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Testosterone responses to competition predict future aggressive behaviour at a cost to reward in men

Justin M. Carré [a,1], Susan K. Putnam [c,2], Cheryl M. McCormick [a,b,*]

[a] Psychology Department, Brock University, St. Catharines, Ontario, Canada
[b] Centre for Neuroscience, Brock University, St. Catharines, Ontario, Canada
[c] Psychology Department, Canisius College, Buffalo, NY, United States

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Summary The extent to which trait factors (baseline testosterone concentrations, trait dominance) and state factors (change in social status, change in testosterone concentrations) would predict reactive aggression in a subsequent task that involved provocation was examined in 99 participants (39 men and 60 women). Participants first competed in same-sex dyads on a Number Tracing Task for which the outcome (win or loss) was rigged. After the competition, participants performed the Point Subtraction Aggression Paradigm (PSAP), a behavioural measure of reactive aggression against an opponent (actually a computer program). Trait dominance predicted baseline testosterone in men, but not women, and men made more aggressive responses than did women. Baseline testosterone concentrations did not predict aggressive behaviour in either men or women. Winners and losers did not differ in competition-induced change in testosterone. However, change in testosterone concentrations predicted aggressive responses in the PSAP for men in the loss condition, and aggressive responses were made at a cost to obtaining reward points. For men in the win condition, aggressive responses were predicted by an interaction between trait dominance and change in testosterone concentrations. These findings suggest that situational changes in testosterone concentrations modulate future aggressive behaviour in men.

1. Introduction

The World Health Organization has estimated that for every death due to physical aggression, another 20—40 youth require hospital treatment for an aggression-related injury (Mercy et al., 2002). The variety of ways in which aggressive behaviour is manifested (e.g., ''road rage'', bullying, child abuse, domestic abuse and workplace violence) indicates the multifaceted nature of this behaviour. Despite the negative consequences of aggressive behaviour, the use (or threat) of

* Corresponding author at: Psychology Department and Centre for Neuroscience, Brock University, 500 Glenridge Ave., St. Catharines, Ontario L2S3A1, Canada. Tel.: +1 905 688 5550x3700.
E-mail addresses: justin.carre@brocku.ca (J.M. Carré), putnams@canisius.edu (S.K. Putnam), cmccormick@brocku.ca (C.M. McCormick).
[1] Tel.: +1 905 688 5550x3109.
[2] Tel.: +1 716 888 2895.

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aggression can be beneficial under certain conditions (e.g., athletic competition, self-defense, derogation of same-sex rivals and establishment of status hierarchies). Psychobiological investigations of the factors contributing to the expression of aggressive behaviour have identified many of the individual differences and situational factors that are associated with aggression, although most investigations in people have relied on self-report measures (see reviews by Anderson and Bushman, 2002; Bettencourt et al., 2006; Trainor and Nelson, 2007).

Dominance is a personality trait that involves the desire to seek control and/or influence over social situations, events, and relationships (Mehrabian, 1996). Although trait dominance is theoretically and empirically related to aggression, there have been few studies of the relationship between the two variables (Bettencourt et al., 2006). Individual differences in trait dominance predicted trait aggression as measured by self-report (Archer and Webb, 2006; Johnson et al., 2007), and men tend to score higher than women on self-report measures of trait dominance (Budaev, 1999; Costa et al., 2001) and on several measures of aggression (Archer, 2004). Given the empirical relationship between trait dominance and self-report aggression, it is plausible that trait dominance would also be related to behavioural aggression.

Testosterone is a biological factor of relevance to aggressive behaviour and to dominance in many species (reviewed in Simon and Lu, 2006; Trainor and Nelson, 2007). There have been reports of a positive association between self-report trait dominance and baseline testosterone concentrations (Cashdan, 1995; Grant and France, 2001; Sellers et al., 2007), although others have failed to replicate this finding (see Josephs et al., 2006; Stanton and Schultheiss, 2007). The relationship between baseline testosterone concentrations and various forms of aggressive behaviour is less evident in studies of people than in other animals (Book et al., 2001; Archer et al., 2005). The inconsistent findings for aggression may be due, in part, to the use of self-report measures as opposed to the direct measurement of aggressive behaviour (but see Pope et al., 2000; Klinesmith et al., 2006). Further, dynamic fluctuations in testosterone concentrations may be more related to aggressive behaviour than are baseline testosterone concentrations (Hermans et al., 2008). We recently found that baseline testosterone concentrations did not predict aggressive behaviour, but that aggressive behaviour was positively correlated with a rise in testosterone (Carré and McCormick, 2008). This result mirrors the findings of a study in non-human primates in which baseline testosterone concentrations did not predict aggressive behaviour, but aggressive behaviour was positively associated with a rise in testosterone concentrations (Ross et al., 2004).

Social interactions are known to modulate testosterone concentrations. For instance, winning competitive interactions (reviewed in Mazur and Booth, 1998; Archer, 2006; van Anders and Watson, 2006), good individual athletic performance (Edwards et al., 2006), the vicarious experience of victory and defeat (Bernhardt et al., 1998), and interactions with an attractive member of the opposite sex (Roney et al., 2003, 2007) all lead to changes in salivary testosterone concentrations. Dynamic shifts in testosterone concentrations have been proposed to influence future competitive and/or aggressive behaviours (Wingfield et al., 1990; Mazur, 1985; Mazur and Booth, 1998). A few studies have directly tested this hypothesis. For example, among losers (but not winners) of a competition, men whose testosterone concentrations had risen were more likely to choose to compete again, whereas men whose testosterone concentrations decreased chose the non-competitive option (Mehta and Josephs, 2006). We have also shown that changes in testosterone concentrations and aggressive behaviour during a competition predicted subsequent choice of a novel competitive task over a non-competitive task (Carré and McCormick, 2008). Furthermore, experimental studies have demonstrated that exogenous testosterone administrations increased cardiac responses to angry faces (van Honk et al., 2001), decreased fear-potentiated startle (Hermans et al., 2006a), increased visuospatial performance (Aleman et al., 2004), increased subcortical responses to angry faces (Hermans et al., 2008), decreased empathetic behaviour (Hermans et al., 2006b), and decreased conscious detection of angry faces (van Honk and Schutter, 2007). Although these studies support the idea that situational or experimental changes in testosterone concentrations are functionally related to future social behaviours, they do not speak to the issue of whether such changes in testosterone concentrations predict future aggressive behaviour.

Evidence from animal models suggests that the relationship between testosterone concentrations and future aggression is causal. A study of castrated male mice on low testosterone replacement found that those receiving a testosterone injection after a successful aggressive encounter were more aggressive in subsequent encounters compared to those that received a saline injection after a successful aggressive encounter (Trainor et al., 2004). One study has investigated the influence of a situation-specific change in salivary testosterone concentrations on future aggressive behaviour in people by comparing men who were given the opportunity to interact with a toy gun or a board game (Klinesmith et al., 2006). Men who interacted with the toy gun were more aggressive (as defined by the amount of hot sauce placed in another's drink) compared to men who interacted with the board game. Importantly, the relationship between type of interaction and extent of aggressive behaviour was mediated by a rise in salivary testosterone concentrations, suggesting that testosterone was a factor influencing aggressive behaviour.

The studies above show relationships between either trait factors and aggressive behaviour or state factors and aggressive behaviour. The General Aggression Model (GAM) (Anderson and Bushman, 2002) posits that trait/personological factors (including personality traits, gender, attitudes and genetic predispositions) and state/situational factors (including features of the situation or environment such as the presentation of provocation, aggression cues, level of frustration and pain) influence various cognitive, emotional, metabolic and arousal mechanisms that mediate aggressive behaviour. However, studies of how trait and state factors interact to predict aggressive behaviour are lacking. We tested the hypothesis, derived from the literature reviewed above, that a competition-induced change in testosterone concentrations would predict subsequent aggressive behaviour as measured using the Point Subtraction Aggression Paradigm (PSAP). We included trait dominance as an individual difference variable and tested how this variable was associated with testosterone concentrations. Furthermore,

based on previous self-report studies (Archer and Webb, 2006; Johnson et al., 2007), we predicted that trait dominance would be positively related to aggressive behaviour. Based on a few previous studies (Grant and France, 2001; Sellers et al., 2007), we also predicted that individual differences in baseline testosterone concentrations would be positively related to trait dominance. We included gender as a variable in our analyses because although men have higher concentrations of testosterone, are more physically aggressive (Archer, 2004), and have higher trait dominance scores (Budaev, 1999; Costa et al., 2001), the research literature is equivocal as to whether the relationships among these variables might differ for men and women (Dabbs and Hargrove, 1997; Mazur et al., 1997; Bateup et al., 2002; Kivlighan et al., 2005; Edwards et al., 2006; Josephs et al., 2006; Mehta et al., 2008).

2. Methods

2.1. Participants

Participants were recruited from the Canisius College Psychology Department, and all procedures were approved by the Canisius College Institutional Review Board. The sample consisted of 39 men (mean age = 19.51, S.D. = 2.86) and 60 women (mean age = 18.88, S.D. = 1.03). An additional two men and two women were not included in the sample because they were taking prescription medications (ritalin, antidepressants and thyroxin).

2.2. Trait dominance questionnaire

Participants first completed a brief 10-item questionnaire assessing trait dominance (International Personality Item Pool Scales (IPIP); Goldberg et al., 2006). The IPIP dominance sub-scale is highly correlated with the 6-item dominance subscale of the 6 factor personality questionnaire ($r = 0.79$) (Goldberg et al., 2006). Internal reliability was high in the current sample (Cronbach alpha = 0.81). Some examples of items measured by the scale include: ''Like having authority over others'', ''Want to be in charge'', and ''Have a strong need for power''. Responses were scored on a Likert scale ranging from −2 (very inaccurate) to +2 (very accurate). The highest obtainable score with this scale is +20 and the lowest is −20.

2.3. Competition using the Number Tracing Task (NTT)

The Number Tracing Task (NTT) is a competitive task that requires participants to compete against each other on a series of puzzles, and was administered according to the methods of Schultheiss and colleagues (Schultheiss et al., 1999; Schultheiss and Rhode, 2002). Briefly, participants were told that the NTT is an important measure of perceptual processing speed that consists of several puzzles containing grids of numbers. Participants were instructed to trace through numbers in sequential order as fast as possible until they reached a highlighted number. Upon reaching the highlighted number, participants were instructed to shout 'done', and this indicated that he/she had completed that particular round of the competitive interaction, with the first to completion designated the winner. Participants competed against each other on 12 puzzles. Unknown to participants, the outcome of the competitive interaction was rigged, in that half of the participants received eight easy and four hard puzzles, and the other half received four easy and eight hard puzzles, experimentally creating a 'winner' and 'loser'. The NTT took approximately 15 min to complete.

2.4. Point Subtraction Aggression Paradigm (PSAP)

The PSAP was originally designed by Cherek (1981) to measure aggressive behaviour in response to provocation in a controlled laboratory environment. Male parolees convicted of violent crimes were significantly more aggressive on the PSAP than male parolees convicted of non-violent crimes (Cherek et al., 1996, 1997), which supports the validity of the PSAP as a measure of aggressive behaviour. Also, other studies have demonstrated that aggressive behaviour on the PSAP is moderately correlated with various self-report measures of aggressive behaviour (Gerra et al., 2001, 2007; Golomb et al., 2007). The original PSAP task takes approximately 3 h to complete, although similar results are obtained with shorter versions (Golomb et al., 2007). We designed a 40 min version of the task (see Carré and McCormick, 2008). In brief, participants were led to believe that they were playing the computer game with the same partner (same-sex) that they were paired with in the previous NTT competition. They were instructed that they could obtain points (later exchangeable for money) by pressing button #1 on a standard keyboard a hundred consecutive times. Once they completed the 100 presses, their point counter would flash several times with positive signs around it and increase by 1 point. Participants were told that throughout the task, their point counter may flash several times with negative signs around it and decrease by 1 point. This indicated that their partner had stolen a point from them. Participants were told that points taken from them would be added to their partner's point total. Participants could respond in one of three ways: continue to hit the point reward option (button #1) or choose to select button #2 or button #3. Hitting button #2 (aggression response) 10 times would result in one point being stolen from their partner. However, participants were instructed that they were randomly assigned to the experimental condition whereby the points that they stole would not be added to their point counter. If participants hit button #3 (protection response) 10 times, this resulted in a provocation-free interval, whereby their point counter would be protected from point subtractions from their partner for a variable amount of time. Thus, the three response options available were option #1 (reward), option #2 (aggression) and option #3 (protection).

2.5. Testosterone assay

Saliva samples were collected in polystyrene culture tubes from participants before the NTT competition and 10 min after the NTT competition. Samples were stored at −20 °C until assayed using commercial enzyme immunoassay kits (DRG International, Inc.). All samples were assayed in duplicate and on the same day. The intra- and inter-assay coefficients of variation reported by DRG were below 10%, and the

Table 1 Mean (S.E.M.) salivary testosterone, trait dominance scores, and Point Subtraction Aggression Paradigm (PSAP) responses for men and women.

	Men	Women	*p*-Value
Baseline testosterone (pg/mL)	119.43 (14.61)	20.74 (3.37)	<0.001
Post-testosterone (pg/mL)	94.77 (9.41)	17.02 (2.73)	<0.001
Trait dominance scores	8.64 (0.88)	5.75 (0.74)	0.01
PSAP responses			
Reward	2421.27 (52.49)	2458.56 (51.76)	0.63
Aggression	280.76 (24.52)	220.37 (19.03)	0.05
Protection	310.85 (20.28)	300.72 (22.00)	0.77

detection limit of the assay is 1.9 pg/mL. The intra-assay coefficient of variation for the current sample was 3.1%. Saliva samples were lost for 12 men (6 winners and 6 losers) and 10 women (5 winners and 5 losers). Therefore, testosterone data were available for 27 men (13 winners and 14 losers) and 50 women (25 winners and 25 losers). For both men and for women, there were no significant differences in trait dominance and aggression between those for whom testosterone concentrations were measured and those for whom testosterone concentrations were not obtained.

2.6. Procedure

Participants were tested between 1300 and 1800 h to control for diurnal variations in testosterone concentrations. Upon arrival, participants completed a brief demographic questionnaire, a trait dominance questionnaire, and also provided a 1–2 mL saliva sample (pre-competition), to later be assessed for testosterone concentrations. Next, participants were paired with a same-sex partner, whom they competed against on the NTT. After the competition, participants completed a brief questionnaire as a manipulation check to ensure their awareness of the outcome (i.e., whether they had won or lost) and to ascertain whether or not they had any suspicion that the outcome had been pre-determined. Ten minutes after completion of the competitive task, participants provided the researcher with a second saliva sample (post-competition). A delay in collecting the second saliva sample was used because it takes approximately 10 min for steroid levels in serum to reach saliva (Riad-Fahmy et al., 1987). After providing the second saliva sample, participants were escorted to separate rooms where they performed the Point Subtraction Aggression Paradigm. Participants were instructed that they would be paired with the same opponent that they had just competed against (although they were actually playing against the computer program). At the end of the task, participants completed a brief questionnaire to assess whether participants believed they were actually playing against another person. Some of the questions were: "Did you earn more or fewer points than your opponent?", "Did you steal more or fewer points than your opponent?", "Did you form an impression of your opponent?"

2.7. Statistical analyses

Statistical analyses consisted of analyses of variance (ANOVAs), independent sample *t*-tests, Pearson correlations and multiple linear regressions. For all analyses, an alpha level of $p < 0.05$ was used to determine statistical significance.

3. Results

3.1. Descriptive statistics and simple correlations

Descriptive statistics for the trait measures (basal testosterone concentrations and trait dominance score) and PSAP responses are presented in Table 1. Outcome (win–loss) was included as a factor in the initial analyses as a manipulation check of the random assignment, and it was never a significant factor. The expected sex differences were observed: men had higher baseline testosterone concentrations ($F_{1,\ 73} = 81.19$, $p < 0.001$) and higher trait dominance scores ($F_{1,\ 97} = 6.25$, $p = 0.01$) than women. Baseline testosterone concentrations and trait dominance were positively correlated in men ($r = 0.53$, $p = 0.005$; see Fig. 1), and not in women ($r = -0.02$, $p = 0.92$).

For the PSAP measures, among men, there were significant correlations between reward and aggression responses ($r = -0.76$, $p < 0.001$), reward and protection responses ($r = -0.73$, $p < 0.001$), and aggression and protection responses ($r = 0.44$, $p < 0.01$). Among women, there were significant correlations between reward and aggression responses ($r = -0.76$, $p < 0.001$); reward and protection

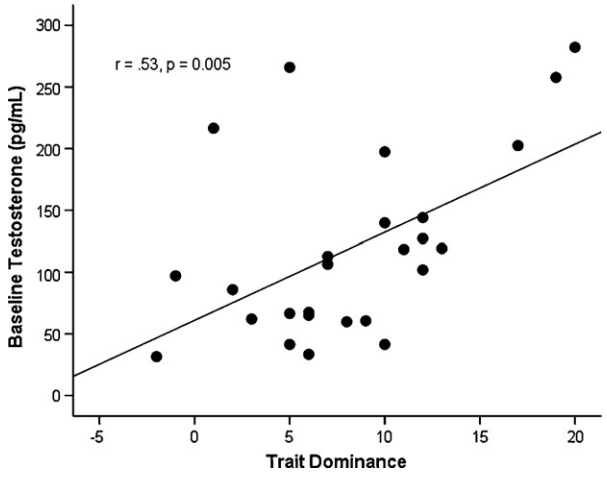

Figure 1 Relationship between trait dominance and baseline testosterone concentrations in men ($n = 26$). $r = 0.53$, $p < 0.01$.

responses ($r = -0.76$, $p < 0.001$); and aggression and protection responses ($r = 0.42$, $p < 0.01$).

3.2. Competition outcome and testosterone responses

Answers to the post-NTT questionnaire demonstrated that participants were not aware that the outcome of the contest was rigged. A mixed factor (sample time × competition outcome × sex) ANOVA was computed to examine whether sex and/or outcome influenced testosterone responses. Competition outcome was not a significant factor ($F_{1,\ 71} = 0.003$, $p = 0.96$). There were main effects of time and sex ($F_{1,\ 71} = 12.35$, $p < 0.001$ and $F_{1,\ 71} = 107.06$, $p < 0.001$, respectively), indicating an overall decrease in testosterone concentrations and higher testosterone concentrations for men relative to women. The 'outcome by sex' and 'outcome by time' interactions were not significant ($F_{1,\ 71} = 0.52$, $p = 0.47$ and $F_{1,\ 71} = 1.06$, p = 0.31, respectively). However, the 'Time by Sex' interaction reached statistical significance ($F_{1,\ 71} = 6.23$, $p = 0.02$). Pre- and post-testosterone concentrations were correlated both for men ($r = 0.69$, $p < 0.001$) and for women ($r = 0.68$, $p < 0.001$). Both men and women decreased in testosterone concentrations from pre- to post-competition, although the decrease was greater for men (men; mean decrease = −24.57, women; mean decrease = −4.14, $t_{73} = 2.50$, $p = 0.015$). The 'time by sex by outcome' interaction was not significant ($F_{1,\ 71} = 1.65$, $p = 0.20$).

3.3. Behavioural responses in the PSAP

Answers to the post-PSAP questionnaire indicated that participants believed they were playing the game with another individual. Men made more aggressive responses than did women on the PSAP ($F_{1,\ 95} = 3.86$, $p = 0.05$; Cohen's $d = 0.40$). There was no main effect of competition outcome ($F_{1,\ 95} = 0.04$, $p = 0.84$) or outcome by gender interaction ($F_{1,\ 95} = 2.24$, $p = 0.14$) on aggressive responses. There was no main effect of either gender or competition outcome, or interaction of the two factors, for reward responses or for protection responses on the PSAP (all p's > 0.43).

3.4. Relationships between trait and state variables and aggressive behaviour

Multiple regression analyses were used to examine the extent to which trait and state variables predicted aggressive behaviour in men and in women separately based on the apparent sex differences found in many of the predictor variables (see Table 1). Trait variables (baseline testosterone concentrations and trait dominance) were entered on the first step and state variables (outcome and post-competition testosterone concentrations) on the second step. All two-way interactions were included on the third step, and three-way interactions were included on the fourth step.

For women, trait dominance and baseline testosterone concentrations did not predict aggressive behaviour ($R^2 = 0.03$, $F_{2,\ 35} = 0.58$, $p = 0.57$), and the addition of post-competition testosterone concentrations and competition outcome did not predict any variance in aggressive behaviour ($R^2_{change} = 0.07$, $F_{2,\ 33} = 1.18$, $p = 0.32$). The two-way and three-way interactions did not predict any variance in aggressive behaviour (all p's > 0.25). For men, trait dominance and baseline testosterone concentrations did not predict aggressive behaviour ($R^2 = 0.09$, $F_{2,\ 23} = 1.18$, $p = 0.32$). The second step of the regression analysis was significant ($R^2_{change} = 0.22$, $F_{2,\ 21} = 3.40$, $p = 0.05$), indicating that the change in testosterone concentrations (post-test concentrations after controlling for pre-competition testosterone) predicted aggressive behaviour ($t_{21} = 2.58$, $p = 0.02$). The addition of the two- and three-way interactions did not predict any variance in aggressive behaviour (all p's > 0.25). However, to further investigate the prediction that the association between change in testosterone concentrations and aggression may differ on the basis of competition outcome (i.e., a stronger association may be observed for losers rather than winners, as in Mehta and Josephs, 2006), separate analyses were conducted for the win and loss conditions.

Trait dominance and pre-competition testosterone concentrations were entered on the first step. Next, post-competition testosterone concentration was entered on the second step, and the interaction between trait dominance and post-competition testosterone concentrations was entered on the third step. For men in the loss condition, pre-competition testosterone concentrations and trait dominance did not predict aggressive behaviour (step 1; $R^2 = 0.14$, $F_{2,\ 10} = 0.79$, $p = 0.48$). As in the analysis with losers and winners combined, the change in testosterone concentrations explained 42% of unique variance in aggressive behaviour (step 2; $R^2_{change} = 0.42$, $F_{1,\ 9} = 8.59$, $p = 0.02$; see Fig. 2), and the change in testosterone by trait dominance interaction did not explain any additional variance in aggressive behaviour (step 3; $R^2_{change} = 0.003$, $F_{1,\ 8} = 0.6$, $p = 0.82$). For men in the win condition, pre-competition testosterone concentrations and trait dominance did not predict aggressive behaviour (step 1; $R^2 = 0.09$, $F_{2,\ 10} = 0.52$, $p = 0.61$), nor did change in testosterone concentrations (step 2: $R^2_{change} = 0.07$, $F_{1,\ 9} = 0.77$, $p = 0.40$). The interaction between change in testosterone concentrations

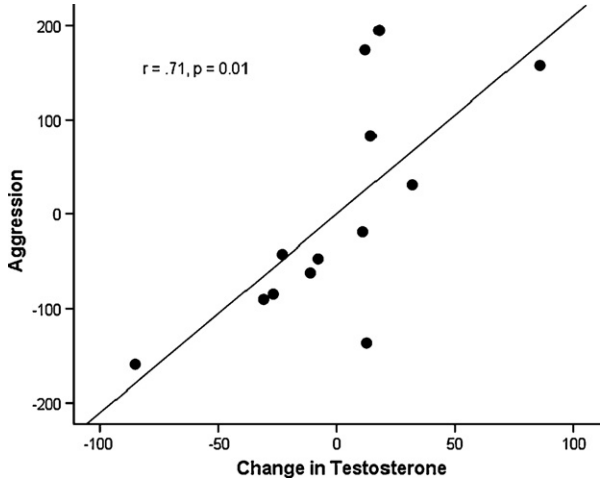

Figure 2 Change in testosterone concentrations and aggressive behaviour among men assigned to loss condition. A partial regression plot (pre-competition testosterone controlled), showing a positive correlation between change in testosterone and aggressive behaviour. Both variables in the partial regression plot are residuals ($n = 13$ men). partial-$r = 0.71$, $p = 0.01$.

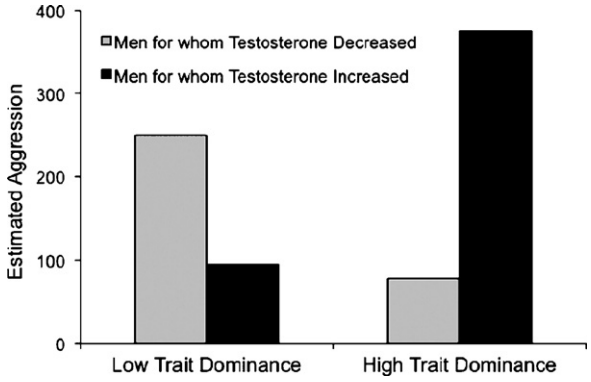

Figure 3 The plot of the interaction of trait dominance and change in testosterone concentrations (using ±1 S.D. of the mean) on aggressive behaviour among men assigned to the win condition ($n = 14$).

and trait dominance explained 38% of unique variance in aggressive behaviour (step 3; $R^2_{change} = 0.38$, $F_{1,\ 8} = 6.74$, $p = 0.03$). Predicted aggression scores were computed by including high and low (±1 S.D.) testosterone change and trait dominance scores into the regression equation (see Fig. 3). Simple slope analyses were conducted using a computer software program (www.quantpsy.org) developed by Preacher and colleagues (2006). A rise in testosterone concentrations was positively related to aggressive behaviour in men with high trait dominance ($\beta = 0.896$, $t_8 = 2.42$, $p = 0.038$) but not in men with low trait dominance ($\beta = -0.770$, $t_8 = -1.52$, $p = 0.16$).

3.5. Mediation analysis

An association between trait and state variables and the PSAP measures was observed among men assigned to the loss condition (see Table 2). That is, there were strong associations between change in testosterone concentrations and aggression and reward responses ($r = 0.71$ and $r = -0.61$, respectively). A hierarchical regression analysis was used to examine the extent to which the association between change in testosterone and reward responding was statistically mediated by aggressive behaviour. Aggressive behaviour as a predictor of reward responses was entered on the first step and change in testosterone concentrations was entered on the second step. The analysis demonstrated that when aggressive responses were controlled statistically, the relationship between change in testosterone concentrations and reward responses decreased ($r = -0.61$ to partial $r = -0.32$), suggesting that aggressive behaviour was the causal pathway by which change in testosterone concentrations reduced point reward responses. Sobel's (1982) test of mediation indicated that the decrease was significant which suggests that aggressive behaviour did in fact statistically mediate the relationship between testosterone change and reward responding: Sobel's test = 2.51, $p = 0.01$.

4. Discussion

The major finding from the current investigation is that testosterone concentrations after a competitive interaction predicted future reactive aggression in men and not women. Notably, men were more aggressive than women, supporting the general finding of higher direct aggression among men compared to women (see Archer, 2004). Furthermore, there was a significant positive association between baseline testosterone concentrations and trait dominance in men but not in women. Overall, these findings demonstrate that trait and state factors interact to influence aggressive behaviour, and thus, that these factors must be considered together when attempting to understand the mechanisms underlying aggressive behaviour.

4.1. Relationship between competition outcome, testosterone and aggressive behaviour

The current study is the first to find that testosterone responses to a competitive interaction predicted future aggressive behaviour among men, although the hypothesis of this relationship has been proposed in the literature (Mazur, 1976, 1985; Wingfield et al., 1990; Mazur and Booth, 1998; Archer, 2006). For example, the 'Challenge Hypothesis' holds that testosterone concentrations rise during the breeding season to facilitate reproductive physiology and increase further during social challenges (male-to-male competition) to support territorial and aggressive behaviours (Wingfield

Table 2 Zero-order correlations between baseline testosterone concentrations, change in testosterone concentrations, trait dominance scores, and Point Subtraction Aggression Paradigm (PSAP) responses. Correlations for women are inside parentheses and for men are outside parentheses.

	Reward	Aggression	Protection
Win condition			
Baseline testosterone	−0.13 (0.40)	0.26 (−0.26)	0.05 (−0.51*)
Testosterone change	−0.10 (0.04)	0.28 (−0.13)	0.33 (−0.03)
Trait dominance scores	0.05 (−0.06)	0.21 (−0.12)	0.13 (0.17)
Loss condition			
Baseline testosterone	−0.29 (0.39)	0.34 (−0.20)	−0.04 (−0.17)
Testosterone change	−0.61** (−0.10)	0.71* (−0.09)	0.34 (0.01)
Trait dominance scores	−0.05 (−0.29)	−0.05 (0.33)	−0.15 (0.07)

* $p < 0.01$.
** $p < 0.05$.

et al., 1990). The relationship between change in testosterone concentrations and subsequent reactive aggression was driven primarily by men assigned to the loss condition. These results are similar to those of Mehta and Josephs (2006), who reported that changes in testosterone concentrations following a competitive loss (but not win) were related to increased willingness to engage in a second competitive interaction. The interaction between trait dominance and change in testosterone concentrations emerged as a significant predictor of aggressive behaviour, but only for men assigned to the win condition. A rise in testosterone concentrations was positively related to aggressive behaviour, but only among men high in trait dominance. That the relationship between change in testosterone concentrations and aggressive behaviour was different for winners and losers suggests that separate mechanisms underlie aggressive behaviour on the PSAP. The different levels of provocation experienced by winners and losers may help explain these findings. For instance, although both groups of participants received the same degree of provocation (points stolen) during the PSAP, the loss condition preceding the PSAP may be an additional source of provocation. Among winners, individual differences in trait dominance interacted with testosterone concentrations to predict aggressive behaviour. For men in this condition, it appeared that testosterone concentrations alone were not sufficient to increase reactive aggression. Consistent with the idea that high trait dominant individuals seek to maintain control over social situations and events, a combination of high trait dominance with elevated testosterone concentrations may serve to increase aggressive behaviour aimed at maintaining high status (Mazur, 1985; Mazur and Booth, 1998). In other words, after a win, reactive aggression was elevated in those men with high dominance scores and an increase in testosterone. The hit to status after a loss may be such that an increase in testosterone alone suffices to increase reactive aggression on the PSAP in men irrespective of trait dominance.

Winners and losers of the Number Tracing Task (NTT) did not differ in testosterone responses, which is consistent with results from other studies using the NTT as a competition (Schultheiss and Rhode, 2002; Mehta and Josephs, 2006). Other studies of competition conducted in laboratory or athletic settings typically report higher post-competition concentrations in winners than in losers (reviewed in Archer, 2006), and the difference may reflect that the NTT competition is of much shorter duration (10 min) than the competition is in other studies, and the resultant "win" or "loss" may not be as salient to, or significant for, the participants as are other competitions. However, there was a significant decrease in pre-to post-competition testosterone concentrations irrespective of outcome that we cannot explain.

4.2. Trait dominance, aggression and baseline testosterone concentrations

There was no relationship between trait dominance and aggressive responses on the PSAP in either men or women. A positive association between trait dominance and self-report measures of aggression has been reported (Archer and Webb, 2006; Johnson et al., 2007). The conflicting findings may be partly due to the fact that the current study involved a behavioural measure of reactive aggression that may be situational, whereas the self-report studies examined the extent to which trait dominance predicted trait aggression. Trait dominance was associated with baseline testosterone concentrations in the present sample of men, a finding consistent with previous research on the relationship between trait dominance and testosterone concentrations (Grant and France, 2001; Sellers et al., 2007) and between implicit dominance (p Power) and testosterone concentrations (Schultheiss et al., 1999).

4.3. PSAP strategy

The inter-correlations among variables measured by the PSAP indicate that selection of aggression and protection responses were made at the expense of reward responses on the PSAP. The mediational analysis used to interpret the relationships among change in testosterone and PSAP variables suggests that men who rose in testosterone concentrations after a competition loss selected the aggressive response more frequently, which led to a decrease in point reward selections. This finding suggests that a rise in testosterone concentrations after losing a competitive interaction may lead to poor economic decision-making. A role for baseline testosterone in decision-making was observed among men performing the Ultimatum Game in which an individual is given a specific sum of money and must decide how much to offer another individual dubbed the 'receiver'. If the receiver accepts the sum offered, both participants receive their respective allotments, but if the receiver rejects the offer, both participants leave with no money. In this game, the rational choice for the receiver is to accept any offer made by the proposer, because any money earned is better than no money at all. Burnham (2007) reported that high testosterone men were more likely to reject low offers than were low testosterone men. Although this may be a poor economic decision, the rejection appears to be based on the desire to punish unfair actions (Ohmura and Yamagishi, 2005). Thus, the financial cost of reactive aggression may be outweighed by the emotional benefits and/or the possibility of influencing future social interactions. Other have found that a loss of status (defined as losing a competition) is associated with poor performance among high testosterone individuals (Josephs et al., 2003, 2006; Newman et al., 2005). Josephs and colleagues (2006) speculate that high testosterone individuals may be distracted by their desire to regain lost status, and as a consequence, perform relatively poorly on cognitive tasks. The findings above suggest that when provoked (by low offers, point subtractions, or a decrease in status due to loss of competition), men with high testosterone are more likely to have impaired performance on strategic and other cognitive tasks. In contrast, in the absence of direct provocation, testosterone may have a positive effect on the gain of reward. Male stock traders had greater overall profits on days in which their morning testosterone concentrations were elevated (Coates and Hebert, 2008), and it was argued that this may be explained by testosterone's influence on persistence, appetite for risk, and/or fearlessness in the face of novelty. The above studies observed relationships between baseline testosterone and performance, whereas in our study, a relationship with behaviour was evident for change in testosterone and not for baseline testosterone.

4.4. Testosterone and aggression in women

No associations were found among trait dominance, testosterone concentrations, and aggressive behaviour in women. One possibility is that other hormones are more important to the prediction of aggressive behaviour for women. Salivary estradiol concentrations (but not testosterone) predicted implicit dominance among women (Stanton and Schultheiss, 2007), whereas salivary testosterone concentrations predicted implicit dominance among men (Schultheiss et al., 1999). It may be that testosterone concentrations were too low to detect any relationship in the current sample of women. Exogenous administration of testosterone increased amygdalar and hypothalamic activation in response to angry faces in women (Hermans et al., 2008). Although their study did not measure aggressive behaviour directly, the authors indicate that these findings suggest that testosterone may modulate neural structures known to mediate reactive aggression. A third possibility is that trait dominance and/or testosterone concentrations may predict sub-types of aggressive behaviour other than reactive aggression in women.

Men and women did not differ in the number of point protection or point reward responses, which suggests that they were equally motivated to gain reward and avoid punishment (point loss). The higher behavioural levels of reactive aggressive in men compared to women is in keeping with the growing body of literature on sex differences in aggressive behaviour (e.g., Allen et al., 1996; Zeichner et al., 2003; Archer, 2004). Sex differences are not always found for behavioural measures of aggression (e.g., Moe et al., 2004), and there is some evidence to suggest that women make use of indirect forms of aggressive behaviour more frequently than do men (Hess and Hagan, 2006).

4.5. Conclusion

The finding from the current study that competition-induced changes in salivary testosterone concentrations predicted reactive aggression among men is consistent with theoretical models of the relationship between dynamic fluctuations in testosterone and aggressive behaviour, such as the Challenge Hypothesis (Wingfield et al., 1990; Goymann et al., 2007) and Biosocial Model of Status (Mazur, 1985; Mazur and Booth, 1998). Importantly, the relationship was stronger for men assigned to the loss condition, but was also significant among winners with elevated trait dominance. Thus, trait and state factors interacted with one another to predict aggression. Further, the aggressive responses associated with higher testosterone were made at a cost to reward. The findings here add to the growing evidence of a role of dynamic changes in endocrine status in shaping behaviour.

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Conflict of interest

There are no conflicts of interest for any of the authors.

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