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Motivational and situational factors and the relationship between testosterone dynamics and human aggression during competition

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A R T I C L E I N F O

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A B S T R A C T

Men engage in aggression at a cost to extrinsic reward, and this behaviour is associated with a rise in testosterone. To characterize the factors underlying aggression, men were assigned to one of the four experimental conditions of a computer game in which they were provoked (points were stolen from them or not) and/or received reward for aggression (received points for aggression or not). Men who were provoked but did not receive reward for aggression enjoyed the task the most, demonstrated an increase in salivary testosterone, and were more likely to choose a competitive versus non-competitive task than men in the other experimental conditions. Moreover, individual differences in aggressive behaviour among these men were positively correlated with the extent to which they enjoyed the task and with testosterone fluctuations. These results indicate that costly aggressive behaviour is intrinsically rewarding, perhaps to regulate future interactions, and that testosterone may be a physiological marker of such reward value.

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Although aggressive behaviour can be costly in terms of energy consumption and the potential for injury and/or death, it may also be adaptive in the context of obtaining and defending valued resources and negotiating status hierarchies (Buss and Shackelford, 1997). Two of the main factors that contribute to the expression of aggressive behaviour are interpersonal provocation and the pursuit of reward (e.g., money, status, and mating opportunities). Accordingly, researchers have generally classified aggressive behaviour as either reactive or proactive. Reactive aggression is typically a defensive response to perceived or actual provocation, and involves retaliation that is characterized by anger and high physiological arousal (Dodge and Coie, 1987; Crick and Dodge, 1996). In contrast, proactive aggression, does not involve provocation, is a behaviour aimed at acquiring a valued resource (e.g., money, territory, social status, and mating opportunities), and does not typically involve physiological arousal (Dodge and Coie, 1987; Crick and Dodge, 1996). Reactive and proactive forms of aggression are found in many competitive settings, such as game play or sport competitions, which can be readily adapted to a laboratory situation.

One effective paradigm used to elicit reactive aggression in the laboratory is the Point Subtraction Aggression Paradigm (PSAP; Cherek, 1981). The PSAP is a computer game in which participants press a button to earn points, which are later exchanged for money. During the task, participants are provoked in that they have points stolen from them by an opponent (a fictitious opponent). In addition to earning points by pressing one button, players can take away points from their opponent by pressing a different button. In most versions of the PSAP, participants are told that they have been randomly assigned to an experimental condition whereby they are not able to keep stolen points. Because participants do not gain any financial reward from stealing points, it is inferred that stealing points serves to punish the opponent, and as such, represents a measure of reactive aggression. Aggressive behaviour on the PSAP is negatively correlated with total points earned during the task, indicating that participants forgo financial reward to punish their partner (Carré and McCormick, 2008; Carré et al., 2009). Although this may appear to be poor economic decision-making, we proposed that the short-term financial costs of reactive aggression may be outweighed by the long-term emotional benefits and/or the possibility of influencing future social interactions (Carré et al., 2009). This possibility is supported by observations from studies of the Ultimatum Game (Güth et al., 1982). In this task, an individual is given a sum of money (proposer) and must decide how much of this money to offer another individual (responder). If the responder accepts the offer, both participants receive their respective allocations, but if the responder rejects the offer, both participants receive nothing. Although the rational choice of the responder would be to accept any offer greater than zero, most individuals reject offers in which they are allocated less than 20% of the total sum of money

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given to the proposer (Camerer and Thaler, 1995). This behaviour, which comes at the expense of extrinsic reward, may function to prevent unfair allocations in future social interactions (Fehr and Gächter, 2000, 2002; Nowak et al., 2000). Thus, aggression on the PSAP may be like refusal of offers in the Ultimatum Game, retaliation to the provocation of unfair behaviour and an attempt to regulate the other player's future behaviour.

That such punishment or aggression comes at the cost of extrinsic monetary reward suggests that this behaviour must have high intrinsic reward value, given that it trumps the motivation for extrinsic financial reward. The latter possibility may be related to our recent finding that individual differences in aggression presses during the PSAP were positively correlated with testosterone responses to the task (Carré and McCormick, 2008). A number of experiments with animal models indicate that testosterone has rewarding properties (see Frye, 2007; Wood, 2008 for reviews). For example, male hamsters self-administer testosterone (Johnson and Wood, 2001; Wood et al., 2004), and male rats develop a preference for locations that were previously paired with testosterone injections versus locations paired with saline injections (Alexander et al., 1994; Packard et al., 1997). Thus, an increase in testosterone may contribute to the intrinsically rewarding nature of reactive aggression.

Here, to better understand the motivational factors underlying aggressive behaviour during the PSAP, we created versions whereby aggressive behaviour would not come at cost to extrinsic financial reward (players would keep the points they stole) to compare to conditions in which aggression is costly (stolen points are not kept and these acts come at the cost of earning points). These two conditions are labelled as Rewarded or Not Rewarded for aggression. The role of provocation in modulating aggression during the PSAP was also investigated by including conditions with and without provocation. These two conditions are labelled as Provoked or Not Provoked. Thus, a two-factor design, Reward × Provocation, was employed. We predicted that participants would be less likely to choose the aggression option in the absence of provocation. Aggression under conditions of no provocation can also be considered the least "fair" or least "socially justifiable", particularly given that optimal gain in external reward can occur in the absence of aggression and given that the aggressive behaviour cannot be viewed as retaliatory. We then investigated the extent to which the relationship between aggressive behaviour and testosterone dynamics was specific to the condition of provocation, or would be evident irrespective of provocation and reward. As an indication of the intrinsic reward value of each PSAP condition, participants rated how enjoyable the task was and were asked to choose between competing again against the same person on a novel task or helping the investigator validate a computer program (i.e., choice of a competitive versus non-competitive task). We hypothesized that the intrinsic reward value of aggression might be greatest when justified by provocation, but especially when it was most costly (condition of no reward but involving provocation). An additional question investigated was whether a change in testosterone concentrations and the extent of aggression during the PSAP predict enjoyment and subsequent choice of a competitive versus non-competitive task in all four conditions or whether such relationships limited to the condition in which there is provocation and the aggression is costly.

1. Methods

1.1. Participants

The participants were 151 undergraduate men recruited from Brock University (mean age = 19.78, SD = 1.93). The majority of participants were self-identified as Caucasian (84.1%). Participants were instructed not to eat 1 h prior to arriving in the laboratory for testing. Eight participants reported taking prescription medication (e.g., SSRIs, glucocorticoids, thyroxin, and Ritalin) and were removed from analyses. Behavioural data from four participants were lost due to computer malfunction. Thus, the final sample consisted of 139 male participants.

1.2. Measures

1.2.1. Point Subtraction Aggression Paradigm (PSAP)

Originally designed by Cherek (1981), the PSAP is used to measure reactive aggression in a laboratory setting. In this task, participants are paired with a fictitious person during experimental sessions and have the opportunity to make money based on their performance. The goal of the task is to gain as many points as possible; the more points earned, the more money participants make. In the original version of the PSAP, participants have points taken from them by a fictitious partner (i.e., they are provoked) throughout the task. They can respond by stealing points back, but they are told that they have been randomly assigned to the experimental condition whereby the points that they steal are not added to their point counter. Thus, given that participants do not gain any financial reward by stealing points and that stealing points actually comes at the expense of gaining points (e.g., Carré and McCormick, 2008; Carré et al., 2009), it can be inferred that participants are stealing points to 'punish' their partner. Here, aggressive behaviour is defined as any behaviour "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 need not be physical in nature, but must be considered as an aversive stimulus by the receiver.

The validity of the PSAP has been established in a number of studies. Male and female parolees with violent histories behaved more aggressively on the PSAP than parolees with non-violent histories (Cherek and Lane, 1999; Cherek et al., 1996, 1997). Furthermore, aggressive behaviour on the PSAP is moderately correlated with various self-report measures of aggression (Gerra et al., 2007; Golomb et al., 2007). Also, consistent with the literature on sex differences in aggression (see Archer, 2004, 2009 for reviews), men are more aggressive on the PSAP than are women (Carré et al., 2009).

Participants were randomly assigned to one of the four experimental conditions in which the PSAP was modified to differ in the extent of provocation and external reward received for aggression (see Table 1 for a breakdown of the conditions). (1) *Provoked/Not Rewarded*: In this condition, similar to our previous studies, participants are provoked (have points stolen) by their fictitious partner and are told that they can steal points from their opponent, but that they had been randomly assigned to the experimental condition in which they do not get to keep stolen points whereas the opponent does. (2) *Not Provoked/Not Rewarded*: In this condition, participants are never provoked during the task and do not get to keep the points that they steal from their partner. (3) *Provoked/Rewarded*: In this condition, participants are provoked during the task and are told that any points stolen from their partner would be added to their own point counter. (4) *Not Provoked/Rewarded*: Participants in this condition are never provoked and are told that any points stolen from their partner would be added to their own point counter. As in our previous studies (Carré and McCormick, 2008; Carré et al., 2009), participants in the current experiment had three response options available to them; Button 1 (point press), Button 2 (aggression press), and Button 3 (protection press). In our previous studies, participants had to hit Button 1 a hundred consecutive times to earn a single point, and had to select Button 2 and Button 3 ten consecutive times to steal a point and protect their points, respectively. In the current experiment, participants had to hit Buttons 1, 2, and 3 fifty consecutive times to earn points, steal points, or protect points, respectively. We chose to keep the number of button presses required for each option equal to ensure that it was never easier to earn points by using the aggression press option than to earn points by using the point press option. Participants were told that they could initiate a provocation-free interval by hitting Button 3 fifty times. When a provocation-free interval was initiated, the computer program did not provoke participants for a minimum of 45 s and a maximum of 90 s after which the random point subtractions would continue to occur every 12–45 s. Once participants selected one of the three response options, they were committed to this option until they completed the fixed ratio of 50 presses, after which they were free to select any other option. For conditions involving provocation, the computer program provoked participants by stealing a point every 12–45 s in the absence of any Button 2 or Button 3

Table 1
Breakdown of the four experimental conditions.

	Provoked	Not Provoked
Rewarded for aggression	Reactive/Proactive condition (n = 34)	Proactive condition (n = 34)
Not Rewarded for aggression	Reactive condition (n = 36)	Control condition (n = 35)

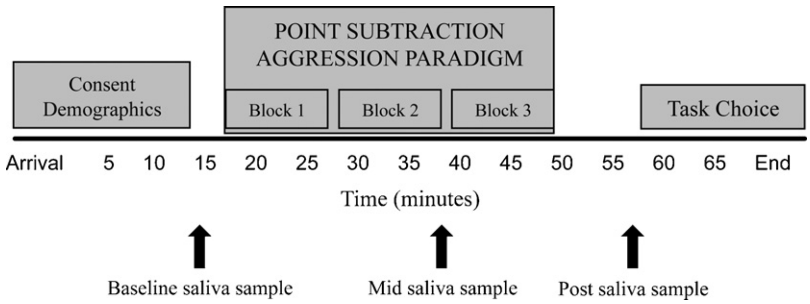

Fig. 1. Timeline of experimental procedures.

selections. For conditions not involving provocation, participants never had points stolen from them.

1.3. Saliva collection procedure and salivary testosterone assay

Saliva samples were collected in polystyrene culture tubes and 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 mean intra-assay coefficient of variation was 3.74%.

1.4. Procedure

All testing took place between 1200 and 1600 h to control diurnal variation in testosterone. Upon arrival, participants completed a consent form along with a short demographic questionnaire. Once completed, participants provided the researcher with a 1–2 ml saliva sample (baseline testosterone). After providing the first saliva sample, participants were randomly assigned to one of the four experimental conditions and were given instructions for the PSAP. Participants were given a 1-min practice session to become familiar with the response options. Next, participants played three 10-min sessions of the PSAP. After the second session (i.e., approximately 24 min after the first saliva sample), participants provided a second 1–2-ml saliva sample (mid-testosterone). At the conclusion of the third session, participants completed a brief Likert-scale questionnaire assessing their thoughts on the task (example of items; "I enjoyed the task", "I obtained more points than my opponent", "I formed a positive impression of my opponent"; scale ranging from −2 very inaccurate to +2 very accurate). As a means to gauge the level of suspicion, participants were asked "During the computer task, did you form any impressions of your opponent (positive or negative)". In total, 24% of participants reported some degree of suspicion as to whether they were actually playing the PSAP with another person (6% Provoked/Not Rewarded condition, 27% Provoked/Rewarded condition, 53% Not Provoked/Rewarded condition and 11% Not Provoked/Not Rewarded condition). Nonetheless, preliminary analyses did not find suspicion a significant factor in analysis, so all participants were kept in future analyses. Examples of suspicious responses included "I was unsure if my opponent was even present because he made no visible attempts to defend himself or fight back", "My impression was that there was no opponent", "Steals were fairly random, was I even playing anyone", "I formed no impression, not even sure if I was playing against another person". Approximately 10 min after completion of the PSAP, participants provided a third saliva sample (post-testosterone). Last, participants were given the option to choose between a competitive or non-competitive task as the final part of the experiment. Participants were told that both tasks took the same amount of time (5 min) and were the same level of difficulty. Option 1—Compete with the same person on a puzzle-solving task, or Option 2—Help the investigator validate a program assessing puzzle-solving abilities. The options were fully counter-balanced within each of the experimental conditions (see Fig. 1 for an overview of the procedure).

1.5. Statistical analyses

Analyses of variance (ANOVA) with Reward and Provocation as between-subject factors were computed to examine the extent to which our manipulation of provocation and reward would produce quantitative differences in aggressive behaviour, points earned (measure of extrinsic reward), and the extent to which participants enjoyed the task (measure of intrinsic reward). Tests of differences in proportions were computed to examine whether experimental groups differed in their task preference. For each experimental condition, chi-square analyses were computed to examine the extent to which individuals demonstrated a task preference (i.e., choice of the competitive versus non-competitive task) after playing the PSAP. Next, within each experimental condition, Pearson correlations were used to examine the association between aggression presses and points earned during the task (i.e., extrinsic reward), the extent to which participants enjoyed the task (i.e., intrinsic reward), and testosterone dynamics. One sample *t*-tests were also used on the percent change in testosterone values (pre- to mid-PSAP and pre- to post-PSAP) to examine whether there were any significant changes in testosterone within each of the experimental conditions. Last, multiple logistic regression analyses were computed separately for each experimental condition to assess whether testosterone dynamics and/or aggressive behaviour would predict subsequent task choice (i.e., choice of a competitive versus non-competitive task).

2. Results

2.1. Descriptive statistics

Descriptive statistics for age, baseline, mid, and post-PSAP testosterone concentrations across experimental conditions are presented in Table 2. Men assigned to be in the provoked conditions had lower baseline testosterone concentrations than men assigned to be in the non-provoked conditions ($F_{1,135} = 3.87$, $p = 0.05$). The other testosterone measures (e.g., mid- and post-PSAP testosterone), and age did not differ across experimental conditions.

2.2. Points earned and aggression presses as a function of provocation and/or reward

Men who were provoked were more aggressive than men who were not provoked ($F_{1,135} = 4.19$, $p = 0.04$), and men who were rewarded for aggression were more aggressive than men who were not rewarded for aggression ($F_{1,135} = 78.54$, $p < 0.001$). There was no interaction between the two factors ($p = 0.72$) (see Fig. 2). Men who were provoked earned fewer points than men who were not provoked ($F_{1,135} = 253.09$, $p < 0.001$) and men who were rewarded for aggression earned more points than men who were not rewarded for aggression ($F_{1,135} = 43.21$, $p < 0.001$). There was a

Table 2
Mean (SEM) age and testosterone concentrations for each experimental condition.

	Experimental conditions			
	Provoked/Not Rewarded	Not Provoked/Not Rewarded	Provoked/Rewarded	Not Provoked/Rewarded
Age	19.69 (0.33)	19.46 (0.26)	19.85 (0.31)	19.88 (0.34)
Pre-testosterone (pg/ml)*	87.00 (6.76)	103.99 (6.98)	85.33 (8.47)	98.07 (7.98)
Mid-testosterone (pg/ml)	94.34 (6.58)	109.00 (8.99)	83.93 (6.07)	92.70 (8.26)
Post-testosterone (pg/ml)	88.05 (6.11)	103.03 (7.88)	85.29 (7.43)	92.69 (7.98)

* $p = 0.05$, main effect of provocation.

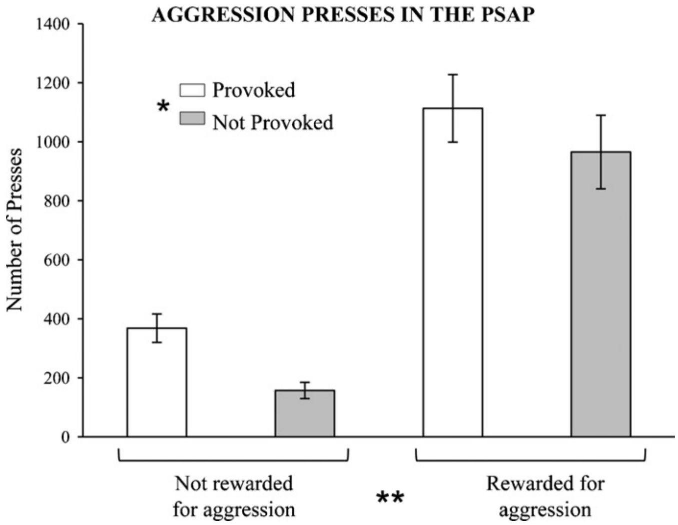

Fig. 2. Mean (SEM) aggression presses as a function of Reward and of Provocation. *Main effect of Provocation ($p = 0.04$). **Main effect of Reward ($p < 0.001$).

Provocation × Reward interaction ($p < 0.001$), indicating that men who received reward for aggression earned more points than men who did not receive reward for aggression, but only if they were provoked during the PSAP.

2.3. Choice of competitive versus non-competitive task

Tests of significant differences in proportions were used to examine if experimental groups differed in the extent to which they had a preference for the competitive versus non-competitive task. A between group analysis found that men in the Provoked/Not Rewarded condition were more likely to choose the competitive task rather than the non-competitive task than were the other experimental groups (all $ps < 0.04$). Men in the Not Provoked/Not Rewarded condition were more likely to choose the competitive versus non-competitive task than were men in the Not Provoked/Rewarded condition ($p = 0.02$). Chi-square analyses were used to examine whether the preference for the competitive task compared to the non-competitive task was significant within each experimental group. Only men in the Provoked/Not Rewarded condition had a task preference, with 29 out of 35 (83%) men choosing the competitive over the non-competitive task ($\chi^2 = 15.11$, $p < 0.001$) (see Fig. 3). In the other conditions, each option was chosen equally often.

2.4. Relationship between aggression presses and points earned within conditions

In both the Provoked/Not Rewarded and the Not Provoked/Not Rewarded conditions, points earned and aggression presses were negatively correlated ($r = -0.77$, $p < 0.001$ and $r = -0.66$, $p < 0.001$ respectively), indicating that aggressive behaviour was costly. For men in the Provoked/Rewarded condition, there was a positive correlation between aggression presses and points earned ($r = 0.55$, $p = 0.001$). There was no relationship between points earned and aggression presses for men in the Not Provoked/Rewarded condition ($r = -0.07$, $p = 0.69$).

2.5. Enjoyment of the PSAP as a function of provocation and/or reward

Men who were provoked enjoyed the PSAP more than men who were not provoked ($F_{1,133} = 8.64$, $p = 0.004$). The effect of Reward

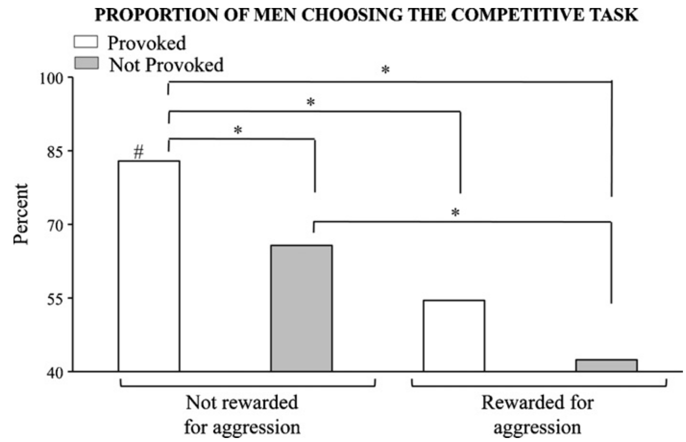

Fig. 3. Percentage of men who chose the competitive versus non-competitive task in each experimental condition. *Significant group differences in percent choosing the competitive task $p < 0.04$. #Significant preference for the competitive task within a condition ($p < 0.001$).

and the interaction of the two factors were not significant ($p = 0.13$ and 0.90) (see Fig. 4). The only group for which there was a significant association between individual differences in the extent to which men enjoyed the PSAP and aggressive behaviour was for men in the Provoked/Not Rewarded condition ($r = 0.41$, $p = 0.02$) (see Table 3 for other correlations).

2.6. Relationship between testosterone dynamics and aggression

Three participants who had change in testosterone scores greater than three standard deviations from the mean were removed from all subsequent analyses involving testosterone dynamics. No main effects of Reward or Provocation were evident when ANOVA was used to compare change in testosterone during the PSAP ($ps = 0.17$ and 0.13, respectively). Also, there was no interaction between the two factors ($p = 0.71$). When each condition was examined separately, the only group for which there was a significant increase in testosterone from baseline (baseline to mid-PSAP) was for men in the Provoked/Not Rewarded condition (mean increase = 14.58%, $t_{34} = 2.23$, $p = 0.03$) (see Fig. 5). Also, for men in this condition, the change in salivary testosterone concentrations

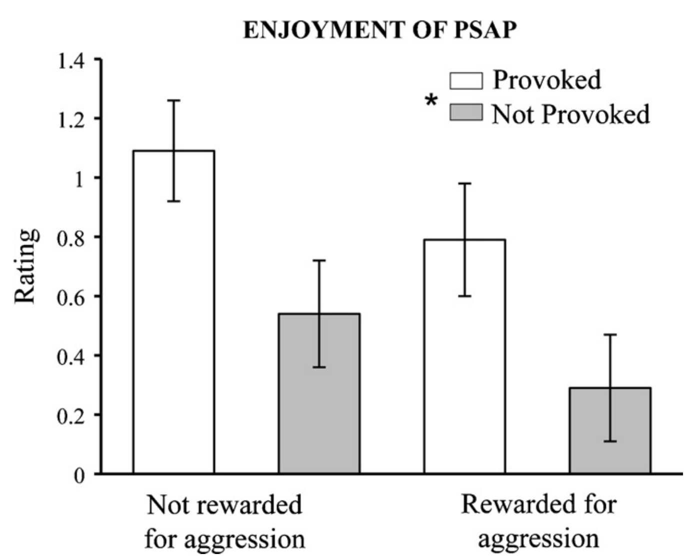

Fig. 4. Mean (SEM) ratings of enjoyment of the Point Subtraction Aggression Paradigm (PSAP) as a function of Reward and of Provocation. *Main effect of Provocation ($p < 0.01$).

Table 3
Pearson correlations of the relationship between aggression presses and either baseline testosterone concentrations, change in testosterone, or task enjoyment for each experimental condition.

	Correlations with aggression presses			
	Provoked/Not Rewarded	Not Provoked/Not Rewarded	Provoked/Rewarded	Not Provoked/Rewarded
Pre-testosterone (pg/ml)	−0.15	0.22	−0.08	0.06
Change in testosterone (pre- to mid-PSAP)	0.34*	0.03	0.21	−0.01
Change in testosterone (pre- to post-PSAP)	0.10	0.12	−0.01	0.02
Task enjoyment	0.41*	0.10	−0.20	0.15

* $p < 0.05$.

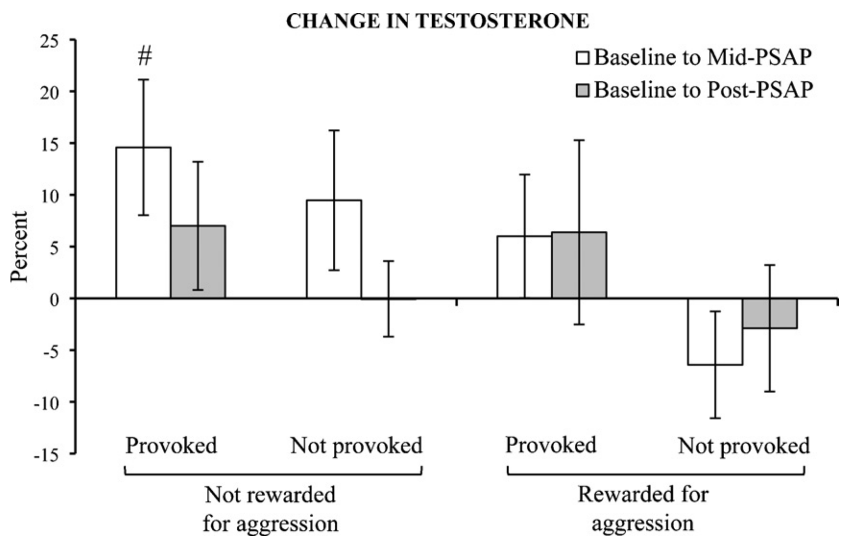

Fig. 5. Mean (SEM) percent change in testosterone from baseline to mid-PSAP and from baseline to post-PSAP as a function of Reward and of Provocation. #Significant increase in testosterone within a condition ($p = 0.03$).

from baseline to mid-PSAP and aggressive behaviour was significant ($r = 0.34$, $p = 0.049$) (see Fig. 6). For the other conditions, no correlation was significant (see Table 3).

2.7. Testosterone dynamics, aggressive behaviour, and willingness to compete

Multiple logistic regression analyses were computed to examine the extent to which aggressive behaviour and change in testosterone concentrations during the PSAP would predict subsequent task preference. Analyses were computed separately for each experimental condition with task preference dummy coded as 1 = choice of a competitive task, 2 = choice of a non-competitive task. For all analyses, the extent to which individuals enjoyed the PSAP was included on the first step and change in testosterone (pre- to mid- and pre- to post-PSAP) and aggressive behaviour were entered on the second step.

For men in the Provoked/Not Rewarded condition, too few individuals chose the non-competitive option ($n = 6$), precluding a multiple logistic regression analysis. For men in the Provoked/Rewarded and Not Provoked/Not Rewarded conditions, the variables of enjoyment, testosterone dynamics, and aggressive behaviour did not predict willingness to compete ($ps > 0.05$). For men in the Not Provoked/Rewarded condition, testosterone dynamics and aggressive behaviour predicted willingness to compete (χ^2 (2, $n = 32$) = 18.97, $p < 0.001$), indicating that both change in testosterone from pre- to post-PSAP ($p = 0.02$) and average aggressive behaviour ($p = 0.02$) predicted subsequent task preference. Specifically, individuals who chose to compete had a larger increase in testosterone (mean = 17.30%) and were more aggressive (mean = 1200.78) than individuals who chose the non-competitive task (mean = −16.70% and 800.43, respectively).

3. Discussion

Previous research has found that individuals engage in punitive or aggressive behaviour even when such behaviour comes at a financial cost (Güth et al., 1982; Fehr and Gächter, 2000, 2002; de Quervain et al., 2004; Carré and McCormick, 2008; Carré et al., 2009), suggesting that such behaviour is associated with high intrinsic reward. We explored this possibility by manipulating the extent to which aggressive behaviour (stealing points) during the PSAP would lead to financial cost by including conditions in which points stolen were not kept by the participant in addition to conditions in which participants kept stolen points. Further, in some conditions, participants were provoked by having their points stolen by the opponent, and in other conditions participants were not provoked, thereby manipulating the extent to which the aggressive behaviour could be justified as retaliatory or not. When both the financial incentive and retaliatory incentive for aggression were absent from the PSAP and the financial cost was high (as indicated by the negative correlation between aggression in this condition and points earned), the aggressive behaviour was very low. In this condition, ratings of enjoyment of the PSAP were low and there was no bias in subsequent choice of a competitive task over a non-competitive task. In contrast, aggressive behaviour was high when there was both a financial and retaliatory incentive for aggression. Nevertheless, despite higher ratings of enjoyment than in the no provocation conditions, there was no bias in this condition (provoked and rewarded) in subsequent preference for a competitive task over a non-competitive task.

The equally high aggressive behaviour of men in the condition of financial reward and no provocation to that of men in the financial reward and provocation condition was unexpected. In this condition, financial reward could be obtained as readily with-

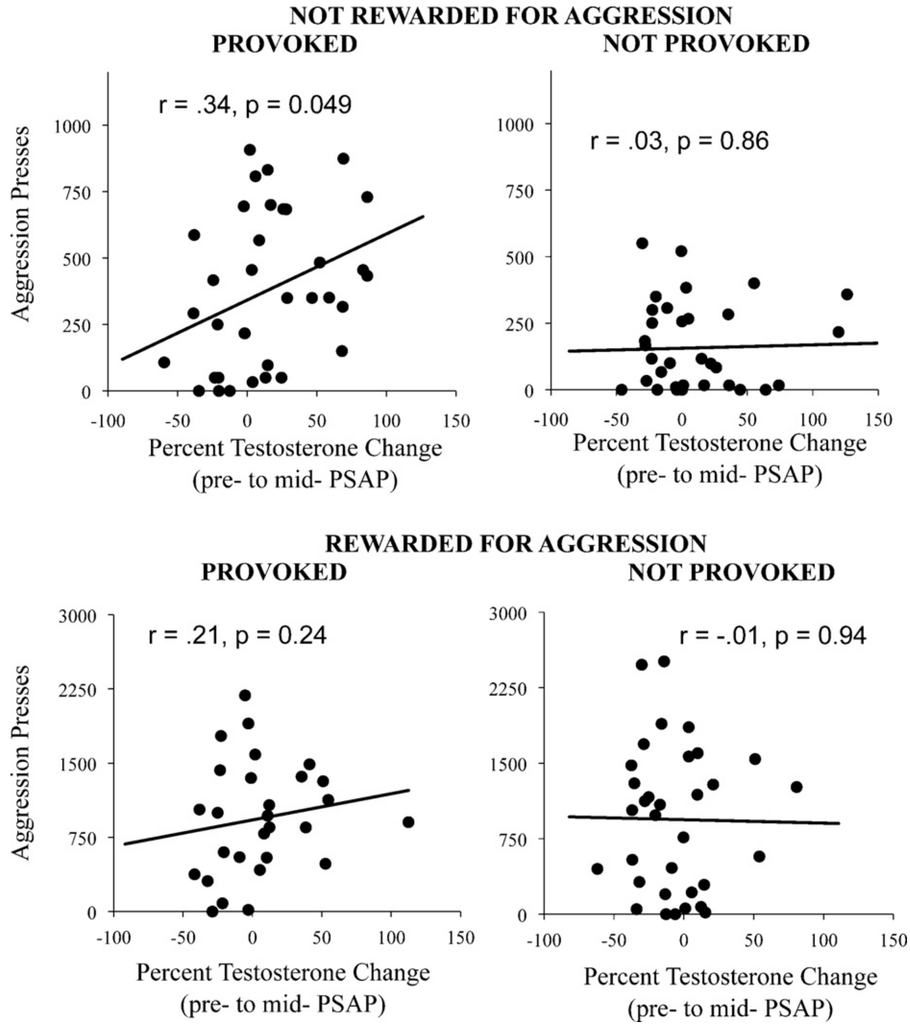

Fig. 6. Relationship between percentage change in testosterone (baseline to mid-PSAP) and aggression presses for each experimental condition.

out aggression as with aggression (50 presses were required to steal points, 50 presses were required to earn points), and there was no correlation between aggression presses and points earned ($r = -0.07$). Thus, aggression in this condition appears unnecessary and unjustifiable. It may be that a condition in which there was no retaliation from an opponent when participants stole points appeared too artificial, and thus participants may have been simply "reality testing" and/or trying to engage their opponent. This possibility is supported by the higher levels of suspicion in this condition compared to the other conditions. Further, ratings of enjoyment were low in this condition, and there was no bias in this condition in subsequent preference for a competitive task over a non-competitive task.

Only in the reactive aggression condition involving provocation and no financial reward was there an association between aggressive behaviour and level of enjoyment of the PSAP. This group also had the highest levels of enjoyment; significantly higher than both no provocation conditions, although not significantly different from that in the provocation and financial reward condition. Further, only in the reactive aggressive condition was there a significant preference for a subsequent competitive task than for a non-competitive task, and with the proportion choosing the competitive task higher in this condition than in the other conditions. Eighty-three percent of men in this condition chose the competitive option, which is similar to the proportion of men (71%) who chose a competitive versus a non-competitive option after the PSAP in our previous study involving the reactive aggression condition (Carré and McCormick, 2008). In sum, the present results provide support for the hypothesis that costly aggressive behaviour in the context of competition may have intrinsic reward value.

Recent imaging research provides supportive evidence for the idea that costly aggressive behaviour may be intrinsically rewarding. de Quervain et al. (2004) found that the amount of money participants were willing to pay to punish unfair participants in a monetary exchange game was positively correlated with activity in the striatum, a brain structure critically involved in processing reward. Another study reported that watching individuals who had played unfairly in monetary exchange game receive painful electric shocks produced increased activation in the striatum/nucleus accumbens relative to watching individuals who had played fairly (Singer et al., 2006). Further, participants' self-reported desire for revenge against unfair players was positively correlated with activation in these areas (Singer et al., 2006). Together, these findings suggest that observing or delivering punishment to unfair others may have intrinsic reward value.

The second main question we investigated was whether our previous finding of a relationship between change in testosterone concentrations and extent of aggression during the PSAP (Carré and McCormick, 2008) is limited to the condition involving provocation and costly aggression (reactive aggression condition), or would it extend to the other conditions. In the present study, although the between group comparisons were not significant, a significant change in testosterone concentrations was found only in the reactive aggression condition. Further, only in the reactive condition was a significant correlation observed between change in testosterone and aggression. The mean increase in the reactive condition group was 14%, similar to the 15% increase we previously reported (Carré and McCormick, 2008). However, in the present study, the increase was found mid-way through the PSAP as opposed to post-PSAP. One possibility for this difference is the lower rates of aggressive point presses in the present study than in our previous study. Aggression had greater extrinsic cost in this experiment, because 50 presses were required to steal a point as opposed to 10 presses in the previous study. The change was necessary to ensure that the benefit of aggressive presses was not greater than that of point presses in the conditions in which participants kept points stolen (50 presses to earn a point, 50 presses to steal a point). Thus, these changes may have affected the temporal dynamics of the relationship between aggression and testosterone. It is also possible that a lack of an association between change in testosterone and aggression for men assigned to conditions not involving provocation was partly due to a restricted range in testosterone responses. That is, unprovoked men had higher baseline testosterone concentrations than provoked men, and thus, may have been less capable of mounting an additional elevation to the PSAP.

Nonetheless, our finding of a relationship between changes in testosterone and aggression (albeit modest) only in the reactive aggression condition is consistent with reviews of the literature in humans indicating that relationships between testosterone and behaviour are most evident in the context of competition and/or when there is a threat to social status (Mazur and Booth, 1998; Archer, 2006). Our finding is also consistent with the proposal that physiological arousal is a feature of reactive, and not of proactive, aggression (Dodge and Coie, 1987; Crick and Dodge, 1996). In the present studies, the possibility of threat to social status is likely greatest in the reactive aggression condition. Further, in male rhesus monkeys, testosterone concentrations were associated with aggressive behaviours during defense and/or establishment of social dominance, but were not associated with maladaptive forms of escalated aggression (Higley et al., 1996), which also highlights that aggressive behaviour comes in many forms, and that relationships between testosterone and aggression are situational- and motivational-specific (see also Griskevicius et al., 2009). We have proposed that what may appear to be irrational economic behaviour in the PSAP situation – retaliation leading to decreased extrinsic reward – may be offset by motivations high in intrinsic reward value (Carré et al., 2009). Retaliation may be such a motivation (Griskevicius et al., 2009). Further, that an association with testosterone only in the condition in which aggression is both costly to extrinsic reward and is retaliatory suggests that changes in testosterone may be a marker of the intrinsic reward value of the aggression.

Studies of laboratory animals have provided evidence of the reward value of elevations in testosterone (see reviews by Frye, 2007; Wood, 2008), and there is evidence to support the hypothesis that one functional outcome of rises in testosterone is the facilitation of the behaviours associated with its rise. For example, in animal models, winning an aggressive encounter leads to a rise in testosterone and a preference for locations associated with such a win (Oyegbile and Marler, 2005; Meisel and Joppa, 1994; Martínez et al., 1995; Farrell and Wilczynski, 2006). Further, a rise in testosterone concentrations following successful aggressive encounters facilitate future aggressive behaviour and increase the probability of winning future competitive interactions (Trainor et al., 2004; Gleason et al., 2009; Oliveira et al., 2009). Thus, a rise in testosterone associated with extrinsically costly retaliatory behaviour may be adaptive because it serves to promote behaviour in an individual that is perhaps costly in the immediate, but with potential future benefit if it serves to alter the behaviour of an opponent.

There is correlational evidence in studies of people that endogenous fluctuations in testosterone influence future competitive and aggressive behaviours (Mehta and Josephs, 2006; Klinesmith et al., 2006; Carré and McCormick, 2008; Carré et al., 2009). Also, exogenous administration of testosterone in studies of people influences a number of factors that may be relevant in future upcoming competitive interactions (van Honk et al., 2001; Aleman et al., 2004; Hermans et al., 2006). Using the reactive aggression form of the PSAP, we previously reported that change in testosterone concentrations and aggressive behaviour predicted subsequent choice of playing a competitive versus non-competitive task (Carré and McCormick, 2008). The sample size of men who chose the non-competitive option (6 of 35) did not allow us to test for such a relationship in the reactive condition in the present study. Inexplicably, a relationship was observed in the Not Provoked/Rewarded condition. Men who were most aggressive and for whom testosterone concentrations increased during the PSAP were more likely to choose the competitive over the non-competitive task. Although men in the Not Provoked/Rewarded condition had the lowest ratings of enjoyment of the PSAP and were the least likely to choose a competitive task, ratings of enjoyment was not a factor in predicting willingness to compete. A recent study that involved a similar PSAP condition (reward for aggression with no provocation) reported that individuals who engaged in high levels of unprovoked aggression scored significantly higher on measures of psychopathy and personality disorders (Nouvion et al., 2007), thus perhaps such factors are involved in the relationship we observed. However, as noted above, the men in the Not Provoked/Rewarded condition had the most suspicion with regard to their fictional opponent and, thus this condition may be the most artificial of the four PSAP conditions.

In summary, the current study adds to our understanding of costly aggressive behaviour that occurs in the context of human competition. Although reactive aggressive behaviour during the PSAP is costly in terms of financial reward, it may have intrinsic reward value in that it is retaliatory, possibly as an attempt to regulate another's "unfair" behaviour. Compared to the other conditions, the reactive aggression condition of the PSAP was the only condition to lead to a significant preference for a subsequent competition and a significant increase in salivary testosterone, and was the condition for which the PSAP was rated as most enjoyable. Self-deception (positive illusion, overconfidence) has been proposed to be a psychological adaptation guiding costly aggressive behaviour in combat (Wrangham, 1999; Johnson et al., 2007), and the intrinsic reward value of costly aggression may be another such adaptation. The extent to which testosterone is one of the biological mechanisms that serves to strengthen the reward value of costly aggressive behaviour requires further investigation.

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