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Postgame Testosterone Levels of Individuals in Team-Based Status Games Are Affected by Genetic Makeup, Gender, and Winning Versus Losing

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Testosterone, a steroid hormone, affects the ability of the prefrontal cortex to regulate the limbic system and therefore has been implicated in a wide range of social behaviors such as facing status challenges, aggression and dominance. Here we use a team-based status game to examine factors that determine the postgame testosterone (T) levels of participants who were on the winning or losing team in a status game. We focused on functional polymorphisms in 2 candidate genes, namely *DRD4* and *COMT* because these genes are densely expressed in the prefrontal cortex and thus affect peoples' self-regulation ability. Being on the winning team does not automatically lead to higher postgame T levels. Postgame T levels were affected by pregame T level and genetic makeup of the *DRD4* gene variants for male and *COMT* gene variants for female participants, respectively. These findings remain robust when we controlled for contextual variables related to game play. Such insights, based on genetic markers, might motivate researchers in neuro-economics to look closer at neuro-biological mechanisms, specifically the prefrontal-limbic connectivity that modifies when people engage in status games.

Keywords: COMT gene, *DRD4* gene, status games, testosterone

> Men are continually in competition for honor and dignity.
>
> —Hobbes

Imagine you are on a team involved in a competitive game in a business setting. Your team faces three other teams that are also motivated to gain the status that comes with winning. The contest is like a rat race with negative externalities: an increase in one team's relative status means a decrease in the relative status of the other teams (Heffetz & Frank, 2009). The theories suggest that when people win a competitive game, a gonadal steroid hormone testosterone (T) is released; T is triggered by the hypothalamic-pituitary-gonadal axis which facilitates the synthesis of T in ovaries in females and Leydig cells in testes in males as well as in the adrenal cortex in both males and females (Eisenegger, Haushofer, & Fehr, 2011). This rise in T levels after winning a contest conforms with the winner effect (Fuxjager & Marler, 2010; Gleason, Fuxjager, Oyegbile, & Marler, 2009) or the biosocial status hypothesis (Mazur, 1985). The two hypotheses indicate that as status is gained on winning the game, T levels rise, thus driving players to protect their gained status. T is also called a dominant hormone

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(Eisenegger et al., 2011) and has been implicated in a wide range of phenomena such as impulsivity, aggression and dominance (e.g., Dabbs, Carr, Frady, & Riad, 1995). Therefore, T is perceived as a hormone that has wide social implications. From a neurobiological perspective, reasons for typical behaviors such as dominance in humans are attributed to a reduction in the connectivity between prefrontal cortex (PFC) and limbic nuclei where higher T levels come with a lowered ability to exert self-control during challenging situations and this lower self-control in turn amplifies T levels in the case of a person winning a contest (e.g., Eisenegger et al., 2011; Hamilton, Carré, Mehta, Olmstead, & Whitaker, 2015; Mehta & Beer, 2010). In this study we build on these neuro-biological mechanisms when developing our hypotheses.

Here we explore T levels of winners versus losers after a management simulation game, in which teams of students in a Business Economics class from a Dutch university competed against each other. Their win or loss was publicly announced on the classroom blackboard as this game was played in class. This social context adheres to a research tradition that uses real tournaments or status contests (such as sporting events) where one's status or reputation is at stake to investigate how winning versus losing affects T levels (e.g., Booth, Shelley, Mazur, Tharp, & Kittok, 1989; Costa & Salvador, 2012; Salvador, 2005). The experimental conditions of this study differ from (rigged) designs that artificially place people in the winning or losing condition (e.g., Schultheiss, Campbell, & McClelland, 1999) or from experimental economics games where T is artificially administered and the results are compared with placebo subjects (see Eisenegger et al., 2011 for an overview). Just before the experiment began, pregame T levels (reflecting both preparation and excitement for the contest) were measured as they were expected to affect postgame T levels. This observation fits the just mentioned biosocial status hypothesis (Mazur, 1985) and also the challenge hypothesis. The latter states that T levels rise in order to prepare a person for a contest.

We do not expect that postgame T levels will rise unconditionally when people win. Indeed, the literature shows that a large set of variables—especially related to individual differences and the social context—moderates postgame T levels (which may rise or lower) on winning a contest. First, individual differences include for instance differences in basal T levels (which might indicate dominance; Sellers, Mehl, & Josephs, 2007) and implicit need for power, which comes with higher T levels when winning is experimentally induced (Schultheiss et al., 1999). Gender is another individual difference associated with changes in T levels during status-related behaviors (Josephs, Mehta, & Carré, 2011). However, rather than focusing on psychology-personality traits, we focus on individual differences based on whether the participants are carriers of two candidate genetic variants (*DRD4* and *COMT*). An endophenotype approach (gene-hormone associations) seeks closer relationship with neuro-biological mechanisms than behavioral phenotypes and they might explain the higher postgame T levels when people win a contest (see Josephs et al., 2012 for a similar endophenotype approach). Second, social context matters; concretely we are studying people as members of the winning team or one of the losing teams (second, third or fourth) and not individuals competing against one another for the winning spot (e.g., Josephs et al., 2011). Therefore we study the moderating effect of possible contextual factors, such as team composition and team size.

The article progresses as follows. First we present an overview of the literature on research about testosterone and social behavior in a variety of different social contexts, as well as the literature on neuro-biological mechanisms that are affected by testosterone changes. In doing we show that the testosterone hormone affects many behaviors and has substantial societal implications related to status, violence, and sexual behavior. However, that does not mean that the conclusions about the correlates of T levels with behavior are always consistent. Using the insights from this literature overview as a foundation, we present a theory on how genetic information might add to better insights into how the outcome of challenges—winning or losing—affect postgame T levels. In addition, we describe our hypotheses on T level changes as a consequence of winning or losing. A method section and results are then presented. Finally we discuss what can be learned from this study.

Literature Overview on T Levels and Social Behavior

The literature on the behavioral correlates of T levels in general reflects two main theories rooted in studies of animal behavior and serving as ultimate explanations for T level changes related to status (Blumstein et al., 2010). First, the biosocial status hypothesis/winner effect states that as individuals compete for status, postgame T levels reflect the outcome of the context such that winners' T levels increase and losers' T levels decrease (Mazur, 1985). The higher T levels prepare the winner to defend their dominance and force the loser to submit to high status people. Hence T levels have a social adaptive function. Second, the challenge hypothesis relates T levels to both reproductive and aggressive functions where T levels rise as the breeding season begins and rises even more when facing challenges, especially in mating status competitions between males hoping to attract females (Archer, 2006; Wingfield, Hegner, Dufty, & Ball, 1990). Once the breeding season/contest ends and the off spring need care, T levels lower which protects the animal from energy loss. Hence T levels serve adaptive functions. In humans the behavioral mechanisms of seeking or defending status are reflected in several social contexts such as sports, organizational life, mating rituals and aggression. The study of T levels involves approximate explanations hence it can be expected that various factors related to the person and environment play a role.

In this literature overview on the relationship between T and social behavior we first focus on the T levels as an antecedent for social cognition and behavior. We then focus on T levels (postgame T levels) that emerge after status challenges are won or lost, such as sports that occur on natural field conditions and games in laboratory settings which, by definition, are artificial conditions. We also focus on aggression in laboratory settings. T levels are related to mating behavior which reflects the challenge hypothesis as animals engage in competition to attract a mate. We then study the relationship between T levels and personality traits, such as implicit status and aggressive behavior. Moreover, we also discuss the contemporary neurobiological literature concerning T levels and the corresponding neural activity and use that as the basis for our theory and hypotheses within our context. Although we seek to provide an overview of the main streams of research on T levels we do not intend to make a complete overview of the literature, as is done in metastudies, which are beyond the scope of this study. In doing so we might have excluded several articles that might have been interesting to various scholars. We consciously limited ourselves to the literature between 1980 and 2015 that which focuses only on adults (not adolescents or children) and excluded T-related research on nonsocial tasks (speed at solving puzzles), T responses related research on random events like lottery, or T levels related to power posing.

T Levels as Antecedents for Social Cognition and Behavior

An important stream of research focuses on how T administration of participants compared to a control group affects psychological and behavioral processes and outcomes when participants engage in laboratory experiments. Other studies look at T baseline levels high versus low and study their correlations with psychological and behavioral processes and outcomes without implying causality. Note however that both streams of research reflect the biosocial status theory meaning higher T levels help a person to defend or gain status or dominance.

T administration in laboratory settings.

T administration and social perception/appraisal. In the van Honk, Peper, and Schutter (2005) study people watched facial emotional expressions when T was administered. Higher T levels reduced the unconscious emotional responses to fearful faces without influencing conscious anxiety. Another study showed that T administration reduced sensitivity to conscious recognition of facial threats (Van Honk & Schutter, 2007). In a study involving mimicry of human facial expressions, T administration reduced people's mimicking ability; hence it reduced their empathy to others (Hermans, Putman, & van Honk, 2006). Van Honk et al. (2011) showed that females watching faces with different emotional expressions when T was administered resulted in impaired cognitive empathy. The cognitive emphatic response was moderated by their D2:D4 ratio; specifically people with a low D2:D4 ratio had greater impairment of cognitive empathy. Administered T also induced accelerated cardiac response to angry faces (van Honk et al., 2001).

Using pictures with negative, positive, or neutral content, T administration reduced participants' stress system responsivity and affective startle modulation to the negative content. This effect was especially strong for highly anxious people (Hermans et al., 2007). Another study focused on T levels' relation to trust; female participants were asked to appraise the trustworthiness of gray scaled faces. The results indicated that administration of T decreased females' interpersonal trust. This decline in trust occurred especially in the high-trusting people (Bos, Terburg, & Van Honk, 2010). Female participants administered with T also show reduced avoidance of social threat and elevated approach toward angry faces (Enter, Spinhoven, & Roelofs, 2014).

T administration and economic decision making. Male participants played an ultimatum game, which resulted in less generous offers by the proposer when T was administered. T administration also interfered with the proposer's ability to read the minds of the receiver (Zak et al., 2009). Interestingly, during an ultimatum game with only female participants administered T participants made more fair offers compared to the control group. However when female participants assumed that T was administered, they made more unfair offers thus indicating that having T administered primed the stereotypical association that a rise in T levels leads to more aggression (Eisenegger & Naef, 2011). In trying to gauge people's pro-social behavior during a social cooperative game (public goods), people with a high D2:D4 ratio showed more cooperation (van Honk, Montoya, Bos, van Vugt, & Terburg, 2012). When postmenopausal female participants played the ultimatum game followed by a dictator game, T administration seemed to have no effect on fairness, trustworthiness, altruism, and behaviors concerning risk taking (Zethraeus et al., 2009). Note, however, that this last study used a continuous method of T administration (4 weeks, daily) versus the acute administration method in Eisenegger and Naef's (2011) study.

Conclusion. (a) In general, T administration affects people's perception and appraisal of facial expression making them less fearful to potential threat which prepares them for a confrontation. Note, however, that in all studies reported here females are the sole participants. (b) T administration during economics games does not reveal a forthright conclusion probably because economic decisions involve more complex cognitive-affective processes than merely watching facial expressions. Several factors, especially gender, age effects on hormonal production, and assumptions about the effects of hormone administration, play a role, as well as other factors such as personal values, self-conscious emotions and social influence.

T levels in laboratory settings.

T levels and social perception and social appraisal. Some studies measure the relationship between actual T levels (using blood serum or saliva sampling) and social cognition using both static and dynamics pictures. Van Honk et al. (1999) show that males and females with higher T levels show more selective attention to angry faces, while people with low T levels are more averse to angry faces. When angry faces were used as part of an implicit learning task; higher T levels were associated with vigorous responses to angry faces, indicating that high basal T levels reduced avoidance of angry faces. After letting males and females watch joyful and angry faces, higher basal T levels in the morning were associated with a decrease of aversion to threat stimuli both in the short term (directly after watching stimuli) and long-term (afternoon) (Wirth & Schultheiss, 2007). Carré, Baird-Rowe, and Hariri (2014) showed that the outcome of a trust game in combination with T level change influences trust ratings. Concretely, participants of an experiment were asked to rate neutral faces on trustworthiness, play a trust game (stealing points from others without gain for oneself), and then redo the same trust evaluation task (rating neutral faces on trustworthiness). Here a rise in T predicted subsequent decreased trust ratings by males but not by females.

Conclusion. All reported studies indicate that higher T levels come with more attention and less aversion both to negative faces and lower trust, for both males and females (except one study). It can be said that the findings on T administration and T levels of participants asked to appraise facial expressions have many similarities as they indicate that T levels prepare males and females to face challenges (biosocial status theory and challenge hypothesis). Note also that these overlapping findings might be due to the restricted social task (watching facial expressions) in laboratory settings; or as Carré and Olmstead (2015) note, facial expressions are honest signals to a threat of status.

Consequences for T Levels in Status Contests

T levels are related to behavioral outcomes in status contests that include various sports played under natural conditions, thus not competitive situations in laboratory environments organized by the researchers.

Effect of sports as status games on T levels. ***Contact sports.*** In judo (an individual contact sport) winning or losing did not affect postgame T levels. The results indicated that after an exercise match one week before the actual match T levels were significantly higher. However, after a competition match, only players with previous successes showed increased T levels (Salvador, Simon, Suay, & Llorens, 1987). Winning versus losing also had no effect on postgame T levels in another study involving judo but this study did find an anticipatory increase of T levels before competition (Suay et al., 1999). Another study showed that both outcome (winning-losing) and physical effort during a contest had no effect on T levels, yet surprisingly, winners before the competition had a worse mood and lower T levels than the losers (Serrano, González-Bono, & Suay, 2000). Mixed results for the anticipation effect were also found by Salvador, Suay, González-Bono, and Serrano (2003), where only some of the players showed an anticipatory rise in T levels accompanied by higher C levels; the rest showed no increase in T levels before the contest. Interestingly, the group with anticipatory rise in T levels also had better outcomes compared with the players without the rise. Noteworthy is another study on judo where not the winners but the losers had higher T levels (Filaire, Maso, Sagnol, Ferrand, & Lac, 2001). These losers also experienced more cognitive anxiety and had less self-confidence before the contest. In another contact sport, wrestling, the winners had greater T increases than losers (Elias, 1981).

Noncontact individual sports. Booth et al. (1989) showed that winners had a higher rise of postgame T levels than losers (who also had raised T levels). Winners also had higher anticipation T levels before the next match, indicating that winning prepares a person to engage in the next contest (biosocial status hypothesis). The study showed that mood played an important role as moderator: winners with a positive mood had greater increases of T compared with those with a negative mood. In tennis, where players teamed up in doubles (dyads), only clear winners had mood elation and increased postgame T while close winners showed declines in T levels (Mazur & Lamb, 1980). This indicates that higher postgame T levels do not necessarily come with winning. One study focused on the continuous effects of competition in golf (stroke play). The results indicated no T elevation during the competition or an anticipation effect for the next holes (Doan, Newton, Kraemer, Kwon, & Scheet, 2007).

Team sports. In a study involving female soccer players, anticipation and elevated mood came with higher T levels, and after the contest winners showed an increase in postgame T levels while losers had a decrease in postgame T levels (Oliveira, Gouveia, & Oliveira, 2009). Note that this soccer match was the final in the league, meaning there were exceptional status gains and losses at stake. The same effect of higher postgame T levels when winning and decrease of postgame T levels when losing was also observed in fans watching a soccer game (Bernhardt, Dabbs, Fielden, & Lutter, 1998). In rugby, pregame T levels were higher in anticipation yet moderated by team bonding (better bonding came with higher T levels). Amazingly, the postgame T levels were independent of game outcome (winning/losing) and self-attribution of performance (Bateup, Booth, Shirtcliff, & Granger, 2002). A basketball study corroborated the results of the previous study concerning players' postgame T levels having no relation with the game outcomes. However, this study did find that postgame T levels of winners correlated negatively with external factors (such as attributing losses to referee). Losers' postgame T levels had a negative correlation with performance but correlated positively with external factors such as referee decisions (Gonzalez-Bono, Salvador, Serrano, & Ricarte, 1999). Another study involving basketball found winners' postgame T levels negatively correlating with external factors such as referee decisions (Gonzalez-Bono, Salvador, Ricarte, Serrano, & Arnedo, 2000). Despite the outcome of games having no effect on players' postgame T levels, the fans' postgame T levels seem to be affected by the results of their team's outcome. A study involving basketball fans showed increased postgame T levels in fans of the winning team, and lower postgame T levels for the fans of the losing team (Bernhardt et al., 1998). Studies show that merely watching a previous victory of your team can result in testosterone increases (Carré & Putnam, 2010).

Intellectual sports contests. In a study involving a prestigious chess tournament, winners had higher postgame T levels and an anticipatory rise in pregame T levels. This anticipation effect was not observed in a less prestigious chess tournament, although winners did have increased postgame T levels (Mazur, Booth, & Dabbs, 1992).

Conclusion. Not surprisingly, winning in the sports described above does not always result in higher postgame T levels because the social contexts are diverse in terms of specific physical, intellectual, or team effort the sport requires as well as in how it is refereed. The studies covered a plethora of, factors such as coping strategies, gender, competition type (contact sport or not), personality traits, closeness of winning-losing, pregame T levels, interaction of C levels and T level mood, importance of reputation at stake and team bonding.

Effect of experimental status challenges on T.

Laboratory experiments involving rigged status positions. Most studies involve creating a competitive environment using questionnaires or rigged competitive situations. In a study using ability-based questionnaires, match loss induced a larger decline of T levels in men. When the task was changed to chance-based questions, the T effect disappeared; indicating the role of effort or self-efficacy. The study concluded that the effect of T in men is based on a function of ability and outcome (Van Anders & Watson, 2007). Using questionnaires designed to measure dominance, high female T levels were related to high dominance levels, indicating that words related to status affect T levels (Grant & France, 2001). Josephs, Sellers, Newman, and Mehta (2006) put dominant people in a losing position and compliant people in a winning situation in a rigged competition. Both dominant and compliant people showed impaired cognitive functioning and performance in the mismatch conditions. This impairment was correlated with heightened heart rate. Similarly, Newman, Sellers, and Josephs (2005) put high T level participants in a high versus low status condition in a rigged competition and found that participants did better in the high status condition and performed worse in the lower status condition, once again showing that mismatch of status can impair cognitive ability.

Saad and Vongas (2009) tried to lower the status of participants by letting a confederate show off with luxury goods in the presence of a male or female moderator. They found no relationship between T and status itself, but the presence of the female moderator increased T levels. Males placed in a rigged winning or losing position showed higher T levels after winning the competition. In the winning group, post T levels but not pregame T levels were related to a facial masculinity index (Pound, Penton-Voak, & Surridge, 2009). When males were put in a rigged winning versus losing position and consequently asked whether they would compete again, only participants who had lost with increased T levels were likely to compete again. This indicates that loss of status can predict subsequent social behavior (Mehta & Josephs, 2006). One study involved a field experiment with rigged status positions. In this elegant study by Saad and Vongas (2009), males driving a luxury car versus a basic car had higher T levels on leaving the luxury car. Driving a luxury car in the city and on the highway came with increase in T levels and driving a basic car in the city came with decrease in T levels.

Status games. When participants played a video game against same sex participants, only males had an anticipatory rise in T levels whereas the outcome had no effect on T levels (Mazur, Susman, & Edelbrock, 1997). In another study involving nonphysical rigged competitive conditions, winners had higher T levels and slower decline of T levels. Whether the outcome was close or decisive had no effect on T levels (Gladue, Boechler, & McCaul, 1989).

T levels and aggression in experimental situations. Carré, Putnam, and McCormick (2009) studied the relationship between T and reactive aggression. In a rigged experiment they put participants in a winning or losing condition and found that the T reactivity (percentage T level changes) predicted subsequent aggression. This link was especially strong among losers. Norman, Moreau, Welker, and Carré (2014) found that the effect of T reactivity on aggressive behavior was moderated by anxiety levels in males. Males low on anxiety show aggressive behavior after increasing T levels, whereas both males high on anxiety show compliant behavior. In a follow up study the authors included females in the experiment and found that the effect applied only to males. The results indicated that men with high anxiety levels showed increased aggressive behavior after winning a video game versus losing it. Carré, Campbell, Lozoya, Goetz, and Welker (2013) used videogames (basketball or boxing) followed by an aggression task (stealing points) to study the interaction between T and aggressive behavior. They found that T fluctuations mediated the outcome of the competition and subsequent aggressive behavior in males but not females. One study showed that increased T levels after being merely excluded in a game of throwing balls was associated with anger but not with other emotions like fear and sadness (Peterson & Harmon-Jones, 2012).

Conclusion. In experimental conditions, gaining or losing status after a challenge did not come with higher T levels or a lower T level. This is similar to the earlier observed field studies of sports. Once more a plethora of factors affected T levels, such as personality traits (dominance, self-efficacy, gender) and environmental factors (such as a mismatch between desired status and position).

Effect of Social Interaction on T Levels

T levels have been associated with sexual selection, mate choice, loyalty to chosen mate, and sensitivity to sexual cues, which fits the challenge hypothesis, except humans have no breeding seasons.

Intimate social interaction. In a laboratory setting where males had a brief interaction with female confederates, males in the afternoon group showed increased T levels. In a follow up study the authors let female confederates physically touch male participants; extravert men (as indicated by the female confederate) showed increased T levels when interacting with the confederate (Roney, Lukaszewski, & Simmons, 2007). Van Anders and Goldey (2010) focused on the long-term effects of relationships on T levels using questionnaires. Males and females showed lower T levels the longer they stayed together. In addition, casually partnered men showed higher T levels than men in long-term relationships. The same authors found that T relates to relationship orientation in men (tendency to enter long-term relationships) and relationship status in woman (currently partnered or not). Frequency of partnered sexual activity and masturbation mediate T levels and partnering in women (meaning high frequency less partnering). Finally, it was found that interest in new partners and not extra partners was related to T levels and partnering in men. Cobey, Nicholls, Leongómez, and Roberts (2015) conducted a study with females only and confirmed that partnered women have lower T levels than single women. Women on contraceptives had overall lower T levels. Couples in a relationship (duration ranging from weeks to years) showed lower T levels when they were more satisfied and committed to their relationship. A person's satisfaction with the relationship was also negatively correlated with their partners' T levels (Edelstein, van Anders, Chopik, Goldey, & Wardecker, 2014).

Sensitivity to stimuli reflecting T levels in diverse modalities. In a study of females watching videos of a handsome man courting a woman, a nature documentary, attractive women, or an ugly older man courting a woman, only females not using contraceptives had higher T levels, solely after watching the video of the handsome man courting the woman (López, Hay, & Conklin, 2009). In an other study, male participants were asked to smell T shirts worn by females during and outside ovulation; here males had higher T levels when smelling the T shirts worn during ovulation period. In a follow-up study the same authors used a larger sample and besides confirming the previous finding, they found that males felt that shirts from the ovulation period smelled better (Miller & Maner, 2010). Note that during the experiments participants were told that the T shirts were from women, which could have contributed to a biased result. In a similar study of men asked to smell gauze pads containing ovulatory sweat, T showed no response after exposure (Roney & Simmons, 2012). When the experimental condition was reversed and females were invited to smell T shirts worn by males; females indicated to prefer the scent of males with high T levels only during the ovulation phase of their menstrual cycle (Thornhill, Chapman, & Gangestad, 2013).

Conclusion. T levels rise as a consequence of multiple contextual variables: long-term relationships reduce T levels and T levels rise as mating motivation is activated. In addition, sensory cues, such as the scent of ovulation, affect T levels, indicating T levels are related to mate-seeking behaviors.

T Levels as a Reflection of Personality Traits

A group of studies looked at the relation between T levels and dispositional characteristics of a person, especially dominance and aggressive behavior.

Dominance. Sellers et al. (2007) found that T levels were associated with dominance in both males and females. Studying the relationship between T, dominance, and implicit power motivation, Schultheiss et al. (1999) found that males with high implicit power had higher T levels after imagining success in a domination contest. The results indicated that males with high implicit power had high T levels after actually winning but not after losing. During a serial response test to measure learning capability, implicit power motivation enhanced implicit learning and increased the T levels of winners while it impaired implicit learning and decreased T levels of losers (Schultheiss et al., 2005). After watching a power-arousing movie, an affiliation-arousing movie, or a control movie, men with high T levels increased T after watching the power-arousing movie compared to the other movies. The opposite effect was found for high T females whose T decreased after watching the power-arousing movie. High T level men showed a decrease in T after watching the affiliation movie, which is in line with research indicating that partnering lowers males' T level (Schultheiss, Wirth, & Stanton, 2004). Finally, Mehta, Welker, Zilioli, and Carré (2015) revealed that people with high T levels engaged in more risk-taking behavior, but only when they had low cortisol levels. Using a subsequent behavioral risk-taking task (BART test), male participants (females were excluded) high on T but low on C engaged in more risk taking.

Aggressive traits and antisocial behavior. Dabbs et al. (1995) found in male prison inmates that high T level compared with low level inmates engaged in more rule violations. The crimes of high T level inmates were also more violent (rape, armed robbery etc.) compared to low T level inmates (drug use, burglary etc.). The higher T levels correlate with familiarity with the victim and intent for homicide, indicating planning the murder (Dabbs, Riad, & Chance, 2001). Likewise, female inmates with high T levels are related to criminal violence and aggressive dominance. However, aging in combination with lower T levels made female inmates less dominant and aggressive (Dabbs & Hargrove, 1997). A study of war veterans found that high T levels correlated with antisocial behavior. Social economic status moderated the relation between T levels and antisocial behavior (concretely, higher socioeconomics status had a weaker relationship; Dabbs & Morris, 1990).

Conclusion. Personality traits, such as implicit dominance in competitive situations (rigged, imagined or real) or watching power-arousing movies, affect T levels. A positive relationship between aggression and higher T levels was consistently found in people with criminal records, and this applied to both males and females.

Neurophysiological Studies

Recently several studies have been looking at the neuro-endocrine pathways involved when administering T levels and observing people with different T levels. Note, however, that these neurophysiological studies take place in a constrained environment, namely an fMRI scanner using standard experiments that allow deeper insight into the neuro-biological processes due to T changes or T levels. Here we focus only on tasks involving facial expressions.

When females were asked to match pictures of facial expressions emotional labels, T administration resulted in reduced coupling of the amygdala with the orbitofrontal cortex and contralateral amygdala, whereas it enhanced coupling with the thalamus (van Wingen, Mattern, Verkes, Buitelaar, & Fernández, 2010). When females watched both angry and happy faces, T administration enhanced their responsiveness to social threat and came with amygdala and thalamus activation (Hermans, Ramsey, & van Honk, 2008). Van Wingen et al. (2009) showed that matching emotional cues with facial expressions activated the amygdala in females which in turn increased fusiform gyrus responses. Bos, van Honk, Ramsey, Stein, and Hermans (2013) showed that T administration increased the activity of the amygdala in response to both dynamic happy and angry faces, indicating that T administration does not reduce fear by down-regulating the amygdala. However, T affected the superficial amygdala and to a lesser extent the basolateral amygdala, both input regions that play a role in adaptive responses to socially relevant stimuli. In an experiment where female participants had to memorize and recognize male and female faces T administration made it easier to encode and retrieve male faces by shifting the memory processes in the hippocampus and interior temporal cortices (van Wingen, Mattern, Verkes, Buitelaar, & Fernández, 2008). Finally, in another Study T administration also increased activity in the amygdala for untrustworthy faces. The increase in T reduced the coupling of the orbitofrontal cortex and amygdala (Bos, Panksepp, Bluthé, & van Honk, 2012).

Volman, Toni, Verhagen, and Roelofs (2011) showed that T levels modulated (lowered) the strength of the connection between the amygdala and ventrolateral PFC/frontal poles in males. Stanton, Wirth, Waugh, and Schultheiss (2009) let both male and female participants watch angry faces and then play odd ball. In general, high T levels came with lower amygdala activation but higher vmPFC activation. Overall the coupling between the vmPFC and the amygdala became lower. Note that these effects only were found for males.

These studies generally show that people with higher (administered) T levels engaged in social tasks (e.g., confrontation with threatening/untrustworthy faces) showed an uncoupling of regions around the PFC (such as vmPFC) and limbic parts of the brain (NAcc, amygdala, temporal poles, etc.). It must be noted that although every study of T administration concerning neural activity was conducted with female participants, males were included in the baseline T level studies so that the findings about uncoupling PFC and limbic parts can be generalized across the genders.

Overall Conclusion

Given the wide range of studies on T levels as an antecedent of behavior, and a correlate or outcome of behavior, testosterone has been shown to be a key hormone affecting behaviors across many social situations relevant to society. Although research on testosterone is inspired by ultimate explanations (biosocial status hypothesis and challenge hypothesis) the findings do not support these hypotheses directly when applied to humans, because searching for proximal explanations is more challenging. When cognitive tasks are simple, as in the perception of facial expressions in a lab, results are more parsimonious probably because angry faces are honest signals of threat, which supports the biosocial status hypothesis (see Carré and Olmstead, 2015, p. 176). However, as tasks become affectively cognitively more complex, as in economics games, and status competitions take place in diverse contexts, relationships between T level changes and behaviors are less parsimonious. This is because a hormone has adaptive functions, meaning that T helps people to maneuver in social conditions and here it modulates the cognition and motivation required to operate in these conditions. Put another way, as different social contexts require different cognitive-emotive and motivational processes, the effects of T levels occur in different neuro-biological pathways. Most important in this literature overview is the rise in neurobiological studies in recent years. They might offer explanations at a level lower than behavioral of how T levels affect cognitive-affective-motivational processes. Here the main effect is on the PFC-limbic connectivity, which is involved in self-regulation.

Theory and Hypotheses

Building on research by Bos et al. (2012, 2010) and Mehta and Beer (2010), we focus on a core neuro-biological mechanism that is influenced by higher T levels, namely the connectivity between regions in the PFC (such as OFC or vmPFC) and the limbic system which includes the amygdala, and NAcc. First, these three nuclei are dense in T receptors (Finley & Kritzer, 1999), and higher T levels weaken the PFC-amygdala/NAcc coupling that affects self-regulation of social emotions when competing with others. In general, people encounter other people with empathic understanding (shared manifold; Gallese, 2003), but this prosocial approach is not adaptive for successful engagement in status contests as is the case in this study. Instead, uncoupling the PFC-amygdala/NAcc prepares a person to act vigilantly and self-confidently (Eisenegger et al., 2011). Mehta, Goetz, and Carré (2013) propose a similar point of view as they focus on PFC-amygdala coupling to study associations between genetic makeup and aggression. This adaptive change in social-emotion regulation when interacting with others comes with more self-confidence, lower empathy for the opponent, lower levels of anxiety about the opponents' abilities, and higher motivation (wanting) to win (e.g., Chichinadze, Lazarashvili, Chichinadze, & Gachechiladze, 2012; Salvador & Costa, 2009).

We reason that postgame rise in T levels negatively affects the PFC-limbic coupling, which may come with more euphoria and pride when winning a contest, meaning that winners may have little compassion for people lower in ranking. However, we argue that postgame T levels do not automatically rise but are moderated by the team participants' genetic makeup. Concretely, because *DRD4* and *COMT* genes are expressed in the PFC and affect regulation of emotions during interactions with others, carriers of *DRD4* and *COMT* variants will show different T levels on winning the contest, as developed below. Second, because genetic markers have dimorphic properties we study whether their effects might be different between males and females (e.g., Harrison & Tunbridge, 2008). Third, we offer an additional hypothesis, related to the effect of pregame T levels on postgame T levels. Based on the earlier observation on PFC-limbic system coupling—that people have with high pregame T levels (indicating eagerness to win and self-confidence)—we hypothesize a stronger likelihood of experiencing higher postgame T levels no matter whether people win or lose the game. Fourth, because social context matters, we also control for contextual factors such as team size and team composition.

Neurobiological Mechanisms When Engaging in a Contest

We begin by describing the basic neurobiological mechanisms that explain how people go about the contest, extending the abovementioned research and presenting molecular mechanisms that allow us to make better connections between neuro-biological mechanisms and genetics.

When people are challenged on game entry, and then win or lose when the game is over, hormonal cascades occur in the peripheral nervous system and the central nervous system (CNS). A status challenge provokes the release of both norepinephrine (NE; arousal) and cortisol (C; stress/anxiety). First, the challenge activates the sympathetic-adrenal-medullary (SAM) axis. Through efferent nerves (in the sympathetic nervous system), the SAM axis targets the medulla of the adrenal cortex, triggering catecholamine release (NE) which positively affects T release in the testes and ovaries (see Stanton & Schultheiss, 2009). Second, the same challenge activates the amygdala, which reflects experienced stress or anxiety, which in turn affects the hypothalamus, which triggers the hypothalamus-pituitary-adrenal axis. The hypothalamus triggers corticotrophin-releasing hormone, which in turn affects the pituitary gland, which releases adrenocorticotrophin hormone in the blood stream to the adrenal cortex where it produces C, which feeds back into the brain affecting the functioning of the amygdala (fear) and hippocampus (memories of danger). Meanwhile, higher C levels also negatively affect T release in the testes (for a review, see Stanton & Schultheiss, 2009). Depending on whether more or less C (stress) or NE (challenge) is released, T levels will lower/rise accordingly.

Higher T levels also affect the brain (CNS) as T crosses the blood–brain barrier (Pardridge & Mietus, 1979). Consistently, fMRI-based research has revealed that higher T levels affect the connectivity between the PFC and the limbic brain nuclei (NAcc, amygdala, and hypothalamus), but other neuro-endocrine processes take place as well, which we will describe now. First, conceiving the contest as a challenge triggers NE release in the locus coeruleus. NE affects PFC functioning (density of α receptors for NE), which is involved in dominance (Cabib & Puglisi-Allegra, 2012). The PFC affects dopamine 2-type (D2) receptors in the NAcc, which activate the NAcc, and this in turn stimulates coping efforts when facing challenges (Cabib & Puglisi-Allegra, 2012). In addition, NE (produced in the locus coeruleus) is known to directly stimulate DA system functioning

(Sara, 2009) which, in turn, affects the NAcc and PFC functioning. Second, because higher T levels stimulate the amygdala, which is dense in T receptors, people are more alert to danger (higher T levels come with greater threat vigilance) (Blair, Morris, Frith, Perrett, & Dolan, 1999; de Souza Silva, Mattern, Topic, Buddenberg, & Huston, 2009; Whalen et al., 2001), and this motivates them to undertake quick action to face challenge from others. It is here that the connectivity between the PFC and amygdala subsequently decreases as the amygdala is intensely activated (see literature overview). For instance, young females administered with T were more prone to react vigilantly to negative-valence stimuli (e.g., Van Honk et al., 2001; see also overview of literature under "T Levels as Antecedents for Social Cognition and Behavior" above). Indeed, higher T levels limit PFC activation (Beer, John, Scabini, & Knight, 2006), and T release leads to lower cross communication between the PFC and amygdala (e.g., Bos et al., 2012; Van Wingen et al., 2010).

Candidate Genes and Their Effect on Postgame T Levels

Carriers of the *DRD4* 7R$^+$ versus *DRD4* 7R$^-$ allele, and carriers of the *COMT* Val$^+$ versus Met/Met allele moderate the PFC-limbic system coupling that undergoes change due to T levels (see Josephs et al., 2012). Both COMT and D$_4$ play key roles in regulating dopamine functioning in the PFC. D$_4$ (a D2-type) is expressed more in the PFC than in other nuclei in the DA system, such as NAcc (which expresses more D$_2$). COMT plays an important role in the PFC because DA transporter genes (*DAT*; which remove DA from the cleft) are less frequently expressed in the PFC, hence COMT becomes the main means by which DA is metabolized thus affecting dopamine functioning (such as in self-regulation).

The *DRD4* gene located on chromosome 11p15.5 codes for the DA D$_4$ (D2 type) receptor and includes in exon III a 48-bp variable number of tandem repeats (VNTR) polymorphism, which contains 2 to 11 repeats. This VNTR is located in a region that encodes the third cytoplasmic loop of the receptor that couples to G-inhibiting (G$_i$) proteins that affect adenylyl cyclase, which in turn affects the intercellular cAMP levels. This influences the cell's excitability and regulation of channels for potassium (K$^+$), which affects the polarization of the cell membrane (Wang et al., 2004). Carriers of the *DRD4* 7R$^+$ have blunted signaling in neurons. Rather than lowering the excitability of the neuron via G$_i$ proteins, they in fact provoke higher excitability than the 7R$^-$ carriers (Oak, Oldenhof, & Van Tol, 2000) and thus make a person more responsive to cues, such as rewards in the environment, both potential rewards (wanting and corresponding risk-taking preferences) and when winning (liking; e.g., Dreber et al., 2009 in a male population for financial risk preferences). In addition, many authors like Belsky et al. (2009) conceive the carriers of the 7R$^+$ as more sensitive to both positive and negative social environmental stimuli. Hence we conceive the 7R$^+$ as the dominant allele and classify people as carriers of 7R$^+$ versus no 7R$^-$.

Because *DRD4* is expressed mostly in the PFC, for the *DRD4* 7R$^+$ we expect the PFC (already negatively affected by T levels; Beer et al., 2006) to have lower control over limbic parts and so amplify the uncoupling of PFC and subcortical nuclei, leading to a change in social emotions. Specifically, players show higher vigilance and intense motivation during the game and this might result in higher T levels when they win (Chichinadze et al., 2012).

The *COMT* gene located at chromosome 22q11.23 codes for catechol-*O*-methyltransferase, an enzyme that breaks down the catecholamines DA and NE. As DA and NE are expressed in the PFC, we elaborate on how the difference in breakdown affects the connectivity between PFC and limbic nuclei (Bilder, Volavka, Lachman, & Grace, 2004). Special interest has been given to the functional single nucleotide polymorphism val158met (rs4680) in the *COMT* gene. The substitution of guanine with adenine results in a valine (Val) to methionine (Met) change at codon 158. Carriers of the *COMT* Val versus Met show quicker break down of catecholamines (NE and DA), and when DA breaks down quickly it affects DA levels. DA levels (heightened due to stress and challenge) affect PFC functioning, which operates according to an inverted U curve: levels too low or too high inhibit DA functioning and thus self-regulation), while middle DA levels show optimal PFC functioning (Meyer-Lindenberg and Weinberger, 2006). The effects in the PFC of the gene variants of *COMT* gene are known to be pleiotropic—one gene affects multiple phenotypic traits (Mier, Kirsch, & Meyer-Lindenberg, 2010)—and here that means that they might affect postgame T levels both when winning and losing. Based on the theory, choosing whether the Val allele or the Met allele is the dominant allele is difficult to decide. In general the carriers of the Met allele are better at self-regulation and thus they might have lower postgame T levels (see Mier et al., 2010). However, other authors (e.g., Dumontheil et al., 2011) simulate the combinations. Therefore we also simulated the Val dominance as the dominant allele and found that the Val dominance model did not result in the same predictions for females; actually none was significant. The reason might be that Met carriers (Met/Met and Met/Val) have better self-regulation and use more cognitive efforts in terms of strategizing, all of which is needed to win an intellectual status battle and makes people proud when winning. Therefore, we divided our population into carriers of the Met/Met and Met/Val variants versus the Val/Val carriers.

We reason that although Met carriers have optimal cognitive functioning (optimal DA levels) they might also be more prone to anxiety on being challenged (e.g., Mier et al., 2010; Meyer-Lindenberg and Weinberger, 2006). In fact, their ability to focus during the contest is higher as they have a lower breakdown of NE, which allows them to cope better, thus positively affecting T release, which is a benefit when engaged in a contest. However, it might also evoke stress and anxiety (C production), as sticking to plans might lead to less successful outcomes (thus T levels will be lower). Overall, we expect the Met^{+} carriers to have higher T levels as they put more effort into the contest and feel more pride in their own efforts on winning the game (Salvador & Costa, 2009). Equally, the carriers of the Val allele might experience less stress as they can switch strategies fast; concretely they might remain vigilant and aggressive as they have lower levels of self-control via PFC (e.g., Mier et al., 2010 finds the Val carriers to be more resilient). Even on losing the game, carriers of the Val allele might remain vigilant and have higher T levels (e.g., Gonzalez-Bono et al., 1999 showed higher T levels for losing basketball players).

Gender Differences

T is a particularly male hormone produced in the gonads (testicles and ovaries). Males might enter the game with different motives and degrees of competitiveness than females. Males are known to deploy a fight or flight strategy, whereas females tend to pursue a "tend and befriend" strategy (e.g., Taylor et al., 2000). In addition, males might be more ego-oriented, and females might be more task-oriented (Costa & Salvador, 2012). We explore whether gender is a significant variable in predicting winners and losers (Josephs et al., 2011). We expect that gender would be an important moderator in differences in postgame T levels on winning or losing the game. If gender is significant, the T levels will be analyzed separately for both populations.

Pregame T Levels Affecting Postgame T Levels

We explore pregame T levels because they are expected to affect postgame T levels when players either win or lose the status contest. The contestants in this study were skilled in this sort of competition; experience with competitions (winning or losing) has significant effects on T levels in both animals and humans (Fuxjager & Marler, 2010; Kloke et al., 2011). For example, winning increases T receptor expression in the ventral tegmental area and nucleus accumbens (NAcc), both part of the dopamine system which raises a person's eagerness and ability to win a contest (e.g., Fuxjager et al., 2010). Higher pregame T levels might indicate anticipation of victory (e.g., Chichinadze et al., 2012), efforts undertaken during the contest (Salvador & Costa, 2009), and previous winning experience (Gleason et al., 2009), which also affect T levels when players either win or lose the contest.

Contextual Variables and Postgame T Levels

Hormones do not cause behaviors but they help people navigate the social environment. Hormone levels are affected by the social environment or social context (e.g., Bartz, Zaki, Bolger, & Ochsner, 2011). We explore whether social environmental factors such as team size and gender composition of the team (males and females or mixed) and offering monetary incentives (yes–no) play any role. No concrete hypotheses will be made.

Method

Participants

A total of 173 Dutch students (107 males and 66 females; average age 25.4 years) earned credits for participating in the research, which was a component of a Master's program in Business Economics. The Medical Ethics Committee of the Erasmus MC Rotterdam approved the study. Participants prepared for the game by reading the game manual, which was given to them well in advance. During the game, participants answered a biographical questionnaire.

The Game

We used a sales management game which is a computer simulation used frequently to train managers operating in teams in how to make better managerial decisions (Patton, 1994). The sales game requires that four teams of "real managers," composed of the participants in this study, manage four virtual sales teams employed by four virtual firms in the world of the computer simulation. The number of real managers might vary (some teams consisted of three to six players). The participants had to discuss and decide how to make their virtual sales team most effective. The team ending with the highest cumulative earnings in the virtual world was designated the winner. Making a team effective requires taking such decisions as which salesperson to hire from a list of salespeople mentioned in the game, and how to compensate, train, and coach the sales teams throughout the game. All decisions are represented as options on a dashboard of the sales management game. Students knew how to play the game as they had played similar business simulations in other classes (e.g., Larréché & Gatignon, 2000). In all conditions, the names of the winning management team were announced on the classroom blackboard.

The game was played in four rounds, representing the four quarters of a year. Decisions are made under pressure and with each quarter the time to make management decisions gradually decreases, from 60 minutes for the first quarter, to 45, 30, and 20 minutes for the second, third, and fourth quarters, respectively. Between rounds, all four sales management teams receive updates on what happened in their sales team and they also could get information about the standings of the other teams.

The games were played by students in class of a Business Economics program, for which they earned credits. Asking students to participate is akin to convenience sampling and implies only limited control over gender, ambition, or other variables that characterize the participants. Thus, we created teams, which we controlled for gender or monetary rewards. Occasionally students did not show up for games (some were ill or had other obligations such as job interviews) and then we reconfigured the teams, based on the people available to us.

In half of the game sessions all participants were promised a monetary reward if they won; in other sessions no participants received monetary rewards. In addition, participants were invited to play the game once or twice (the second time with completely new team members) depending on the availability of places and their opportunity to play; NB: not all participants did actually play twice. We controlled for this contingency in the data analyses.

Procedure

One week before the start, participants were reminded of the upcoming game. They were asked to maintain their usual daily rhythms in terms of sports and sleep the day before and on the day of the game. They were asked to refrain from smoking, consuming alcohol, chocolate, tea, or coffee during the game, but they could drink water. All participants received verbal information about the study and signed the written consent form.

The game was played between 11.30 a.m. and 5.00 p.m. to minimize the effects of circadian fluctuations in T levels (Touitou & Haus, 2000). On arrival, students were randomly assigned to a team in a four-team market. Sales management teams had two, three, four, and five participants. At the onset, all sales management teams gathered in the instruction room for a detailed explanation of the aims and rules of the game, even though all participants had been asked to read the game manual in preparation. During this session, participants were instructed not to smoke, eat, or drink (except water). Immediately after the introduction, 30 minutes after entering the room, precontest saliva samples were collected.

Each team was placed in a separate room, equipped with a computer on which to play the game. In a fifth room, the researchers monitored the game and provided feedback. At the close of each quarter, the sales management teams sent their proposed strategy to the central computer that calculated the new results and produced a quarterly report, including information on the outcomes of decisions, such as sales revenue, company profits, and a list of current staff (indicating successful or failed attempts to hire new salespeople). The researchers handed these progress reports to the teams at the onset of each new round. The reports included data on the performance of the other sales management teams, thus giving teams their current ranking and setting the stage for status comparisons.

After the fourth round, all teams met back in the instruction room to hear the final ranking announcement. Students waited an additional 25 minutes, during which they filled in the questionnaires and refrained from smoking, eating, and drinking. Finally, the postgame saliva sample was collected.

Biological Assessments

Hormone assays. Saliva samples were obtained with Sarstedt Salivette devices following standard salivary hormone collection procedures (Schultheiss & Stanton, 2009). The participants chewed on a synthetic swab at the onset of the game, and 25 minutes after disclosure of the final sales management team rankings. The samples were stored at −20°C until analyzed for T concentrations.

Free testosterone levels in saliva were analyzed with a commercially available ELISA kit (Demeditec Diagnostics, Kiel, Germany). The limit of detection was 34.7 pmol/L. The inter- and intraassay coefficient of variation was lower than 10%.

Genetic testing. All genotyping was performed blind to demographic and clinical data. DNA from saliva was collected using the Oragene DNA Self-Collection Kit (DNA Genotek, Ottawa, Ont., Canada) and purified from 500-μl aliquots using the ethanol precipitation protocol as described by the manufacturer. Purified DNA was dissolved in 100-μl of TE buffer [10 mM Tris-HCl, 1 mM ethylenediaminetetraacetic acid (EDTA), pH 8.0] and stored at −20°C.

Results

From the 173 respondents in the data set, we deleted participants with incomplete hormonal or DNA analysis, which reduced the sample size to 157 (99 men and 58 women). To test whether the business game situation affected participants' hormonal reactions, we computed t tests comparing the average T level before and after the game. The postgame T level was significantly lower than the pregame one (men: pregame $M = 209.1$ pmol/L, postgame $M = 187.3$ pmol/L; mean difference = 21.8, $t = 3.00$, $p = .003$; women: pregame $M = 112.5$ pmol/L, postgame $M = 96.9$ pmol/L; mean difference = 15.6 pmol/L, $t = 2.38$, $p = .021$) suggesting that testosterone production occurs mostly in anticipation of a contest (Wingfield, 2005; see Table 1).

All analyses below were conducted for males and females separately because of natural differences in testosterone concentration between genders, as shown in Table 1. To test for the influence of achieved status after the game (i.e., winning or losing), genetic makeup on DA receptor D4 (*DRD4*), and catechol-O-methyltransferase gene (*COMT*), we conducted an ANOVA using *DRD4* (7R$^+$ vs. other variants), *COMT* (Met/Met and Val/Met variants vs. Val/Val), and game ranking (win/lose) as independent variables and the T level as measured after

Table 1
Differences Between Pre- and Postgame Testosterone Levels for Men and Women

Gender	Pregame testosterone *M* (*SD*)	Postgame testosterone *M* (*SD*)	*t* value		Pregame testosterone *M* (*SD*)	Postgame testosterone *M* (*SD*)
Men	209.103 (96.703)	187.318 (89.935)	3.00 ($p = .003$)	Win	191.104 (74.217)	193.848 (123.060)
				Lose	215.184 (102.931)	185.112 (76.550)
Women	112.522 (58.657)	96.921 (47.608)	2.38 ($p = .021$)	Win	110.454 (60.383)	113.408 (71.391)
				Lose	113.120 (58.831)	92.158 (37.982)

the game as the dependent variable. The genotype frequencies for *DRD4* are 7R$^+$ $N = 48$ (31%) and the other variants $N = 109$ (69%); the genotype frequencies for *COMT* are Val $N = 37$ (24%) and the other variants $N = 120$ (76%).

Table 2 shows the gender composition of the genetic groups. The relative frequencies of the genotypes in our study are comparable with earlier findings, for example, another study conducted in Hungary found that 29% of the nonclinical sample (in our Study 31%) showed at least one 7-repeat allele (Lakatos et al., 2000), and a study on Caucasians in the U.K. by Hoda et al. (1996) found that 23% of their nonclinical sample showed *COMT* Val/Val variant (in our Study 24%).

In addition, the genotypes of the *DRD4* and the *COMT* gene are in Hardy-Weinberg equilibrium (e.g., for *COMT*: men – sum chi-square = 0.462, $p = .497$; women – sum chi-square = 0.610, $p = .435$; for main *DRD4* genotypes 4/4, 4/7, and 7/7: men – sum chi-square = 0.054, $p = .816$; women – sum chi-square = 0.054, $p = .817$).

We controlled for the pregame T level as measured before the game. T is an indication of implicit dominance, motivating individuals to achieve or maintain status (Eisenegger et al., 2011) and it affects vigilance during a status contest (Stanton & Schultheiss, 2009). Because some participants played the game twice, we included an additional control variable denoting whether participants were participating for the first or second time. Next, because some sessions had a monetary incentive and others not, half the participants were promised a monetary reward if they won. We also controlled whether participants were in the monetary condition or not. Because the sales management teams consisted of two to five players (because of nonavailability of students), team size was another control variable. Finally, teams differed randomly in terms of gender composition, that is, some teams consisted only of male participants, others only of female participants, and others had a mixed gender composition. We therefore added gender composition of the team (only male, only female, mixed male and female) as an additional control variable to the analyses. The partial eta-squared (η^2) was calculated to show the explained variance of a particular variable on postgame T level as an estimate of the effect size. We computed the observed power per variable.

Table 3 shows the ANOVA results. In step 1, we computed only the main effects of the variables. In step 2, we added the two interaction effects between status information and genetic dispositions of the participants. For male participants, we found a significant interaction effect between status information (winning vs. losing) and *DRD4*, $F = 4.46$, $p = .038$. The effect of the pregame T level was also significant, $F = 74.68$, $p < .001$. The four other control variables had no significant effect on the postgame T level (game played for money: $F = 1.74$, $p = .190$; game played first or second time: $F = 0.07$, $p = .784$; team size: $F = 0.87$, $p = .355$; team gender composition: $F = 0.39$, $p = .534$).

For female participants, the interaction effect between status information and *DRD4* variants was not significant, $F = 2.39$, $p = .129$. Instead, we found a significant interaction between winning versus losing and the *COMT* gene variants on postgame T level, $F = 6.92$, $p = .011$ for females (but not for males). The effect of the pregame T level was also significant for females, $F = 25.86$, $p < .001$, whereas the other control variables had no significant effect on postgame T level (game played for money: $F = 1.16$, $p = .287$; game played first or second time: $F = 2.91$, $p = .094$; team size: $F = 0.21$, $p = .652$); team gender composition: $F = 0.96$, $p = .333$).

Figure 1 illustrates the direction of the significant interaction effect found for male participants. To facilitate interpretation of the significant interaction between an individual's rank in the contest and their genetic disposition, we plotted the relationship between status and postgame T level for the 7R$^+$ variant versus other variants of the *DRD4* gene. Figure 1 shows the results. Male participants with the *DRD4* 7R$^+$ variant in the winning condition clearly showed the highest postgame T level of all groups. The

Table 2
Genotype Frequencies of DRD4 and COMT Genes in Men and Women

Gender	*DRD4* 7R $^+$	*DRD4* other variant	*COMT* Val/Val	*COMT* other variant
Men	33	66	29	70
Women	15	43	8	50

Table 3
ANOVA Results for Postgame T Level

	Step 1				Step 2			
Measure	*F*	*p*	η^2	Observed power	*F*	*p*	η^2	Observed power
Men (*n* = 99)								
Status (win/lose)	2.732	.102	.029	.373	3.098	.082	.034	.413
DRD4	.108	.744	.001	.062	1.472	.228	.016	.224
Status × *DRD4*					**4.459**	.038	.048	.551
COMT	.010	.920	.000	.051	.086	.770	.001	.060
Status × *COMT*					.189	.665	.002	.071
Pregame T level	**77.204**	.000	.462	1.000	**74.678**	.000	.459	1.000
Team size	1.513	.222	.017	.229	.866	.355	.010	.151
Played for money (yes/no)	1.842	.178	.020	.269	1.743	.190	.019	.257
Round played (first/second)	.126	.724	.001	.064	.076	.784	.001	.059
Team gender composition	.404	.526	.004	.096	.389	.534	.004	.095
Women (*n* = 58)								
Status (win/lose)	4.045	.050	.076	.505	.973	.329	.020	.162
DRD4	.181	.673	.004	.070	2.451	.124	.050	.335
Status × *DRD4*					2.388	.129	.048	.328
COMT	1.992	.164	.039	.283	.136	.714	.003	.065
Status × *COMT*					**6.922**	.011	.128	.731
Pre-game T level	**27.365**	.000	.358	.999	**25.855**	.000	.355	.999
Team size	.084	.773	.002	.059	.206	.652	.004	.073
Played for money (yes/no)	1.842	.181	.036	.265	1.161	.287	.024	.184
Round played (first/second)	3.939	.053	.074	.494	2.914	.094	.058	.387
Team gender composition	1.665	.203	.033	.244	.957	.333	.020	.160

Note. Bold values indicate statistical significance at the level of $p < .05$.

T levels of the three other groups were similar to one another.

Figure 2 shows the direction of the significant interaction effect found for female participants. Here, we plotted the relationship between status and postgame T level for the Val variant versus other variants of the *COMT* gene. Female participants with the *COMT* Val/Val variant

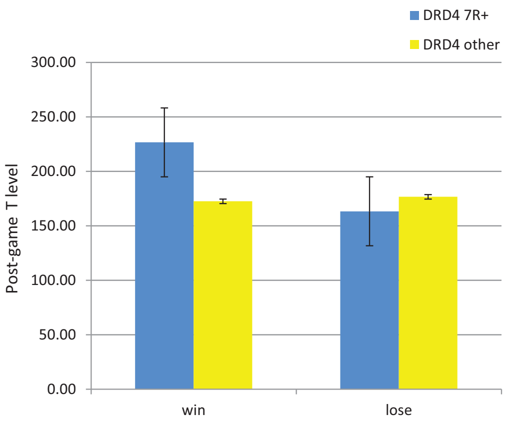

Figure 1. Interaction effect of status/*DRD4* on postgame T level (pmol/L) for male participants (error bars are ± 1 standard error from the mean). See the online article for the color version of this figure.

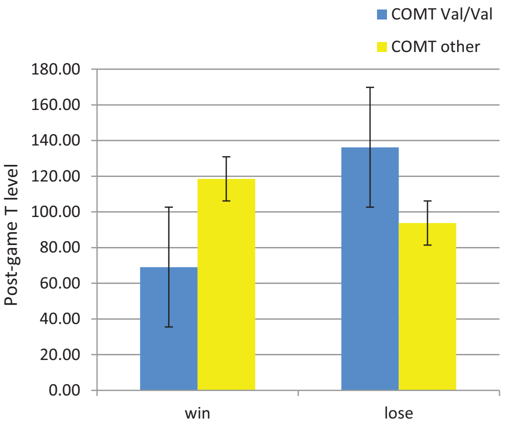

Figure 2. Interaction effect of status/*COMT* on postgame T level (pmol/L) for female participants (error bars are ± 1 standard error from the mean). See the online article for the color version of this figure.

showed the lowest postgame T level of all groups in the winning condition and the highest postgame T level of all groups in the losing condition. Female participants with one of the other variants of the *COMT* gene showed the opposite pattern. Their postgame T level was lower in the losing than in the winning condition.

To confirm the moderation effect of gender we also computed the same analysis as described above for the overall combined sample of males and females (with gender added only as a control variable). Indeed, both interaction effects of the *DRD4* and the *COMT* gene reported above dropped to a nonsignificant level ($F = 2.00$, $p = .159$, and $F = 3.26$, $p = .073$, respectively), here indicating that gender acts as a statistically reliable moderator of these interactions.

Discussion

T levels are known to affect the vigilance of people in various status challenging situations which fits the biosocial status and challenge hypotheses, both of which are ultimate explanations (Blumstein et al., 2010). However, research thus far on the relationship between T levels and status challenging situations for humans show that the findings based on these biology-based hypotheses are far from parsimonious (see literature review under “T Levels as Antecedents for Social Cognition and Behavior” above). The main reason is that proximal explanations are sensitive to how people with different personality traits strategize in specific social contexts. Here we explored postgame T levels and focused on whether the T levels of players were affected by membership in the winning versus losing team in a team status game; specifically a sales management game. In general, we expected that winning a contest will not automatically result in higher postgame T levels but is moderated by a variety of factors such as coping styles and personality variables (see literature overview under “T Levels as Antecedents for Social Cognition and Behavior” above, especially Salvador, 2005). We followed well-established literature on how T levels affect the PFC-limbic system coupling (e.g., Beer, Lombardo, & Bhanji, 2010) and argued that it affects emotion regulation when people are confronted with others, resulting in lower empathy, higher self-confidence and eagerness to attain status.

We focused on three main hypotheses about postgame T levels once higher status was gained. First, as *COMT* and *DRD4* genes are densely expressed in the PFC they affect regulation of emotions when confronted with others who challenged their status (e.g., lower compassion with people lower in the ranking). Actually, in this study the polymorphisms of these genes moderated postgame T levels. Second, we explored the possible moderating effect of gender and found that it had a significant effect on the T levels on winning. Therefore, we did separate analyses for males and females and found that the moderating effect of genes differed by gender. This splitting of the data is not surprising given the fact that the genetic literature has shown gender differences in genetic dimorphisms such as the *COMT* gene (e.g., Harrison & Tunbridge, 2008). Third, we hypothesized that higher pregame T levels come with higher postgame T levels no matter whether players win or lose. Finally, we controlled for contextual variables because postgame T levels are sensitive to how people interact with their social environment, as indicated in the literature overview (under “T Levels as Antecedents for Social Cognition and Behavior” above). Here we explored the possible effects without actually making a hypothesis.

Two notes need mentioning before we delve into the discussion. First, note that we used pregame T levels (which affect the PFC-limbic coupling during the game) and not baseline T levels (measured a day before the game) as this is in accordance with biosocial status theory and the challenge hypothesis. Second, pregame T levels were higher than postgame levels which fits some ideas expressed in the challenge hypothesis that T levels lower after a contest (Wingfield et al., 1990). This might be typical for the study population: given that the players were business students seeking prestigious jobs, their motivation to gain status played an important role in their minds. Once the game starts it actives this mind-set indicating a high degree of anticipation to win or the desire to defend one’s established reputation (e.g., Chichinadze et al., 2012).

Male but not female carriers of *DRD4* $7R^{+}$, compared with $7R^{-}$, experienced greater T change on winning versus losing. In general, carriers of the *DRD4* 7R$^+$ have blunted cellular signaling which lowers PFC control, making them more vigilant when winning over competitors. More specifically, carriers of the *DRD4* 7R$^+$ exhibit strong reward dependencies and will remain excited about winning. Comings et al. (2001) show that carriers of *DRD4* 7R$^+$ undertake pathological behaviors such as gambling more often and others have shown that carriers engage in sensation seeking, risk taking, and novelty seeking when a situation gives them the opportunity (Dreber et al., 2009).

Female, but not male, carriers of the *COMT* Met allele, who win versus lose, break down NE and DA less quickly in the PFC, leading to optimal self-regulation, which allows them to develop stable strategies during the game. When they win, because of their cognitive efforts, their T levels rise. This makes them feel truly dominant over others and proud of their own efforts in the game (Costa & Salvador, 2012). Surprisingly, female carriers of the *COMT* Val-Val allele metabolize DA more quickly, leading to lower PFC control over processes in the striatum and amygdala (making them "warriors"), and when they lose they show higher T levels, which resonates with Mier et al. (2010) observation that the carriers of the Val-Val are more resilient in the face of anxious moments. Note that Filaire et al. (2001) made a similar observation that losers had high T values compared to winners, yet this was in a male population. In other terms, carriers of the Val-Val *COMT* gene respond more vigilantly to a challenge (higher T levels), which in this case also occurs on having lost the game. These findings, that the same gene comes with two genotypes, are noteworthy as they confirm that the *COMT* gene has pleiotropic effects (Mier et al., 2010).

Neither team size nor team composition (male-female-mixed) had any effect on the postgame T levels, which might indicate that by focusing on neural-biological mechanisms social context matters less in our team-based status game. Remarkably, playing for money (or not) made no difference in the postgame T levels achieved. Loch, Yaziji, and Langen (2001) observed that when people compete for status, financial stimuli do not matter much, because seeking (and achieving) status is in itself sufficient. Note that being announced winner in the class (on the blackboard) might be perceived as a reward and in turn, this might indicate that status alone is enough of a reward. In this regard, it might be productive to speculate somewhat differently about the game. Salvador (2012, p. 79) argues, "[P]articipation in competitive sports is one way that aggressive behavior is ritualized among humans." Similarly, our status contest involves a competitive element but it might be framed as a serious game in which people implicitly learn management strategies (see also Schultheiss & Schiepe-Tiska, 2013). The "gamification" perspective (Werbach & Hunter, 2012) conceives this status contest as a game, making it akin to a magic circle separated from the rest of the world. People step into this magic circle, suspending the rules of the real world, and explore it as if it were real. Huizinga regards gaming as an essential part of being human and thus calls us Homo Ludens (Man the Player) because people essentially love to play and create new ideas (e.g., Kerr & Apter, 1991). Gaming is not just typical of humans. Young animals also enjoy play (it triggers the reward system) during which they practice various repertoires, ranging from boxing to pinning down prey, allowing them to learn social and nonsocial behaviors (Trezza, Baarendse, & Vanderschuren, 2010).

Exploring status contests is ecologically valid and advantageous in that they entail high ego involvement (e.g., Salvador, 2005). However, they make it harder to pinpoint the complex endocrine/neural mechanisms that explain postgame T release compared to clear experiments, where T is administered, or when winning or losing is experimentally induced (see literature overview under "T Levels as Antecedents for Social Cognition and Behavior" above and also Eisenegger et al., 2011). However, Josephs et al. (2012) used a set of heterogeneous experiments (status threats, cognitive/perceptual failure, and physical competence) to study the relationship between human genetic makeup (*5-HTTLPR* variants) and T and C levels (see also Mehta et al., 2013, for an overview on genetic makeup and aggressive behavior in a variety of contexts). More to the point, the associations between postgame T levels and genetic variants should be conceived of as associations not causal mechanisms, yet that should not deter us from making theoretical statements.

We did find lower postgame T levels, which besides confirming components of the challenge hypothesis (lower levels of T after the challenge) might have been the result of late collection of saliva. There is no agreement on when exactly to ask people to donate saliva to gauge postgame T levels. Just some examples: Lopez et al. (2009) and Apicella, Dreber, and Mollerstrom (2014) use 30 minute-window; Van Anders and Watson (2007) use a 25-min time window; Pound et al. (2009) take a 20-min time window; Carré et al. (2009) uses a 10-min time window while Booth et al. (1989) take a smaller time window (i.e., directly after the contest). Future research should consider different time frames after a contest to gauge postgame T levels.

Future research could study baseline T levels in addition to pregame T levels study, that is, not in anticipation but one or more days before the game (as the social-based status theory and the challenge hypothesis would indicate). Baseline T levels would then reflect a personality trait and this could add new information (see literature overview under "T Levels as Antecedents for Social Cognition and Behavior" above). However, T levels vary considerably during the day, so these T level measures should be gathered at many times of the day, making data collection more complex and expensive.

Future research should study the questions raised by the design of our study: people could play the game anonymously with no public consequences (experimental condition) and, as in our study, with public consequences in all conditions. Would this design affect pregame T levels (e.g., longer anticipation in-group experiment) and postgame T levels on winning? Would the associations of *DRD4* and *COMT* polymorphisms with postgame T levels found in our study still hold?

Further research is needed on T levels in relation to reward. Could people with high pregame T levels be (more) addicted to winning and/or gaming? In different environments (schools, organizations), people take part in many games, both formal and informal. Would people display similar behavior/ambitions in these different game contexts?

To the extent that serious gaming is an important tool for studying status contests—where players are intrinsically motivated to compete—we should not only study whether people win or not, but how they win in terms of the strategies they use or how they develop strategies together with teammates. We might ask such questions as, "What did you learn from this game?" or "Do you look at the game differently now that you have won (or lost)?" or "Did you explore this game systematically, alone or with a few people?" Again, would carriers of *DRD4* 7R$^+$, known to love exploration and who focus on opportunities, turn out to be better explorers or learners?

Finally, our study has a relatively small sample size and therefore interpretations should be done cautiously, as goes for many other studies as well (e.g., Little et al., 2009).

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