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SOCIAL NEUROENDOCRINOLOGY OF HUMAN AGGRESSION: EXAMINING THE ROLE OF COMPETITION-INDUCED TESTOSTERONE DYNAMICS

J. M. CARRÉ * AND N. A. OLMSTEAD

Department of Psychology, Nipissing University, North Bay, ON, Canada

Abstract—A large body of evidence indicates that individual differences in baseline concentrations of testosterone (T) are only weakly correlated with human aggression. Importantly, T concentrations are not static, but rather fluctuate rapidly in the context of competitive interactions, suggesting that acute fluctuations in T may be more relevant for our understanding of the neuroendocrine mechanisms underlying variability in human aggression. In this paper, we provide an overview of the literature on T and human competition, with a primary focus on the role of competition-induced T dynamics in the modulation of human aggression. In addition, we discuss potential neural mechanisms underlying the effect of T dynamics on human aggression. Finally, we highlight several challenges for the field of social neuroendocrinology and discuss areas of research that may enhance our understanding of the complex bi-directional relationship between T and human social behavior.

Key words: social neuroendocrinology, testosterone, competition, aggression.

Contents

INTRODUCTION

Aggression, defined as any behavior directed toward another individual with the intent to cause harm (Baron and Richardson, 1994), evolved in the context of intraspecific competition for valued resources (e.g., food, shelter, mating opportunities, status). Thus, although aggression is widely regarded as a "negative" behavior – it is a quintessential component of our lives that can serve important adaptive functions. Despite progress in identifying some of the neurobiological factors associated with aggression (see Nelson and Trainor, 2007 for review), we know very little about the causal role of such factors in shaping variability in human aggression. Testosterone (T), a steroid hormone produced primarily by the gonads, is a prime biological candidate for mediating aggressive behavior within the context of human competition. The idea that T is related to human aggression comes from various sources: Men are generally more aggressive than women (Archer, 2009), have much higher T concentrations than women (Dabbs, 1990), and at a time when T concentrations are surging (e.g., ages 21–35), there is an increase in male-to-male aggressive behavior (Daly and Wilson,

*Corresponding author.
E-mail address: justinca@nipissingu.ca (J. M. Carré).
Abbreviations: ACC, anterior cingulate cortex; BMS, Biosocial Model of Status; GnRH, gonadotropin releasing hormone; HPG, hypothalamic–pituitary–gonadal; LH, luteinizing hormone; OFC, orbitofrontal cortex; PAG, periaqueductal gray; PSAP, Point Subtraction Aggression Paradigm; T, testosterone; UG, Ultimatum Game.

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1988). Despite T's clear association with aggression in animal models (see Simon and Lu, 2006) and its apparent link to human aggression, research indicates that individual differences in baseline levels of T are only weakly correlated with various indices of human aggression (r = .08, see Archer et al., 2005 for meta-analysis).

There are likely many reasons why the association between T and aggression is relatively weak in humans. First, it may be that only extreme, or supraphysiological concentrations of T are linked to aggression (see Pope et al., 2000), whereas normal variation in T is not. Second, it may be a measurement issue whereby human studies usually rely on self-report measures of aggression, which may not represent the most bias-free way to assess aggression. Notably, studies that use behavioral measures of aggression typically find stronger correlations between baseline levels of T and aggression (see Archer et al., 2005 for meta analysis). Third, researchers usually do not differentiate between reactive and proactive forms of aggression, which may in part underlie some of the inconsistencies observed in the literature. Reactive aggression is a defensive response to perceived or actual provocation and is characterized by anger, impulsivity, disinhibition, affective instability, and high levels of bodily arousal (Dodge and Coi, 1987). In contrast, proactive aggression occurs in the absence of direct provocation and is a goal-oriented behavior aimed at the acquisition of a valued resource (Dodge and Coi, 1987). Only a few studies have examined associations between individual differences in T and measures of reactive and proactive aggression. One study reported that baseline levels of T were positively correlated with reactive and proactive aggression in adolescent males (van Bokhoven et al., 2006), whereas another study found that baseline levels of T were positively correlated with reactive, but not proactive aggression (Olweus et al., 1988). Finally, many studies have relied on single measurements of T when examining correlations with self-report measures of aggression. This is quite problematic given that T concentrations are highly variable, fluctuating throughout the day (diurnal variation), the season, and in response to various social interactions. Indeed, a large body of work in both humans and non-human species indicates that competitive interactions rapidly potentiate T release (Wingfield et al., 1990; Archer, 2006; Oliveira, 2009; Oliveira and Oliveira, 2014). Thus, some have argued that acute fluctuations in T within the context of social competition may be more relevant to our understanding of individual differences in mating effort (including aggression) than baseline levels of T (McGlothlin et al., 2007). In this paper we review recent human work examining the relationship between T dynamics and competitive/aggressive behavior and draw comparisons to evidence from animal models. We also discuss recent neuroimaging work and speculate about a potential neural mechanism underlying links between T dynamics and human aggression. Finally, we highlight challenges to progress and suggest future research directions. Before reviewing the empirical work, we first present an overview of the 'Challenge Hypothesis' and the 'Biosocial Model of Status', two of the main theoretical models guiding current research on the bidirectional relationship between T and aggressive behavior.

TESTOSTERONE RESPONSES TO INTRA-SEXUAL COMPETITION

Challenge Hypothesis

The 'Challenge Hypothesis' was originally developed in an attempt to explain intra- and inter-species variation in T secretion in birds. Wingfield and colleagues (1990) noted that T concentrations fluctuate around three levels during the season: Level A, constitutive baseline; Level B, breeding baseline; and Level C, physiological maximum. In monogamous male birds that provide paternal care, T concentrations remain low during the non-breeding season (Level A). T increases (Level B) at the start of the breeding season as a means to initiate spermatogenesis, expression of secondary sex characteristics and the full display of male reproductive behavior. Finally, T may further increase (Level C) in response to intra-sexual competitive interactions as a means to facilitate territorial and aggressive behavior. When intra-sexual competition decreases, T concentrations return to Level A. It has been proposed that the costs associated with maintaining elevated T concentrations throughout the season (e.g., decreased paternal care, increased risk for physical injury/death, depressed immune function, increased energetic demands) may have led to a highly flexible endocrine system capable of modulating T concentrations in response to changes in the social environment (Wingfield et al., 2001). Although originally proposed to account for the trade-off between mating and parental efforts in birds, support for the Challenge Hypothesis has now been obtained in numerous taxa including fish (Oliveira, 2009), non-human primates (Bernstein et al., 1974; Sobolewski et al., 2013), humans (Archer, 2006), and insects (Tibbetts and Crocker, 2014).

Biosocial Model of Status

The 'Biosocial Model of Status' (BMS; Mazur, 1976, 1985; Mazur and Booth, 1998) is a conceptually similar theoretical model adopted primarily by researchers studying human competition and aggression. One important difference between the 'Challenge Hypothesis' and the BMS is that the latter makes the additional prediction that T concentrations during competition will vary as a function of the outcome of the competitive interaction with T concentrations increasing in winners and decreasing in losers. Although the BMS has mainly been studied within the context of human competition, its main predictions were guided by research in male rhesus monkeys. In a series of experiments, Rose and colleagues (1972, 1975) found that male rhesus monkeys successful in aggressive interactions (i.e., winners) experienced marked elevations in T, while unsuccessful males (i.e., losers) experienced decreased T concentrations. A number of studies have examined this 'winner/loser effect' in humans and have found elevated T concentrations in winners relative to

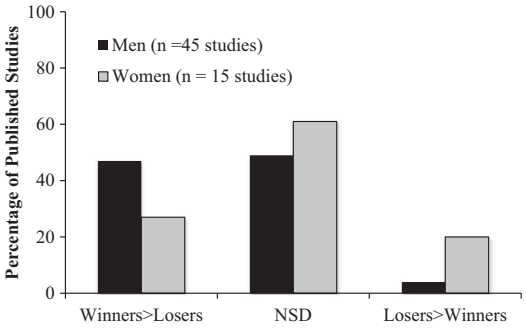

Fig. 1. Effect of competition outcome on testosterone (T) reactivity in men and women. Winners > Losers indicates that winners showed a significantly greater increase, or smaller decrease, in T than losers. Losers > Winners indicates that losers showed a significantly greater increase, or smaller decrease in T than winners. NSD indicates no statistically significant difference between winners and losers.

losers in athletic competition (Mazur and Lamb, 1980; Elias, 1981; Booth et al., 1989; Jiménez et al., 2012), political elections (Stanton et al., 2009b), rigged laboratory tasks (Gladue et al., 1989; Pound et al., 2009; Carré et al., 2013a) and sport spectators (Bernhardt et al., 1998). Although most of this work has been conducted exclusively in men, studies that have combined men and women have found that winners have elevated T concentrations relative to losers in men, but not women (Stanton et al., 2009b; van Anders and Watson, 2007; Carré et al., 2013a; but see Jiménez et al., 2012). See Fig. 1 and Table 1 for a summary of the 'winner/loser effect' in men and women. Examination of Fig. 1 suggests that although a sizeable number of studies have reported that male winners have elevated T concentrations relative to losers (47% of studies), an equal number of studies have failed to find significant differences between winners and losers (49% of studies). There are several factors that may contribute to the heterogeneity in findings reported in Fig. 1 and Table 1. It will be critical to perform a formal meta-analysis (e.g., Archer, 2006) to provide an estimate of the true effect size of the relationship between competition outcome and T release and to examine factors that may moderate the effect of competition outcome on T release (e.g., timing of post-competition saliva/serum sampling, personality traits, participant sex, type of competition, etc.).

The reciprocal component of Mazur's model suggests that changes in T during competition will serve to modulate future dominance-related behaviors. Specifically, Mazur (1985) reasoned that winners of competitive interactions may face additional challenges for social 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. Thus, from an evolutionary perspective, these divergent T responses may enable people to rapidly adjust future social behavior according to changes in the social environment. In the following section I review evidence supporting the reciprocal component of Mazur's model.

FUNCTIONAL ROLE OF TESTOSTERONE DYNAMICS

Competitive motivation and performance

There is now a growing body of evidence in humans examining the extent to which acute changes in T during competition map onto ongoing and/or future social behavior. In one experiment, Mehta and Josephs (2006) had men participate against each other in a rigged laboratory competition in which half were randomly assigned to a loss condition and half to a win condition. After the competition, participants were asked whether they wanted to compete again against the same opponent on the same task, or whether they would prefer to fill out a questionnaire on food, music and entertainment preferences (i.e., a measure of willingness to avoid competition). Results indicated that individual differences in T responses to the competition predicted future motivation to compete. Here, men who increased in T were more likely to approach a future competitive task, whereas men who decreased in T were more likely to approach the non-competitive task. There was no relationship between baseline levels of T and willingness to compete, highlighting the importance of considering competition-induced changes in T. Also, although the interaction between competition outcome and T reactivity was not statistically significant (p = .32; Mehta P.H., personal communication), the effect of T reactivity on willingness to compete was significant in losers (p = .034), but not winners (p = .32). The authors attribute this outcome dependent effect to the fact that winners had nothing to gain from re-challenging the losers to another competition. Similarly, Carré and McCormick (2008) found that a rise in T was positively correlated with ongoing aggressive behavior during a competitive task and predicted increased willingness to approach a subsequent competitive task. Other work has investigated the extent to which acute changes in T during a sport motivational intervention would influence subsequent athletic performance and physical strength. Cook and Crewther (2012a) reported that athletes receiving positive feedback from their coaches prior to a competitive interaction demonstrated both a rise in T concentrations and better athletic performance. In a subsequent study, the authors reported that watching motivational and aggressive video clips increased T concentrations and improved subsequent physical strength as indexed by squat performance (Cook and Crewther, 2012b).

The studies reviewed in this section indicate that a rise in T concentrations predicted competitive behavior and performance measured shortly after the change in T was detected (usually within 10–15 min). However, it may be that T responses to competition exert effects on behavior long after the change in T is detected. In support of this possibility, research in male California mice indicates that an acute increase in T in response to a victory influences aggressive behavior measured more than 24 h after the change in T occurs (Trainor et al., 2004). It has been speculated that the acute T response to victory may serve to reinforce learning processes associated with winning competition (Gleason

Table 1. Review of the testosterone responses to victory and defeat

Year	Author	Paradigm	Sample	Win vs. loss
2013	Aguilar et al.	Field Hockey	♂ (7)	W > L
2014	Apicella et al.	Rock/Paper/Scissors	♂ (49)	W > L
1989	Booth et al.	Tennis	♂ (6)	W > L
1998	Bernhardt et al.	Basketball/Soccer Fans	♂ (8)/♂ (21)	W > L/W > L
2013a	Carré et al.	Xbox Video Game	♂ (114)	W > L
1981	Elias	Wrestling	♂ (15)	W > L
2012	Flinn et al.	Dominoes	♂ (27)	W > L
2011	Fry et al.	Wrestling	♂ (12)	W > L
1989	Gladue et al.	Reaction Time Task	♂ (39)	W > L
2012	Jiménez et al.	Badminton	♂ (27)	W > L
1980	Mazur and Lamb	Tennis	♂ (14)	W > L
1992	Mazur et al.	Chess	♂ (16)	W > L
1992	McCaul et al.	Coin Toss	♂ (28)/♂ (32)	W > L/W > L
2009	Pound et al.	Sumo Wrestling	♂ (57)	W > L
2009b	Stanton et al.	Political Elections	♂ (57)	W > L
2014	Trumble et al.	Hunting	♂ (31)	W > L
2007	van Anders and Watson	Vocabulary Task	♂ (37)	W > L
2012	Zilioli and Watson	Tetris	♂ (70)	W > L
2014	Zilioli and Watson	Tetris	♂ (84)	W > L
2012	Costa and Salvador	Squares with Letters Task	♀ (40)	W > L
2013	Denson et al.	Taylor Aggression Task	♀ (49)	W > L
2012	Jiménez et al.	Badminton	♀ (23)	W > L
2009b	Oliveira et al.	Soccer	♀ (29)	W > L
2010	Carré and Putnam	Hockey	♂ (21)	NSD
2009	Carré et al.	Number Tracing Task	♂ (39)	NSD
2013	Crewther et al.	Rugby	♂ (5)	NSD
1999	Gonzalez-Bono et al.	Basketball	♂ (16)	NSD
2000	Gonzalez-Bono et al.	Basketball	♂ (17)	NSD
2008	Hasegawa et al.	Shogi	♂ (90)	NSD
2008	Maner et al.	Number Tracing Task	♂ (23)	NSD
1997	Mazur et al.	Video Game	♂ (28)/♂ (32)	NSD/NSD
2006	Mehta and Josephs	Number Tracing Task	♂ (50)	NSD
2010	Oxford et al.	Video Game	♂ (42)	NSD
1987	Salvador et al.	Judo	♂ (14)	NSD
2002	Schultheiss and Rohde	Number Tracing Task	♂ (66)	NSD
1999	Schultheiss et al.	Number Tracing Task	♂ (42)	NSD
2005	Schultheiss et al.	Serial Response Task	♂ (95)	NSD
2000	Serrano et al.	Judo	♂ (12)	NSD
2009b	Stanton et al.	Political Elections	♀ (106)	NSD
2010	Steiner et al.	Poker	♂ (32)	NSD
1999	Suay et al.	Judo	♂ (26)	NSD
2012	Trumble et al.	Soccer	♂ (82)	NSD
2012	van der Meij et al.	'Intelligence' Task	♂ (84)	NSD
2002	Wagner et al.	Dominoes	♂ (8)	NSD
2014	Welker and Carré	Number Tracing Task	♂ (80)	NSD
2002	Bateup et al.	Rugby	♀ (17)	NSD
2009	Carré et al.	Number Tracing Task	♀ (60)	NSD
2013a	Carré et al.	Video Game	♀ (123)	NSD
2006	Edwards et al.	Soccer	♀ (18)	NSD
2009	Hamilton et al.	Wrestling	♀ (13)	NSD
2008	Mehta et al.	Number Tracing Task	♀ (61)	NSD[a]
2007	Stanton and Schultheiss	Serial Response Task	♀ (49)	NSD
2007	van Anders and Watson	Vocabulary Task	♀ (38)	NSD
2001	Filaire et al.	Judo	♂ (18)	W < L
2006	Parmigiani et al.	Judo	♂ (22)	W < L
2013	Oliveira et al.	Number Tracing Task	♀ (34)	W < L
2014	Zilioli et al.	Number Tracing Task	♀ (72)/♀ (56)	W < L/W < L

Note: ♂ = males; ♀ = females. W > L: Winners showed a greater increase, or smaller decrease, in testosterone than losers. W < L: Losers showed a greater increase, or smaller decrease in testosterone than winners. NSD: No significant difference between winners and losers. We cannot exclude the possibility that a lack of significant differences between winners and losers (i.e., NSD) is due to Type II errors.

[a] Personal communication with P.H. Mehta (September 7, 2014).

et al., 2009). Consistent with the animal literature, Zilioli and Watson (2014) found that a rise in T during a Tetris competition predicted better performance 24 h later on the same Tetris task indicating that acute fluctuations in T can modulate human behavior long after the changes in neuroendocrine function have occurred. Notably, the

positive relationship between T reactivity to the first competition and performance 24 h later was found in both winners and loses.

Testosterone dynamics and aggressive behavior

A larger body of work has examined the extent to which acute fluctuations in T may serve to modulate aggressive behavior. In one experiment, Carré and colleagues (2009) had men and women compete in same-sex dyads on a rigged laboratory competition wherein half were randomly assigned to a win condition and half to a loss condition. After the competitive interaction, participants performed the Point Subtraction Aggression Paradigm (PSAP), a well-established behavioral measure of reactive aggression in humans (Cherek et al., 2006). In this task, participants were led to believe that they were playing a computer game with another same-sex participant (in reality, this was a fictitious opponent). Participants had to hit a button a hundred consecutive times to earn a point. They were told that their payment at the conclusion of the study would be based on the number of points they earned during the task. Throughout the task, points were stolen from participants and this was attributed to their fictitious opponent who kept all the stolen points. Participants were able to respond by ignoring the provocation (i.e., continue to earn points), by stealing points back, or by protecting their points from subtraction. In this task, stealing points back is a costly behavior because participants do not get to keep the stolen points and engaging in such behavior detracts from points earned during the game. Stealing points in this game serves the function of retaliating against one's opponent, and is considered a form of reactive aggression. Results indicated that a rise in T during the competitive interaction predicted increased aggressive behavior in men, but not women (Carré et al., 2009). Similar to Mehta and Josephs (2006), there was no significant interaction between competition outcome and T reactivity ($p = .43$). However, post-hoc analysis indicated that the effect of T dynamics on aggressive behavior was significant in male losers ($p = .01$), but not winners ($p = .37$). In more recent work, we modeled competition using an Xbox Kinect video game in a relatively large sample of men and women ($n = 237$, Carré et al., 2013a). In this experiment, participants were randomly assigned to experience a string of victories or defeats after which aggression was assessed using the PSAP. Results indicated that male winners had elevated T concentrations and aggressive behavior compared to male losers. Moreover, the effect of winning on subsequent aggressive behavior was statistically mediated by heightened T concentrations after the victory (Carré et al., 2013a). A number of other studies using variations of the PSAP and manipulations of other contextual variables (e.g., provoked vs. unprovoked; socially rejected vs. accepted) have provided additional support for the idea that acute changes in T during competition are positively correlated with human reactive aggression and antagonistic behavior (Carré et al., 2010; Geniole et al., 2011, 2013; see Carré et al., 2011 for review).

IIn more recent work, we have found that a long-term intervention program designed to curtail antisocial behavior in 'at-risk' youth was successful, in part, because it dampened T responses to social provocation. This intervention was implemented in kindergarten and the children assigned to the intervention condition received social-cognitive-behavioral therapy, while those assigned to the control condition received no such treatment. When tested 20 years later, the intervention group demonstrated less aggression on the PSAP and decreased T reactivity to social provocation compared to the control group. Notably, the association between assignment to the intervention condition and decreased aggression was statistically mediated by decreased T reactivity to provocation (Carré et al., 2014a). Collectively, the data reviewed in this section 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. Importantly, the findings diverge to some extent from predictions of Mazur's BMS. Specifically, Mazur (1985) argued that winners would increase in T and that this would promote subsequent dominance behavior, whereas losers would decrease in T and that this would promote subsequent submissive behavior. The work reviewed here indicates that winners typically have elevated T concentrations relative to losers (consistent with the BMS) – however, T responses among winners *and* losers are positively correlated with subsequent competitive motivation and aggression. Thus, a rise in T translates into more competitive/aggressive behavior, whereas a decrease in T translates into less competitive/aggressive behavior in both winners and losers alike. These findings indicate that although competition outcome modulates T reactivity patterns – the resulting neuroendocrine responses have similar effects on subsequent behavior in winners and losers.

Animal models of competition, testosterone and aggression

One clear limitation of the research reviewed in sections 'Competitive motivation and performance' and 'Testosterone dynamics and aggressive behavior' is that it is correlational. Specifically, because T concentrations were not experimentally manipulated, it is not possible to make strong causal claims concerning T's role in modulating competitive and aggressive behavior. Research with animal models is particularly useful for testing causal mechanisms shaping complex social behavior. In a number of experiments, administration of T to male California mice after winning a competitive interaction produced increased aggressive behavior in subsequent interactions (Trainor et al., 2004; Gleason et al., 2009; Fuxjager et al., 2010) and increased their probability of winning subsequent interactions (Gleason et al., 2009; Fuxjager et al., 2011). In addition, Oliveira and colleagues (2009a) 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 during competitive interactions were less likely to win a subsequent aggressive

interaction (relative to control males). In contrast, losers treated with an androgen (11-ketotestosterone, the primary metabolite of T in fish) were not more likely to win a subsequent aggressive interaction. These findings indicate that the 'winner effect' (but not the 'loser effect') depends critically on acute fluctuations in T. In contrast, work in male Japanese quail found that T administration to losers increased subsequent aggressive behavior (i.e., reversed the loser effect), whereas T blockade to winners had no effect on subsequent behavior (Hirschenhauser et al., 2013). As the authors of the latter study noted "if testosterone is part of the mechanism underlying the observed 'winner and loser effects', we would expect that these mechanisms are evolutionary conserved throughout the vertebrates" (Hirschenhauser et al., 2013). Thus, it remains unclear what may account for the divergent effects in observed in fish and quail. In other work with male cichlid fish, unresolved social conflicts increased the probability of winning future competitive interactions – an effect that was in part due to heightened T concentrations after the unresolved conflict (Dijkstra et al., 2012). In addition to demonstrating the importance of post-competition T responses in modulating future behavior – this study indicates that the objective outcome of the competition (i.e., victory vs. defeat) may not be the critical factor driving T responses to competition. Going beyond the role of circulating T concentrations, Fuxjager and colleagues (2010) reported that the 'winner effect' was in part due to an up-regulation of androgen receptors in several key brain regions involved in reward and motivation (e.g., nucleus accumbens and ventral tegmental area) as well as social aggression (bed nucleus of the stria terminalis). The extent to which such upregulation of AR expression in the nucleus accumbens and ventral tegmental area plays a causal role in modulating the 'winner effect' remains to be seen. Collectively, experiments in animal models provide compelling support for the role of competition-induced T dynamics in mediating ongoing and/or future competitive and aggressive behavior.

NEURAL CORRELATES OF HUMAN AGGRESSION

Neural circuitry of aggression

A key question for future work will be to elucidate the neural mechanisms through which competition-induced T dynamics modulate human aggression. Extensive work in animal models indicates that several interconnected cortical and subcortical structures within the so-called social behavior network (Newman, 1999) are involved in the modulation of reactive aggression (Nelson and Trainor, 2007). One specific model that has received extensive support from both lesion and electrical/chemical stimulation experiments indicates that a neural circuitry comprising the medial amygdala, medial hypothalamus and periaqueductal gray (PAG) positively modulates reactive aggression (Siegel et al., 2007; Blair, 2010). Briefly, the medial amygdala provides excitatory input to glutamatergic neurons in the medial hypothalamus, which exert excitatory drive on PAG neurons, ultimately mediating reactive aggression (Siegel et al., 2007). Aggression research in human studies has focused mainly on the role of the orbitofrontal cortex (OFC). Specifically, many studies have reported that patients with localized lesions to the OFC engaged in heightened reactive aggression (see Siever, 2008 for review). Given the extensive projections from the OFC to the hypothalamus and amygdala, it has been proposed that the propensity to engage in reactive aggression may emerge from impaired regulatory control of the OFC over these subcortical structures (see Davidson et al., 2000 and Nelson and Trainor, 2007 for reviews).

Threat-processing and propensity for aggression

One research approach aimed at elucidating the neurobiological mechanisms of human aggression examines behavioral and neural responses to angry facial expressions. Angry facial expressions represent honest signals of threat and depending on the dominance relationship between sender and receiver, these threat stimuli may elicit fight or flight behavior from the receiver. Dominant individuals may perceive an angry facial expression as a challenge to their status, whereas submissive individuals may perceive the same angry facial expression as an enforcement of the prevailing relationship, thus promoting approach and avoidance behaviors, respectively (van Honk and Schutter, 2007). Importantly, androgen and estrogen receptors are widely distributed throughout the neural circuitry underlying reactive aggression (Newman, 1999; Murphy et al., 1999; Wood and Newman, 1999; Fernández-Guasti et al., 2000; Donahue et al., 2000; Roselli et al., 2001), suggesting that T and/or its metabolites (e.g., estradiol) may directly modulate this circuitry by interacting with steroid hormone receptors in these regions. Given the high concentration of androgen and estrogen receptors in the amygdala and related structures within the social behavior network, it is reasonable to predict that enhanced neural and behavioral reactivity to angry facial expressions may vary as a function of T concentrations. Indeed, behavioral studies indicate that endogenous T concentrations are positively correlated with attentional biases toward angry facial expressions in men and women (van Honk et al., 1999; Wirth and Schultheiss, 2007). Moreover, functional neuroimaging studies reported that individual differences in baseline T concentrations were positively correlated with amygdala reactivity to facial expressions of anger and fear in men (Derntl et al., 2009; Manuck et al., 2010; but see Stanton et al., 2009a) and negatively correlated with OFC responses to social provocation in men and women (Mehta and Beer, 2010). Also, developmental work indicates that adolescent boys and girls who demonstrate a relatively large increase in pubertal T concentrations demonstrated heightened amygdala reactivity to angry and fearful expressions (Spielberg et al., 2014a) and decreased amygdala-OFC functional coupling during processing of angry and fearful expressions (Spielberg et al., 2014b). Finally, exogenous administration of T to healthy young women increased attention toward angry faces (Terburg et al., 2012), increased cardiac reactivity to angry

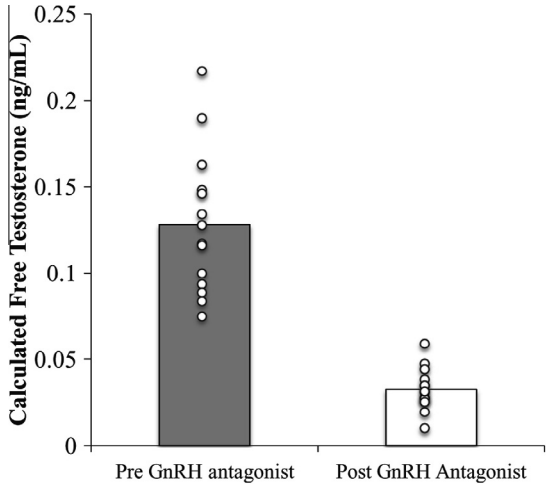

Fig. 2. Gonadotropin release hormone (GnRH) antagonist suppresses and reduces variability in testosterone concentrations. Redrawn from Goetz et al., 2014.

faces (van Honk et al., 2001), enhanced amygdala and hypothalamic reactivity to angry and fearful faces (Hermans et al., 2008; van Wingen et al., 2009; Bos et al., 2013) and decreased amygdala–OFC coupling during processing of angry and fearful facial expressions (van Wingen et al., 2010). These findings suggest that acute fluctuations in T may influence aggressive behavior by enhancing amygdala reactivity and/or decreasing prefrontal cortex (PFC)-amygdala functional coupling during the processing of social threat (e.g., angry facial expressions, social provocation). See Fig. 2 for a summary of these data.

The above findings are particularly noteworthy in light of behavioral and neuroimaging studies indicating that individuals prone to anger and reactive aggression (e.g., 'low expression' carriers of the MAOA gene; intermittent explosive disorder; borderline personality disorder) display attentional biases, enhanced amygdala reactivity, and decreased OFC–amygdala coupling during processing of angry facial expressions (Meyer-Lindenberg et al., 2006; see Siever, 2008 and Coccaro et al., 2011 for reviews). Also, studies in non-clinical samples indicated that even normal variation in constructs linked to reactive aggression (e.g., approach motivation, trait anger, psychopathy) were positively correlated with amygdala reactivity to angry faces (Beaver et al., 2008; Carré et al., 2012, 2013b). Other research has found that individual differences in approach motivation are associated with decreased ventral anterior cingulate cortex (ACC)-amygdala functional coupling during processing of angry facial expressions (Passamonti et al., 2009). Given the important role of highly interconnected prefrontal regions (e.g., ventral ACC, OFC) in mediating top-down regulation of amygdala driven emotional reactivity (see Davidson et al., 2000 and Siever, 2008 for reviews), such decreased functional coupling may in part explain the positive link observed between approach motivation and aggressive behavior (Harmon-Jones, 2003). In summary, clinical and pre-clinical data converge on a model in which relatively increased amygdala reactivity and/or decreased coupling of prefrontal regions (ventral ACC, OFC) with the amygdala during processing of threat-related stimuli may bias one's propensity to engage in reactive aggression and may ultimately underlie the relationship between T and human aggression.

CHALLENGES TO PROGRESS

Individual differences in testosterone responses to competition

Although several studies indicate that male winners have elevated T concentrations relative to losers (see Archer, 2006 for meta-analysis and Table 1 for a summary of these data), there is an enormous amount of variability in T responses within winners and losers (see Fig. 3 for an example). Some studies suggest that individual difference factors (e.g., personality traits) and social contextual variables underlie variability in T reactivity to winning and losing. Schultheiss and colleagues (1999, 2002, 2005) have found that individual differences in one's implicit need for power/dominance interacted with competition outcome to predict the pattern of T release. For instance, male winners had elevated T concentrations relative to losers, but only to the extent that they scored high on a measure of implicit power motive (Schultheiss et al., 2005). Others have noted that an individual's personal contribution to the outcome may play an important role in modulating T release (Gonzalez-Bono et al., 1999; Trumble et al., 2012). In one study, Trumble and colleagues (2012) reported that T concentrations only rose among individuals who self-reported relatively good individual performance. In addition, other work suggests that the 'competition effect' only occurs in the context of inter-group competition, whereby effects of competition outcome on T release are only observed when people compete with members of their 'outgroup' (Oxford et al., 2010; Flinn et al., 2012). Finally, one study suggests that the location of a competitive interaction modulates T secretion in winners. In a study of male hockey players, Carré (2009) found that T responses to victory were much more pronounced when the victory occurred in the team's home venue relative to their opponents' venue. These findings are remarkably similar to work in California mice in which T levels increased in response to winning in one's home cage, but not in a neutral cage (Fuxjager et al., 2009). Collectively, these findings indicate that although winners typically have elevated T concentrations relative to losers – there are important individual difference factors and social contextual variables that influence T responses to competition. It will be critical for future research to include a wider range of individual difference factors in order to more fully account for the emergent variability in T responses to victory and/or defeat. In the pursuit of identifying individual difference factors that may moderate the effect of competition outcome on T secretion, it will be important for researchers to have well-powered studies in order to avoid potential spurious moderation effects.

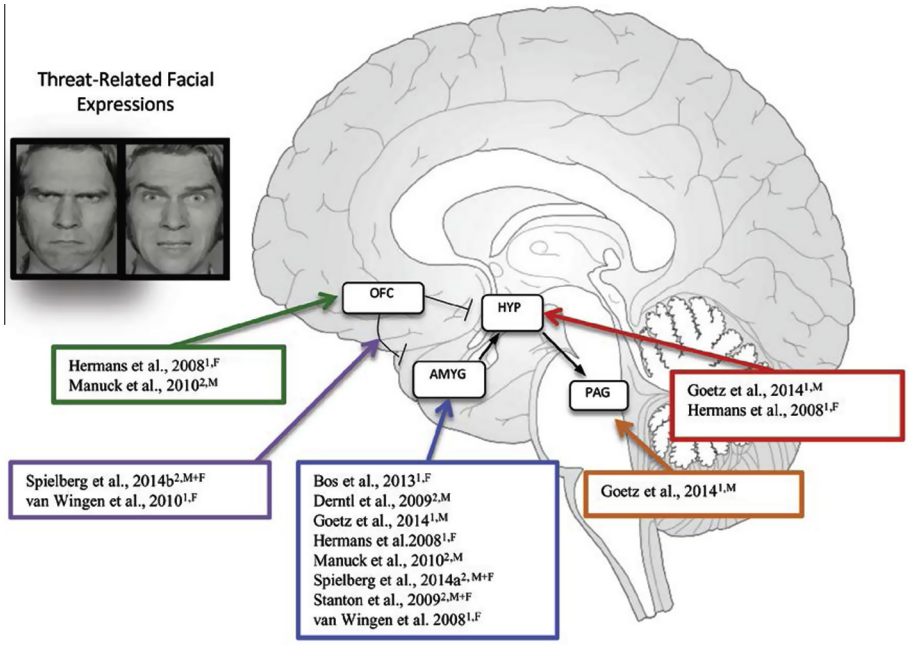

Fig. 3. Relationship between testosterone (T) and neural responses to threat-related facial stimuli. 1 = exogenous T administration, 2 = endogenous T concentrations. M = males, F = females. OFC = orbitofrontal cortex; HYP = hypothalamus; AMYG = amygdala; PAG = periaqueductal gray.

Mechanisms underlying the rapid increase in testosterone during competition

Some researchers have speculated that the increase in T observed during competition is too fast (within 10–15 min) to be mediated by the hypothalamic–pituitary–gonadal (HPG) axis (Schultheiss et al., 2005; Flinn et al., 2012). In support of this proposition, basic physiology work has demonstrated a 40–70 min time lag between luteinizing hormone (LH) administration and T response (Veldhuis and Iranmanesh, 2004) and the rapid T response to physical exercise occurs in the absence of an LH response (Sutton et al., 1973). These findings suggest that the rapid increases in T during competition may be due to a non-HPG mediated mechanism. Evidence in humans and non-human primates suggests that this rapid T response may be mediated by sympathetic catecholamines. In one study, Jezova and Vigas (1981) demonstrated that administration of propranolol, a beta-adrenergic blocker (i.e., beta-blocker), abolished the rapid increase in T that occurred in young men during physical exercise. Also, it has been demonstrated that high-ranking male baboons demonstrate a relatively rapid increase in T concentrations in response to capture/immobilization stress (Sapolsky, 1986), an effect that is completely abolished by the administration of chlorisondamine, a sympathetic ganglionic blocker which attenuates stress-induced release of epinephrine and norepinephrine (Sapolsky, 1986). Collectively, these findings converge on the idea that sympathetic catecholamines may underlie the rapid increase in T observed during human competition. More basic research will be needed to determine whether interference with this putative mechanism (e.g., beta-blocker) would attenuate and/or eliminate the effect of competition on T reactivity.

Development of exogenous testosterone administration protocols

The most effective way to demonstrate a cause-and-effect relationship is through pharmacological manipulation of T concentrations. As described in section 'Threat-processing and propensity for aggression', this work indicates that a single administration of T enhances amygdala and hypothalamus reactivity to angry and fearful faces and decreases amygdala–OFC functional connectivity during processing of angry faces. A notable limitation of this body of work is that it has been conducted exclusively in young women. To address this shortcoming, we developed a novel two-step pharmacological challenge protocol and investigated the role of T in potentiating threat-related neural function in healthy young men (Goetz et al., 2014). A major consideration when developing this protocol was that endogenous T concentrations are highly variable in young men and this variability may impact men's physiological and behavioral responses to a standard dose of T. Thus, we used a gonadotropin releasing hormone (GnRH) antagonist to reduce inherent variability in baseline levels of endogenous T. The GnRH antagonist rapidly suppressed and significantly reduced variability in T concentrations (see Fig. 4). Eight hours after receiving the GnRH antagonist, men received a single dose of T gel (Androgel®, 100 mg) or placebo (double-blind, counter-balanced) and then performed a well-validated emotional face-processing task during acquisition of blood-oxygenated level dependent (BOLD) fMRI. Results indicated that T increased amygdala, hypothalamus, and PAG reactivity to angry facial expressions within just 90 min of administration (Goetz et al., 2014). These findings are remarkably similar to single T administration work conducted in young women in which T

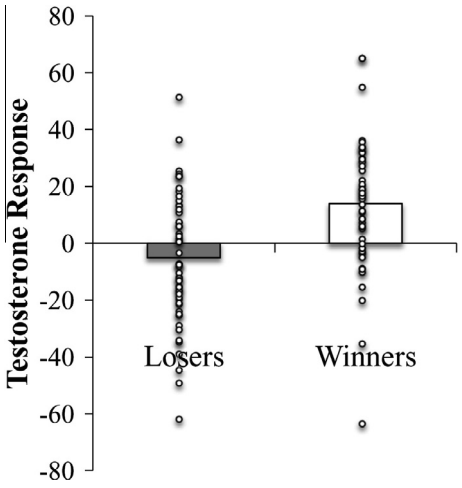

Fig. 4. Effects of competition outcome on testosterone (T) reactivity. Male winners demonstrated increased T concentrations (M = 13.96, SD = 21.36) relative to losers (M = −5.07, SD = 20.86), $t(107)$ = 4.71, p < .001, Cohen's d = .90. Note the substantial variability in T reactivity within winners and losers. Redrawn from Carré et al., 2013a.

increased amygdala and hypothalamic reactivity to threat-related stimuli (e.g., Hermans et al., 2008; van Wingen et al., 2009; Bos et al., 2013) and also provides the first causal support for the role of acute T elevations on threat-related neural function in men.

One key difference between our protocol and that of van Honk and colleagues is that the latter studies typically allow 4 h between the time of T administration and the assessment of outcome variables. The 4-hour time lag is based on a landmark study by Tuiten and colleagues (2000). In this study, women were administered 0.5 mg of T sublingually and vaginal pulse amplitude was continually assessed in response to visual sexual stimuli. The authors found that T concentrations peaked within just 15 min and returned to baseline within 90 min. Notably, T increased vaginal pulse amplitude to sexual stimuli, but only approximately 3 h after T administration. Dozens of studies have since used this time lag when assessing effects of T on various physiological and behavioral outcomes (see Bos et al., 2012 for a review of these studies). Although this time lag is well grounded in earlier validation work (Tuiten et al., 2000), some studies in women have demonstrated that a single administration of T increased amygdala reactivity to angry/fearful faces (van Wingen et al., 2009) and decreased amygdala–OFC connectivity in response to angry/fearful faces within just 45 min of administration (van Wingen et al., 2010). Thus, an important question for future work will be to examine the extent to which T has rapid and/or delayed effects on physiological and behavioral processes in men and women. This approach has been used in research on the effects of exogenous cortisol administration on amygdala responses to fearful and happy expressions. In this work, Henckens and colleagues (2010) found that cortisol inhibited amygdala reactivity to fear expressions when administered 75 min prior to fMRI. In contrast, amygdala reactivity to fearful expressions was restored to baseline if administered 285 min prior to fMRI. Thus, it appears that steroid hormones may exert both rapid and delayed effects on neural processing of threat. A more recent study found that cortisol administration 30 min prior to an emotional encoding task impaired, while cortisol administration 210 min prior to the emotional encoding task enhanced, memory recall performance 24 h later (van Ast et al., 2013). These studies highlight the importance of considering both rapid and delayed effects of steroid hormones on neural and behavioral processes.

The behavioral studies reviewed in this paper (see sections 'Competitive motivation and performance' and 'Testosterone dynamics and aggressive behavior') report that changes in T map onto *future* competitive and aggressive behavior in men assessed approximately 15 min after the changes in T are detected. In addition, although we have focused on the extent to which T responses to competition map onto future competitive and aggressive behaviors – it remains possible that changes in T within the context of competition serves to rapidly modulate *ongoing* social behavior. To the extent that competition-induced changes in T play a causal role in mediating ongoing and/or subsequent competitive motivation and aggressive behavior – it must do so through a relatively rapid mechanism. Research in animal models has identified extranuclear androgen and estrogen receptors in the hippocampus, amygdala, hypothalamus, and cortex (Blaustein et al., 1992; McEwen, 2001; DonCarlos et al., 2003; Tabori et al., 2005). These extranuclear androgen and estrogen receptors are well positioned to regulate rapid membrane and cytoplasmic signaling in axons and dendrites (Sarkey et al., 2008), thus facilitating the modulation of brain function and social behavior through non-genomic mechanisms (Trainor et al., 2008; Laredo et al., 2014).

Sex differences and similarities in the association between testosterone and aggression

A key unresolved issue is whether the link between T and aggressive behavior holds across men and women (Josephs et al., 2011). My colleagues and I have found that changes in T during competition positively predict subsequent aggressive behavior in men, but not women (Carré et al., 2009, 2013a), indicating that competition-induced fluctuations in T may serve to modulate future aggression in a sex dependent manner. In contrast, research examining the association between baseline levels of T and aggression has reported similar relationships in men and women (see Archer et al., 2005 for meta analysis). Indeed, although relatively weak, associations between baseline levels of T and aggression are significantly stronger in women (r = .13) compared to men (r = .08; see Archer et al., 2005). Also, despite using different time courses and drug doses, the neuroimaging research reviewed in this paper (see section 'Threat-processing and propensity for aggression') indicates that T has similar effects on threat-related neural function in women (Hermans et al., 2008; van Wingen et al., 2009) and men (Goetz et al., 2014).

Interestingly, other T administration work has found divergent effects of T on Ultimatum Game (UG)

behavior in men and women. The UG is a behavioral economics task whereby a proposer is given a sum of money and has the opportunity to offer as much, or as little money to a receiver. Once the offer is made, the receiver has the choice to either accept or reject the offer. If the offer is accepted, both participants receive their split of the money. If the receiver rejects the offer, both participants leave with no money. Standard economic theory predicts that proposers should offer the smallest sum of money, while receivers should accept any offer greater than zero. However, years of behavioral economics research indicates that proposers typically offer about 50% of the total sum of money, and receivers normally reject offers that are below 20% of the total sum (Camerer and Thaler, 1995). It has been argued that concerns about one's social status may motivate proposers to make relatively fair offers, particularly among proposers with high T concentrations (Eisenegger et al., 2010). Specifically, proposers face the possibility of having an unfair offer rejected by the receiver, and to avoid this threat to status (i.e., rejection), they may resort to making relatively fair offers. T administration studies have found opposing effects of exogenous T on proposer behavior in men and women. While T administration caused women to make higher offers in the role of proposer (Eisenegger et al., 2010), it caused men to make lower offers (Zak et al., 2009).

It could be argued that rejection behavior in the UG is also related to concerns about one's relative social status. Specifically, receivers may be motivated to reject low offers as a means to avoid being low status relative to the proposer who made the unfair offer. Rejection behavior by the receiver can also be considered a form of aggressive behavior as it is committed with the intent to cause harm (i.e., financial) to another individual (Mehta and Beer, 2010). Two studies have reported that men and women with relatively high baseline concentrations of T are more likely to reject unfair offers (Burnham, 2007; Mehta and Beer, 2010). However, acutely elevated T concentrations through exogenous T did not affect rejection behavior in men or women (Zak et al., 2009; Eisenegger et al., 2010). The UG studies reviewed here suggest both similarities and differences in the role of T in proposer and receiver behavior in men and women. Differences in study design (e.g., within- vs. between-subjects), time lag between T administration and measurement of behavior (4 h in Eisenegger et al., 2010; 18 h in Zak et al., 2009), and/or dosage of T used (supraphysiological in Eisenegger et al., 2010; normal range in Zak et al., 2009) may account for the divergent results obtained in men and women. In order to resolve such conflicting findings, it will be critical to examine effects of T on UG behavior in men and women in the same experimental protocol.

Moderators of the relationship between T dynamics and aggression

Although acute changes in T during competition predict subsequent aggressive behavior in young men (reviewed in section 'Testosterone dynamics and aggressive behavior'), more recent work suggests that individual differences in personality traits may moderate the relationship between T dynamics and human aggression. In two studies, Norman and colleagues (2014) reported that individual differences in trait anxiety moderated the effect competition-induced T dynamics on subsequent aggressive behavior. Specifically, T responses to competition were positively correlated with subsequent aggressive behavior, but only among men scoring relatively low on trait anxiety. Other unpublished research from our laboratory suggests that individual differences in self-construal – or the extent to which the self is defined independently of others or interdependently with others – moderates the relationship between T (baseline and reactivity), aggressive behavior, and risk-taking (Welker et al., unpublished). This work indicates that T (baseline and reactive) is positively correlated with aggression and risk-taking, but among individuals with independent self-construals.

Notably, a surge of research examining the effect of oxytocin administration on human behavior finds that individual difference factors and social context play an important role in moderating the effect of this hormone on cognitive and behavioral processes (see Bartz et al., 2011 for review). Collectively, research with T and oxytocin highlight the importance of considering individual difference factors and social context when studying hormone–behavior associations in people.

Beyond aggression – effects of T on social cognition, risk-taking and mate-seeking behavior

Although the main focus of this paper was to highlight research on the neuroendocrinology of human aggression, there is a growing body of work examining relationships between acute T dynamics and social cognition, risk-taking and mate-seeking behavior. In this section I provide a brief summary of the main findings in each of these domains.

Testosterone and social cognitive processes. Several studies have investigated relationships between endogenous T (both baseline T and reactive T) and exogenous T on empathic cognition/behavior, interpersonal trust, moral decision-making, and social cooperation (see Eisenegger et al., 2011 and McCaul and Singer, 2012 for reviews). Recent studies have reported that individual differences in baseline T concentrations were negatively correlated with empathic accuracy (Ronay and Carney, 2013) and positively correlated with utilitarian decision-making (Carney and Mason, 2010) in both men and women. Also, one recent study investigated the relationship between T (baseline and reactive) and trust ratings of emotionally neutral male faces. Results indicated that although baseline levels of T were unrelated to trust ratings, a rise in T within the context of a competitive interaction predicted decreased ratings of trust in men, but not women (Carré et al., 2014b). The latter findings are consistent with the idea that acute fluctuations in T during competition may serve

to fine-tune social behavior according to changes in the environment.

Research in women has found that a single administration of T decreased ratings of trust from emotionally neutral faces (Bos et al., 2010), decreased cognitive and affective empathy (Hermans et al., 2006; van Honk et al., 2011), inhibited trust during a social exchange paradigm (Boksem et al., 2013), increased utilitarian moral decision making (Montoya et al., 2013) and increased social cooperation and reciprocity (van Honk et al., 2012; Boksem et al., 2013). Notably, some of these studies found that the effects of T on social cognition depended on variability 2D:4D ratio – a putative measure of prenatal androgen exposure (van Honk et al., 2011, 2012; Montoya et al., 2013). The latter findings suggest that T's activational effects on behavior may depend critically on T's early organizational effects on neural architecture underlying social cognitive processes.

Testosterone and risk-taking behavior. There are significant risks associated with engaging in aggressive behavior (e.g., injury, loss of status) and thus, it is perhaps not surprising that researchers have documented links between endogenous T concentrations and risk-taking behavior. For instance, in a recent laboratory experiment, Apicella and colleagues (2014) collected saliva samples prior to and at the end of a competitive interaction and then assessed risk preferences in a behavioral economics task. The authors reported that irrespective of randomly assigned competition outcome, men ($n = 49$) for whom T concentrations increased in response to the competition were less risk averse compared to men for whom T concentrations decreased. In a more recent study with a larger sample of men ($n = 153$), we found that the relationship between T responses to competition and subsequent risk-taking behavior (measured using the Balloon Analogue Risk Task) was moderated by competition outcome (Welker et al., unpublished). Here, T responses to competition were positively correlated with subsequent risk-taking behavior in winners, but not losers. In another study that did not involve competition, it was found that a simple power posture manipulation influenced both T concentrations and risk-taking behavior. In this study, Carney and colleagues (2010) randomly assigned men and women to hold brief dominant or submissive postures, after which they performed a risk-taking task. Results indicated that dominant postures increased T concentrations and risk-taking behavior relative to submissive postures (Carney et al., 2010), an effect that was found irrespective of participant sex (see Stanton, 2011 for a discussion of the limitations of this work).

Other work indicates that acutely elevating T concentrations through pharmacological challenge influences measures of risk-taking in both men (Goudriaan et al., 2010) and women (van Honk et al., 2004). Also, baseline levels of T are positively correlated with measures of risk-taking in both men and women (Apicella et al., 2008; Sapienza et al., 2009; Stanton et al., 2011a; Evans and Hampson, 2014). Finally, there is some evidence for a curvilinear relationship between baseline levels of T and measures of risk-preference in men and women (Stanton et al., 2011b). Collectively, the research summarized here indicates that measures of T reactivity (endogenous and pharmacological challenge) and baseline concentrations of T map onto broad measures of risk-taking in both men and women. At least for men, it may be that the effects of competition-induced T responses on subsequent aggressive behavior (reviewed in section 'Testosterone dynamics and aggressive behavior') may in part be mediated by T's effects on one's propensity to engage in risky behavior (Wilson et al., 2009).

Testosterone dynamics and mate-seeking behavior. A separate body of work has examined T responses among men interacting with potential mating partners. This work has revealed that men demonstrate a rapid increase in T when interacting with attractive women (Roney et al., 2003, 2007, 2010). Moreover, such changes in T were positively correlated with the extent to which men engaged in courtship behavior (Roney et al., 2003, 2007). Even the scent of an ovulating woman rapidly increases T concentrations in men (Miller and Maner, 2010; Cedra-Molina et al., 2013; but see Roney and Simmons, 2012). Similar increases in T have been observed in male mice and rats exposed to receptive females (Amstislavskaya and Popova, 2004) and in male common marmosets exposed to the scent of ovulatory females (Ziegler et al., 2005). Moreover, rapid changes in T concentrations increase the expression of copulatory behavior in house mice (James and Nyby, 2002). Thus, research in both humans and animal models suggest that acute changes in T in response to brief exposure to potential mates (or the scent of potential mates) may serve to modulate mate-seeking and sexual behavior.

SUMMARY

Testosterone plays a key role in a number of physiological and behavioral processes critical to survival and reproduction (Ketterson and Nolan, 1992). In the current paper, we highlighted research indicating that T concentrations are not static, but rather fluctuate rapidly in the context of competitive interactions. Furthermore, this work indicates that such rapid fluctuations in T may enable an individual to rapidly modulate their behavior according to changes in the social environment. Despite these advances, there remain a number of challenges that need to be addressed in order to further enhance our knowledge of the social neuroendocrine mechanisms underlying competitive and aggressive behavior. A multi-method approach combining techniques from experimental and social psychology, neuroscience, behavioral economics, and pharmacology will be critical to advancing the field of social neuroendocrinology. Moreover, a focus on sex differences/similarities, social context, and individual difference factors (e.g., personality traits) may help to resolve inconsistencies in the literature and will enable a greater understanding of the complex bi-directional relationship between T and human competitive/aggressive behavior.

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