposed to T, although both are relevant. Most of the research in this field has been done with non-human animals because it is unethical to socially subjugate human participants. Bullying is a spontaneously occurring form of social subjugation in humans, and so provides an opportunity to apply the animal models to humans non-experimentally.

For the purposes of this review, we will focus on rodent studies that use a chronic resident-intruder paradigm. The resident-intruder paradigm is a commonly used method to induce social defeat in non-human animals and involves placing the subject (intruder) in the home cage of an older and larger conspecific (resident). The resident-intruder paradigm provides a controlled environment for studying the effects of social defeat. Other ways to examine social subordination include the Visible Burrow System, (Tamashiro et al. 2005), or social hierarchies in primates with aggressive dominants (e.g., ring-tailed lemurs, rhesus macaques, baboons; Sapolsky 2005; Virgin and Sapolsky 1997), but these models do not guarantee severe, chronic social defeat. The size discrepancy in the resident-intruder paradigm ensures that the resident will defeat the intruder. Exposure to a resident is generally done over a period of days to weeks, and is a reasonable approximation of bullying exposure in humans.

Social Defeat Can Alter Glucocorticoid Responses

The effects of chronic (usually 1–2 weeks) social defeat on basal hormones in non-human animals were mixed with some studies showing that chronically defeated animals (males) had elevated basal corticosterone (e.g., hamsters, Wommack and Delville 2003; tree shrews, Wang et al. 2013; mice, Warren et al. 2013; Dadomo et al. 2011), while others showing no difference in corticosterone compared to non-defeated animals (e.g., hamsters, Chester et al. 2010; Wommack et al. 2004). To understand these different results, researchers have started looking at moderators. Some initial findings indicate that when comparing socially defeated animals that have elevated morning corticosterone to those who have low morning corticosterone, the latter group had behaviors and neural changes indicative of worse functioning (Bowens et al. 2012). Similarly, when comparing “active” mice to “passive” mice and controls after chronic social defeat, passive mice showed low basal corticosterone compared to controls, while active mice showed elevated levels of corticosterone. Low levels of corticosterone were related to more negative neural effects, indicating that these low levels are the worse outcome (Gomez-Lazaro et al. 2011). Taken as a whole, these studies indicate that decreased basal corticosterone after chronic social defeat indicates more severe negative effects of social defeat than elevated corticosterone. However, most of the studies found links between elevated basal corticosterone and negative outcomes, as well.

In addition to changes in basal levels of corticosterone, there are potential alterations in hormonal responses to acute stress in socially defeated rodents. In response to acute stress, adolescent male hamsters showed blunted corticosterone after defeat, but after a 4-week recovery period, there were no significant differences between controls and socially defeated animals, suggesting that recovery after social subjugation in puberty is possible (Wommack et al. 2004). Two additional studies of acute stress responses in adolescent rats found no differences in corticosterone responses to stress between those who had been chronically socially defeated and those who had not (Bourke and Neigh 2011; Weathington et al. 2012). Sapolsky (1982, 1991) has shown that dominant male baboons show the fastest and strongest C responses to stressors, while subordinates show blunted acute stress responses. Healthy, dominant, non-human animals will show a more robust stress response and recover quickly. This finding has also been replicated in humans who perceive themselves as high status (Gruenewald et al. 2006). Of the few studies that have looked at female rodents, when comparing socially-defeated to non-

defeated animals, some have found that females had blunted corticosterone responses to acute stressors (Bourke and Neigh 2011; Weathington et al. 2012), while others have not (Bourke and Neigh 2012).

In contrast to the non-human animal research, human studies on the relationship between bullying and C have been more consistent. These studies have focused on either differences in diurnal C or on responses to acute stressors between those who have experienced chronic bullying to those who have not. This line of research has been primarily focused on adolescents, but as workplace bullying becomes a more well-known issue, researchers have also begun to study the hormonal effects of being bullied in adults. Studies on diurnal C have found fairly consistently that bullied participants (both males and females) are hypocortisolemic compared to controls (Hansen et al. 2011; Hogh et al. 2012; Knack et al. 2011; Vaillancourt et al. 2011). One exception to this was Vaillancourt et al. (2008), who found that although the overall effect of bullying in their sample of 12-year olds was diurnal hypocortisolism (when controlling for sex, puberty, age, and psychopathology), when boys and girls were analyzed separately, girls had lower C levels, while boys had higher C levels. Another study found no differences in diurnal C between people bullied at work vs. controls (Lac et al. 2012), although bullied workers showed greater psychopathology, which was related to their dehydroepiandrosterone-sulfate (DHEAS) levels. Both hypo- and hypercortisolism have been seen in patients with posttraumatic stress disorder (PTSD) and depression. Both extremes can indicate HPA axis dysregulation (reviewed by Miller et al. 2007).

In studies of acute stress responses in participants with and without experiences being bullied, the research on adolescents has shown that participants who have been bullied show a blunted C response compared to non-bullied peers when exposed to an acute stressor (Trier Social Stress Task) in a lab setting (Ouellet-Morin et al. 2011a). Blunted C responses to acute stress have been linked with behavioral and psychological problems (Ouellet-Morin et al. 2011b) and worse health outcomes (Knack et al. 2011). Neither of these studies examined the role of gender in C response. In a study of university students who had been bullied in high school and junior high, bullied males showed a blunted C response to the acute stressor compared to control males, but there were no differences in the C responses of bullied and control females. There were no differences in self-reported stress across the groups. This suggests that the psychological experience of the stress is not blunted, only the HPA axis response (Hamilton, Rivers, Josephs, & Delville, unpublished data). Two studies of adolescents did not find a difference between groups in their acute C responses to stress, but both used mild stressors that failed to evoke a C response in control participants as well (Hamilton et al. 2008; Kliewer et al. 2012).

Social Defeat is Related to Reduced Testosterone

The few studies that have examine the effect of social defeat on T in hamsters have found that, as expected from the status literature, basal T is significantly lower in socially defeated males compared to controls (Ferris 2003; Huhman et al. 1991). Only one study has assessed the relationship between T and bullying, and results indicated that in 12–13 year old adolescents, being bullied was related to increased basal T in boys but decreased basal T in girls. This difference was attributed to the differences in

coping styles of boys and girls, particularly that girls are more likely to internalize stress, while boys are more likely to develop externalizing and aggressive behaviors in response to bullying (Vaillancourt et al. 2009).

Health Effects of Chronic Social Defeat

Overall, the evidence is fairly clear that chronic social subjugation can alter HPA axis function in humans. In turn, these alterations in function can have detrimental effects on health. Problems with the HPA axis, and C output specifically, have been linked to a number of physical and psychological health problems including depression (Staufenbiel et al. 2013) and all-cause mortality, especially due to cardiovascular disease (Kumari et al. 2010). Coping strategies and responses to social defeat/bullying likely play a role in attenuating or accelerating the negative effects of this stressor.

Future Directions

Although our understanding of the interaction between status, T, and C in humans has grown rapidly in recent years, there are still many avenues of study to pursue and many gaps in the literature to fill. Below we outline a brief list of key areas that we have identified as being top priorities.

Longitudinal Studies

In humans, there have only been a few studies on fluctuations in hormones and status over time (e.g., Zilioli and Watson 2014). We know that high status individuals generally have high T and low C, and that winning a competition can increase T, at least for males, but we do not know how the increases in T from winning adjust over time. Is it a gradual increase in basal T? Does the increase in T attenuate or increase after multiple wins? In the context of status hierarchies, does basal T increase after someone is promoted to a higher status position or do increases in T precede promotion? Longitudinal studies will also be beneficial for identifying individual differences in behavioral and hormonal responses over time.

Manipulating Stable Versus Unstable Hierarchies

More work on social moderators within hierarchies will expand our understanding of the biosocial mechanisms of status. For example, most work on humans has focused on the negative association between status and C within stable status hierarchies. But in unstable hierarchies, high status individuals may fear losing their status (Jordan et al. 2011), undermining their sense of control and increasing their psychological stress. Low status individuals may hope for a better position in the hierarchy, and a “nothing-to-lose” perspective may result in lower stress. Hence, C and stress may be higher in high status compared to low status individuals in unstable hierarchies. Evidence supports this possibility in some species of primates

(Sapolsky 2005). While some recent studies with humans have begun to look at manipulating hierarchy stability (e.g., Zilioli and Watson 2014; Zilioli et al. 2014), the effects of hierarchical stability versus instability on endocrine function and status in humans remains relatively understudied.

Functional Outcomes of Changes in Hormones and Status

Although there has been some work in the competition literature about the behavioral outcomes of winning, losing, and associated changes in hormones, there are still unanswered questions about why and how hormonal changes occur and how they are related to behavior. For example, recent work suggests that changes in T do not necessarily map onto future dominance-related behaviors in everyone. Specifically, in two studies, Norman et al. (2014) reported that a rise in T during competition was positively correlated with subsequent aggression, but only in men scoring relatively low on a trait measure of anxiety. Thus, it will be critical to consider individual difference factors that may moderate effects of T reactivity on behavioral outcomes of relevance to status.

In addition, it will be important to examine functional effects of reductions in T after losing. Mazur (1985) proposed that the alteration may protect the organism from harm, but there may also be psychological effects of decreases in T after losing. Are there other benefits to the reduction in T? Similarly, there is some evidence that blunted C reactivity in bullied/subjugated subjects is maladaptive, but is there any benefit to this change? A question of critical relevance to the social defeat literature is why bullying leads to increased aggression in individuals, but submissiveness in others.

Studying health outcomes of status and hormones is also important. We know from decades of research that high stress/altered HPA axis activity is detrimental to health, but how do changes in status and T affect health outcomes? Much of the health-related research focuses exclusively on C and stress, so it would be beneficial to expand this work to include T effects and interactions with C and health.

Gender/Sex

A better understanding of the sex differences and similarities in social neuroendocrinology of status is needed. The nature of the research biases towards a focus on males and “male” hormones (T). For the research on basal hormones and status, studies that have included both males and females have either found no sex differences, have not separated their analyses by sex, or have only studied males. It is unclear if sex of the participant is a moderator of the relationship between hormones and status. For effects of competition, most of the studies have included only men, and only four studies include both men and women in the same paradigm. Both lines of research would benefit from including both men and women in the same studies, as well as ensuring sample sizes are adequately sized to have enough power to detect sex differences if they exist. Additional areas of focus for future research include gaining a better understanding of how gender role and socialization affect both T and status in both men and women (van Anders 2013),

the role of estradiol in status (see below), and integrating the research on sex differences in stress response.

Moreover, it will be critical to include males and females in future T administration studies as T may exert sex-dependent effects on neural and behavioral responses to dominance related cues. In support of this possibility, exogenous T increases prosocial behavior in behavioral in women (Eisenegger et al. 2011), but decreases prosocial behavior in men (Zak et al. 2009).

Additional Hormones

There is a great deal of interaction within the endocrine system, so our understanding of the relationship between hormones and status would benefit from the inclusion of more hormones in single studies. Our understanding of the neuroendocrinology of status has been clarified by the dual-hormone hypothesis and would likely benefit from even more attention to hormonal interactions. Another theory that addresses the interaction between hormonal systems is the *steroid/peptide theory of social bonds* (van Anders et al. 2011), which states that both steroid hormones (e.g., T) and peptide hormones (e.g., oxytocin and vasopressin) can jointly influence behavior. Different combinations of these hormone levels are related to different behaviors (e.g., High T and high vasopressin would predict defensive aggression, while high T with low vasopressin would predict antagonistic aggression; van Anders et al. 2011.)

Estradiol is a potential status-related hormone, particularly for females, that has been relatively understudied. The findings related to T and status in females have been somewhat tenuous. One possibility is that T may not serve the same functions in females as it does in males. Much of the T administration research in female animals that found important effects used large pharmacological doses of T, which may have different effects than endogenously circulating T (Goymann and Wingfield 2014). It is possible that estradiol, which plays a large role in fertility and reproductive behavior in females could also be related to female status-seeking and dominant behavior (Stanton and Schultheiss 2007, 2009). Higher basal estradiol concentrations relate to higher measures of implicit dominance motives, an indication of a preference for power and higher ranking in hierarchies (Stanton and Schultheiss 2007). The few human studies on estradiol and status, combined with evidence from primate research on estradiol suggest this is an area in need of future studies in humans.

Pro-social Routes to Status

Social endocrinology research has focused almost exclusively on dominance as a behavioral route to individual status attainment, but humans rise in social hierarchies not only through dominance but also through pro-social behaviors, such as building social connections and sharing expertise (Anderson and Kilduff 2009; Cheng et al. 2013). More research is needed on the social and neuroendocrine mechanisms for these additional routes to status. Although some theory and research suggest that T suppresses cooperative behaviors (Mehta et al. 2009; van Anders 2013), recent work has suggested that the context and motivation for cooperative behavior can affect whether

or not it is related to higher levels of T (van Anders et al. 2011; van Anders 2013). A recent study showed that T enhances pro-sociality in contexts where such behaviors may be beneficial for status (Boksem et al. 2013).

Neural Mechanisms

Although it was outside of the scope of this paper, there has been extensive non-human animal research on the neural mechanisms through which hormones and status work, and this is an area that needs more attention in humans. Studies on hormones and functional magnetic resonance imaging (fMRI) have focused primarily T's role in threat processing (e.g., Höfer et al. 2013) and C's role in stress (e.g., Dedovic et al. 2009).

One mechanism through which T may influence human dominance-related behaviors is through interactions between subcortical regions and the prefrontal cortex in response to social threat. Studies in men and women indicate that a single administration of T leads to increased amygdala and hypothalamus reactivity to threat-related stimuli (e.g., Bos et al. 2013; Hermans et al. 2008; Goetz et al. 2014) and decreased amygdala-orbitofrontal cortex (OFC) coupling (van Wingen et al. 2010). Critically, these neural structures are rich in both androgen and estrogen receptors and form part of the neural circuitry underlying reactive aggression (Nelson and Trainor 2007). Moreover, other work has directly investigated the neural mechanisms through which T modulates complex dominance-related behavior. Specifically, Mehta and Beer (2010) reported that endogenous T concentrations modulate rejections of unfair offers in the ultimatum game through dampening OFC reactivity to social provocation.

T and C may also influence status-seeking behavior through reward processing mechanisms. T has been linked to reward-seeking behaviors and anticipation of reward in both human and non-human animal studies through its interactions with dopamine in the ventral striatum (e.g., Packard et al. 1997; Fuxjager et al. 2010; Hermans et al. 2010). While T increases activation, C down-regulates striatal activity (Montoya et al. 2014). These same reward systems have also been linked to status-seeking behaviors and social status. For example, research on the *winner effect* indicates that a rise in T after winning a contest increases the probability of winning a subsequent dominance contest, in part through androgen receptor upregulation in the ventral striatum (e.g., nucleus accumbens) (Fuxjager et al. 2010). Future work will benefit by combining pharmacological challenge, fMRI, and the assessment of human dominance using well-validated behavioral tasks.

Conclusion

The relationship between status and hormones is complex and reciprocal. T and C play an integral role in competing for status, motivation for status, and maintenance of status. In turn, competition, motivation, sex, and social context all affect levels of T and C. Our understanding of these relationships is enhanced by including more moderating variables in our research models as well as administering hormones to get a better understanding of causal effects. Individual psychological differences, social and

environmental contexts, and each person's hormonal milieu contribute to the interaction between hormones and status. Future work should continue to address these moderators in order to develop a complete biopsychosocial model of the social neuroendocrinology of status.

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