Adaptive Human Behavior and Physiology

Social Neuroendocrinology of Status: A Review and Future Directions

--Manuscript Draft--

Manuscript Number:	AHBP-D-14-00016R2
Full Title:	Social Neuroendocrinology of Status: A Review and Future Directions
Article Type:	Original Article
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.
Corresponding Author:	Lisa Dawn Hamilton, Ph.D. Mount Allison University Sackville, NB CANADA
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Mount Allison University
Corresponding Author's Secondary Institution:	
First Author:	Lisa Dawn Hamilton, Ph.D.
First Author Secondary Information:	
Order of Authors:	Lisa Dawn Hamilton, Ph.D.
	Justin M Carre
	Pranjal H Mehta
	Nathan Olmstead
	Jeffrey D Whitaker
Order of Authors Secondary Information:	
Author Comments:	Dear Dr. van Anders, Please find enclosed our revised manuscript titled: "Social Neuroendocrinology of Status: A Review and Future Directions." Sincerely, Lisa Dawn Hamilton

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.

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 & 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, Willer, Kilduff, & Brown, 2012;) or that there are benefits of low T (Aucoin & Wassersug, 2006; Mehta, Wuehrmann, & Josephs, 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 & 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, cortisol 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, Shirtcliff, Booth, Kivlighan, & Schwartz, 2004; Liening, Stanton, Saini, & Schultheiss, 2010; Sellers, Mehl, & Josephs, 2007). For example, in one study male and female participants provided saliva samples between noon and 4 PM over five days (Study 1, Sellers et al., 2007). The intraclass correlation for T concentrations across the five days was $r = .94$ for males and $r = .81$ 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 testosterone should be related to status-seeking behaviors and in turn higher social status (Mazur & 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 testosterone 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, Maughan, Worthman, Costello, & Angold, 2004). Another study of men in college did not find any relationship between T and rankings of status by their suitemates (McIntyre, Li, Chapman, Lobson, & Ellison, 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 cortisol 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, LaRue, & Williams, 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

[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.

behavior in low, but not high SES men (Dabbs & 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 & Wrangham, 2004; male and female baboons, Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2006; Beehner, Phillips-Conroy, & Whitten, 2005; Sapolsky, 1991; male fish, Oliveira, Almada, & Canario, 1996; male & female lemurs Cavigelli & Pereira, 2000; von Engelhard, Kappeler, & Heistermann, 2000). Most social neuroendocrinology research on T's role in social behavior examines males, but similar effects of T on dominance have also been reported in some female 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, McCormick, & Hariri, 2011; Eisenegger, Haushofer, & Fehr, 2011; Mazur & Booth, 1998). As 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 & 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, Aarts, & van Honk, 2012; Wirth & 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 & 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 & 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, Montoya, Bos, van Vugt, & Terberg, 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, Hegner, Dufty, & Ball, 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 taken 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 cortisol 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, Nguyen, & Sakai, 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 ones 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 & 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, Simanek, & Aiello, 2009; Kristenson, Eriksen, Sluiter, Starke, & Ursin, 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 & Kemeny, 2004; Uchino, 2006).

When examining the relationship between status and cortisol 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 (rainbow trout, DiBattista, Anisman, Whitehead, & Gilmour, 2005). Future research is needed to test the mechanisms through which cortisol 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, Loerbroks, Schneider, Thayer, & Fischer, 2011).

Overall, the evidence does seem to point to a link between status and cortisol, although the direction and strength of the relationship varies. As demonstrated in non-human primate studies, the relationship between status and cortisol changes depending on the social dynamics of the group and other contextual factors. Although there have only been a few studies assessing cortisol 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 testosterone will be elevated in times of challenge. The challenge hypothesis states that in species (of birds) with parental males, testosterone 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.

Cortisol 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 & 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, Jurkovic, & Frady, 1991; Edwards & Casto, 2013; Mehta & Josephs, 2010; Pfattheicher, Landhäußer, & Keller, 2013; 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 & 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 & 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, cortisol 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, Turner, & Clark., 2000; Viau, 2002), which all may lead to an inhibitory effect of C on T's behavioral effects. Second, the influence of T on 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, Ronay, von

Hippel, & Schira., 2013; Hermans, Ramsey, & van Honk, 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. Testosterone is implicated in an implicit desire for status (Stanton & 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 & Mehta, 2011; Maner, Gailliot, Menzel, & Kuntsman, 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 on 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 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 testosterone and aggression among individuals *high* in cortisol, but not low in cortisol (Denson, Mehta, & Ho Tan, 2013; social exclusion condition of Geniole, Carré, & McCormick, 2011; Welker, Lozoya, Campbell, Neumann, & Carré, 2014), and yet other studies have found non-significant interactions between basal T and C (e.g., Geniole, Busseri, & McCormick, 2013; Mazur & 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., 2013) 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 testosterone 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 results in increased 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 & Oliveira, 2014; van Anders & 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, Maso, Sagnol, Lac, & Ferrand, 2001; Oliveira, Uceda, Oliveira, Fernandes, Garcia-Marques, & Oliveira, 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, Dabbs, Fielden, & Lutter, 1998), among voters of political elections (Stanton, Beehner, Saini, Kuhn, & LaBar, 2009) and among athletes watching themselves compete on a video recording (Carré & 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 females. 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., 2013; Zilioli, Mehta, & Watson, 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 males, there has only been one study showing a decrease in cortisol 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 females; n = 24 studies with males), 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 males and females the increased T concentrations in winners relative to losers occurs in males, but not females (Carré, Campbell, Lozoya, Goetz, & Welker, 2013; Stanton et al., 2009; van Anders & Watson, 2007). Nevertheless, one study did report similar findings (winners>losers) in both sexes (Jiménez, Aguilar, & Alvero-Cruz, 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 males compared to females.

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, males have much higher levels of T than women, so the effects may be more robust and/or easier to detect in males. 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, Sherry, Lachlan, Lucas, & Homstrom, 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, Welsh, & Schultheiss, 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, Salvador, Serrano, &

Ricarte, 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, Ponzi, & Muehlenbein, 2012; Oxford, Ponzi, & Geary, 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, Mast, Becker, & Marler, 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 and colleagues (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, Sellers, Newman, & Mehta, 2006).

Functional Effects of Testosterone Changes on Behavior

Endogenous testosterone. As suggested by Mazur (1985) and others (e.g., Oliveira & Oliveira, 2014; Wingfield et al., 1990; Gleason, Fuxjager, Oyegbile, & Marler, 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, males demonstrating a rise in T during competition were more willing to approach a subsequent competitive interaction relative to males demonstrating a decrease in T (Carré & McCormick, 2008; Mehta & Josephs, 2006). An

increase in T was also shown to predict subsequent aggression in males, but not females (Carré et al., 2013; Carré, Putnam, & McCormick, 2009). Aggressive behavior in this work was assessed using the Point Subtraction Aggression Paradigm, a well-validated behavioral measure of reactive aggression (Cherek, Tcheremissine, & Lane, 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 & 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, Iselin, Welker, Hariri, & Dodge, 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, Bird, & Marler, 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 hours 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 males (Carré et al., 2009; Carré et al., 2013), and thus, it remains unclear whether acute changes in T during competition exert effects on competitive and aggressive behaviors in females. 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, Silva, and Canario (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.

Testosterone 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, Putman, & van Honk, 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 effects 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 & Sapolsky, 1997; Wommack & 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 & 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 Reponses

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 & 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, Bonu, & Demas, 2010; Wommack, Salinas, Melloni, & Delville, 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, Heydendael, Bhatnagar, & Jacobson, 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 & Neigh, 2011; Weathington, Arnold, & Cooke, 2012). Sapolsky (1982; 1991) has shown that dominant male baboons show the fastest and strongest cortisol 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, Kemeny, & Aziz, 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 & Neigh, 2011; Weathington et al., 2012), while others have not (Bourke & 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, Hogh, & Persson, 2011; Hogh, Hansen, Mikkelsen, & Persson, 2012; Knack, Jensen-Campbell, & Baum, 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, Dutheil, Brousse, Triboulet-Kelly, & Chamoux, 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, Chen, & Zhou, 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, Danese, et al., 2011). Blunted C responses to acute stress have been linked with behavioral and psychological problems (Ouellet-Morin, Odgers, et al., 2011) 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, Newman, Delville, & Delville, 2008; Kliewer, Dibble, Goodman, & Sullivan, 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, Moore, Ferris, Mougey, & Meyerhoff, 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, deCatanzaro, Duku, & Muir, 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, Penninx, Spijker, Elzinga, & van Rossum, 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., Zilloli & 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, Sivanathan, & Galinsky, 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 & Watson, 2014; Zilioli, Mehta, & Watson, 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 and colleagues (in press) 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 testosterone effects and interactions with cortisol 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 males and females 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 females (Eisenegger et al., 2011), but decreases prosocial behavior in males (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 greatly from the inclusion of more hormones in single studies. Our understanding of the neuroendocrinology of status has been greatly 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, Goldey, & Kuo, 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 & 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 & 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 & 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 & Kilduff, 2009; Cheng, Tracy, Foulsham, Kingstone, & Henrich, 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 testosterone's role in threat processing (e.g., Höfer, Lanzenberger, & Kasper, 2013) and cortisol's role in stress (e.g., Dedovic, D'Aquiar, & Pruessner, 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, van Honk, Ramsey, Stein, & Hermans, 2013; Hermans, et al., 2008; Goetz et al., 2014) and decreased amygdala-orbitofrontal cortex (OFC) coupling (van Wingen, Mattern, Verkes, Buitelaar, & Fernández, 2010). Critically, these neural structures are rich in both androgen and estrogen receptors and form part of the neural circuitry underlying reactive aggression (Nelson & 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.

Testosterone and cortisol may also influence status-seeking behavior through reward processing mechanisms. Testosterone 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, Cornell, Alexander, 1997; Fuxjager et al., 2010; Hermans et al., 2010). While T increases activation, C down-regulates striatal activity (Montoya, Bos, Terburg, Rosenberger, & Van Honk, 2014). These same reward systems have also been linked to status-seeking behaviors and social status. For example, research on the *winner effec*t 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.

References

Abbott, D., Keverne, E., Bercovitch, F., Shively, C., Mendoza, S., Saltzman, W., … Sapolsky, R. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*(1), 67–82.

Adler, N. E., & Ostrove, J. M. (1999). Socioeconomic status and health: What we know and what we don't. *Annals of the New York Academy of Sciences*, *896*(1), 3–15.

Agbedia, O. O., Varma, V. R., Seplaki, C. L., Seeman, T. E., Fried, L. P., Li, L., … Carlson, M. C. (2011). Blunted diurnal decline of cortisol among older adults with low socioeconomic status. *Annals of the New York Academy of Sciences*, *1231*(1), 56–64.

Anderson, C., & Kilduff, G. J. (2009). The pursuit of status in social groups. *Current Directions in Psychological Science*, *18*, 295–298.

Anderson, C., Willer, R., Kilduff, G. J., & Brown, C. E. (2012). The origins of deference: When do people prefer lower status? *Journal of Personality and Social Psychology*, *102*(5), 1077–1088.

Archer, J. (2006). Testosterone and human aggression: An evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, *30*(3), 319–345.

Aucoin, M. W., & Wassersug, R. J. (2006). The sexuality and social performance of androgen-deprived (castrated) men throughout history: Implications for modern day cancer patients. *Social Science & Medicine*, *63*(12), 3162–3173.

Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M., & Whitten, P. L. (2006). Testosterone predicts future dominance rank and mating activity among male chacma baboons. *Behavioral Ecology and Sociobiology*, *59*(4), 469–479.

Beehner, J. C., Phillips-Conroy, J. E., & Whitten, P. L. (2005). Female testosterone, dominance rank, and aggression in an Ethiopian population of hybrid baboons. *American Journal of Primatology*, *67*(1), 101–119.

Bernhardt, P. C., Dabbs Jr, J. M., Fielden, J. A., & Lutter, C. D. (1998). Testosterone changes during vicarious experiences of winning and losing among fans at sporting events. *Physiology & Behavior*, *65*(1), 59–62. doi:10.1016/S0031-9384(98)00147-4

Boksem, M. A. S., Mehta, P. H., Van den Bergh, B., van Son, V., Trautmann, S. T., Roelofs, K., … Sanfey, A. G. (2013). Testosterone inhibits trust but promotes reciprocity. *Psychological Science*, *24*(11), 2306–2314.

Bos, P. A., van Honk, J., Ramsey, N. F., Stein, D. J., & Hermans, E. J. (2013). Testosterone administration in women increases amygdala responses to fearful and happy faces. *Psychoneuroendocrinology*, *38*(6), 808–817.

Bourke, C. H., & Neigh, G. N. (2011). Behavioral effects of chronic adolescent stress are sustained and sexually dimorphic. *Hormones and Behavior*, *60*(1), 112–120.

Bourke, C. H., & Neigh, G. N. (2012). Exposure to repeated maternal aggression induces depressive-like behavior and increases startle in adult female rats. *Behavioural Brain Research*, *227*(1), 270–275.

Bowens, N., Heydendael, W., Bhatnagar, S., & Jacobson, L. (2012). Lack of elevations in glucocorticoids correlates with dysphoria-like behavior after repeated social defeat. *Physiology & Behavior*, *105*(4), 958–965.

Burnstein, K., Maiorino, C., Dai, J., & Cameron, D. (1995). Androgen and glucocorticoid regulation of androgen receptor cDNA expression. *Molecular and Cellular Endocrinology, 115,* 177–186.

Carney, D. R., & Mason, M. F. (2010). Decision making and testosterone: When the ends justify the means. *Journal of Experimental Social Psychology*, *46*(4), 668–671.

Carré, J. M. (2009). No place like home: Testosterone responses to victory depend on game location. *American Journal of Human Biology*, *21*(3), 392–394. doi:10.1002/ajhb.20867

Carré, J. M., Campbell, J. A., Lozoya, E., Goetz, S. M. M., & Welker, K. M. (2013). Changes in testosterone mediate the effect of winning on subsequent aggressive behaviour. *Psychoneuroendocrinology*, *38*(10), 2034–2041.

Carré, J. M., Iselin, A. M. R., Welker, K. M., Hariri, A. R., & Dodge, K. A. (2014). Testosterone reactivity to provocation mediates the effect of early intervention on aggressive behavior. *Psychological Science*, *25*(5), 1140–1146. doi:10.1177/0956797614525642

Carré, J. M., & Mehta, P. H. (2011). Importance of considering testosterone-cortisol interactions in predicting human aggression and dominance. *Aggressive Behavior, 37*(6), 1-3.

Carré, J. M., & McCormick, C. M. (2008). Aggressive behavior and change in salivary testosterone concentrations predict willingness to engage in a competitive task. *Hormones and Behavior*, *54*(3), 403–409.

Carré, J. M., McCormick, C. M., & Hariri, A. R. (2011). The social neuroendocrinology of human aggression. *Psychoneuroendocrinology*, *36*(7), 935–944.

Carré, J. M., & Putnam, S. K. (2010). Watching a previous victory produces an increase in testosterone among elite hockey players. *Psychoneuroendocrinology*, *35*(3), 475–479.

Carré, J. M., Putnam, S. K., & McCormick, C. M. (2009). Testosterone responses to competition predict future aggressive behaviour at a cost to reward in men. *Psychoneuroendocrinology*, *34*(4), 561–570.

Cashdan, E. (1995). Hormones, sex, and status in women. *Hormones and Behavior*, *29*(3), 354–366.

Cashdan, E. (2003). Hormones and competitive aggression in women. *Aggressive Behavior,* 29, 107-115.

Cavigelli, S. A., & Pereira, M. E. (2000). Mating season aggression and fecal testosterone levels in male ring-railed lemurs (lemur catta). *Hormones and Behavior*, *37*(3), 246–255.

Chen, S., Wang, J., Yu, G., Liu, W., & Pearce, D. (1997). Androgen and glucocorticoid receptor heterodimer formation. A possible mechanism for mutual inhibition of transcriptional activity. *The Journal of Biological Chemistry, 272,* 14087–14092.

Cheng, J. T., Tracy, J. L., Foulsham, T., Kingstone, A., & Henrich, J. (2013). Two ways to the top: Evidence that dominance and prestige are distinct yet viable avenues to social rank and influence. *Journal of Personality and Social Psychology*, *104*(1), 103–125.

Cherek, D. R., Tcheremissine, O. V., Lane, S. D. (2006). Psychopharmacology of human aggression: Laboratory and clinical studies. In *Biology of Aggression*. RJ Nelson (Ed.). Oxford University Press. New York, NY.

Chester, E. M., Bonu, T., & Demas, G. E. (2010). Social defeat differentially affects immune responses in Siberian hamsters (Phodopus sungorus). *Physiology & Behavior*, *101*(1), 53–58.

Cook, C. J., & Crewther, B. T. (2012a). The effects of different pre-game motivational interventions on athlete free hormonal state and subsequent performance in professional rugby union matches. *Physiology and Behavior*, *106*, 683-688

Cook, C. J, & Crewther, B. T. (2012b). Changes in salivary testosterone concentrations and subsequent voluntary squat performance following the presentation of short video clips. *Hormones and Behavior*, *61*, 17-22.

Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology & Evolution*, *16*(9), 491–497.

Dabbs, J. M. J., Jurkovic, G. J., & Frady, R. L. (1991). Salivary testosterone and cortisol among late adolescent male offenders. *Journal of Abnormal Child Psychology*, *19*(4), 469–478.

Dabbs, J. M., de la Rue, D., & Williams, P. M. (1990). Testosterone and occupational choice: Actors, ministers, and other men. *Journal of Personality and Social Psychology*, *59*(6), 1261-1265.

Dabbs, J. M., & Morris, R. (1990). Testosterone, social class, and antisocial behavior in a sample of 4,462 men. *Psychological Science*, *1*(3), 209-211.

Dadomo, H., Sanghez, V., Di Cristo, L., Lori, A., Ceresini, G., Malinge, I., … Bartolomucci, A. (2011). Vulnerability to chronic subordination stress-induced depression-like disorders in adult 129SvEv male mice. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, *35*(6), 1461–1471.

Dedovic, K., D'Aquiar, C., & Pruessner, J. C. (2009). What stress does to your brain: A review of neuroimaging studies. *Canadian Journal of Psychiatry*, *54*(1), 6–15.

Denson, T. F., Mehta, P. H., & Ho Tan, D. (2013). Endogenous testosterone and cortisol jointly influence reactive aggression in women. *Psychoneuroendocrinology*, *38*(3), 416–424.

Denson, T. F., Ronay, R., von Hippel, W., & Schira, M. M. (2013). Endogenous testosterone and cortisol modulate neural responses during induced anger control. *Social Neuroscience*, *8*(2), 165-177.

DiBattista, J. D., Anisman, H., Whitehead, M., & Gilmour, K. M. (2005). The effects of cortisol administration on social status and brain monoaminergic activity in rainbow trout Oncorhynchus mykiss. *Journal of Experimental Biology*, *208*(14), 2707–2718.

Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, *130*(3), 355–391.

Dowd, J., Simanek, A., & Aiello, A. (2009). Socio-economic status, cortisol and allostatic load: A review of the literature. *International Journal of Epidemiology*, *38*(5), 1297–1309.

Edwards, D. A., & Casto, K. V. (2013). Women's intercollegiate athletic competition: Cortisol, testosterone, and the dual-hormone hypothesis as it relates to status among teammates. *Hormones and Behavior*, *64*(1), 153–160.

Eisenegger, C., Haushofer, J., & Fehr, E. (2011). The role of testosterone in social interaction. *Trends in Cognitive Sciences*, *15*(6), 263–271.

Eisenegger, C., Naef, M., Snozzi, R., Heinrichs, M., & Fehr, E. (2010). Prejudice and truth about the effect of testosterone on human bargaining behaviour. *Nature*, *463*(7279), 356–359.

Ellis, L. (1994). *Social stratification and socioeconomic inequality, Vol. 2: Reproductive and interpersonal aspects of dominance and status*. Westport, CT: Praeger

Ferris, C. F. (2003). Using an animal model to assess the long-term behavioral and biological consequences of adolescent abuse and exposure to alcohol. *Annals of the New York Academy of Sciences*, *1008*, 69-78.

Filaire, E., Maso, F., Sagnol, M., Lac, G., & Ferrand, C. (2001). Anxiety, hormonal responses and coping during a judo competition. *Aggressive Behavior*, *27*(1), 55-63.

Flinn, M. V., Ponzi, D., & Muehlenbein, M. P. (2012). Hormonal mechanisms for regulation of aggression in human coalitions. *Human Nature*, *23*(1), 68–88.

Fuxjager, M. J., Forbes-Lorman, R. M., Coss, D. J., Auger, C. J., Auger, A. P., & Marler, C. A. (2010). Winning territorial disputes selectively enhances androgen sensitivity in neural pathways related to motivation and social aggression. *Proceedings of the National Academy of Sciences*, *107*(27), 12393–12398.

Fuxjager, M. J., Mast, G., Becker, E. A., & Marler, C. A. (2009). The "home advantage" is necessary for a full winner effect and changes in post-encounter testosterone. *Hormones and Behavior*, *56*(2), 214–219.

Gadinger, M. C., Loerbroks, A., Schneider, S., Thayer, J. F., & Fischer, J. E. (2011). Associations between job strain and the cortisol/DHEA-S ratio among management and nonmanagement personnel. *Psychosomatic Medicine*, *73*(1), 44-52.

Geniole, S. N., Busseri, M. A., & McCormick, C. M. (2013). Testosterone dynamics and psychopathic personality traits independently predict antagonistic behavior towards the perceived loser of a competitive interaction. *Hormones and Behavior*, *64*(5), 790–798.

Geniole, S. N., Carré, J. M., & McCormick, C. M. (2011). State, not trait, neuroendocrine function predicts costly reactive aggression in men after social exclusion and inclusion. *Biological Psychology*, *87*(1), 137–145.

Gesquiere, L. R., Learn, N. H., Simao, M. C. M., Onyango, P. O., Alberts, S. C., & Altmann, J. (2011). Life at the top: Rank and stress in wild male baboons. *Science*, *333*(6040), 357–360.

Gleason, E. D., Fuxjager, M. J., Oyegbile, T. O., & Marler, C. A. (2009). Testosterone release and social context: When it occurs and why. *Frontiers in Neuroendocrinology*, *30*(4), 460–469.

Goetz, S. M. M., Tang, L., Thomason, M. E., Diamond, M. P., Hariri, A. R., & Carré, J. M. (2014). Testosterone rapidly increases neural reactivity to threat in healthy men: A novel two-step pharmacological challenge paradigm. *Biological Psychiatry*, *76*, 324-331.

Gomez-Lazaro, E., Arregi, A., Beitia, G., Vegas, O., Azpiroz, A., & Garmendia, L. (2011). Individual differences in chronically defeated male mice: Behavioral, endocrine, immune, and neurotrophic changes as markers of vulnerability to the effects of stress. *Stress*, *14*(5), 537–548.

Gonzalez-Bono, E., Salvador, A., Serrano, M. A., & Ricarte, J. (1999). Testosterone, cortisol, and mood in a sports team competition. *Hormones and Behavior*, *35*(1), 55–62.

Goymann, W., & Wingfield, J. C. (2014). Male-to-female testosterone ratios, dimorphism, and life history—What does it really tell us? *Behavioral Ecology*. *25*(4), 685-699. doi:10.1093/beheco/aru019

Granger, D. A., Shirtcliff, E. A., Booth, A., Kivlighan, K. T., & Schwartz, E. B. (2004). The "trouble" with salivary testosterone. *Psychoneuroendocrinology*, *29*(10), 1229–1240.

Greenberg, B. S., Sherry, J., Lachlan, K., Lucas, K., & Homstrom, A. (2010). Orientations to video games among gender and age groups. *Simulation & Gaming*, *41(*2), 238-259.

Greenspan, F. S., & Gardner, D. S. (2001). *Basic & Clinical Endocrinology* (6th ed.). New York: McGraw Hill.

Gruenewald, T. L., Kemeny, M. E., & Aziz, N. (2006). Subjective social status moderates cortisol responses to social threat. *Brain, Behavior, and Immunity*, *20*(4), 410–419.

Hajat, A., Diez-Roux, A., Franklin, T. G., Seeman, T., Shrager, S., Ranjit, N., … Kirschbaum, C. (2010). Socioeconomic and race/ethnic differences in daily salivary cortisol profiles: The multi-ethnic study of atherosclerosis. *Psychoneuroendocrinology*, *35*(6), 932–943.

Hamilton, L. D., Newman, M. L., Delville, C. L., & Delville, Y. (2008). Physiological stress response of young adults exposed to bullying during adolescence. *Physiology & Behavior*, *95*(5), 617–624.

Hansen, A. M., Hogh, A., & Persson, R. (2011). Frequency of bullying at work, physiological response, and mental health. *Journal of Psychosomatic Research*, *70*(1), 19-27.

Hellhammer, J., Fries, E., Schwisthal, O. W., Schlotz, W., Stone, A. A., & Hagemann, D. (2007). Several daily measurements are necessary to reliably assess the cortisol rise after awakening: State- and trait components. *Psychoneuroendocrinology*, *32*, 80 – 86.

Hermans, E. J., Putman, P., & van Honk, J. (2006). Testosterone administration reduces empathetic behavior: A facial mimicry study. *Psychoneuroendocrinology*, *31*(7), 859–866.

Hermans, E. J., Ramsey, N. F., & van Honk, J. (2008). Exogenous testosterone enhances responsiveness to social threat in the neural circuitry of social aggression in humans. *Biological Psychiatry*, *63*(3), 263–270.

Hermans, E. J., Bos, P. A., Ossewaarde, L., Ramsey, N. F., Fernandez, G. & van Honk, J. (2010). Effects of exogenous testosterone on the ventral striatal BOLD response during reward anticipation in healthy women. *Neuroimage, 52(1)*, 277-283.

Höfer, P., Lanzenberger, R., & Kasper, S. (2013). Testosterone in the brain: Neuroimaging findings and the potential role for neuropsychopharmacology. *European Neuropsychopharmacology*, *23*(2), 79–88.

Hogh, A., Hansen, Å. M., Mikkelsen, E. G., & Persson, R. (2012). Exposure to negative acts at work, psychological stress reactions and physiological stress response. *Journal of Psychosomatic Research*, *73*(1), 47–52.

Huhman, K. L., Moore, T. O., Ferris, C. F., Mougey, E. H., & Meyerhoff, J. L. (1991). Acute and repeated exposure to social conflict in male golden hamsters: Increases in plasma POMC peptides and cortisol and decreases in plasma testosterone. *Hormones and Behavior, 25,* 206-216.

Jiménez, M., Aguilar, R., & Alvero-Cruz, J. R. (2012). Effects of victory and defeat on testosterone and cortisol response to competition: Evidence for same response patterns in men and women. *Psychoneuroendocrinology*, *37*(9), 1577–1581.

Johnston, S. D., Ward, D., Lemon, J., Gunn, I., MacCallum, C. A., Keeley, T., & Blyde, D. (2007). Studies of male reproduction in captive African wild dogs (Lycaon pictus). *Animal Reproduction Science*, *100*(3–4), 338–355.

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

Josephs, R. A., Sellers, J. G., Newman, M. L., & Mehta, P. H. (2006). The mismatch effect: When testosterone and status are at odds. *Journal of Personality and Social Psychology*, *90*(6), 1999-1013.

Kliewer, W., Dibble, A. E., Goodman, K. L., & Sullivan, T. N. (2012). Physiological correlates of peer victimization and aggression in African American urban adolescents. *Development and Psychopathology*, *24*(2), 637–650.

Knack, J. M., Jensen-Campbell, L. A., & Baum, A. (2011). Worse than sticks and stones? Bullying is associated with altered HPA axis functioning and poorer health. *Brain and Cognition*, *77*(2), 183-190. doi:10.1016/j.bandc.2011.06.011

Kristenson, M., Eriksen, H., Sluiter, J., Starke, D., & Ursin, H. (2004). Psychobiological mechanisms of socioeconomic differences in health. *Social Science & Medicine*, *58*(8), 1511–1522.

Kumari, M., Badrick, E., Chandola, T., Adler, N. E., Epel, E., Seeman, T., … Marmot, M. G. (2010). Measures of social position and cortisol secretion in an aging population: Findings from the Whitehall II study. *Psychosomatic Medicine*, *72*(1), 27-34.

Lac, G., Dutheil, F., Brousse, G., Triboulet-Kelly, C., & Chamoux, A. (2012). Saliva DHEAS changes in patients suffering from psychopathological disorders arising from bullying at work. *Brain and Cognition*, *80*(2), 277–281.

Liening, S. H., Stanton, S. J., Saini, E. K., & Schultheiss, O. C. (2010). Salivary testosterone, cortisol, and progesterone: Two-week stability, interhormone correlations, and effects of time of day, menstrual cycle, and oral contraceptive use on steroid hormone levels. *Physiology & Behavior*, *99*(1), 8–16.

Maner, J. K., Gailliot, M. T., Menzel, A. J., & Kunstman, J. W. (2012). Dispositional anxiety blocks the psychological effects of power. *Personality and Social Psychology Bulletin*, *38*(11), 1383-1395.

Mazur, A. (1985). A biosocial model of status in face-to-face primate groups. *Social Forces*, *64*(2), 377–402.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences*, *21*, 353–363.

Mazur, A., & Booth, A. (2014). Testosterone is related to deviance in male army veterans, but relationships are not moderated by cortisol. *Biological Psychology*, *96*, 72–76. doi:10.1016/j.biopsycho.2013.11.015

McIntyre, M. H., Li, A. Y., Chapman, J. F., Lipson, S. F., & Ellison, P. T. (2011). Social status, masculinity, and testosterone in young men. *Personality and Individual Differences*, *51*(4), 392–396.

Mehta, P. H., & Beer, J. (2010). Neural mechanisms of the testosterone–aggression relation: The role of orbitofrontal cortex. *Journal of Cognitive Neuroscience*, *22*(10), 2357–2368.

Mehta, P. H., Jones, A. C., & Josephs, R. A. (2008). The social endocrinology of dominance: Basal testosterone predicts cortisol changes and behavior following victory and defeat. *Journal of Personality and Social Psychology*, *94*(6), 1078–1093.

Mehta, P. H., & Josephs, R. A. (2006). Testosterone change after losing predicts the decision to compete again. *Hormones and Behavior*, *50*(5), 684–692.

Mehta, P. H., & Josephs, R. A. (2010). Testosterone and cortisol jointly regulate dominance: Evidence for a dual-hormone hypothesis. *Hormones and Behavior*, *58*(5), 898–906.

Mehta, P. H., Wuehrmann, E. V., & Josephs, R. A. (2009). When are low testosterone levels advantageous? The moderating role of individual versus intergroup competition. *Hormones and Behavior*, *56*(1), 158–162.

Miller, G. E., Chen, E., & Zhou, E. S. (2007). If it goes up, must it come down? Chronic stress and the hypothalamic-pituitary-adrenocortical axis in humans. *Psychological Bulletin*, *133*(1), 25–45.

Montoya, E. R., Bos, P. A., Terburg, D., Rosenberger, L. A., & van Honk, J. (2014). Cortisol administration induces global down-regulation of the brain's reward circuitry, *Psychoneuroendocrinology*, *47*, 31-42.

Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the "challenge hypothesis." *Animal Behaviour*, *67*(1), 113–123.

Nelson, R. J., & Trainor, B. C. (2007). Neural mechanisms of aggression. *Nature Reviews Neuroscience*, *8*(7), 536–546.

Norman, R. E., Moreau, B. J. P., Welker, K. M., & Carré, J. M. (in press). Trait anxiety moderates the relationship between testosterone responses to competition and aggressive behavior. *Adaptive Human Behavior and Physiology*.

Oliveira, G. A., & Oliveira, R. F. (2014). Androgen responsiveness to competition in humans: The role of cognitive variables. *Neuroscience and Neuroeconomics*, *2014*(3), 19–32.

Oliveira, G. A., Uceda, S., Oliveira, T. F., Fernandes, A. C., Garcia-Marques, T., & Oliveira, R. F. (2014). Testosterone response to competition in males is unrelated to opponent familiarity or threat appraisal. *Frontiers in Psychology*, *5*, 1240.

Oliveira, R. F., Almada, V. C., & Canario, A. V. M. (1996). Social modulation of sex steroid concentrations in the urine of male cichlid fish Oreochromis mossambicus. *Hormones and Behavior*, *30*(1), 2–12.

Oliveira, R. F., Silva, A., & Canário, A. V. M. (2009). Why do winners keep winning? Androgen mediation of winner but not loser effects in cichlid fish. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1665), 2249–2256.

Ouellet-Morin, I., Danese, A., Bowes, L., Shakoor, S., Ambler, A., Pariante, C. M., … Arseneault, L. (2011). A discordant monozygotic twin design shows blunted cortisol reactivity among bullied children. *Journal of the American Academy of Child and Adolescent Psychiatry*, *50*(6), 574-582.

Ouellet-Morin, I., Odgers, C. L., Danese, A., Bowes, L., Shakoor, S., Papadopoulos, A. S., … Arseneault, L. (2011). Blunted cortisol responses to stress signal social and behavioral problems among maltreated/bullied 12-year-old children. *Biological Psychiatry*, *70*(11), 1016–1023.

Oxford, J., Ponzi, D., & Geary, D. C. (2010). Hormonal responses differ when playing violent video games against an ingroup and outgroup. *Evolution and Human Behavior*, *31*(3), 201–209.

Parmigiani, S., Bartolomucci, A., Palanza, P., Galli, P., Rizzi, N., Brain, P. F., & Volpi, R. (2006). In judo, randori (free fight) and kata (highly ritualized fight) differentially change plasma cortisol, testosterone, and interleukin levels in male participants. *Aggressive Behavior*, *32*(5), 481-489.

Pfattheicher, S., Landhäußer, A., & Keller, J. (2014). Individual differences in antisocial punishment in public goods situations: The interplay of cortisol with testosterone and dominance. *Journal of Behavioral Decision Making*, *27*(4), 340-348.

Popma, A., Vermeiren, R., Geluk, C. A. M. L., Rinne, T., van den Brink, W., Knol, D. L., … Doreleijers, T. A. H. (2007). Cortisol moderates the relationship between testosterone and aggression in delinquent male adolescents. *Biological Psychiatry*, *61*(3), 405–411.

Pruessner, J. C., Gaab, J., Hellhammer, D. H., Lintz, D., Schommer, N., & Kirschbaum, C. (1997). Increasing correlations between personality traits and cortisol stress responses obtained by data aggregation. *Psychoneuroendocrinology*, *22*(8), 615-625.

Roelofs, K., van Peer, J., Berretty, E., Jong, P. D., Spinhoven, P., & Elzinga, B. M. (2009). Hypothalamus–pituitary–adrenal axis hyperresponsiveness is associated with increased social avoidance behavior in social phobia. *Biological Psychiatry*, *65*(4), 336-343.

Ronay, R., & Carney, D. R. (2013). Testosterone's negative relationship with empathic accuracy and perceived leadership ability. *Social Psychological and Personality Science*, *4*(1), 92–99.

Rowe, R., Maughan, B., Worthman, C. M., Costello, E. J., & Angold, A. (2004). Testosterone, antisocial behavior, and social dominance in boys: Pubertal development and biosocial interaction. *Biological Psychiatry*, *55*(5), 546–552.

Sapolsky, R. M. (1982). The endocrine stress-response and social status in the wild baboon. *Hormones and Behavior*, *16*(3), 279–292.

Sapolsky, R. M. (1991). Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology*, *16*(4), 281–293.

Sapolsky, R. M. (1992). Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology*, *17*(6), 701–709.

Sapolsky, R. M. (2002). Endocrinology of the stress-response. In *Behavioral Endocrinology* (2nd ed., pp. 409–450). Cambridge, MA: Massachusetts Institute of Technology Press.

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science*, *308*(5722), 648–652.

Schultheiss, O., Wirth, M., Torges, C., Pang, J., Villacorta, M., & Welsh, K. (2005). Effects of implicit power motivation on men's and women's implicit learning and testosterone changes after social victory or defeat. *Journal of Personality and Social Psychology, 88*, 174-188.

Sellers, J. G., Mehl, M. R., & Josephs, R. A. (2007). Hormones and personality: Testosterone as a marker of individual differences. *Journal of Research in Personality*, *41*(1), 126–138.

Sherman, G. D., Lee, J. J., Cuddy, A. J. C., Renshon, J., Oveis, C., Gross, J. J., & Lerner, J. S. (2012). Leadership is associated with lower levels of stress. *Proceedings of the National Academy of Sciences*, *109*(44), 17903–17907.

Stanton, S. J., Beehner, J. C., Saini, E. K., Kuhn, C. M., & LaBar, K. S. (2009). Dominance, politics, and physiology: Voters' testosterone changes on the night of the 2008 United States presidential election. *PLoS ONE*, *4*(10), e7543. doi: 10.1371/journal.pone.0007543

Stanton, S. J., & Schultheiss, O. C. (2007). Basal and dynamic relationships between implicit power motivation and estradiol in women. *Hormones and Behavior*, *52*(5), 571–580.

Stanton, S. J., & Schultheiss, O. C. (2009). The hormonal correlates of implicit power motivation. *Journal of Research in Personality*, *43*(5), 942-949.

Staufenbiel, S. M., Penninx, B. W. J. H., Spijker, A. T., Elzinga, B. M., & van Rossum, E. F. C. (2013). Hair cortisol, stress exposure, and mental health in humans: A systematic review. *Psychoneuroendocrinology*, *38*(8), 1220–1235.

Tackett, J. L., Herzhoff, K., Harden, K. P., Page-Gould, E., & Josephs, R. A. (2014). Personality x hormone interactions in adolescent externalizing psychopathology. *Personality Disorders: Theory, Research, and Treatment*, *5*(3), 235-246.

Tamashiro, K. L. K., Nguyen, M. M. N., & Sakai, R. R. (2005). Social stress: From rodents to primates. *Frontiers in Neuroendocrinology*, *26*(1), 27–40.

Terburg, D., Aarts, H., & van Honk, J. (2012). Testosterone affects gaze aversion from angry faces outside of conscious awareness. *Psychological Science*, *23*(5), 459–463.

Tilbrook, A. J., Turner, A. I., & Clarke, I. J. (2000). Effects of stress on reproduction in non-rodent mammals: the role of glucocorticoids and sex differences. *Reviews of Reproduction, 5*, 105–113.

Trainor, B. C., Bird, I. M., & Marler, C. A. (2004). Opposing hormonal mechanisms of aggression revealed through short-lived testosterone manipulations and multiple winning experiences. *Hormones and Behavior, 45(2),* 115–121.

Trumble, B. C., Cummings, D., von Rueden, C., O'Connor, K. A., Smith, E. A., Gurven, M., & Kaplan, H. (2012). Physical competition increases testosterone among Amazonian forager-horticulturalists: A test of the "challenge hypothesis." *Proceedings of the Royal Society B: Biological Sciences*, *279*(1739), 2907–2912.

Uchino, B. (2006). Social support and health: A review of physiological processes potentially underlying links to disease outcomes. *Journal of Behavioral Medicine*, *29*(4), 377–387.

Vaillancourt, T., deCatanzaro, D., Duku, E., & Muir, C. (2009). Androgen dynamics in the context of children's peer relations: An examination of the links between testosterone and peer victimization. *Aggressive Behavior*, *35*(1), 103–113.

Vaillancourt, T., Duku, E., Becker, S., Schmidt, L. A., Nicol, J., Muir, C., & MacMillan, H. (2011). Peer victimization, depressive symptoms, and high salivary cortisol predict poorer memory in children. *Brain and Cognition*, *77*(2), 191–199.

Vaillancourt, T., Duku, E., Decatanzaro, D., Macmillan, H., Muir, C., & Schmidt, L. A. (2008). Variation in hypothalamic–pituitary–adrenal axis activity among bullied and non-bullied children. *Aggressive Behavior*, *34*(3), 294–305.

van Anders, S. M. (2013). Beyond masculinity: Testosterone, gender/sex, and human social behavior in a comparative context. *Frontiers in Neuroendocrinology*, *34*(3), 198–210.

van Anders, S. M., Goldey, K. L., & Kuo, P. X. (2011). The Steroid/Peptide Theory of Social Bonds: Integrating testosterone and peptide responses for classifying social behavioral contexts. *Psychoneuroendocrinology*, *36*(9), 1265–1275.

van Anders, S. M., & Watson, N. V. (2006). Social neuroendocrinology. *Human Nature*, *17*(2), 212–237.

van Anders, S. M., & Watson, N. V. (2007). Effects of ability- and chance-determined competition outcome on testosterone. *Physiology & Behavior*, *90*(4), 634–642.

van Honk, J., Montoya, E. R., Bos, P. A., van Vugt, M., & Terburg, D. (2012). New evidence on testosterone and cooperation. *Nature*, *485*(7399), E4-E5.

van Honk, J., Tuiten, A., Verbaten, R., van den Hout, M., Koppeschaar, H., Thijssen, J., & de Haan, E. (1999). Correlations among salivary testosterone, mood, and selective attention to threat in humans. *Hormones and Behavior*, *36*(1), 17–24.

van Kesteren, F., Sillero-Zubiri, C., Millar, R., Argaw, K., Macdonald, D. W., & Paris, M. (2012). Sex, stress and social status: Patterns in fecal testosterone and glucocorticoid metabolites in male Ethiopian wolves. *General and Comparative Endocrinology*, *179*(1), 30–37.

van Wingen, G., Mattern, C., Verkes, R. J., Buitelaar, J., & Fernández, G. (2010). Testosterone reduces amygdala–orbitofrontal cortex coupling. *Psychoneuroendocrinology*, *35*(1), 105–113.

Viau, V. (2002). Functional cross-talk between the hypothalamic-pituitary-gonadal and - adrenal axes. *Journal of Neuroendocrinology, 14*, 506–513.

Virgin, C. J., & Sapolsky, R. M. (1997). Styles of male social behavior and their endocrine correlates among low-ranking baboons. *American Journal of Primatology*, *42*(1), 25-39.

von Engelhard, N., Kappeler, P. M., & Heistermann, M. (2000). Androgen levels and female social dominance in Lemur catta. *Proceedings of the Royal Society of London*. *Series B: Biological Sciences*, *267*(1452), 1533–1539.

Wang, J., Chai, A., Zhou, Q., Lv, L., Wang, L., Yang, Y., & Xu, L. (2013). Chronic clomipramine treatment reverses core symptom of depression in subordinate tree shrews. *PloS One*, *8*(12), e80980. doi:10.1371/journal.pone.0080980

Warren, B. L., Vialou, V. F., Iniguez, S. D., Alcantara, L. F., Wright, K. N., Feng, J., … Bolanos-Guzman, C. A. (2013). Neurobiological sequelae of witnessing stressful events in adult mice. *Biological Psychiatry*, *73*(1), 7-14.

Weathington, J. M., Arnold, A. R., & Cooke, B. M. (2012). Juvenile social subjugation induces a sex-specific pattern of anxiety and depression-like behaviors in adult rats. *Hormones and Behavior*, *61*(1), 91–99.

Welker, K. M., Lozoya, E., Campbell, J. A., Neumann, C. S., & Carré, J. M. (2014). Testosterone, cortisol, and psychopathic traits in men and women. *Physiology & Behavior*, *129*(0), 230–236.

Welsh, T. H., Kemper-Green, K. N., & Livingston, K. N. (1999). Stress and reproduction. In *Encyclopedia of Reproduction* (pp. 662–674). San Diego, CA: Academic Press.

Wingfield, J. C., Hegner, R. E., Dufty, A. M., & Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, *136*(6), 829–846.

Viau, V. (2002). Functional cross talk between the hypothalamic pituitary gonadal and adrenal axes. *Journal of Neuroendocrinology*, *14*(6), 506-513.

Wirth, M. M., & Schultheiss, O. C. (2007). Basal testosterone moderates responses to anger faces in humans. *Physiology & Behavior*, *90*(2–3), 496–505.

Wirth, M. M., Welsh, K. M., & Schultheiss, O. C. (2006). Salivary cortisol changes in humans after winning or losing a dominance contest depend on implicit power motivation. *Hormones and Behavior*, *49*(3), 346–352.

Wommack, J. C., & Delville, Y. (2003). Repeated social stress and the development of agonistic behavior: Individual differences in coping responses in male golden hamsters. *Physiology & Behavior*, *80*(2), 303–308.

Wommack, J. C., Salinas, A., Melloni, R. H. J., & Delville, Y. (2004). Behavioural and neuroendocrine adaptations to repeated stress during puberty in male golden hamsters. *Journal of Neuroendocrinology*, *16*(9), 767–775.

Zak, P. J., Kurzban, R., Ahmadi, S., Swerdloff, R. S., Park, J., Efremidze, L., … Matzner, W. (2009). Testosterone administration decreases generosity in the ultimatum game. *PLoS ONE*, *4*(12).

Zilioli, S., Mehta, P., & Watson, N. V. (2014). Losing the battle but winning the war: Uncertain outcomes reverse the usual effect of winning on testosterone. *Biological Psychology, 103,* 54-62.

Zilioli, S., & Watson, N. V. (2012). The hidden dimensions of the competition effect: Basal cortisol and basal testosterone jointly predict changes in salivary testosterone after social victory in men. *Psychoneuroendocrinology*, *37*(11), 1855–1865.

Zilioli, S., & Watson, N. V. (2014). Testosterone across successive competitions: Evidence for a "winner effect" in humans? *Psychoneuroendocrinology*, *47,* 1-9.

Table
Click here to download Table: Table TxC_Final.docx

Table 1

Review of Basal T x 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	Pfattheicher 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 Day 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 & Mehta, 2011).
2013	Denson et al.	53 F	1 Afternoon	Aggression	T (+) DV at high C, but not at mean or low C.
2014	Welker et al.	114 M | 123 F	1 Early Afternoon	Psychopathy	T (+) DV at high C, T (-) DV at low C (in men).

Note: 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 & Mehta (2011).[c] = effect size of T x C x Inclusion/Exclusion.[d] = reported in Geniole et al., 2011.

Supplementary Material

Click here to download Supplementary Material: T_Table_Final.docx

Table 1

Review of the Win/Lose Effect on Testosterone in Published Literature

Year	Author	Paradigm	Sample	Win Vs. Lose
2013	Aguilar et al	Field Hockey	M (7)	W>L
2014	Apicella et al	Financial Task	M (49)	W>L
1998	Bernhardt et al	Watching Basketball	M (8)	W>L
1998	Bernhardt et al	Watching Soccer	M (21)	W>L
1989	Booth et al	Tennis	M (6)	W>L
2010	Carre & Putnam	Hockey	M (23)	W=L
2009	Carre et al	PSAP and NTT	M (39)	W=L
2013	Carre et al	Video Game	M (114)	W>L
2013	Crewther et al	Rugby	M (5)	W=L
1981	Elias	Wrestling	M (15)	W>L
2001	Filaire et al	Judo	M (18)	W<L
2012	Flinn et al	Dominoes	M (27)	W>L
2011	Fry et al	Wrestling	M (12)	W>L
1989	Gladue et al	RT Task	M (39)	W>L
1999	Gonzalez-Bono et al	Basketball	M (16)	W=L
2000	Gonzalez-Bono et al	Basketball	M (17)	W=L
2008	Hasegawa et al	Shogi	M (90)	W=L
2012	Jiminez et al	Badminton	M (27)	W>L
2008	Maner et al	NTT	M (23)	W=L
1980	Mazur and Lamb	Tennis	M (14)	W>L
1992	Mazur et al	Chess	M (16)	W>L
1997	Mazur et al*	Video Game	M (28) / M (32)	W=L / W/=L
1992	McCaul et al	Coin Toss	M (28) / M (32)	W>L / W>L
2006	Mehta and Josephs	NTT	M (50)	W=L
2010	Oxford et al	Video Game	M (42)	W=L
2006	Parmigiani et al	Judo	M (22)	W<L

2009	Pound et al	Sumo Wrestling	M (57)	W>L
1987	Salvador et al	Judo	M (14)	W=L
2002	Schultheiss and Rohde	NTT	M (66)	W=L
1999	Schultheiss et al	Lab Task	M (42)	W=L
2005	Schultheiss et al	SRT	M (95)	W=L
2000	Serrano et al	Judo	M (12)	W=L
2009	Stanton et al	Elections	M (57)	W>L
2010	Steiner et al	Poker	M (32)	W=L
1999	Suay et al	Judo	M (26)	W=L
2012	Trumble et al	Soccer	M (82)	W=L
2014	Trumble et al	Hunting	M (31)	W>L
2007	van Anders and Watson	Competitive Lab Task	M (37)	W>L
2010	van der Meij et al	Computer Task	M (84)	W=L
2002	Wagner et al	Dominoes	M (8)	W=L
2014	Welker & Carre	NTT	M (80)	W=L
2012	Zilioli et al	Tetris	M (70)	W>L
2014	Zilioli et al	Tetris	M (84)	W>L
2002	Bateup et al	Rugby	F (17)	W=L
2009	Carre et al	PSAP and NTT	F (60)	W=L
2013	Carre et al	Video Game	F (123)	W=L
2012	Costa and Salvador	Competitive Task	F (40)	W>L
2013	Denson et al	Reactive Aggression Task	F (49)	W>L
2006	Edwards et al	Soccer	F (18)	W=L
2009	Hamilton et al	Wrestling	F (13)	W=L
2012	Jiminez et al	Badminton	F (23)	W>L
2008	Mehta et al	Intelligence Lab Task	F (61)	W=L
2009	Oliveira et al	Soccer	F (29)	W>L
2013	Oliveira et al	NTT	F (34)	W<L
2007	Stanton and Schultheiss	SRT	F (49)	W=L

2007	van Anders and Watson	Competitive Lab Task	F (38)	W=L
2014	Zilioli, Mehta & Watson	Number Tracing Task	F(65)	W<L
2014	Zilioli, Mehta & Watson	Tetris	F(53)	W<L

Note. W>L: Winners showed a greater increase, or smaller decrease, in T than losers. W<L: Losers showed a greater increase, or smaller decrease in T than winners. W=L: No statistically significant difference between winners and losers. Note: These are published studies obtained from a search using PubMed and Google Scholar.

References

1. Aguilar, R., Jiménez, M., and Alvero-Cruz, J. (2013). Testosterone, cortisol and anxiety in elite field hockey players. Physiology & Behavior, 119, 38-42.
2. Apicella, C., Dreber, A., and Mollerstrom, J. (2014). Salivary testosterone change following monetary wins and losses predicts future financial risk-taking. Psychoneuroendocrinology, 39, 68-64.
3. Bateup, H., Booth, A., Shirtcliff, E., and Granger, D. (2002). Testosterone, cortisol, and women's competition. Evolution and Human Behavior, 23, 181-192.
4. Bernhardt, P., Dabbs, J Jr., Fielden, J., and Lutter, C. (1998). Testosterone changes during vicarious experiences of winning and losing among fans at sporting events. Physiology and Behavior, 65, 59-62.
5. Booth, A., Shelley, G., Mazur, A., Tharp, G., and Kittok, R. (1989). Testosterone, and winning and losing in human competition. Hormones and Behavior, 23, 556-571.
6. Carré, J., Campbell, J., Lozoya, E., Goetz, S., and Welker, K. (2013). Changes in testosterone mediate the effect of winning on subsequent aggressive behavior. Psychoneuroendocrinology, 38, 2034-2041.
7. Carré, J. M., & Putnam, S. K. (2010). Watching a previous victory produces an increase in testosterone among elite hockey players. Psychoneuroendocrinology, 35, 475–479.
8. Carré, J., Putnam, S., and McCormick, C. (2009). Testosterone responses to competition predict future aggressive behavior at a cost to reward in men. Psychoneuroendocrinology, 34, 561-570.
9. Costa, R., and Salvador, A. (2012). Associations between success and failure in a face-to-face competition and psychobiological parameters in young women. Psychoneuroendocrinology, 37, 1780-1790.
10. Crewther, B., Sanctuary, C., Kilduff, L., Carruthers, J., Gaviglio, C., and Cook, C. (2013). The workout responses of salivary-free testosterone and cortisol concentrations and their association with the subsequent competition outcomes in professional rugby league. Journal of Strength and Conditioning Research, 27, 471-476.
11. Denson, T., Mehta, P., and Ho Tan, D. (2013). Endogenous testosterone and cortisol jointly influence reactive aggression in women. Psychoneuroendocrinology, 38, 416-424.
12. Edwards, D., Wetzel, K., and Wyner, D. (2006). Intercollegiate soccer: saliva cortisol and testosterone are elevated during competition, and testosterone is related to status and social connectedness with teammates. Physiology and Behavior, 87, 135-143.
13. Elias, M. (1981). Serum cortisol, testosterone, and testosterone-binding globulin responses to competitive fighting in human males. Aggressive Behavior, 7, 215-224.
14. Filaire, E., Maso, F., Sagnol, M., Ferrand, C., and Lac, G. (2001). Anxiety, hormonal responses, and coping during a judo competition. Aggressive Behavior, 27, 55-63.
15. Flinn, M., Ponzi, D., and Muehlenbein, M. (2012). Hormonal mechanisms for regulation of aggression in human coalitions. Human Nature, 23, 68-88.
16. Fry, A., Schilling, B., Fleck, S., and Kraemer, W. (2011). Relationships between competitive wrestling success and neuroendocrine responses. Journal of Strength and Conditioning Research, 25, 40-45

17. Gladue, B., Boechler, M., and McCaul, K. (1989). Hormonal response to competition in human males. Aggressive Behavior, 15, 409-422.
18. Gonzalez-Bono, E., Salvador, A., Serrano, M.A., and Ricarte, J. (1999). Testosterone, cortisol, and mood in a sports team competition. Hormones and Behavior, 35, 55-62.
19. Gonzalez-Bono, E., Salvador, A., Ricarte, J., Serrano, M.A., and Arnedo, M. (2000). Testosterone and attribution of successful competition. Aggressive Behavior, 26, 235-240.
20. Hamilton, L., van Anders, S., Cox, D., and Watson, N. (2009). The effect of competition on salivary testosterone in elite female athletes. International Journal of Sports Physiology and Performance, 4, 538-542.
21. Hasegawa, M., Toda, M., and Morimoto, K. (2008). Changes in salivary physiological stress markers associated with winning and losing. Biomedical Research, 29, 43-46.
22. Jiménez, M., Aguilar, R., and Alvero-Cruz, J. (2012). Effects of victory and defeat on testosterone and cortisol response to competition: evidence for same response patterns in men and women. Psychoneuroendocrinology, 37, 1577-1581.
23. Maner, J. K., Miller, S. L., Schmidt, N. B., & Eckel, L. A. (2008). Submitting to defeat: Social anxiety, dominance threat, and decrements in testosterone. Psychological Science, 19(8), 764–768.
24. Mazur, A., and Lamb, T. (1980). Testosterone, status, and mood in human males. Hormones and Behavior, 14: 236-246.
25. Mazur, A., Booth, A., and Dabbs, J. Jr. (1992). Testosterone and chess competition. Social Psychology Quarterly, 55, 70-77.
26. Mazur, A., Susman, E., and Edelbrock, S. (1997). Sex differences in testosterone response to a video game contest. Evolution and Human Behavior, 18, 317-326.
27. McCaul, K., Gladue, B., and Joppa, M. (1992). Winning, losing, mood, and testosterone. Hormones and Behavior, 26, 486-504.
28. Mehta, P., Jones, A., and Josephs, R. (2008). The social endocrinology of dominance: basal testosterone predicts cortisol changes and behavior following victory and defeat. Journal of Personality and Social Psychology, 94, 1078-1093.
29. Mehta, P., and Josephs, R. (2006). Testosterone change after losing predicts the decision to compete again. Hormones and Behavior, 50, 684-692.
30. Oliveira, T., Gouveia, M., and Oliveira, R. (2009). Testosterone responsiveness to winning and losing experiences in female soccer players. Psychoneuroendocrinology, 34, 1056-1064.
31. Oliveira, G., Uceda, S., Oliveira, T., Fernandes, A., Garcia-Marques, T., and Oliveira, R. (2013). Threat perception and familiarity moderate the androgen response to competition in women. Frontiers in Psychology, 4.
32. Oxford, J., Ponzi, D., and Geary, D. (2010). Hormonal responses differ when playing violent video games against an ingroup and outgroup. Evolution and Human Behavior, 31, 201-209.
33. Parmigiani, S., Bartolomucci, A., Palanza, P., Galli, P., Rizzi, N., Brain, P., and Volpi, R. (2006). In judo, Randori (free fight) and Kata (highly ritualized fight) differentially change plasma cortisol, testosterone, and interleukin levels in male participants. Aggressive Behavior, 32, 481-489.
34. Pound, N., Penton-Voak, Ian., and Surridge, A. (2009). Testosterone responses to competition in men are related to facial masculinity. Proceedings of the Royal Society, 276, 153-159.
35. Salvador, A., Simon, V., Suay, F., and Llorens, L. (1987). Testosterone and cortisol responses to competitive fighting in human males: a pilot study. Aggressive Behavior, 13, 9-13.
36. Schultheiss, O., Kenneth, C., and McClelland, D. (1999). Implicit power motivation moderates men's testosterone responses to imagined and real dominance success. Hormones and Behavior, 36: 234-241.
37. Schultheiss, O., and Rohde, W. 2002. Implicit power motivation predicts men's testosterone changes in implicit learning in a contest situation. Hormones and Behavior, 41, 195-202.

38. Schultheiss, O., Wirth, M., Torges, C., Pang, J., Villacorta, M., and Welsh, K. (2005). Effects of implicit power motivation on men's and women's implicit learning and testosterone changes after social victory or defeat. Journal of Personality and Social Psychology, 88, 174-188.
39. Serrano, M., Salvador, A., Gonzalez-Bono, E., Sanchis, C., and Suay, F. (2000). Hormonal responses to competition. Psicothema, 12, 440-444.
40. Stanton, S., Beehner, J., Saini, E., Kuhn, C., and LaBar, K. (2009). Dominance, politics, and physiology: voters' testosterone changes on the night of the 2008 United States presidential election. PLoS ONE, 4, e7543.
41. Stanton, S., and Schultheiss, O. (2007). Basal and dynamic relationships between implicit power motivation and estradiol in women. Hormones and Behavior, 52, 571-580.
42. Steiner, E., Barchard, K., Meana, M., Hadi, F., and Gray, P. (2010). The deal on testosterone responses to poker competition. Current Psychology, 29, 45-51.
43. Suay, F., Salvador, A., Gonzalez-Bono, E., Sanchis, C., Martinez-Sanchis, S., Simon, V.M., and Montoro, J.B. (1999). Effects of competition and its outcome on serum testosterone, cortisol, and prolactin. Psychoneuroendocrinology, 24, 551-566.
44. Trumble, B., Cummings, D., von Rueden, C., O'Connor, K., Smith, E., Gurven, M., and Kaplan, H. (2012). Physical competition increases testosterone among Amazonian forager-horticulturalists: a test of the 'challenge hypothesis'. Proceedings of the Royal Society, 279, 2907-2912.
45. Trumble, B. C., Smith, E. A., O'Connor, K. A., Kaplan, H. S., & Gurven, M. D. (2014). Successful hunting increases testosterone and cortisol in a subsistence population. Proceedings of the Royal Society B: Biological Sciences, 281(1776). doi:10.1098/rspb.2013.2876
46. van Anders, S., and Watson, N. (2007). Effects of ability- and chance-determined competition outcome on testosterone. Physiology and Behavior, 90, 634-642
47. van der Meij, L., Buunk, A., Almela, M., and Salvador, A. (2010). Testosterone responses to competition: The opponent's psychological state makes it challenging. Biological Psychology, 84, 330-335.
48. Wagner, J., Flinn, M., and England, B. (2002). Hormonal response to competition among male coalitions. Evolution and Human Behavior, 23, 437-442.
49. Welker, K. M., & Carré, J. M. (2014). Individual differences in testosterone predict persistence in men. European Journal of Personality. doi:10.1002/per.1958
50. Zilioli, S., and Watson, N. (2012). The hidden dimensions of the competition effect: basal cortisol and basal testosterone jointly predict changes in salivary testosterone after social victory in men. Psychoneuroendocrinology, 37, 1855-1865.
51. Zilioli, S., and Watson, N. (2014). Testosterone across successive competitions: Evidence for a winner effect in humans?. Psychoneuroendocrinology, 47. doi:10.1016/j.psyneuen.2014.05.001

Table 2

Review of the Win/Lose Effect on Cortisol in Published Literature

Year	Author	Paradigm	Sample	Win Vs. Lose
2013	Aguilar et al	Field Hockey	M (7)	W>L
1989	Booth et al	Tennis	M (6)	W=L
2013	Crewther et al	Rugby	M (5)	W=L
1981	Elias	Wrestling	M (15)	W>L
2001	Filaire et al	Judo	M (18)	W=L
2009	Filaire et al	Tennis	M (8)	W<L
2011	Fry et al	Wrestling	M (12)	W=L
1989	Gladue et al	RT Task	M (39)	W=L
1999	Gonzalez-Bono	Basketball	M (16)	W=L
2008	Hasegawa et al	Shogi	M (90)	W=L
2012	Jiminez et al	Badminton	M (27)	W<L
1997	Mazur et al	Video Game	M (28)	W=L
1992	McCaul et al	Coin Toss	M (28) M (101)	W=L W=L
2008	Mehta et al	Dog Agility Competition	M (83)	W<L
2010	Oxford et al	Video Game	M (42)	W=L
2006	Parmigiani et al	Judo	M (22)	W=L
1987	Salvador et al	Judo	M (14)	W=L
2000	Serrano et al	Judo	M (12)	W=L
2010	Stanton	Election	M (61)	W<L
1999	Suay et al	Judo	M (26)	W=L
2002	Wagner et al	Dominoes	M (8)	W=L
2006	Wirth et al	NTT	M (66)	W>L
2012	Zilioli et al	Tetris	M (70)	W=L
2002	Bateup et al	Rugby	F (17)	W<L
2012	Costa and Salvador	Competitive Task	F (40)	W=L
2013	Denson et al	Reactive Aggression	F (49)	W=L

		Paradigm		
2006	Edwards et al	Soccer	F (18)	W=L
2009	Filaire et al	Tennis	F (8)	W<L
2012	Jiminez et al	Badminton	F (23)	W<L
1997	Mazur et al	Video Game	F (32)	W=L
2008	Mehta et al	Dog Agility Competition	F (57)	W<L
2009	Oliveira et al	Soccer	F (29)	W=L
2013	Oliveira et al	NTT	F (34)	W=L
2010	Stanton et al	Election	F (122)	W<L

Note. W>L: Winners showed a greater increase, or smaller decrease, in T than losers. W<L: Losers showed a greater increase, or smaller decrease in T than winners. W=L: No statistically significant difference between winners and losers. Note: These are published studies obtained from a search using PubMed and Google Scholar.

References

1. Bateup, H., Booth, A., Shirtcliff, E., and Granger, D. (2002). Testosterone, cortisol, and women's competition. Evolution and Human Behavior, 23, 181-192.
2. Booth, A., Shelley, G., Mazur, A., Tharp, G., and Kittok, R. (1989). Testosterone, and winning and losing in human competition. Hormones and Behavior, 23, 556-571.
3. Costa, R., and Salvador, A. (2012). Associations between success and failure in a face-to-face competition and psychobiological parameters in young women. Psychoneuroendocrinology, 37: 1780-1790.
4. Crewther, B., Sanctuary, C., Kilduff, L., Carruthers, J., Gaviglio, C., and Cook, C. (2013). The workout responses of salivary-free testosterone and cortisol concentrations and their association with the subsequent competition outcomes in professional rugby league. Journal of Strength and Conditioning Research, 27, 471-476.
5. Denson, T., Mehta, P., and Ho Tan, D. (2013). Endogenous testosterone and cortisol jointly influence reactive aggression in women. Psychoneuroendocrinology, 38, 416-424.
6. Edwards, D., Wetzel, K., and Wyner, D. (2006). Intercollegiate soccer: saliva cortisol and testosterone are elevated during competition, and testosterone is related to status and social connectedness with teammates. Physiology and Behavior, 87, 135-143.
7. Elias, M. (1981). Serum cortisol, testosterone, and testosterone-binding globulin responses to competitive fighting in human males. Aggressive Behavior, 7, 215-224.
8. Filaire, E., Maso, F., Sagnol, M., Ferrand, C., and Lac, G. (2001). Anxiety, hormonal responses, and coping during a judo competition. Aggressive Behavior, 27, 55-63.
9. Filaire, E., Alix, D., Ferrand, C., and Verger, M. (2009). Psychophysiological stress in tennis players during the first single match of a tournament. Psychoneuroendocrinology, 34, 150-157.
10. Fry, A., Schilling, B., Fleck, S., and Kraemer, W. (2011). Relationships between competitive wrestling success and neuroendocrine responses. Journal of Strength and Conditioning Research, 25, 40-45.

11. Gladue, B., Boechler, M., and McCaul, K. (1989). Hormonal response to competition in human males. Aggressive Behavior, 15, 409-422.
12. Gonzalez-Bono, E., Salvador, A., Serrano, M.A., and Ricarte, J. (1999). Testosterone, cortisol, and mood in a sports team competition. Hormones and Behavior, 35, 55-62.
13. Hasegawa, M., Toda, M., and Morimoto, K. (2008). Changes in salivary physiological stress markers associated with winning and losing. Biomedical Research, 29, 43-46.
14. Jiménez, M., Aguilar, R., and Alvero-Cruz, J. (2012). Effects of victory and defeat on testosterone and cortisol response to competition: evidence for same response patterns in men and women. Psychoneuroendocrinology, 37, 1577-1581.
15. Mazur, A., Susman, E., and Edelbrock, S. (1997). Sex differences in testosterone response to a video game contest. Evolution and Human Behavior, 18, 317-326.
16. McCaul, K., Gladue, B., and Joppa, M. (1992). Winning, losing, mood, and testosterone. Hormones and Behavior, 26, 486-504.
17. Mehta, P., Jones, A., and Josephs, R. (2008). The social endocrinology of dominance: basal testosterone predicts cortisol changes and behavior following victory and defeat. Journal of Personality and Social Psychology, 94, 1078-1093.
18. Oliveira, T., Gouveia, M., and Oliveira, R. (2009). Testosterone responsiveness to winning and losing experiences in female soccer players. Psychoneuroendocrinology, 34, 1056-1064.
19. Oliveira, G., Uceda, S., Oliveira, T., Fernandes, A., Garcia-Marques, T., and Oliveira, R. (2013). Threat perception and familiarity moderate the androgen response to competition in women. Frontiers in Psychology, 4. doi: 10.3389/fpsyg.2013.00389.
20. Oxford, J., Ponzi, D., and Geary, D. (2010). Hormonal responses differ when playing violent video games against an ingroup and outgroup. Evolution and Human Behavior, 31, 201-209.
21. Parmigiani, S., Bartolomucci, A., Palanza, P., Galli, P., Rizzi, N., Brain, P., and Volpi, R. (2006). In judo, Randori (free fight) and Kata (highly ritualized fight) differentially change plasma cortisol, testosterone, and interleukin levels in male participants. Aggressive Behavior, 32, 481-489.
22. Salvador, A., Simon, V., Suay, F., and Llorens, L. (1987). Testosterone and cortisol responses to competitive fighting in human males: a pilot study. Aggressive Behavior, 13, 9-13.
23. Serrano, M., Salvador, A., Gonzalez-Bono, E., Sanchis, C., and Suay, F. (2000). Hormonal responses to competition. Psicothema, 12, 440-444.
24. Stanton, S., LaBar, K., Saini, E., Kuhn, C., and Beehner, J. 2010. Stressful politics: voters' cortisol responses to the outcome of the 2008 United States presidential election. Psychoneuroendocrinology, 35, 768-774.
25. Suay, F., Salvador, A., Gonzalez-Bono, E., Sanchis, C., Martinez-Sanchis, S., Simon, V.M., and Montoro, J.B. (1999). Effects of competition and its outcome on serum testosterone, cortisol, and prolactin. Psychoneuroendocrinology, 24, 551-566.
26. Wagner, J., Flinn, M., and England, B. (2002). Hormonal response to competition among male coalitions. Evolution and Human Behavior, 23, 437-442.
27. Wirth, M., Welsh, K., and Schultheis, O. (2006). Salivary cortisol changes in humans after winning or losing a dominance contest depend on implicit power motivation. Hormones and Behavior, 49, 346-352.
28. Zilioli, S., and Watson, N. (2012). The hidden dimensions of the competition effect: basal cortisol and basal testosterone jointly predict changes in salivary testosterone after social victory in men. Psychoneuroendocrinology, 37, 1855-1865.