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Aggressive behavior and change in salivary testosterone concentrations predict willingness to engage in a competitive task

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ABSTRACT

The current study investigated relationships among aggressive behavior, change in salivary testosterone concentrations, and willingness to engage in a competitive task. Thirty-eight male participants provided saliva samples before and after performing the Point Subtraction Aggression Paradigm (a laboratory measure that provides opportunity for aggressive and defensive behavior while working for reward; all three involve pressing specific response keys). Baseline testosterone concentrations were not associated with aggressive responding. However, aggressive responding (but not point reward or point protection responding) predicted the pre- to post-PSAP change in testosterone: Those with the highest aggressive responding had the largest percent increase in testosterone concentrations. Together, aggressive responding and change in testosterone predicted willingness to compete following the PSAP. Controlling for aggression, men who showed a rise in testosterone were more likely to choose to compete again ($p=0.03$) and controlling for testosterone change, men who showed the highest level of aggressive responding were more likely to choose the non-competitive task ($p=0.02$). These results indicate that situation-specific aggressive behavior and testosterone responsiveness are functionally relevant predictors of future social behavior.

Introduction

Despite much animal research demonstrating that testosterone is associated with aggressive and/or dominant behaviors (reviewed in Simon and Lu, 2006; Trainor and Nelson, 2007), the findings from studies in people are less consistent (Archer, 1991; Archer et al., 1998; Book et al., 2001; Archer, 2006). Perhaps contributing to the inconsistencies is that most studies have utilized self-reported measures of aggression, and only a few studies have assessed the relationship between testosterone and aggression in well-controlled laboratory paradigms (see Kouri et al., 1995; Pope et al., 2000; Berman et al., 1993). Stronger relationships between testosterone and human aggression possibly would be revealed when basal and dynamic fluctuations in neuroendocrine function are considered within the context of readily observable aggressive and/or competitive situations.

In studies of several different species (non-human primates: Muller and Wrangham, 2004; Cristobal-Azkarate et al., 2006; birds: Wingfield et al., 1990; rodents: Oyegbile and Marler, 2005; fish: Oliveira et al., 1996; insects: Trumbo, 2007; Scott, 2006), testosterone concentrations were found to be highly responsive to situational cues, particularly cues signaling intra-sexual competition. Such findings are consistent with the ‘Challenge Hypothesis’, originally derived from studies of monogamous birds, which predicts that during times of social instability (such as during the reproductive season), males typically demonstrate a rise in testosterone concentrations, which in turn facilitates various forms of aggressive and dominant behaviors (Wingfield et al., 1990).

The ‘Challenge Hypothesis’ has been applied to studies of human social interactions (reviewed in Archer, 2006). Some studies have found that testosterone concentrations in men rise during face-to-face interactions with women (Roney et al., 2007; Roney et al., 2003), in anticipation of competition (Suay et al., 1999; Bateup et al., 2002; but see Mazur et al., 1997; Carré et al., 2006), and are sometimes, but not always, elevated in winners relative to losers post-competition (Mazur and Lamb, 1980; Elias, 1981; Gladue et al., 1989; Booth et al., 1989; Mazur et al., 1992; van Anders and Watson, 2007 Edwards et al., 2006; Gonzalez-Bono et al., 1999). Related to the ‘Challenge Hypothesis’ some investigators have proposed a ‘Biosocial Model of Status’ whereby a rise in testosterone concentrations following a successful competitive interaction may serve to facilitate future behaviors aimed at maintaining or gaining status (Mazur, 1985; Mazur and Booth, 1998). This idea was recently examined in a well-controlled laboratory study involving mice (Trainor et al., 2004). Castrated mice administered testosterone following a successful aggressive encounter (resident–intruder paradigm) were more aggressive in subsequent encounters whereas those administered saline (following a successful encounter) showed no change in aggressive behavior, indicating a key role of testosterone in modulating future behavior.

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There is also some support for a relationship between dynamic changes in testosterone concentrations and behavior in people from studies that involved exogenous administration of testosterone. In a series of studies conducted with women, a single sublingual administration of testosterone (0.5 mg) significantly increased cardiac responses to angry faces (van Honk et al., 2001), improved visuospatial abilities (Aleman et al., 2004), reduced fear-potentiated startle (Hermans et al., 2006), increased subcortical (amygdalar and hypothalamic) responses to angry faces (Hermans et al., 2008), and reduced conscious detection of angry faces (van Honk and Schutter, 2007).

Only a few studies have investigated the functional relevance of endogenous fluctuations in testosterone concentrations on future behavior. In a series of studies using implicit-power motive as a measure of trait dominance, Schultheiss and colleagues (2002, 2005) have reported that, for those high in implicit dominance, winners (of a rigged challenge) demonstrated better performance on a visuomotor task than did losers, and that this effect was partially mediated by the competition-induced change in testosterone concentrations. In another study in which the outcome of the competition also was rigged, Mehta and Josephs (2006) demonstrated that an increase in salivary testosterone concentrations predicted the willingness of participants to compete again. However, this relationship was found only among the losers of the competition, and not among the winners. Klinesmith et al. (2006) found that men who interacted with a toy gun were more aggressive compared to those who interacted with a board game (aggressiveness was defined as how much hot sauce was placed in an opponent's drink when given the opportunity). Importantly, the relationship between interacting with the toy gun and aggressive behavior was mediated by a rise in salivary testosterone concentrations. That is, when the authors statistically controlled for change in testosterone, the relationship between interacting with the gun and aggressive behavior diminished, suggesting that testosterone was one of the causal mechanisms mediating the expression of aggressive behavior.

In the present experiment, we investigated the relationship between situationally-determined behavior, changes in testosterone concentrations, and future behavior using a competitive laboratory task that provided the opportunity to win points that could be exchanged for monetary reward and the opportunity for aggressive behavior, although without a clear designation of “winner” and “loser” (i.e., participants were not aware of the final performance outcome of their opponent). We used a modified version of the Point Subtraction Aggression Paradigm (PSAP), an externally valid measure of aggressive behavior. Cherek and colleagues (1996, 1997) demonstrated that parolees convicted of violent crimes demonstrated significantly higher levels of aggressive responding on the PSAP compared to parolees convicted of non-violent crimes. Other laboratories have also demonstrated that aggressive responding on the PSAP is related to self-report measures of aggression (Gerra and colleagues, 2001, 2004, 2007; Golomb et al., 2007). The PSAP allowed us to directly investigate the relationship between testosterone concentrations and aggressive behavior, and the extent to which these measures predict future behavior in men. Our first hypothesis was that there would be a positive correlation between basal testosterone and aggressive responses. We also examined whether behavior on the PSAP (aggression, point reward, protection) predicted the change in testosterone concentrations. Furthermore, we predicted that when given the option to choose their next activity, either another competitive task or a similar non-competitive task, men with the highest increase in salivary testosterone levels would be more likely to choose the competitive task.

Materials and methods

Participants

Forty-three men were recruited from the Brock University campus using advertisements and participant pools. Five were excluded because they were taking prescription medications (four taking corticosteroids and one taking antidepressants), resulting in a sample of 38 men (71% Caucasian, 18% Asian, 10% Other; mean age of 21.03, SD = 2.96). The participants were told that they would be playing a computer game for points, and that the number of points that they earned would be exchanged for money. At the end of the experiment, participants were fully debriefed, and were paid $10 irrespective of their performance on the task.

Procedure

The study was approved by the Brock University Research Ethics Board. All testing took place between 1300 h and 1700 h to control for diurnal variation in testosterone concentrations. After completion of the informed consent form, participants completed a brief demographic questionnaire and then provided the researcher (male) with a 1–2 ml saliva sample. After providing the first saliva sample, participants began the Point Subtraction Aggression Paradigm (described below), which requires approximately 40 min to complete. At the conclusion of the PSAP, participants completed a series of open-ended brief questions. One question asked whether the participant thought he had gained more or fewer points than his opponent in the previous competition to assess whether the perception of the participant was that he had “won” or “lost”. 25 of the participants (66%) reported that they thought they earned more points than their partner (subjective winners) and 13 participants (34%) reported that they thought their partner had earned more points (subjective losers). A second question was used to probe indirectly whether the participants were suspicious as to whether the opponent was real or not by asking them to describe any impressions they had formed of their opponent during the task. The responses of the participants suggested that each believed that he was playing against an actual opponent. Some typical responses were: “Negative impression because he seemed to take a lot of points at inconvenient times”, “Once I started to steal his points, he did it back to me.”, “I saw him as a negative thief.”, “I thought my competitor was pretty good at this game as he took a lot of points from me.”, “He probably played similar to me but I was trying to out-think him at times.”

A second saliva sample was obtained 10 min after completion of the PSAP (a timer was used to ensure consistency, and all participants completed the questionnaires within the 10-minute interval). A 10-minute interval was used so that salivary concentrations would reflect plasma testosterone concentrations at the conclusion of the task. A 10–15-minute interval between task completion and saliva sampling is commonly used (e.g., Gonzalez-Bono et al., 1999; Mehta and Josephs, 2006) based on the time required for testosterone to reach saliva (Riad-Fahmy et al., 1987). After providing the second sample, participants were asked to complete a forced-choice questionnaire that asked which type of task they would prefer to perform for the last part of the experiment. The forced-choice was based on Mehta and Josephs (2006), but instead of providing the participants with the option of performing the same competition again or the option of filling out a questionnaire on music, food, and entertainment preferences, here both options for participation were new (i.e., the choice of competing on PSAP again was not an option) and were either of a competitive or cooperative nature. The two options were: 1) Compete with the same individual on solving a series of puzzles; or 2) Help the investigator validate a program assessing puzzle-solving abilities. The order of the choices was counter-balanced, and participants were told that both options took the same amount of time to complete and that they were of the same level of difficulty.

Point Subtraction Aggression Paradigm (PSAP)

The PSAP was originally designed by Cherek (1981) to measure aggressive behavior in a controlled laboratory environment. The original PSAP takes 3 h to administer, and recent evidence has demonstrated that an abbreviated version of the PSAP (a 25-minute session) maintains good psychometric properties, in that aggressive responding to this abbreviated version was positively correlated with scores on questionnaires assessing recent aggressive behaviors (Golomb et al., 2007). Our version takes 40 min to complete and includes 2-minute rest breaks at the 12 min intervals.

Participants were tested individually. Each was told that he would have the opportunity to earn money based on his performance on a computer game, during which he would be paired with another male participant (who, in actuality was a fictitious partner; the opponent was the computer program) and that their goal was to gain as many points as possible because these points would be exchangeable for money. Participants sat in front of a computer monitor and keyboard and had three response options available to them: Option 1 was the point reward button; Option 2 was the point steal button (aggressive response); Option 3 was the point protection button (protective response). The response options corresponded to numbers 1, 2, and 3 of a standard computer keyboard.

Participants were told that hitting Option 1 a hundred consecutive times would cause their point counter to enlarge, flash several times with positive signs around it, and that their point counter would *increase* by 1 point, indicating that they had gained a point. Participants were instructed that throughout the task, their point counter may turn red, flash several times with negative signs around it, and that their point counter would *decrease* by 1 point. These series of events indicated that their partner (actually the computer program) had stolen a point from them. Participants were told that these ‘stolen’ points would be added to their partner's point counter. Participants were instructed that they could also choose to select Option 2 or Option 3. They were told that hitting Option 2 ten times would steal a point from their partner, but despite the fact that their partner lost a point, they had been randomly assigned to the experimental condition in which they did not get to keep the points that they stole from their partner. Since participants did not gain any financial reward from stealing, it can be inferred that stealing points served to 'punish' one's partner, and as such, represents the primary measure of aggressive behavior. Aggressive responding on the PSAP is consistent with the widely used operational definition of aggression as being "any form of behavior directed toward the goal of harming or injuring another living being who is motivated to avoid such treatment" (Baron and Richardson, 1994, p. 7). Importantly, the harm or injury does not need to be physical, but simply needs to be considered as an aversive stimulus by the receiver. In addition to offering participants the opportunity to select Option 2 (aggressive responses), participants were also told that they could select Option 3 (protective responses). Pressing Option 3 ten times would protect their counter from point subtractions for a variable amount of time, thus, providing a non-aggressive option.

The PSAP task was programmed using E-Prime (Version 1.0). The computer program was designed to provoke (or steal) from participants every 6 to 60 s in the absence of any Option 2 or Option 3 selections. Cherek's (1981) original PSAP provoked participants every 6 to 120 s. We chose to use a smaller interval of provocations due the abbreviated nature of the PSAP used in this study. If participants completed 10 presses on Option 2 or Option 3, this would initiate a provocation-free interval (PFI). Participants were made aware that Option 3 (protection) initiated a PFI, but were not explicitly told that Option 2 (aggression) would also initiate a PFI. When a PFI was initiated, the computer program did not provoke participants for a minimum of 60 s and a maximum of 120 s, after which the random point subtractions would continue to occur every 6 to 60 s.

Another important parameter of the task was that once participants selected one of the three options they were committed to this option until they completed the fixed ratio. For example, if participants first selected Option 1 (reward responses), they had to complete the 100 presses prior to selecting another option. Equally, if participants selected Option 2 (aggression) or 3 (protection), they had to complete 10 presses prior to choosing another option. Last, the computer was set up in such a way that participants had to allow 170 ms between each button press. In sum, the measures obtained from the PSAP were (1) point reward responses, (2) aggressive responses, (3) protective responses, and (4) provocations received, all of which influenced (5) points earned.

Saliva collection procedure and salivary testosterone assay

Saliva samples were collected using polystyrene culture tubes. Saliva samples were stored at −20 °C until assayed using commercial enzyme immunoassay kits (DRG International, Inc). All saliva samples were measured in duplicate and on the same day. Briefly, frozen samples were first warmed to room temperature and then centrifuged (3000 rpm) for 15 min. Duplicate 100 µl aliquots of saliva were assayed according to the instructions of the kit. Optical densities were determined using a Bio-tek Synergy plate reader at 450 nm. The intra- and inter-assay coefficients of variation reported by DRG were below 10%, and the detection limit of the assay is 1.9 pg/ml. The intra-assay coefficient of variation for the current sample was 3.99%.

Statistical analyses

Change in testosterone concentration was calculated as a percent change (post-testosterone minus pre-testosterone / pre-testosterone × 100) as in other studies of salivary testosterone and behavior (van Anders and Watson, 2007; Edwards et al., 2006; Bateup et al., 2002). Pearson correlations were used to examine the bivariate relationships between variables measured on the PSAP. Hypotheses were tested using logistic and linear regression analyses. An alpha level of $p<0.05$ (two-tailed) was used to determine statistical significance.

Results

Descriptive statistics for the Point Subtraction Aggression Paradigm and salivary testosterone concentrations are presented in Table 1. Point reward responses were negatively correlated with aggressive responses and with protection responses, and positively correlated with points earned and with provocations received (see Table 2). In other words, participants who spent more time hitting the point reward button obtained more points, were less aggressive, protected their points less often, and were provoked more frequently. The number of provocations received was not related to aggressive responses and was negatively related to protection responses. That is, the more times participants protected their points, the less often they were provoked because of the resulting provocation-free interval. The average number of points earned was negatively related to the average number of aggression and protection responses. 27 of the participants chose the competitive task and 11 chose the non-competitive task. 18 of the 25 (72%) of the 'subjective winners' chose the competitive task and 9 of the 13 (69%) 'subjective losers' chose the competitive task.

Table 1
Descriptive statistics for PSAP and salivary testosterone measures

	Mean	SEM	Minimum	Maximum
Behavioral options of the PSAP				
Reward responses	2597.6	58.8	1400.0	3314.7
Aggression responses	229.2	27.0	13.3	732.0
Protection responses	219.8	22.7	10.0	605.7
Testosterone measures (pg/l)				
Baseline	97.5	8.3	30.2	272.0
Post-test	101.1	6.4	37.7	216.4
% change	15.1[1]	6.3	−65.0	141.1

SEM = Standard error of the mean.
[1]The % change in testosterone was significant ($t_{37}=2.39$, $p=0.02$).

Table 2
Bivariate correlations among variables measured with the PSAP

	Reward	Aggression	Protection	Provocations
Reward				
Aggression	−0.78***			
Protection	−0.67***	.23		
Provocations	.31**	−0.14	−0.49***	
Points	.85***	−0.68***	−0.42*	−0.20

*** $p<0.001$, ** $p<0.01$, * $p<0.05$.

Baseline salivary testosterone concentrations and aggressive behavior

Baseline salivary testosterone was not correlated with aggressive, protective, or reward responses or with decision to compete or with perceived outcome (all $p>0.18$, all $r<0.22$, using Pearson or Spearman correlations where appropriate).

Aggressive behavior and change in salivary testosterone concentrations

A linear regression analysis was performed with age, point reward responses, aggressive responses and protection responses simultaneously entered as predictors of change in salivary testosterone concentrations. All three behavioral responses from the PSAP (aggression, protection and reward) were included in the analysis to determine which, if any, of the behavioral responses predicted the change in salivary testosterone concentration. Age was included as a predictor because it was significantly correlated with change in testosterone ($r=0.43$, $p=0.007$). The overall model accounted for 32% of the variance ($R^2=0.32$, $F_{4,\ 33}=3.82$, $p=0.01$), with aggressive responding ($t_{33}=2.39$, $p=0.02$) and age ($t_{33}=3.34$, $p=0.002$) as the only significant predictors of change in testosterone concentrations. See Table 3 for regression coefficients. Adding perceived outcome (winner/loser) to the linear regression model did not predict any additional variance in change in testosterone concentrations ($t_{32}=-0.53$, $p=0.60$).

Aggression, change in testosterone, and choice of competitive/non-competitive task

Multiple logistic regression analysis found that aggressive behavior and change in testosterone significantly predicted willingness to

Table 3
Regression analysis predicting changes in salivary testosterone concentrations ($n=38$)

	Beta	t	p	Zero-order r	Partial r
PSAP responses					
Reward	0.75	1.82	0.08	−0.10	0.30
Aggression	0.74	2.39	0.02	0.23	0.38
Protection	0.41	1.56	0.13	0.02	0.26
Age	0.49	3.31	0.001	0.43	0.50

Full model $R^2=0.32$.

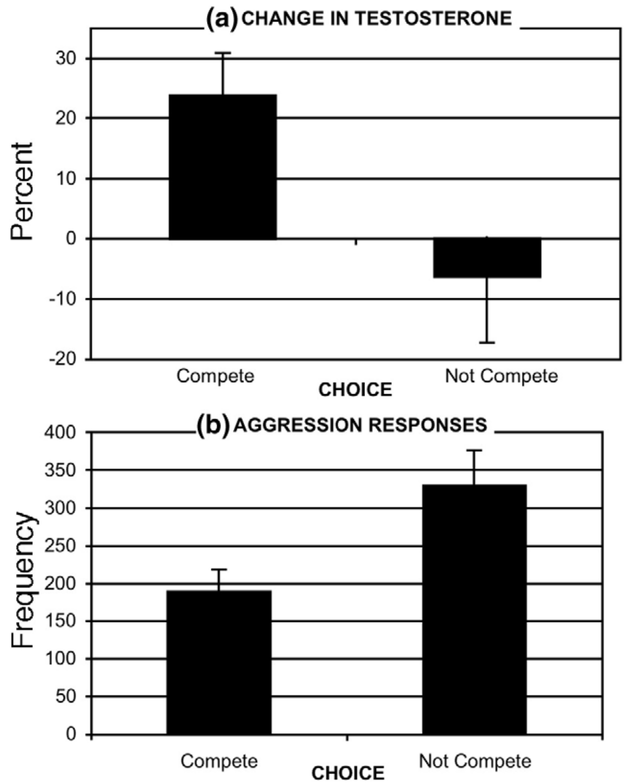

Fig. 1. Estimated marginal means and S.E.M. for (a) change in testosterone (with aggressive responses as a covariate) and (b) aggression responses (with change in testosterone as a covariate) as a function of choice: competitive task (n=27) or non-competitive task (n=11).

compete (χ^2(2, n=38)=9.06, p=0.01). Likelihood ratio tests indicated that the inclusion of both predictors was significantly higher than either predictor alone (−2LL were χ^2(1)=5.09, $p<0.025$ and χ^2(1)= 4.33, $p<0.05$, respectively; simple logistic regression using only aggressive behavior approached statistical significance, p=0.07, as did using only change in testosterone, p=0.09). Analysis of covariance was used to interpret and illustrate the relationship between willingness to compete and each predictor while controlling for the other (see Fig. 1). Controlling for aggression, men who chose the competitive task had a higher rise in salivary testosterone concentrations than did those who chose the non-competitive task ($F_{1,\,35}$=4.86, p=0.03). Controlling for change in salivary testosterone concentrations, men who chose to compete had fewer aggressive responses than did those who chose the non-competitive task ($F_{1,\,35}$=6.11, p=0.02).

Likelihood ratio test indicated that adding perceived outcome (winner/loser) to the multiple logistic regression model did not increase the prediction of willingness to compete (χ^2(1)=0.01, ns).

Discussion

The major findings of the present experiment are, first, that aggressive behavior in a competitive situation was associated with an increase in testosterone concentrations and, second, that together these situation-dependent factors predicted future social behavior.

Baseline testosterone concentrations and aggressive behavior

There was no significant relationship between baseline testosterone concentrations and aggressive behavior in response to provocation. Meta-analyses have revealed a small, yet significant, relationship between baseline testosterone concentrations and various measures of aggressive behavior (Book et al., 2001; Archer et al., 2005). Given the wide variety of measures used to assess the subtypes of aggression, it is perhaps not surprising that the findings have been inconsistent. The current study assessed aggressive behavior in response to provocation and can thus be considered a form of reactive aggression, which may not be associated with basal levels of testosterone. Another possible reason for the lack of a relationship between baseline testosterone and aggressive behavior in the current study is that testosterone may interact with other biological variables to predict aggressive behavior (Dabbs et al., 1991; Popma et al., 2007). For example, Popma et al. (2007) demonstrated that baseline testosterone was positively correlated with aggression, but only among those with low baseline cortisol levels. Furthermore, Hermans et al. (2008) reported that the ratio of basal testosterone to basal cortisol was related to activation of neural structures mediating social aggression, whereas basal testosterone on its own was not.

Aggressive behavior predicts change in salivary testosterone concentrations

Although no relationship was found between baseline testosterone and aggressive responding, there was a relationship between aggressive responding and change in testosterone concentrations, and thus provides further evidence that human social interactions modulate testosterone concentrations (e.g., van Anders and Watson, 2006; Archer, 2006; Mazur and Booth, 1998). Aggression during this competitive social interaction appears to be the specific behavioral modulator of salivary testosterone concentrations since neither point reward nor point protection responding was associated with the change in salivary testosterone concentrations. This finding complements other research that has demonstrated that contextual and situational factors modulate testosterone concentrations. For example, winning (see Archer, 2006; Mazur and Booth, 1998; van Anders and Watson, 2006), competing in one's home venue (Carré et al., 2006; Neave and Wolfson, 2003), vicariously experiencing a victory (Bernhardt et al., 1998) and successful individual performance (Edwards et al., 2006) have all been associated with higher testosterone concentrations. Our findings are also consistent with recent studies in non-human primates that indicate associations between aggressive behavior and change in testosterone concentrations (e.g., Muller and Wrangham, 2004; Ross et al., 2004). For example, male resident marmosets that responded most aggressively toward an intruder showed the largest increase in testosterone concentrations following the interaction, but there was no association between baseline testosterone concentrations and aggressive behavior (Ross et al., 2004).

The PSAP as a competitive task and as a measure of aggression

Although not a conventional form of competition, the PSAP can be considered a competitive task in that the reward earned by performing the PSAP depends on the performance (number of button presses) and strategy (which buttons are pressed) of the player and the performance of the competitor (number of provocations given). The relationships among these factors are evident in the table of correlations (Table 2) and speak to which strategy of button pressing optimizes reward (total points earned) and minimizes losses (aggression presses or protection presses both lead to the same provocation-free time interval and thus both protect points, but at the cost of pressing the reward button; hence the high correlations among these variables). Point reward responses were positively associated with the total points earned, whereas protection and aggression responses were negatively associated with total points earned. Further, aggression responses detracted more from total points earned than did protective responses, and the number of provocations a participant received was not associated significantly with points earned. Thus, the best strategy is to simply hit the point reward button throughout the task.

The evidence that aggressive responding comes at a cost to a financial reward (or "winning"), suggests that the increase in testosterone concentrations is likely very different than testosterone increases that have been reported for overt winners of a competition irrespective of whether there was opportunity for aggression in the competition (Mazur and Lamb, 1980; Elias, 1981, Gladue et al., 1989; Booth et al., 1989; Mazur et al., 1992; van Anders and Watson, 2007; but see Edwards et al., 2006; Gonzalez-Bono et al., 1999). In the current study, perceived outcome did not influence testosterone levels or aggressive behavior. It would be of interest to test whether aggressive behavior and ongoing awareness of one's actual performance in relation to one's competitor would have additive effects on testosterone levels. Additionally, it is important to distinguish the type of aggressive behavior that is measured by the PSAP. Because the task measures aggressive behavior in response to provocation, it fits the subtype of reactive aggression. The classification of aggressive behavior as reactive aggression is based on the taxonomical scheme of Gendreau and Archer (2005) whereby classification begins by considering whether or not there is a proximal contextual elicitor (if not, the aggression is proactive; if there is, it is reactive), and then by considering the consequences for the individual [harm-induced pleasurable reward (hostile aggression) or social/material gain (instrumental aggression)], and then following the consequences, reinforcement occurs. Thus, the aggression here with the PSAP fits the classification of reactive, hostile aggression, and the findings may not extend to other subtypes of aggressive behavior.

Change in testosterone concentrations and aggression predict willingness to compete

We also addressed whether the aggressive behavior and the competition-induced changes in testosterone concentrations are relevant to future social behavior. The reciprocal model suggests that situation-specific neuroendocrine changes can in turn feedback to influence future social behaviors (Mazur and Booth, 1998; Mazur, 1985). In animal models, the increase in future aggression that occurs after winning an aggressive encounter is dependent on testosterone concentrations after the aggressive encounter (Trainor et al., 2004). Some recent studies in people have found that situation-induced rises in testosterone concentrations alter subsequent behavior. In a series of studies using implicit-power motive as a measure of trait dominance, Schultheiss and colleagues (2002, 2005) have reported that, for those high in implicit dominance, winners (of a rigged challenge) demonstrated better performance on a visuomotor task than did losers, and that this effect was partially mediated by the competition-induced change in testosterone concentrations. In addition, Klinesmith et al. (2006) have reported that interacting with a toy gun was associated with a rise in testosterone, and this in turn led to an increase in aggressive behavior. Mehta and Josephs (2006) found that a dynamic change in testosterone concentrations was associated with willingness to re-engage in the same competitive activity with the same individual. However, this relationship was only observed for losers of the competition and when the sample was restricted to those individuals among the highest and lowest thirds of the range of change in testosterone [i.e., middle third of the losers were removed from the analysis].

Our results, which included the whole range of testosterone responses, provide an important extension of the findings reported by Mehta and Josephs (2006). However, our results also indicated that the relationship between change in testosterone and willingness to compete only became statistically significant when aggressive behavior was included in the logistic regression model. Another difference between our study and that of Mehta and Josephs (2006) is that we did not manipulate the outcome of the competitive encounter. Mehta and Josephs (2006) interpreted their findings from a status perspective, indicating that, "losers who increased in T chose to compete again as an attempt to reclaim their lost status" (p. 689). Furthermore, the authors argued that the rewarding properties of testosterone could also explain their findings such that those who rose in testosterone in response to the competition may have associated this event with reward, and as such, may have learned to repeat the competition. However, this interpretation does not explain why testosterone changes among winners did not predict willingness to compete. In their study, Mehta and Josephs (2006) asked participants whether they wanted to compete with the same individual on the same task. In contrast, our participants were asked whether they wanted to compete with the same individual on another competitive task. Although this is a subtle difference, it may be theoretically important. Perhaps a change in testosterone would have predicted willingness to compete in both winners and losers in the Mehta and Josephs (2006) study if they were given the opportunity to compete with the same person on a novel competitive task.

In the current study, perception of outcome did not appear to be a critical factor in the association between change in testosterone and willingness to compete. First, change in testosterone concentrations was not associated with reward presses or points earned but it was associated with aggressive behavior. Second, there was no difference in the choice of subsequent task between those who perceived themselves to have performed better than their fictitious opponent and those who did not. However, there are important limitations to our use of 'perceived outcome' as a measure. Perceived outcome may have been related to individual differences not measured in the current study such as trait dominance (Sellers et al., 2007) or power motive (Schultheiss et al., 2005), which in turn could have influenced both change in testosterone and willingness to compete. In addition, it is important to note that our measure of perceived outcome was quite different from that of Mehta and Josephs (2006) who specifically assigned participants to win/lose conditions, and thus, a direct comparison of our findings regarding 'win/lose', change in testosterone and willingness to compete cannot be made. It is possible that the participants in our study who demonstrated a rise in testosterone concentrations in response to the task may have chosen the competitive task because they found the competitive nature of the PSAP in and of itself rewarding. Although this interpretation is speculative, it is consistent with animal studies of self-administration of testosterone and testosterone-associated conditioned place preference (see reviews by Wood, in press; Frye, 2007).

An unexpected result was that whereas aggressive responses on its own did not predict choice of competitive over non-competitive task, it became a significant predictor when included in the logistic regression model with change in testosterone concentrations. Interestingly, men with higher aggressive responses were more likely to choose the non-competitive task over the competitive task. This finding is counter-intuitive given that aggressive behavior and change in testosterone concentrations were positively related to each other. Thus, whether there truly is a joint effect of aggressive behavior and change in testosterone on choice of task will require more investigation. Furthermore, recent evidence in rodents has also demonstrated that aggressive behavior (much like testosterone) is rewarding and produces its effects via the dopaminergic reward system (Couppis and Kennedy, 2008). That there was a significant negative relationship between aggressive behavior and willingness to compete suggests that individual differences not measured in this experiment, such as whether the task was enjoyable or frustrating to the participant may be important variables to consider. Some spontaneous comments made by participants after completing the PSAP exemplify variable reactions to the task [e.g., "I thought my partner was pretty good at this game as he took quite a few points from me", "As simple a game it was, I felt aggressive towards my partner" and "I had a negative impression of my partner. He kept stealing my hard earned points. It was more frustrating than anything"], and could be examined more systematically in future studies. Others have shown that individual differences in variables such as the implicit-power motive (Schultheiss et al., 2005) and/or trait dominance (Sellers et al., 2007) may influence testosterone–behavior relationships, and such individual differences may be related to aggressive responding on the PSAP.

Conclusion

In sum, we found that aggressive responses (but not point reward or point protection responses) predicted the change in testosterone concentrations in response to the PSAP and that aggressive behavior and change in testosterone concentrations predicted willingness to re-engage in another competitive task. How situation-specific behavior and neuroendocrine changes influence the decision to compete is still unknown, although testosterone's influence on the dopaminergic reward system and its effect on status-seeking behavior have both been suggested as possible factors of relevance (see Mehta and Josephs, 2006; Edwards, 2006). It will be important to determine the extent to which the relationships observed are specific to situations involving provoked aggression, and to men, particularly in view of the 'Challenge hypothesis' (Wingfield et al., 1990), which was originally proposed to describe the important role of testosterone fluctuations in facilitating male-to-male competitive behavior.

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