

SOCIAL NEUROENDOCRINOLOGY OF COMPETITION

by

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ABSTRACT

The relationship between testosterone concentrations and aggressive behaviour in studies of people has produced very inconsistent findings. However, one consistent finding that has emerged is that competitive and aggressive interactions potentiate testosterone release in both human and non-human species. It has been argued that socially-induced alterations in testosterone concentrations may function to influence ongoing and/or future social behaviour. Nonetheless, few studies have empirically tested this hypothesis. The current series of experiments was designed to address the extent to which competition-induced fluctuations in testosterone concentrations were associated with ongoing and/or subsequent social behaviour. In Study 1, men ($n = 38$) provided saliva samples prior to, and at the conclusion of, the Point Subtraction Aggression Paradigm (PSAP). Although baseline testosterone concentrations were not related to aggressive behaviour, there was a positive correlation between change in testosterone and aggressive behaviour such that men who were most aggressive on the PSAP demonstrated the largest increase in testosterone concentrations. Furthermore, a rise in testosterone during the PSAP predicted willingness to choose a subsequent competitive task. In Study 2, men and women provided saliva samples prior to and after competing against a same-sex opponent on the Number Tracing Task (NTT). The outcome of the competition was rigged such that half of the individuals won most of the races, while the other half lost most of the races, thus experimentally creating a winner and loser in the laboratory. Following the competitive interaction, men and women played the PSAP with their same-sex partner. Results indicated that men selected the aggressive response (but not reward or protection responses), more frequently than women. For men assigned to the loss condition, an

increase in testosterone concentrations in response to the NTT predicted subsequent aggressive behaviour. For men assigned to the win condition, an increase in testosterone concentrations in response to the NTT predicted subsequent aggressive behaviour, but only among those men who scored high on trait dominance. Change in testosterone and trait dominance did not predict aggressive behaviour in women. In Study 3, men provided saliva samples prior to, during, and at the end of the PSAP. They were randomly assigned to one of four experimental conditions that differed in the extent to which they were provoked and whether they received reward for behaving aggressively (i.e., stealing points). Results indicated that baseline testosterone concentrations did not correlate with aggression in any of the experimental conditions. Consistent with Study 1, there was a positive correlation between change in testosterone and aggressive behaviour among men who were provoked, but did not receive reward for aggression (i.e., reactive condition). Men who were provoked but did not receive reward for aggression enjoyed the task the most and were more likely to choose the competitive versus non-competitive task relative to men assigned to the other experimental conditions. Also, individual differences in aggressive behaviour among these men were positively correlated with the extent to which they enjoyed the task. Together, these studies indicate that testosterone dynamics within the context of competition influence subsequent competitive and aggressive behaviours in humans and that testosterone may be a marker of the intrinsically rewarding nature of costly aggressive behaviour.

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CHAPTER 1 - GENERAL INTRODUCTION

“To an evolutionary biologist, testosterone may be one of the most interesting hormones because it is so intimately associated with reproduction and affects such a wide variety of traits” (Ketterson & Nolan, 1992, p. 34).

The steroid hormone testosterone is of interest to researchers in many disciplines because once secreted into the blood stream, it may interact with receptors in various tissues to modulate a wide range of morphological, physiological, and behavioural characteristics. For instance, during gestation, testosterone is responsible for the sexual differentiation of internal and external genitalia, as well as the sexual differentiation of various brain structures implicated in the regulation of social behaviour (see Arnold & Gorski, 1984 for review). In adults, testosterone is responsible for the development of secondary sex characteristics, growth of bones and muscles, the initiation of spermatogenesis (see Porterfield, 2001 for review), and is also associated with sexual behaviour, physical strength, and aggression (see Zitzmann and Nieschlag, 2001 for review). Thus, testosterone has the potential to influence various processes that are critical to survival and reproduction (Ketterson & Nolan, 1990).

Despite the benefits of testosterone, prolonged exposure to this hormone may carry substantial costs. Chronically elevated testosterone concentrations may interfere with paternal behaviour, increase exposure to predation, increase risk of injury, increase metabolism, impair immune system functioning, and may have oncogenic effects (see Wingfield, Lynn, & Soma, 2001 for review). However, research has demonstrated that testosterone concentrations are not static, but instead, fluctuate throughout the season (e.g., breeding versus non-breeding) and in response to social interactions (see Wingfield, Hegner, Dufty, & Ball, 1990; Oliveira, 2009 for reviews). Thus, acute fluctuations in

testosterone may provide a physiological mechanism for maximizing processes relevant to survival and reproduction while also avoiding the costs of maintaining elevated testosterone concentrations (see Wingfield et al., 2001 for review). In male rodents, testosterone concentrations rise with exposure to female rodents and in response to sexual behaviour (see Nyby, 2008 for review). Similarly, testosterone concentrations in men rise in response to viewing sexually explicit movies (Hellhammer, Hubert, & Schumeyer, 1985), during conversations with attractive women (Roney, Lukaszewski, & Simmons, 2007; Roney, Simmons, & Lukaszewski, 2009), and during sexual intercourse (see van Anders & Watson, 2006 for review). Testosterone concentrations are also highly responsive to male-to-male competitive interactions (see Wingfield et al., 1990; Mazur, 1985; Oliveira, 2009), and the outcome of such interactions influences the pattern of testosterone release (see Mazur, 1985; Archer, 2006 for reviews). Together, these findings indicate that there is a complex reciprocal relationship between testosterone and behaviour whereby testosterone concentrations both influence, and respond to, social behaviour (Oliveira, 2009).

Socially-induced testosterone fluctuations are generally interpreted from a functional perspective whereby a rise in testosterone may fine-tune ongoing and/or future behavioural responses (see Wingfield et al., 1990; Mazur, 1985; Nyby, 2008; Oliveira, 2009 for reviews). Recent evidence in non-human animals provide compelling support for this hypothesis (e.g., Ramage-Healey & Bass, 2006; Trainor et al., 2004; Gleason, Fuxjager, Oyegbile, & Marler, 2009; Oliveira, Silva, & Canario, 2009). However, the extent to which socially-induced fluctuations in testosterone are associated with ongoing and/or future human social behaviour has received very little attention.

In this dissertation, I investigate associations between testosterone dynamics and aggressive behaviour within the context of competition. The rationale for using aggression as the main criterion variable is based on the following: 1) Androgen receptors are located in key regions of the brain that are known to mediate aggressive behaviour (see Newman, 1999; Simon & Lu, 2006 for reviews); 2) There is a rich literature on the relationship between baseline testosterone concentrations and aggressive behaviour in many species, including humans (see Simon & Lu, 2006; Archer, 2006 for reviews); 3) Changes in testosterone during competitive interactions coincide with aggressive behaviour in non-human animals (see Wingfield et al., 1990; Oliveira, 2004; 2009 for reviews); 4) Testosterone responses to competitive interactions influence future aggressive behaviour (mice, Trainor, Bird, & Marler, 2004; Gleason et al., 2009; fish, Oliveira et al., 2009), and 5) Human aggression can be readily assessed in a controlled laboratory setting. In this Chapter, I provide a general review of the literature on testosterone and competitive/aggressive behaviour. Section 1 begins with a basic overview of testosterone and Section 2 provides a brief review of the literature on the relationship between baseline testosterone concentrations and human aggression. In Section 3, I summarize the evidence for the role of competitive interactions in modulating testosterone release, with an emphasis on the 'Challenge Hypothesis' and 'Biosocial Model of Status'. In Section 4, I review recent evidence for the functional role of testosterone fluctuations in modulating ongoing and/or future social behaviour. Results from Studies 1, 2, and 3 will be presented in Chapters 2, 3, and 4, respectively. Finally, Chapter 5 will provide a summary and a general discussion of the main findings.

Section 1. TESTOSTERONE BASICS

Testosterone is a steroid hormone synthesized by the Leydig cells of the testes in men, the thecal cells of the ovaries and placenta of women, and the zona reticularis of the adrenal cortex of both men and women. Testosterone secretion is governed by the hypothalamic pituitary gonadal axis (HPG). More specifically, neurons within the hypothalamus secrete gonadotropin-releasing hormone (GnRH) into the hypophyseal portal system, which binds to receptors in the anterior pituitary and stimulates the release of luteinizing hormone (LH) and follicular stimulating hormone (FSH). LH travels through the blood stream, binding to receptors on the Leydig cells of the testes and the thecal cells of the ovaries, stimulating the secretion of testosterone. The regulation of testosterone is governed by classic negative feedback, such that testosterone binding to receptors located in the anterior pituitary and hypothalamus decreases subsequent secretion of LH and GnRH, respectively.

Testosterone is particularly relevant to psychologists because of its ability to cross the blood-brain-barrier and interact with receptors located in key brain structures known to mediate social behaviour (Newman, 1999). In the brain, testosterone may act on pre- and/or post-synaptic neuron membranes to alter the permeability to neurotransmitters, modulate production of enzymes and hormone receptors, enzymes for production of neurotransmitters, neuropeptides and their receptors, ion channels, proteins for building and repairing axons, and many other physiological effects (see McEwen, Davis, Parsons, & Pfaff, 1979; Adkins-Regan, 2005 for reviews). How does testosterone influence such complex processes? Adkins-Regan (2005) simplifies the process by stating that steroid

hormones such as testosterone “tickle the genome” (p. 13). Specifically, testosterone may act within target cells by binding directly to intracellular androgen receptors (AR) and modulating gene transcription. Testosterone may also be metabolized to dihydrotestosterone or estradiol and subsequently bind to androgen or estrogen receptors, respectively. Studies indicate that androgen and estrogen receptors are located in key neural structures known to mediate aggressive behaviour, including the bed nucleus of the stria terminalis, the medial pre-optic area, the lateral septum, and the medial amygdala (see Newman, 1999; Simon, 2002 for reviews). These findings indicate that testosterone and/or its metabolites have the potential to modulate aggressive behaviour by acting on intracellular receptors located in these key limbic structures.

In addition to its slow genomic mode of action (i.e., it takes several minutes to hours for testosterone to influence gene transcription and subsequent protein formation), testosterone may influence physiological processes within seconds, suggesting that testosterone may be acting via non-genomic, membrane-bound receptors (see Michels & Hoppe, 2008 for review). Testosterone’s fast acting effects through membrane-bound receptors and/or ion channels may also trigger downstream second messenger processes within the cell, which, in turn, may modulate gene transcription. Thus, testosterone has the potential to influence behavioural processes by acting through both slow- and/or fast-acting biological mechanisms. Of particular interest to the current dissertation is testosterone’s role in modulating aggressive behaviour in humans. The following section will provide a brief review of the literature on the relationship between baseline testosterone concentrations and aggressive behaviour in humans.

Section 2. TESTOSTERONE AND HUMAN AGGRESSION

“We require, as a team, proper levels of pugnacity, testosterone, truculence and belligerence. That's how our teams play. I make no apologies for that. Our team plays a North American game. We're throwbacks. It's black-and-blue hockey. It's going to be more physical hockey here than people are used to” (Brian Burke, General Manager, Toronto Maple Leafs Hockey).

The idea that testosterone is related to human aggression comes from various sources. Research in humans indicates that men are generally more aggressive than women (Archer, 2004; 2009), have much higher testosterone concentrations than women (Dabbs, 1990), and at a time when testosterone concentrations peak (e.g., ages 21-35), there is an increase in male-to-male aggressive behaviour (Daly & Wilson, 1988). Thus, in the words of Robert Sapolsky “testosterone [is] found on the scene repeatedly with no alibi when some aggression has occurred” (Sapolsky, 1997, p. 47). Nevertheless, studies of the relationship between baseline testosterone concentrations and aggressive behaviour in people have produced mixed results (see Archer, 1991; Archer, Birring, & Wu, 1998; Archer, Graham-Kevan, & Davis, 2005 for reviews). Before reviewing the evidence, it is important to briefly define what I mean by ‘aggression’.

2.1 Operational definition of aggression

Baron and Richardson (1994) state that “aggression is any form of behaviour directed toward the goal of harming or injuring another living being who is motivated to avoid such treatment” (p. 7). This definition allows for aggressive behaviour to be physical or non-physical in nature. Physical aggression may involve pushing, slapping, kicking, punching, or any type of behaviour that inflicts physical damage to another

living being who, in turn, is motivated to avoid such treatment. Non-physical aggression can involve name-calling, issuing threats, and spreading nasty rumours. In both cases, the behaviour of the aggressor is intentional, and the victims of such behaviour clearly do not welcome such treatment. This definition of aggression would exclude non-intentional forms of aggression such as accidentally stepping on another person's toe, or bumping into someone in a crowded room.

Two of the main factors contributing to aggressive behaviour are interpersonal provocation and the pursuit of some desired goal (e.g., money, territory, status, mates). Accordingly, researchers have typically classified aggressive behaviour as either reactive/affective/hostile or proactive/instrumental. Reactive aggression is a defensive response to perceived or actual provocation and involves retaliation (Dodge & Coi, 1987). Commonly referred to as 'hot-blooded', reactive aggression is characterized by anger and impulsivity and is often accompanied by disinhibition, affective instability, and high levels of bodily arousal. On the other hand, proactive aggression, also referred to as instrumental aggression, occurs in the absence of direct provocation and is a goal-oriented behaviour aimed at the acquisition of a valued resource (Dodge & Coi, 1987). In contrast to reactive aggression, proactive aggression is a 'cold blooded' type of aggression characterized by low physiological arousal. Despite evidence for a two-factor model of aggression (Poulin & Boivin, 2000), few studies examining the relationship between testosterone and aggression have attempted to differentiate between the two forms of aggression.

In this section I will provide a brief review of the literature on the relationship between baseline testosterone concentrations and various measures of aggressive

behaviour in humans (see Archer, 1991; Archer et al., 1998; Archer et al., 2005 for detailed reviews and meta-analyses). Researchers have used three main methodological approaches to the study of testosterone and human aggression: Self-report questionnaires, comparison of violent versus non-violent offenders, and direct behavioural measures.

2.2 Self-report measures of aggression

The majority of studies examining the relationship between testosterone and human aggression have relied on self-report measures of aggression. The first published study on this topic found that 'aggressive feelings' were positively correlated with serum testosterone concentrations in a small sample ($n = 18$) of healthy young men ($r = .49$; Persky, Smith, & Basu, 1971). Despite this earlier report, studies with much larger sample sizes (e.g., $n = 100-250$) have failed to find any association between baseline testosterone concentrations and self-report measures of aggression (e.g., Monti, Brown, & Corriveau, 1977; Archer et al., 1998; Popma et al., 2007). Nevertheless, a recent meta-analysis by Archer and colleagues (2005) reported a positive (albeit small) relationship between testosterone and various self-report measures of aggression (Cohen's $d = .17$, 95% CI = .17 to .28).

One main limitation of studies employing self-report measures of aggression is that these questionnaires assess general behavioural tendencies across situations (i.e., trait aggression). This issue is especially problematic given that studies in non-human animals indicate that the relationship between testosterone and aggressive behaviour may be context dependent (e.g., Wingfield et al., 1990; Sapolsky, 1983; Cavigelli & Pereira, 2000; Muller & Wrangham, 2004). Another problem is that someone who scores high on a self-report measure of reactive aggression (e.g., "I generally respond aggressively when

people provoke me”) may not necessarily behave aggressively when provoked in the ‘real world’ or in a laboratory setting (Baumeister, Vohs, & Funder, 2007). Finally, most studies have failed to differentiate between reactive and proactive aggression. In the one study that did differentiate between reactive and proactive aggression, the authors reported that baseline testosterone concentrations were positively correlated with a self-report measure of reactive, but not proactive, aggression (Olweus, Mattsson, Schalling, & Low, 1980). Thus, perhaps some of the inconsistencies in the literature are, in part, related to a general failure to consider the multidimensional nature of aggressive behaviour.

2.3 Prisoners and aggression

Another research strategy has been to compare testosterone concentrations from prisoners convicted of violent versus non-violent crimes. These studies typically report that men convicted of violent crimes have higher testosterone concentrations relative to those convicted of non-violent offences (Kreuz & Rose, 1972; Ehrenkranz, Bliss, & Sheard, 1974; Dabbs, Frady, Carr, & Besch, 1987; Dabbs, Jurkovic, & Frady, 1991; Brooks & Reddon, 1996). In the first of such studies, Kreuz and Rose (1972) reported that men with a history of aggressive behaviour during adolescence had higher testosterone concentrations than men without such a history (Kreuz & Rose, 1972). In a similar study, men convicted of violent crimes had significantly higher testosterone concentrations compared to men convicted of non-violent crimes (Ehrenkranz et al., 1974).

The main limitation to studies conducted with prison populations is that these studies are based on correlations between current testosterone concentrations and previous aggressive behaviours. Implicit in this research strategy is that testosterone

concentrations are stable across time and that current testosterone concentrations should reflect testosterone concentrations at the time of the crime. Although there is evidence that baseline testosterone concentrations are relatively stable across days, weeks, and months (e.g., r -values between .59 and .78; Dabbs, 1990; Sellers, Mehl, & Josephs, 2007), other studies indicate that testosterone concentrations fluctuate in response to social interactions, including dominant and aggressive behaviours (reviewed in Section 3). This finding presents a problem in interpreting data from prison populations. Does elevated testosterone predispose men to commit aggressive crimes, or does aggressive behaviour while in prison produce elevated testosterone concentrations? One way to get around this problem would be to collect longitudinal data and examine whether testosterone concentrations prior to criminal behaviour differs as a function of the type of crimes committed later in life (violent versus non-violent), or whether testosterone differences emerge as a function of current behaviour while in prison.

2.4 Behavioural measures of aggression

A third research strategy has been to examine the relationship between baseline testosterone concentrations and behavioural measures of aggression. One 'field' study reported positive correlations (average r -value = .38) between pre-competition testosterone concentrations and various behavioural measures of aggression in male judo fighters (Salvador, Suay, Martinez-Sanchez, Simon, & Brain, 1999). Other studies have utilized laboratory paradigms to assess the relationship between testosterone and aggression. For instance, Berman and colleagues (1993) reported that individual differences in baseline testosterone concentrations were positively correlated ($r = .41$) with aggressive behaviour on the Taylor Aggression Paradigm (TAP). The TAP is a

laboratory task in which participants compete against a fictitious opponent on a reaction time task. Prior to each trial, participants are required to set a shock (or noise blast) intensity which will be administered to their fictitious opponent if he/she loses the trial. The number of trials that are won or lost can be manipulated by the researcher. Aggressive behaviour in this task is defined as the average shock (or noise blast) intensity that participants deliver to their opponent on win trials (Giancola & Parrott, 2008). One limitation to this paradigm is that the rules of the game require the participant to set a shock (or noise blast) intensity prior to each trial, and as a result, the TAP does not provide participants with a non-aggressive response option (Tedeschi & Quigley, 1996).

Some recent studies have reported that testosterone concentrations are positively correlated with the extent to which participants reject unfair offers in the Ultimatum Game (UG; Burnham, 2007; Mehta & Beer, in press, but see Eisenegger, Naef, Snozzie, Heinrichs, & Fehr, in press). The UG is a behavioural economics task whereby a 'proposer' is given a sum of money (e.g., \$10), and has the opportunity to offer as much, or as little money to a 'receiver'. Once the offer is made, the 'receiver' has the choice to either accept or reject the offer. If the offer is accepted, both participants receive their split of the money. If the 'receiver' rejects the offer, both participants leave with no money. Standard economic theory predicts that 'receivers' should accept any offer greater than zero – after all, some money is better than no money. However, years of behavioural economics research indicates that proposals that are below 20% of the sum (e.g., \$2) are generally rejected (Camerer & Thaler, 1995). Rejection behaviour on the UG can be considered a form of aggressive behaviour as it is committed with the intent to cause

harm to another individual (i.e., financial harm), who, in turn, is motivated to avoid such treatment.

Other researchers have used the Point Subtraction Aggression Paradigm (PSAP, Cherek, 1981) to examine the association between baseline testosterone concentrations and aggressive behaviour (Gerra et al., 1997; Kouri, Lukas, Pope, & Oliva, 1995; Pope, Kouri, & Hudson, 2000). The PSAP is a computer task in which participants are paired with a fictional opponent and the main goal of the task is to gain as many points as possible – the more points earned, the more money participants receive. During the task, participants have points taken from them by their fictitious opponent (actually a computer program). Participants have three response options available to them; 1) reward response; 2) steal response; and 3) protection response (full details of the PSAP are described below). Thus, one major advantage of the PSAP is that it circumvents the problem (see Tedeschi & Quigley, 1996) of not having a non-aggressive response option. Gerra and colleagues (1997) reported a positive association between baseline testosterone concentrations and aggressive behaviour (Gerra et al., 1997) in a small sample of young men ($n = 30$). One limitation to this study was that the authors pre-selected groups of highly aggressive ($n = 15$) and non-aggressive ($n = 15$) individuals, based on self-report questionnaires, limiting the study's generalizability. Nevertheless, in a recent randomized, placebo-controlled, cross over study, Pope and colleagues (2000) reported that 6 weeks of testosterone treatment increased aggressive behaviour in healthy men tested on the PSAP. It is important to note that the authors found no change in self-reported aggression following testosterone treatment, indicating that the behavioural measure of aggression was more sensitive to the effects of testosterone treatment. This finding is consistent with

a recent review of the literature indicating that testosterone is more strongly correlated with aggression when using behavioural measures compared to self report measures (Cohen's $d = .26$, 95% CI = .15 to .37 and Cohen's $d = 0.15$, 95% CI = .11 to .20, respectively).

2.5 Point Subtraction Aggression Paradigm (PSAP)

Given the stronger associations between baseline testosterone and aggression obtained when using behavioural measures, I decided to use the Point Subtraction Aggression Paradigm (PSAP) in the studies reported in this dissertation. This task requires participants to press the point reward button (option 1) 100 consecutive times in order to gain points that are exchangeable for money. After completing 100 consecutive button presses on option 1, participants' point counter enlarges, flashes several times with positive signs around it, and increases by 1 point (see Figure 1). Points earned are displayed at the top of the computer screen throughout the task. Participants are told that they are playing with an opponent who is in another room (but the participant actually plays against a computer program). At various times during the task, participants have points deducted from them by the fictitious opponent who keeps all the points stolen. When participants have points stolen from them by their opponent, this causes their point counter to enlarge, flash several times with negative signs around it, and decreases by 1 point. The participant can respond by either continuing to hit the point-reward button (option 1), or selecting the 'steal' button (option 2) or the 'protect' button (option 3). Selecting the 'steal' button results in the deduction of a point from his/her fictitious partner. However, participants are told that they have been randomly assigned to the experimental condition wherein the points that they steal are not added to their own point

counter, meaning that the only reward for the participant is punishing the other participant. Stealing money from the fictitious partner is considered aggressive because it is a behaviour directed towards another individual with the intent to cause harm to the target (Baron & Richardson, 1994). Alternatively, the participant may choose the 'protection' option, which will protect his/her point counter from future subtractions for a variable amount of time.

Several studies have demonstrated that the PSAP is a valid laboratory measure of aggressive behaviour. For example, male and female violent offenders select the aggressive response option (but not the reward or protection options) more frequently than non-violent offenders (Cherek, Schnapp, Moeller, & Dougherty, 1996; Cherek, Moeller, Schnapp, & Dougherty, 1997; Cherek & Lane, 1999). Men and women with a history of drug dependence emitted more aggressive responses on the PSAP compared to healthy aged-matched controls (Allen, Dougherty, Rhoades, & Cherek, 1996). Moreover, athletes from contact sports emit more aggressive responses than those from non-contact sports (Huang, Cherek, & Lane, 1999). Also, several studies have found moderate, positive correlations between various self-report measures of aggression and aggressive behaviour as measured using the PSAP (Golomb, Cortez-Perez, Jaworski, Mednick, & Dimsdale, 2007; Gerra et al., 2001; Gerra et al., 2007). Finally, research indicates that decreased serotonin levels in humans are associated with elevated aggression and experiments that acutely reduce serotonin levels in healthy participants (using tryptophan depletion) have found increases in aggressive behaviour (but not reward or protection responses) as measured using the PSAP (Moeller, Dougherty, Swann, Collins, Davis, & Cherek, 1996; Bjork, Dougherty, Moeller, Cherek, & Swann, 1999).

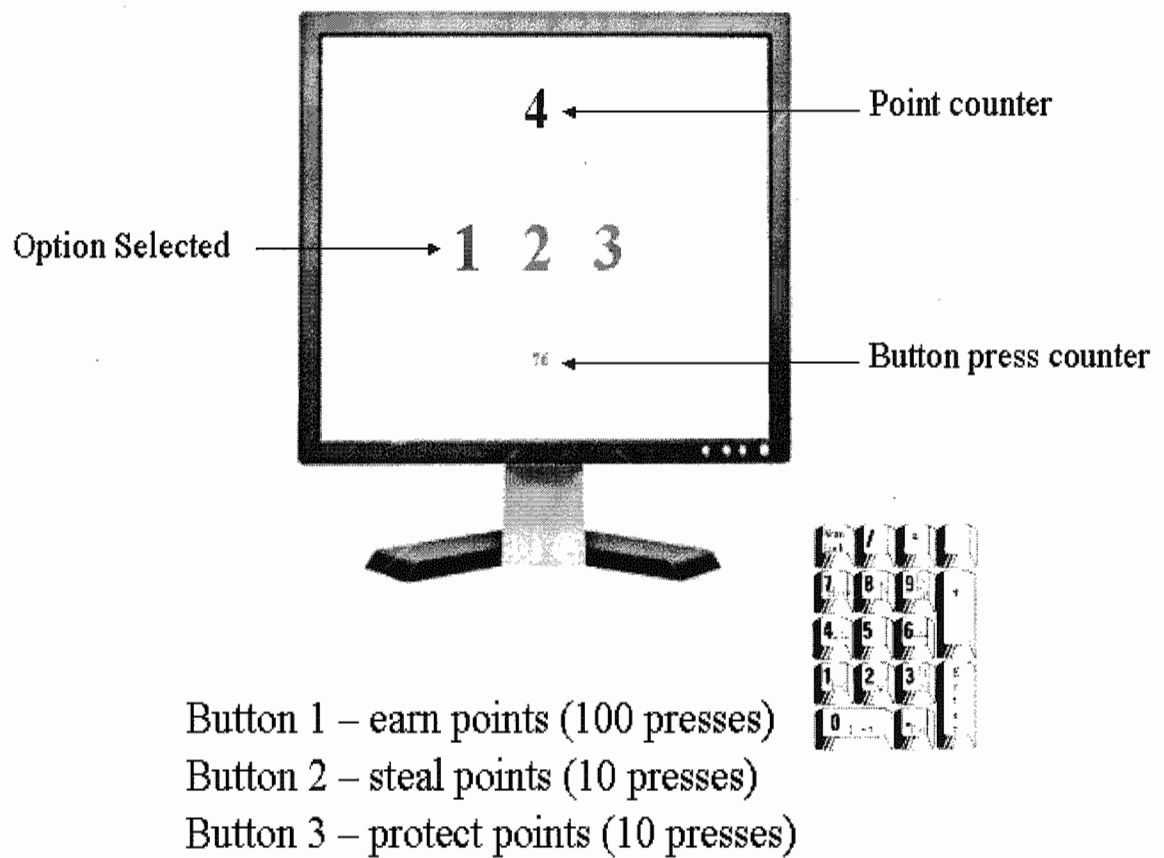


Figure 1. Screen displayed to participants competing on the Point Subtraction Aggression Paradigm (PSAP). See text for description of the task.

Summary

The data reviewed in this section provide evidence for a small, positive correlation between baseline testosterone concentrations and various measures of human aggression. Notably, the relationship between baseline testosterone concentrations and aggression is stronger in studies that have employed behavioural measures. However, it is increasingly apparent that testosterone concentrations fluctuate rapidly during competitive interactions, suggesting that testosterone dynamics may play an important role in modulating ongoing and/or future aggressive behaviour. In the following section, I will review comparative data indicating that testosterone concentrations are highly responsive to competitive and aggressive interactions.

Section 3. TESTOSTERONE DYNAMICS AND SOCIAL BEHAVIOUR

“Short-term changes [in testosterone] are particularly interesting because in many species, they are induced by social stimuli and occur during the production of mate-acquisition behaviour, such as territorial aggression and courtship. Because of its association with behaviour, variation in transient testosterone elevations may be more relevant to the mating effort/parental effort trade-off than is baseline circulating testosterone” (McGlothlin, Jawor, & Ketterson, 2007, p. 864).

Traditionally, research on the neuroendocrine basis of aggressive behaviour has taken a unidirectional approach focusing on testosterone’s role in promoting aggression (see Simon & Lu, 2006 for review). However, competitive interactions are known to potentiate testosterone release (see Wingfield et al., 1990; Oliveira, 2004; 2009 for reviews), suggesting that the relationship between testosterone and aggressive behaviour is much more complex than previously thought. In fact, testosterone concentrations are highly responsive to competitive interactions in a number of taxa including birds (see Wingfield et al., 1990 for review), fish (see Oliveira, 2004 for review), non-human primates (see Bernstein, Rose, & Gordon, 1974 for review), humans (see Archer, 2006 for review), and even insects (Scott, 2006, Trumbo, 2007; Kou, Chou, Huang, & Yang, 2008; Kou, Chou, Chen, & Huang, 2009)! This section will present an overview of this literature beginning with a description of the ‘Challenge Hypothesis’ and the ‘Biosocial Model of Status’, two of the main theoretical models guiding current research on the bidirectional relationship between testosterone and aggressive behaviour.

3.1 Challenge Hypothesis

The ‘Challenge Hypothesis’ is perhaps one of the most influential theoretical models guiding current research on the relationship between testosterone and behaviour (Wingfield et al., 1990). This hypothesis was originally developed in an attempt to

explain intra- and inter- species variation in the pattern of testosterone secretion in birds (Wingfield et al., 1990). The 'Challenge Hypothesis' posits that the pattern of testosterone secretion varies as a function of mating system (e.g., monogamous versus polygynous species). Wingfield and colleagues (1990) noted that testosterone concentrations fluctuate around three levels during the season: 1) Level A, constitutive baseline; 2) Level B, breeding baseline; and 3) Level C, physiological maximum. In monogamous males that provide paternal care, testosterone concentrations remain low during the non-breeding season (Level A); increase at the start of the breeding season as a means to initiate spermatogenesis, expression of secondary sex characteristics, and the full display of male reproductive behaviour (Level B); and further increase in response to male-to-male competitive interactions as a means to support aggressive behaviour (Level C). When inter-male competition decreases, testosterone concentrations also decrease to support paternal care. Polygynous male birds that do not provide paternal care maintain testosterone concentrations at a physiological maximum (i.e., Level C) throughout the breeding season, concurrent with elevated male-to-male aggressive behaviour. Thus, the 'Challenge Hypothesis' predicts that testosterone concentrations will be associated with aggressive behaviour, but only during times of social instability characterized by elevated male-to-male competitive interactions (Wingfield, Ball, Dufty, Hegner, & Ramenofsky, 1987; Wingfield et al., 1990). Reviews of data obtained from fish and birds provide compelling support for the idea that testosterone is linked to aggressive behaviour during periods of social instability and that the pattern of testosterone release during the breeding season and in response to social challenges vary as a function of mating system

(Wingfield et al., 1990; 2000; Hirschenhauser, Taborsky, Oliveira, Canario, & Oliveira, 2004).

Thus, in male birds of a monogamous mating system, there is a trade-off between mating and paternal efforts, which appears to be mediated by testosterone concentrations (Wingfield et al., 1990; Ketterson & Nolan, 1992). An increase in testosterone concentrations at the beginning of the breeding season facilitates mating effort (e.g., sexual and aggressive behaviour), whereas a decrease in testosterone concentrations (in monogamous males) facilitates paternal behaviour. For monogamous birds, it has been proposed that the costs associated with maintaining elevated testosterone concentrations throughout the breeding season may have led to the evolution of a highly flexible endocrine system capable of modulating testosterone concentrations in response to changes in the social environment (Wingfield et al., 2001).

Although the 'Challenge Hypothesis' was originally proposed to account for hormone-behaviour relationships in birds, it has since been extended to include several other vertebrates and invertebrates. The finding that some predictions derived from the 'Challenge Hypothesis' also apply to non-human primates (Cavigelli & Pereira, 2000, Ross, French, & Patera, 2004; Muller & Wrangham, 2004) is particularly intriguing given that non-human primates are more closely related to humans. In a recent study with male ring-tailed lemurs, Cavigelli and Pereira (2000) reported that males had elevated testosterone concentrations during periods of social instability (when females were sexually receptive), and that individual differences in testosterone concentrations during this time were positively correlated with aggressive behaviour ($r = .75$). Also, male wild chimpanzees demonstrated an increase in testosterone during periods of social instability,

characterized by intense male-to-male aggressive behaviour. Notably, during this period, there was a strong positive relationship between individual differences in testosterone concentrations and male dominance ($r = .62$). Together, these findings suggest that predictions derived from the 'Challenge Hypothesis' may also apply to primates.

3.2 Biosocial Model of Status

A conceptually similar theoretical model concerning the relationship between testosterone and social behaviour is known as the 'Biosocial Model of Status' (Mazur, 1976; 1985; 2005; Mazur & Booth, 1998). One important difference between the 'Challenge Hypothesis' and the 'Biosocial Model of Status' is that the latter makes the specific prediction that testosterone concentrations during competition will vary as a function of the outcome of the interaction: Winners of competitive interactions will experience an increase in testosterone, whereas losers will experience a decrease in testosterone. Furthermore, the increase in testosterone in response to victory may serve to promote future aggressive and competitive behaviours aimed at maintaining and/or gaining further status, whereas the decrease in testosterone in response to defeat may serve to promote submissive behaviours aimed at avoiding further loss of status and/or physical injury (See Figure 2). From an evolutionary perspective, these divergent testosterone responses may enable organisms to adjust future social behaviour according to changes in the social environment.

'Outcome Effects'. Although the 'Biosocial Model of Status' has mainly been studied within the context of human competition, its main predictions come from research conducted in male rhesus monkeys (Rose, Gordon, & Bernstein, 1972; Rose, Bernstein, & Gordon, 1975). In a series of experiments, Rose and colleagues (1972; 1975) reported

that aggressive interactions in male rhesus monkeys modulated testosterone release. Specifically, the authors found that male rhesus monkeys that were successful in aggressive interactions experienced marked elevations in testosterone, while unsuccessful males experienced decreased testosterone concentrations (Rose et al., 1972; 1975). Most current research testing hypotheses derived from the 'Biosocial Model of Status' comes from studies involving sport competitions (see Salvador, 2005; van Anders & Watson, 2006; Archer, 2006; Salvador & Costa, 2009). Competitive sports provide an ideal environment in which to study hormone/behaviour relationships as they have clear rules and regulations and offer the possibility to study the effects of competition outcome and social context (i.e., home versus away) on testosterone concentrations. The first study in humans to demonstrate the effect of competition outcome on testosterone responses was based on a small sample ($n = 4$) of male varsity tennis players. The authors reported that men had an increase in testosterone after a victory and a decrease in testosterone after a defeat (Mazur & Lamb, 1980). A similar effect was observed in a relatively larger study of male varsity wrestlers ($n = 15$), in which winners had elevated post-competition testosterone concentrations relative to losers (Elias, 1981). Similarly, another study in male tennis players reported an increase in testosterone among winners relative to losers (Booth, Shelley, Mazur, Tharp, & Kittok, 1989). However, only winners who experienced elated mood demonstrated a reliable increase in testosterone (Booth et al., 1989), suggesting that the subjective evaluation of the competitive interaction plays an important role in modulating testosterone release.

The importance of the objective outcome (i.e., winner or loser), in modulating testosterone release is corroborated by a recent study in male cichlid fish (*Oreochromis*

mossambicus). In that study, the authors took advantage of the fact that cichlid fish cannot recognize their own image in a mirror, and as a result, attack their image vigorously as if the image were that of another fish. The authors reasoned that if aggressive behaviour is the factor responsible for modulating testosterone release, then these fish should have an increase in testosterone in the 'mirror-challenge' condition (Oliveira, Carneiro, & Canario, 2005). In contrast, if the outcome of the interaction is critical to modulating testosterone release, then no testosterone change would be expected based on the fact that there was no clear outcome (i.e., it ended in a draw). Their results were consistent with the latter hypothesis; testosterone concentrations were non-responsive to the mirror-elicited challenge, despite the finding that the fish increased their rate of aggressive behaviour during the testing period (Oliveira et al., 2005).

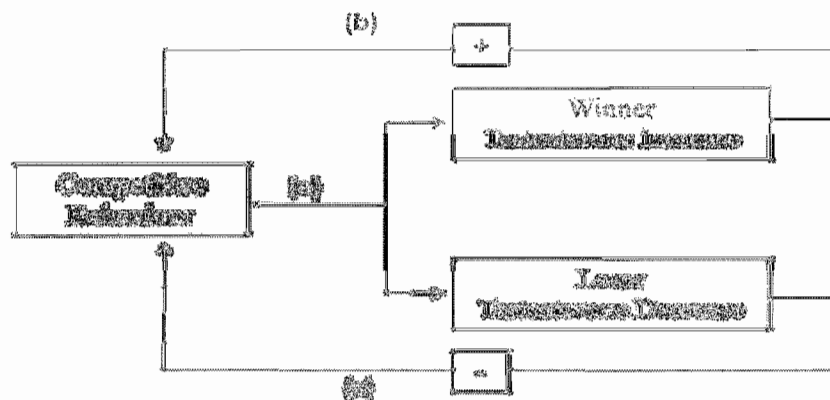


Figure 2. A representation of Mazur's (1985) Biosocial Model of Status. (a) Following a competitive interaction, testosterone concentrations increase in winners and decrease in losers. (b) The increase in testosterone for the winners promotes future competitive and aggressive behaviours. (c) The decrease in testosterone for the losers promotes future avoidant/submissive behaviours.

One methodological limitation to research involving athletic competition is that physical activity is known to potentiate testosterone release (see Kraemer & Ratamess,

2005 for review). Therefore, it is possible that the greater increase in testosterone observed among winners relative to losers may be in part attributed to differential physical effort involved in victory versus defeat. In response to this methodological concern, several studies have examined the extent to which competition outcome would have divergent effects on testosterone release in non-physically taxing competitive tasks. Studies involving men engaged in reaction-time tasks, chess tournaments, and coin toss competitions have all reported that post-competition testosterone concentrations are elevated in winners relative to losers (Gladue, Boechler, & McCaul, 1989; Mazur, Booth, & Dabbs, 1992; McCaul, Gladue, & Joppa, 1992). These findings indicate that the 'triumph' of victory and/or the 'agony' of defeat, rather than physical activity *per se*, may contribute to the differential testosterone responses observed.

'Spectator Effects'. Some studies suggest that the effect of competition outcome on testosterone release may occur in individuals not directly involved in the competitive interaction, an effect which I will refer to as the 'spectator effect'. The first observation of the 'spectator effect' was reported by Bernhardt and colleagues (1998) who obtained pre- and post- game saliva samples from male spectators attending college basketball and professional soccer games. Supporters of the winnings and losing teams demonstrate an increase and decrease in testosterone, respectively. This finding supports the idea that the vicarious experience of victory and/or defeat had similar effects on the endocrine system to that previously observed in athletes directly involved in the competitive interaction (Bernhardt et al., 1998). A recent study involving elite NCAA varsity hockey players provides a conceptual replication of this effect. In two studies, male varsity hockey players watched videos of themselves engaged in a previous victory, previous defeat,

and/or a neutral documentary film. Saliva samples were collected prior to, and at the conclusion of, each video. Carré and Putnam (2010) reported that testosterone concentrations increased significantly after watching a video of a previous victory, but not after a defeat or a neutral video. Examination of testosterone response patterns among players who did not play in the games that were viewed demonstrated a similar pattern; testosterone increased after watching a win, but not a loss (Carré & Putnam, 2010). This finding provides additional evidence that the vicarious experience of victory and/or defeat has a similar effect on the neuroendocrine system than does the actual experience of victory and/or defeat. A recent study has extended these findings to the political domain, reporting that men (but not women) who voted for John McCain the night of the 2008 US Presidential election had decreased testosterone concentrations after the vote, whereas those who voted for Barack Obama voters experienced no change in testosterone (Stanton, Beehner, Saini, Kuhn, & Labar, 2009). It is unclear why Obama voters did not experience a rise in testosterone. However, the differential testosterone response is consistent with the idea that the outcome of competition may influence the pattern of testosterone release (Mazur, 1985).

A similar 'spectator effect' has been observed in male cichlid fish (*Oreochromis mossambicus*). In their experiment, Oliveira and colleagues (2001) allowed male fish to watch two isolated conspecific male neighbours through a one-way mirror. After a period of habituation, the opaque partition separating the two neighbours was removed, allowing the bystander fish to observe their neighbours engaged in a 1-hour aggressive interaction. Urine samples were collected 2 hours prior to removal of the partition, and again 30, 120, and 360 minutes after the aggressive interaction. Urine samples were also collected at the

same time points from a control group not exposed to an aggressive interaction. Results indicated that the experimental bystanders exposed to an aggressive interaction had significantly higher testosterone and 11-ketotestosterone concentrations relative to the control bystanders not exposed to an aggressive interaction. Together, these findings indicate that the vicarious experience of competitive and/or aggressive interactions may be sufficient to elicit a testosterone response.

'Home Advantage'. Other recent evidence indicates that the social context in which a competitive interaction takes place influences testosterone concentrations in men. Two studies have found that testosterone concentrations are higher prior to competition played in the home venue versus the opponents' venue (male soccer players; Neave & Wolfson, 2003; male hockey players; Carré, Muir, Putnam, & Bélanger, 2006), providing a potential biological mechanisms for the well-known home advantage observed in competitive sports. Also, Carré (2009) recently reported that male hockey players had a much larger increase in salivary testosterone after a victory that took place in their home venue compared to a similar victory (against the same team) that took place in their opponents' venue. Consistent with this observation is the finding that male California mice had elevated testosterone concentrations after a victory in their home cage, but not after a victory in a neutral cage (Fuxjager & Marler, in press).

'Anticipatory Effects'. Although the 'Biosocial Model of Status' is mainly concerned with the effects of testosterone fluctuations following competitive interactions on subsequent behaviour, Mazur and Booth (1998) also argued that a rise in testosterone prior to competition may 'prime' individuals for future competition. Studies involving tennis players (Booth et al., 1989), judo fighters (Suay et al., 1999), and soccer players

(Neave & Wolfson, 2003) have found that testosterone concentrations were significantly higher prior to competition relative to testosterone concentrations obtained on non-competition days. Opponents who were greater rivals elicited a steeper anticipatory rise in testosterone relative to non-rival teams (Neave & Wolfson, 2003). In addition to human research, a recent study indicates that male cichlid fish can learn to mount an increase in testosterone in anticipation of an aggressive interaction (Antunes & Oliveira, 2009). In this study, male fish were exposed to multiple pairings of a light (conditioned stimulus) and the introduction of a male intruder (unconditioned stimulus). After multiple pairings, the fish were exposed to the light alone, which elicited a significant increase in testosterone concentrations, similar to that observed in response to an aggressive interaction (Antunes & Oliveira, 2009).

Women and Testosterone Dynamics. Most of the studies on competition and testosterone have been conducted using samples of men. However, predictions derived from the 'Challenge Hypothesis' and the 'Biosocial Model of Status' may also apply to women. In fact, evidence from studies of people indicate that competitive interactions produce an increase in testosterone among female athletes (e.g., Bateup, Booth, Shirtcliff, & Granger, 2001; Kivlighan, Granger, & Booth, 2005; Edwards, Wetzel, & Wyner, 2006; Hamilton, van Anders, Cox, & Watson, 2009). Also, recent evidence indicates that testosterone concentrations in women rise in anticipation of competition (Bateup et al., 2002), and remain elevated in winners relative to losers (Oliveira, Gouveia, & Oliveira, 2009). Clearly, future research is needed to elucidate the extent to which predictions derived from the 'Challenge Hypothesis' and 'Biosocial Model of Status' extend to women.

3.3 Individual differences and testosterone dynamics

It is important to note that not all studies have found that competition outcome influences testosterone release (e.g., Salvador, Simon, Suay, & Llorens, 1987; Gonzalez-Bono, Salvador, Serrano, & Ricarte, 1999; Suay et al., 1999; Schultheiss, Wirth, Torges, Pang, Villacorta, & Welsh, 2005; Mehta & Josephs, 2006; Metha, Jones, & Josephs, 2008; Maner, Miller, Schmidt, & Eckel, 2008). Some of the inconsistencies may be due to differences in the methodologies used (e.g., timing differences in obtaining post-competition saliva samples). Another possibility is that there may be important variables that moderate the extent to which competition outcome influences testosterone responses (see Archer, 2006; Salvador, 2005; Salvador & Costa, 2009 for reviews). Oliver Schultheiss' group has reported that individual differences in implicit need for power (i.e., implicit measure of trait dominance) moderates the effect of competition outcome on testosterone responses. Using the Number Tracing Task (NTT; a laboratory competition task), it was found that individual differences in power motive were positively correlated with testosterone responses to a victory, but negatively correlated with testosterone responses to a defeat (Schultheiss & Rohde, 2002; Schultheiss, Wirth, Torges, Pang, Villacorta, & Welsh, 2005). Another study using the NTT reported no difference in testosterone responses between winners and losers, but reported that losers who scored high on a trait measure of social anxiety demonstrated a much steeper decline in testosterone in response to defeat relative to losers who scored low on this measure (Maner et al., 2008). Studies with athletes indicate that personal contribution to the outcome of the competitive interaction and causal attributions of the outcome (i.e., lucky versus earned) have an important influence on post-competition testosterone

concentrations. For example, some studies indicated that a rise in testosterone during competition was positively correlated with objective measures of individual performance (e.g., soccer players; Edwards et al., 2006; basketball players; Gonzalez-Bono et al., 1999; hockey players; Carré, 2007), and negatively correlated with external attributions of success (Gonzalez-Bono et al., 1999).

The 'Challenge Hypothesis' and 'Biosocial Model of Status' are not typically concerned with individual differences in testosterone responses. For instance, the 'Challenge Hypothesis' predicts that all monogamous males will have elevated testosterone concentrations during periods of social instability (i.e., beginning of breeding season), and will demonstrate a further rise in testosterone during male-to-male aggressive interactions (Wingfield et al., 1990). Do all males demonstrate this pattern of testosterone release at the beginning of the breeding season? Do they all demonstrate a similar increase in testosterone during social challenges? Recent studies in male dark-eyed juncos have found that there is indeed a great deal of variability in testosterone responses to social challenges, and that individual differences in the magnitude of the increase in testosterone during social challenges are correlated with variability in aggressive behaviour (McGlauthlin et al., 2007). This finding is important because it suggests that individual differences in natural fluctuations in testosterone in response to competition may explain variability in aggressive behaviour.

Similarly, the 'Biosocial Model of Status' predicts that testosterone concentrations will rise in winners, and decrease in losers of competitive interactions and that these divergent endocrine responses will facilitate dominant and submissive behaviours, respectively (Mazur, 1985). However, as reviewed in this section, there are individual

differences that influence the extent to which testosterone concentrations rise and/or fall following a victory or defeat, respectively. Mazur's model does not make any specific predictions concerning the extent to which individual differences in testosterone responses to victory or defeat influence subsequent behaviour. However, as discussed in the following section, individual differences in testosterone responses to a competitive interaction may have an important impact on subsequent human behaviour.

Summary. The studies reviewed in this section provide compelling support for the influence of competitive interactions on testosterone release. However, there have been few studies that have directly examined the functional consequences of these acute endocrine responses. In other words, does a rise in testosterone serve to promote future competitive and/or aggressive behaviour? Alternatively, does a decrease in testosterone promote future submissive behaviours? These questions represent the reciprocal aspect of the 'Biosocial Model of Status' (Figure 2, pathways b and c) in which changes in testosterone in response to competition serve to influence future social behaviour. Most studies that have found support for the effect of competition outcome on testosterone release have speculated that these divergent testosterone responses may be functional. However, few studies have examined this issue in people. In the following section I will review evidence from studies in non-humans animals as well as humans suggesting that testosterone dynamics during competition may be functionally relevant to subsequent social behaviour.

Section 4. FUNCTIONAL ROLE OF SOCIALLY-INDUCED CHANGES IN TESTOSTERONE

“The other side to the Challenge Hypothesis – and indeed its whole point in adaptive terms – is that the testosterone surge should increase aggressiveness in competitive situations” (Archer, 2006, p. 329).

Theorists have long speculated that competition-induced fluctuations in testosterone are adaptive, possibly enabling organisms to rapidly adjust current and/or future social behaviour according to changes in the environment (Mazur, 1976; 1985; Wingfield et al., 1990; Oliveira, 2004; 2009). Mazur (1976; 1985) has argued that a rise in status may bring about future challenges by lower status individuals attempting to increase their social status, and that a rise in testosterone may serve to increase one’s readiness to engage in future competitive interactions. Despite the intuitive appeal of bidirectional models, few studies have empirically investigated whether testosterone dynamics during competitive interactions influence subsequent social behaviour.

One of the most robust behavioural observations in animal studies is that winning a competitive interaction increases the probability of winning a subsequent interaction (Dugatkin, 1997). This winner effect has been observed in a wide range of taxa (fish; Hsu and Wolf, 1999; insects: Moore, Ciccone, & Breed, 1988; rodents; Oyegbile & Marler, 2005; Fuxjager & Marler, in press). The psychological effects of winning/losing streaks are well-known among individuals who play competitive sports. For example, reflecting on his experience in competitive sports, Hooke (2005) states that “a little success generates in me a feeling of confidence which, as long as it lasts, makes me do better than usual... a few failures can destroy this confidence, after which for a while I can’t do anything right (p. 241). The finding that testosterone concentrations are elevated in

winner relative to losers across the animal kingdom suggests that testosterone may be one of the biological mechanisms contributing to the 'winner effect'. Thus, the "feedback between high testosterone and dominant demeanor may explain the momentum often associated with strings of triumphs. Success begets a high testosterone response, which begets more dominant behavior, which begets more success" (Mazur, 2005, p. 121).

4.1 Evidence in animal models

It is perhaps surprising that the functional consequences of competition-induced fluctuations in testosterone have only recently been explored in animal studies. In a study of intact male California mice (*Peromyscus californicus*), it was found that winning three consecutive aggressive interactions (compared to winning only 1 or 2 previous aggressive interactions) increased the probability of winning a fourth aggressive interaction (Oyegbile & Marler, 2005; Fuxjager & Marler, in press). These behavioural findings were mirrored by elevated endogenous testosterone concentrations (observed only after three consecutive wins), providing some evidence that testosterone may be one of the biological mechanisms contributing to the 'winner effect' (Oyegbile & Marler, 2005; Fuxjager & Marler, in press). One interesting finding is that white-footed mice (*Peromyscus leucopus*), which are closely related to California mice, do not increase their probability of winning a competitive interaction after three previous winning experiences, nor do they demonstrate an increase in testosterone concentrations (Fuxjager & Marler, in press).

In a similar study involving intact California mice, Gleason and colleagues (2009) found that testosterone administration on its own (without previous winning experience) increased subsequent aggressive behaviour, but did not increase the animal's probability

of winning subsequent interactions. In contrast, previous winning experience paired with testosterone injections following each victory was associated with increased aggressive behaviour (higher than those administered testosterone without previous winning experience), and an increase in the probability of winning subsequent interactions. A more definitive test of the interactive role of testosterone and previous experience on mediating the winner effect would require demonstrating that winning experience in the absence of an increase in testosterone fails to generate a robust winner effect.

Unpublished data from the same laboratory provides empirical support for this hypothesis (Oyegbile, 2006). To control for natural fluctuations in testosterone that occur in response to a successful aggressive interaction (e.g., Oyegbile & Marler, 2005), male California mice were castrated and injected with low doses of testosterone concentrations. The authors examined the extent to which previous winning experience and/or testosterone administration would influence the probability of winning a subsequent competitive interaction. Male mice were assigned to one of four experimental groups; 1) previous winning experience + testosterone injection; 2) previous winning experience + saline injection; 3) no previous winning experience + testosterone injection; 4) no previous winning experience + saline injection. The authors reported that previous winning experience or testosterone administration on their own were not associated with an increased probability of winning a future competitive interaction, whereas previous winning experience paired with testosterone injection did produce a robust winner effect. Together, these studies indicate that, in male California mice, both winning experience and post-competition testosterone surges are required to produce a full 'winner-effect'.

Using a similar research design, Trainor and colleagues (2004) examined the extent to which testosterone concentrations following multiple victories would be necessary to influence subsequent aggressive behaviour (e.g., attack frequency, attack latency, bites, chases) (Trainor et al., 2004). The mice were assigned to one of three experimental conditions: One group of mice received a testosterone injection after each of three consecutive successful interactions (win + testosterone); the second group of mice received a saline injection after each of three consecutive successful interactions (win + saline); and the third group of mice received an aromatase inhibitor prior to each aggressive interaction, coupled with a testosterone injection after each of the three consecutive successful interactions (win + aromatase inhibitor + testosterone). This third group was used to examine whether testosterone's influence on subsequent behaviour was mediated via an androgen-dependent and/or estrogen-dependent pathway. The results indicated that groups receiving testosterone (with or without the aromatase inhibitor) were significantly more aggressive in the fourth competitive interaction relative to the group that received a saline injection (Trainor et al., 2004). This finding indicated that previous winning experience on its own did not modulate subsequent aggressive behaviour, but that an increase in testosterone concentrations following a successful competitive interaction was causally related to subsequent behaviour. Moreover, the authors argued that these effects were likely mediated via androgen receptors (Trainor et al., 2004), although the possibility that membrane-bound receptors may also be involved cannot be ruled-out.

Oliveira and colleagues (2009) examined the role of testosterone in mediating the 'winner' and 'loser' effects in male Mozambiquan tilapia (*Oreochromis mossambicus*). In

control fish, winners of a first aggressive interaction were more likely to win subsequent interactions (88% won second fight), whereas losers were more likely to lose subsequent interactions (87 % lost second fight). In the experimental groups, winners were treated with an anti-androgen (cyproterone acetate) and losers were treated with an androgen (11-ketotestosterone). If testosterone is critically involved in mediating the 'winner/loser' effects, winners treated with an anti-androgen should be less likely to win a second interaction, and losers treated with an androgen should increase their probability of winning a second interaction. Oliveira and colleagues (2009) found partial support for this hypothesis finding that winners treated with an anti-androgen had a reduced probability of winning a subsequent aggressive interaction (relative to control males), whereas the androgen treatment to losers did not increase their probability of winning a subsequent interaction. Thus, the 'winner effect' appears to be mediated by testosterone, whereas the 'loser effect' does not appear to depend on testosterone. The major difference between the 'winner effect' observed in mice and that observed in fish has to do with timing. Fish treated with an anti-androgen following a victory were tested immediately in a second interaction. In contrast, the effects of testosterone on mice were only examined 1 day after injection. Thus, it appears that testosterone may have immediate and lasting effects on behaviours that influence the probability of winning an aggressive interaction.

4.2 Evidence from human studies

There have only been three published studies from human samples that have examined the extent to which natural fluctuations in testosterone during social interactions were associated with future social behaviour. In the first published study examining functional role of testosterone fluctuations in humans, Mehta and Josephs

(2006) had men participate against each other in a rigged competition in which half were randomly assigned to the 'loss' condition and the other half were assigned to the 'win' condition, experimentally creating a 'winner' and 'loser' in the laboratory. Saliva samples were collected prior to, and at the conclusion of, the competition. After collecting the second saliva sample, participants were asked whether they wanted to compete again against the same opponent on the same task, or whether they would prefer to fill out a questionnaire on food, music, and entertainment preferences. The authors found that among men assigned to the 'loss' condition, an increase in testosterone predicted willingness to choose the competitive option, whereas a decrease in testosterone predicted willingness to choose the non-competitive option. This was the first demonstration that natural fluctuations in testosterone concentrations within the context of a competitive interaction were associated with future social behaviour.

In another study, Klimesmith and colleagues (2006) randomly assigned men to one of two experimental conditions; 1) interact with a realistic-looking toy gun ($n = 15$); or 2) interact with a board game ($n = 15$). The authors hypothesized that interacting with a toy gun would represent a 'challenge' (e.g., Wingfield et al., 1990; Archer, 2006), and that in accordance with research on the effects of challenges, this would produce an increase in testosterone concentrations. After providing the second saliva sample, participants were given a cup of water that was laced with hot sauce. They then had the opportunity to put as much, or as little amount of hot sauce in a glass of water which would later be consumed by another participant. The amount of hot sauce placed in the cup served as the primary measure of aggression (see Lieberman et al., 2003 for validation of the task). As predicted, men who interacted with the toy gun demonstrated an increase in testosterone,

whereas men who interacted with the board game showed no change in testosterone. Also, interacting with the toy gun was associated with more aggressive behaviour (i.e., these men put more hot sauce in the cup). The relationship between interacting with the toy gun and aggressive behaviour was mediated by testosterone responses to the task. This finding suggests that short-term fluctuations in testosterone are among the causal factors eliciting aggressive behaviour in this laboratory task.

A more recent study examined the extent to which the presence of an attractive female research assistant would produce a rise in testosterone concentrations in young men, and whether such endocrine responses would influence subsequent risk-taking behaviour (Ronay & von Hippel, 2010). In this study, risk-taking was assessed as the frequency with which male skateboarders aborted a difficult trick (i.e., more aborted tricks was interpreted as less risky behaviour). Testosterone concentrations were higher in men who interacted with the attractive female research assistant compared to men who interacted with the male research assistant. Also, risk-taking behaviour was higher in men who interacted with an attractive female research assistant compared to those who interacted with the male research assistant. After controlling for differences in testosterone concentrations between experimental groups, the relationship between interacting with an attractive female research assistant and elevated risk-taking behaviour was attenuated, indicating that testosterone partially mediated the effect of experimenter sex on subsequent risk-taking behaviour. One limitation to this study was that only one saliva sample was collected after each participant interacted with the female or male research assistant. Based on this limitation, one cannot conclude that men who interacted with the female research assistant demonstrated an increase in testosterone because no

baseline measure was obtained. Although random assignment was used, it remains possible that men who interacted with the attractive female research assistant had elevated testosterone concentrations prior to the interaction than men who interacted with the male research assistant. Thus, without pre- and post- measures of testosterone, it is impossible to determine the extent to which interacting with an attractive female research assistant produced a rise in testosterone relative to interacting with a male research assistant.

4.3 Evidence using exogenous testosterone manipulations in humans

Although most work on the social modulation of testosterone concentrations has been carried out in men, van Honk and colleagues have examined the functional consequences of testosterone dynamics in healthy women. In their studies, healthy women were given an acute sublingual administration of testosterone (or a sublingual administration of placebo) and subsequent behaviour was assessed. In general, their results indicate that acute administration of testosterone influenced physiological and behavioural factors that may be relevant within the context of human competition. For example, testosterone administration increased cardiac responses to angry faces (van Honk, Tuiten, Hermans, Putnam, Koppeschaar, Thijssen, Verbaten, & van Doornen, 2001), decreased fear potentiated startle (Hermans, Putnam, Baas, Koppeschaar, & van Honk, 2006), increased visuospatial abilities (Aleman, Bronk, Kessel, Koppeschaar, & van Honk, 2004) and increased subcortical (e.g., amygdala, hypothalamus) activation to angry faces (Hermans, Ramsey, & van Honk, 2008). Together, these studies provide evidence that acutely elevating testosterone concentrations may modulate subsequent social behaviour by acting on the neural circuitry subserving human social behaviour. One limitation to this work is that the 0.5 mg dose of testosterone undecanoate used

produces testosterone concentrations that are well outside the normal range of testosterone concentrations observed in healthy women (e.g., testosterone administration; 660 ng/dL versus normal range; 14-58 ng/dL). Thus, although these findings are important in that they indicate that acutely elevating testosterone influences various behavioural and physiological outcomes in healthy women, it remains to be seen whether fluctuations in testosterone within the normal range would produce meaningful effects on behaviour.

4.4 Goal of the dissertation

In summary, social interactions (e.g., competitive and sexual behaviour) alter testosterone concentrations in a wide range of vertebrate and invertebrate species (see Mazur & Booth, 1998; Archer, 2006; Nyby, 2008; Gleason et al., 2009; Oliveira, 2004; 2009 for reviews). The fact that this phenomenon is observed throughout the animal kingdom suggests that acute fluctuations in testosterone may play some functional role in regulating behaviours that are relevant to survival and/or reproduction. Indeed, researchers have typically discussed the social modulation of testosterone concentrations from a functional perspective whereby acute fluctuations in testosterone serve to modulate ongoing and/or future social behaviour (see Mazur, 1985; Wingfield et al., 1990; Oliveira, 2004; 2009; Nyby, 2008 for reviews). Recent evidence from non-human animal experiments provides compelling support for this idea (Trainor et al., 2004; Gleason et al., 2009; Oliveira et al., 2009). In studies of people, there is ample support for the role of competitive interactions in modulating testosterone release (see Figure 2, pathway a). However, with the exception of a few recent studies, there is currently a large gap in the literature regarding the influence of such fluctuations in testosterone on future

human behaviour (see Figure 2, pathways b and c). Thus, the main goal of this dissertation was to try to fill this gap by investigating the extent to which acute fluctuations in testosterone during competitive interactions influence subsequent social behaviour in humans.

In Study #1, I tested the hypothesis that changes in testosterone concentrations in response to the Point Subtraction Aggression Paradigm (PSAP) would influence subsequent decision to choose a competitive versus non-competitive task. In Study #2, I examined the extent to which a change in testosterone in response to a rigged competitive interaction would predict subsequent aggressive behaviour. In this study, I also examined the extent to which the relationship between change in testosterone and aggressive behaviour would be influenced by sex, competition outcome, and individual differences in trait dominance. In Study #3, I examined whether costly aggressive behaviour in the context of a competitive interaction was intrinsically rewarding. Also, I examined whether the association between change in testosterone and aggressive behaviour on the PSAP would be specific to conditions in which participants were provoked and/or receive external reward for behaving aggressively (see Table 1 for a summary the studies).

Table 1.
Summary of studies

	Measures	Research Questions
Study 1	<ul style="list-style-type: none"> -Point Subtraction Aggression Paradigm (PSAP). -Task choice: competitive versus non-competitive task. -Pre- and post- saliva for testosterone analysis. 	<ul style="list-style-type: none"> -Do baseline testosterone concentrations predict aggressive behaviour? -Does behaviour on PSAP influence testosterone concentrations? -Does change in testosterone in response to the PSAP influence subsequent choice of a competitive versus non-competitive task?
Study 2	<ul style="list-style-type: none"> -Point Subtraction Aggression Paradigm (PSAP). -Number Tracing Task (NTT). -Trait dominance questionnaire. -Pre- and post- NTT saliva for testosterone analysis. 	<ul style="list-style-type: none"> -Does change in testosterone in response to the NTT predict subsequent aggressive behaviour on the PSAP? -Does competition outcome moderate the relationship between change in testosterone and subsequent aggression on the PSAP? -Does trait dominance moderate relationship between change in testosterone and subsequent aggression on the PSAP?
Study 3	<ul style="list-style-type: none"> - Four different versions of the Point Subtraction Aggression Paradigm. - Task choice: competitive versus non-competitive task. -Extent to which participants enjoyed the task. -Pre-, mid- and post- PSAP saliva for testosterone analysis. 	<ul style="list-style-type: none"> -Is there a relationship between aggressive behaviour and the extent to which participants enjoyed the PSAP? -If so, is this association apparent across each version of the PSAP? -Is the relationship between change in testosterone and aggressive behaviour specific to reactive aggression?

CHAPTER 2: AGGRESSIVE BEHAVIOUR AND CHANGE IN SALIVARY TESTOSTERONE PREDICT WILLINGNESS TO ENGAGE IN A COMPETITIVE TASK

Note: This section is based on the following article, with permission: Carré, J.M. & McCormick, C.M. (2008). Aggressive behaviour and change in salivary testosterone concentrations predict willingness to engage in a competitive task. *Hormones & Behavior*, 54, 403-409.

Abstract

The current study investigated relationships among aggressive behaviour, 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 behaviour 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 (Cohen's $d = .82$) and controlling for testosterone change, men who showed the highest level of aggressive responding were more likely to choose the non-competitive task (Cohen's $d = .90$). These results indicate that situation-specific aggressive behaviour and testosterone responsiveness are functionally relevant predictors of future social behaviour.

Introduction

Despite much animal research demonstrating that testosterone is associated with aggressive and/or dominant behaviours (reviewed in Simon & Lu, 2006; Nelson & Trainor, 2007), the findings from studies in people are less consistent (Archer, 1991; Archer et al., 1998; Book, Starzyk, & Quinsey, 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 taxa (non-human primates: Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2006; Muller & Wrangham, 2004; Cristobal-Azkarate, Chavira, Boeck, Rodriguez-Luna, & Veal, 2006; birds: Wingfield et al., 1990; rodents: Oyegbile & Marler, 2005; fish: Oliveira, Almada, & Canario, 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 behaviours (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., 2003; Roney et al., 2007), in anticipation of competition (Suay et al., 1999; Bateup et al., 2002; but see Mazur, Susman, & Edelbrock, 1997; Carré, Muir, Belanger, & Putnam, 2006), and are sometimes, but not always, elevated in winners relative to losers post-competition (Mazur & Lamb, 1980; Elias, 1981; Gladue et al., 1989; Booth et al., 1989; Mazur et al., 1992; van Anders & 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 behaviours aimed at maintaining or gaining status (Mazur, 1985; Mazur & Booth, 1998). This idea was recently examined in a well-controlled laboratory study involving mice (Trainor et al., 2004). Castrated mice that received a testosterone injection 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 behaviour, indicating a key role of testosterone in modulating future behaviour.

There is also some support for a relationship between dynamic changes in testosterone concentrations and behaviour 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., 2007), and reduced conscious detection of angry faces (van Honk & Schutter, 2007).

Only a few studies have investigated the functional relevance of endogenous fluctuations in testosterone concentrations on future behaviour. 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 and colleagues (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). The relationship between interacting with the toy gun and aggressive behaviour 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 behaviour diminished, suggesting that testosterone was one of the causal mechanisms mediating the expression of aggressive behaviour.

In the present experiment, we investigated the relationship between situationally-determined behaviour, changes in testosterone concentrations, and future behaviour using a competitive laboratory task that provided the opportunity to win points that could be exchanged for monetary reward and the opportunity for aggressive behaviour, 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 behaviour. 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 et al., 2001; 2004; 2007; Golomb et al., 2007). The PSAP allowed us to directly investigate the relationship between testosterone concentrations and aggressive behaviour, and the extent to which these measures predict future behaviour in men. Our first hypothesis was that there would be a positive correlation between basal testosterone and aggressive responses. We also examined whether behaviour 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.

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 1300h and 1700h 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 minutes 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”. Twenty-five of the participants (66%) reported that they thought they had 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 had been 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."; and "He probably played similar to me but I was trying to out-think him at times."

A second saliva sample was obtained 10 minutes after completion of the PSAP (a timer was used to ensure consistency, and all participants completed the questionnaires within the 10 minute interval). A ten 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 & Josephs, 2006) based on the time required for testosterone to reach saliva (Riad-Fahmy, Read, Walker, Walker, & Griffiths, 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 behaviour in a controlled laboratory environment. The original PSAP takes 3 hours 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 behaviours (Golomb et al., 2007). Our version takes 40 minutes to complete and includes two-minute rest breaks at 12 minute intervals.

Participants were tested individually. Each participant 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 his 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 might turn red, flash several times with negative signs around it, and that their point counter would *decrease* by 1 point. This 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' their partner, and as such, represents the primary measure of aggressive behaviour. Aggressive responding on the PSAP is consistent with the widely used operational definition of aggression as being "any form of behaviour directed toward the goal of harming or injuring another living being who is motivated to avoid such treatment" (Baron & Richardson, 1994, p. 7). It is important to note that the harm or injury does not have to be physical, but simply has to be considered 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 seconds in the absence of any Option 2 or Option 3 selections. Cherek's (1981) original PSAP provoked participants every 6 to 120 seconds. 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 seconds and a maximum of 120 seconds, after which the random point subtractions would continue to occur every 6 to 60 seconds.

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. Similarly, 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, (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. Frozen samples were first warmed to room temperature and then centrifuged (3000 rpm) for 15 minutes. Duplicate 100 μ l 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 x 100] as in other studies of salivary testosterone and behaviour (van Anders & 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 multiple 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 2. 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 3). Due to the nature of the PSAP, 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. Twenty-seven of the participants chose the competitive task and 11 chose the non-competitive task.

Eighteen 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 2.

Descriptive statistics for PSAP and salivary testosterone measures.

	Mean	SD	Minimum	Maximum
Behavioural options of the PSAP				
Reward responses	2597.6	362.34	1400.0	3114.7
Aggression responses	229.2	166.44	13.3	732.0
Protection responses	219.8	140.05	10.0	605.7
Testosterone measurements (pg/mL)				
Baseline	97.5	51.22	30.2	272.0
Post-task	101.1	39.20	37.7	216.4
% change	15.1	38.83	-65.0	141.1

Table 3.

Bivariate correlations among variables measured with the PSAP.

	Reward	Aggression	Protection	Provocations
Reward				
Aggression	-.78***			
Protection	-.67***	.23		
Provocations	.31**	-.14	-.49***	
Points	.85***	-.68***	-.42*	-.20

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

Baseline Salivary Testosterone Concentrations and Aggressive Behaviour

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 Behaviour 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 concentrations¹. All three behavioural responses from the PSAP (aggression, protection and reward) were included in the analysis to determine which, if any, of the behavioural 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 and age as

¹ Examination of predictor variables indicated that all were relatively normally distributed. Also, examination of regression residuals showed no major violations of the assumptions of independence, homoscedasticity, or normality.

the only significant predictors of change in testosterone concentrations. See Table 4 for regression coefficients. Perceived outcome (winner/loser) did not predict any variance in change in testosterone concentrations ($p = 0.40$).

Table 4.

Regression analysis predicting change in salivary testosterone concentrations (n = 38)

	Beta	<i>t</i>	<i>p</i>	Zero order r	Semi-partial r
PSAP response					
Reward	0.75	1.82	0.08	-.10	.26
Aggression	0.74	2.39	0.02	.23	.34
Protection	0.41	1.56	0.13	.02	.22
Age	0.49	3.31	0.001	.42	.48

Full Model $R^2 = 0.32$

Predicting willingness to compete

Multiple logistic regression analysis was performed to examine the extent to which changes in testosterone concentrations and aggressive behaviour predicted choice of a future competitive versus non-competitive task. Results indicated that aggressive behaviour and change in testosterone significantly predicted willingness to compete ($\chi^2(2, n = 38) = 9.06, p = 0.01$). Likelihood ratio tests indicated that the inclusion of both predictors in the model was significantly better than inclusion of either predictor alone (-2LL were $\chi^2(1) = 5.09, p < 0.025$ and $\chi^2(1) = 4.33, p < 0.05$, respectively). Separate simple logistic regression analyses including aggressive behaviour and change in testosterone on their own did not predict willingness to compete ($p = 0.07$ and $p = 0.09$, respectively). Analysis of covariance was used to interpret and illustrate the relationship between willingness to compete and each predictor while controlling for the other (see Figure 3). 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 ($F_{1,35} = 4.86, p = 0.03$; Cohen's $d = .82$). 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 ($F_{1,35} = 6.11, p = 0.02$; Cohen's $d = .90$).

The 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 ($\chi^2(1) = 0.01, ns$).

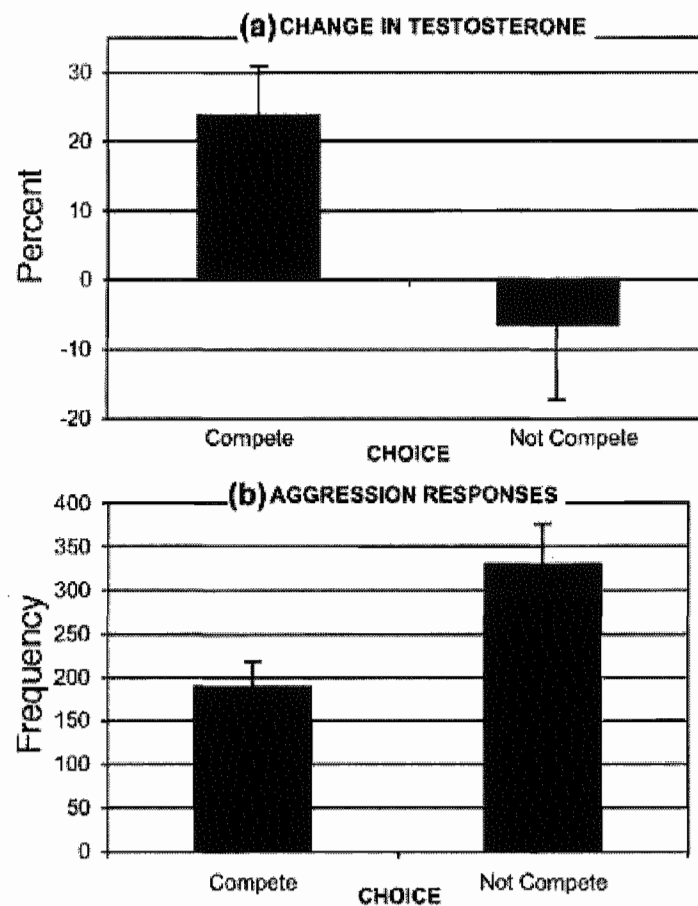


Figure 3. Estimated marginal means for (a) change in testosterone (with aggressive responses as a covariate) and (b) aggressive responses (with change in testosterone as a covariate) as a function of choice: competitive task ($n = 27$) or non-competitive task ($n = 11$). Error bars represent SEM.

Discussion

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

Baseline Testosterone Concentrations and Aggressive Behaviour

There was no significant relationship between baseline testosterone concentrations and aggressive behaviour in response to provocation. Meta-analyses have revealed a small, yet significant, relationship between baseline testosterone concentrations and various measures of aggressive behaviour (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 behaviour in response to provocation, 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 behaviour in the current study is that testosterone may interact with other biological variables to predict aggressive behaviour (Dabbs et al., 1991; Popma et al., 2007). For example, Popma and colleagues (2007) demonstrated that baseline testosterone was positively correlated with aggression, but only among those with low baseline cortisol levels. Furthermore, Hermans and colleagues (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 Behaviour 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 providing further evidence that human social interactions modulate testosterone concentrations (e.g., van Anders & Watson, 2006; Archer, 2006; Mazur & Booth, 1998). Aggression during this competitive social interaction appears to be the specific behavioural 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 & Booth, 1998; van Anders & Watson, 2006), competing in one's home venue (Carré et al., 2006; Neave & 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 nonhuman primates that reported associations between aggressive behaviour and change in testosterone concentrations (e.g., Muller & 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 behaviour (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 3) 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 from testosterone increases that have been reported for overt winners of a competition irrespective of whether there was opportunity for aggression in the competition (Mazur & Lamb, 1980; Elias, 1981, Gladue et al., 1989; Booth et al., 1989; Mazur et al., 1992; van Anders & 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 behaviour. It would be of interest to test whether aggressive behaviour and ongoing awareness of actual performance in relation to the competitor would have additive effects on testosterone levels. Additionally, it is important to distinguish the type of aggressive behaviour that is measured by the PSAP. Because the task measures aggressive behaviour in response to provocation, it fits the subtype of reactive aggression. The classification of aggressive behaviour 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 behaviour.

Change in Testosterone Concentrations and Aggression Predict Willingness to Compete

We also addressed whether the aggressive behaviour and the competition-induced changes in testosterone concentrations are relevant to future social behaviour. The reciprocal model suggests that situation-specific neuroendocrine changes can, in turn, feed back to influence future social behaviours (Mazur & 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 behaviour. In a series of studies using

implicit-power motive as a measure of trait dominance, Schultheiss and colleagues (2002; 2005) 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, Klimesmith and colleagues (2006) reported that interacting with a toy gun was associated with a rise in testosterone, and this, in turn, led to an increase in aggressive behaviour. 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 behaviour 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 had been 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 behaviour. 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, Mehl, & Josephs, 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, 2008; Frye, 2007).

An unexpected result was that whereas the number of 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. Men with higher aggressive responses were more likely to choose the non-competitive task over the competitive task. This finding is counterintuitive given that aggressive behaviour and change in testosterone concentrations were positively related to each other. Thus, whether there truly is a joint effect of aggressive behaviour and change in testosterone on choice of task will require more investigation. Furthermore, recent evidence in rodents has also demonstrated that aggressive behaviour (much like testosterone) is rewarding and produces its effects via the dopaminergic reward system (Couppis & Kennedy, 2008). That there was a significant negative relationship between aggressive behaviour 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-behaviour relationships, and such individual differences may be related to aggressive responding on the PSAP.

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 behaviour and change in testosterone concentrations predicted willingness to engage in another competitive task. How situation-specific behaviour 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 behaviour have both been suggested as possible factors of relevance (see Mehta & 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 behaviour.

Rationale for Study #2

Results from Study 1 indicated that testosterone responses to the PSAP predicted whether individuals chose a subsequent competitive versus non-competitive task. Specifically, controlling for aggressive behaviour, a rise in testosterone during the PSAP predicted willingness to choose a competitive versus a non-competitive task. Mehta and Josephs (2006) reported a similar effect in men tested in a rigged laboratory competition task. However, in that case, change in testosterone only predicted subsequent behaviour among men experimentally assigned to the loss condition. Furthermore, when they restricted their analysis to those individuals who had a clear increase in testosterone (top third of the distribution) and those individuals who had a clear decrease in testosterone (bottom third of distribution), they found that an increase in testosterone predicted willingness to compete, whereas a decrease in testosterone predicted willingness to choose the non-competitive task. A similar supplemental analysis with data from Study 1 indicated that individuals who showed an increase in testosterone were more likely to choose a competitive versus non-competitive task ($\chi^2 = 5.26, p = 0.02$), whereas those who showed a decrease in testosterone did not display a task preference ($p = 0.20$). Also, our data did not provide any evidence for a role of competitive outcome on the relationship between change in testosterone and willingness to compete. However, an important limitation is that we did not specifically assign participants to win or loss conditions (as in Mehta & Josephs, 2006), nor did we provide participants with any explicit information concerning their performance relative to their opponents'. One goal of Study 2 was to investigate more systematically the extent to which competition outcome influences the relationship between testosterone dynamics and future behaviour.

Another interesting finding that emerged from Study 1 was that aggressive responses were positively correlated with changes in testosterone concentrations during the PSAP. This finding may indicate one of two possibilities; 1) that a rise in testosterone during the PSAP increased aggressive behaviour, or 2) that aggressive behaviour on the PSAP produced an increase in testosterone concentrations. Because both variables were measured at the same time, it is impossible to determine the direction of causation. On the one hand, research in non-human primates suggests that aggressive interactions produce a rise in testosterone concentrations (Ross et al., 2004). On the other hand, recent studies in non-human models indicate that testosterone fluctuations rapidly modulate current social behaviours (Aikey, Nyby, Anmuth, & James, 2002; Remage-Healey & Bass, 2006; Trainor, Lin, Finy, Rowland, & Nelson, 2007; Trainor, Finy, & Nelson, 2008).

In Study 2, I assessed change in testosterone concentrations in response to a rigged competitive interaction, and then examined whether such testosterone dynamics would influence subsequent aggressive behaviour. Another goal of this study was to investigate the extent to which individual differences in trait dominance would be associated with aggressive behaviour on the PSAP. Although recent studies have reported moderate associations between individual differences in trait dominance and aggressive behaviour using self-report measures (Johnson, Burk, & Kirkpatrick, 2007; Archer & Webb, 2006), there are no studies that have examined whether trait dominance is also associated with situational aggression. Also, it was of interest to examine the extent to which trait dominance would interact with testosterone dynamics to predict subsequent aggressive behaviour. Finally, I included women in this study to examine whether the effects of testosterone dynamics on behaviour in men (e.g., Mehta & Josephs, 2006; Carré

& McCormick, 2008) would also apply to women. In summary, Study 2 examines the extent to which trait (e.g., baseline testosterone, trait dominance, sex) and state factors (e.g., competition outcome and change in testosterone) influence aggressive behaviour.

CHAPTER 3

TESTOSTERONE RESPONSES TO COMPETITION PREDICT FUTURE AGGRESSIVE BEHAVIOUR AT A COST TO REWARD IN MEN

Note: This section is based on the following article, with permission: Carré, J.M., McCormick, C.M., & Putnam, S.K. (2009). Testosterone responses to competition predict future aggressive behaviour at a cost to reward in men. *Psychoneuroendocrinology*, 34, 561-570.

Abstract

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.

Introduction

The World Health Organization has estimated that for every death in youth due to physical aggression, another 20 to 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 potential negative consequences of aggressive behaviour for the aggressor, the use (or threat) of 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 & Bushman, 2002; Bettencourt, Talley, Benjamin, & Valentine, 2006; Nelson & Trainor, 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 & Webb, 2006; Johnson et al., 2007), and men tend to score higher than women on self-report measures of trait dominance (Budaev, 1999; Costa, Terracciano, &

McCrae, 2001) and on several self-report and behavioural measures of aggression (Archer, 2004). Given the empirical relationship between trait dominance and self-reported 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 & Lu, 2006; Nelson & Trainor, 2007). There have been reports of a positive association between self-reported trait dominance and baseline testosterone concentrations (Cashdan, 1995; Grant & France, 2001; Sellers et al., 2007), although others have failed to replicate this finding (see Josephs, Sellers, Newman, & Mehta, 2006; Stanton & 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 & 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 example, winning competitive interactions (reviewed in Mazur & Booth, 1998; Archer, 2006; van Anders & 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 & 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 & 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 & 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., 2006), increased visuospatial performance (Aleman et al., 2004), increased subcortical responses to angry faces (Hermans et al., 2008), decreased empathic behaviour (Hermans, Putnam, & van Honk, 2006), and decreased conscious detection of angry faces (van Honk & 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. 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 & Bushman, 2002) posits that trait/personological factors (including personality traits, 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 & 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 & 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 sex 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 & 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).

Methods

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 (M age = 19.51, SD = 2.86) and 60 women (M age = 18.88, SD = 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).

Measures

Trait dominance. 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 consistency reliability was high in the current sample (Cronbach's 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.

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, Campbell, & McClelland, 1999; Schultheiss & 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 quickly as possible until they reached a highlighted number. Upon reaching the highlighted number, participants were instructed to shout 'done', and this indicated that they 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 minutes to complete.

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 hours to complete, although similar results are obtained with shorter versions (Golomb et al., 2007). We designed a 40-minute version of the task (see Carré & 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).

Testosterone Assay. Saliva samples were collected in polystyrene culture tubes from participants before the NTT competition and 10 minutes 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 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.

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 and a trait dominance questionnaire, and provided a 1-2 mL saliva sample (pre-competition), to be assessed later for testosterone concentrations. Next, participants were paired with a same-sex partner against whom they competed 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 minutes 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?”

Statistical Analyses. Statistical analyses consisted of analyses of variance (ANOVAs), independent samples t-tests, Pearson correlations and multiple linear

regressions. For all analyses, an alpha level of $p < 0.05$ was used to determine statistical significance.

Results

Descriptive Statistics and simple correlations

Independent samples t-tests were used to examine whether basal testosterone concentrations and/or trait dominance scores differed as a function of competition outcome (i.e., win or loss conditions). Results indicated that winners and losers did not differ in trait dominance or basal testosterone (all $ps > 0.22$). Trait measures (basal testosterone concentrations and trait dominance scores) and PSAP responses are presented in Table 5. 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 Figure 4), but 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 responses ($r = -0.76, p < 0.001$); and aggression and protection responses ($r = 0.42, p < 0.01$).

Table 5.

Mean (SD) salivary testosterone, trait dominance scores, and Point Subtraction Aggression Paradigm (PSAP) responses for men (n = 39) and women (n = 60)

	Men		Women	
	Mean	SD	Mean	SD
Baseline Testosterone (pg/mL)	119.43	74.46	20.74	23.59
Post Testosterone (pg/mL)	94.77	48.90	17.02	19.30
Trait Dominance Scores	8.64	5.48	5.75	5.72
PSAP Responses				
Reward	2421.27	327.78	2458.56	400.90
Aggression	280.76	153.10	220.37	147.38
Protection	310.85	126.61	300.72	170.43

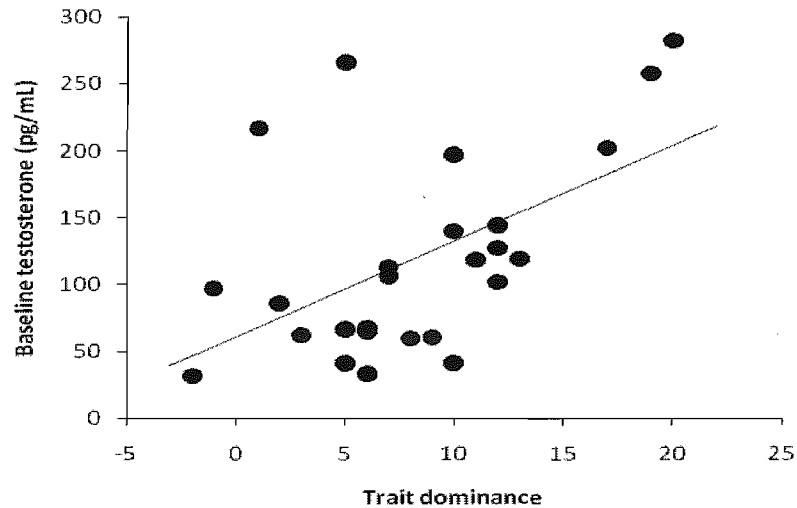


Figure 4. Relationship between trait dominance and baseline testosterone concentrations in men ($n = 26$). $r = .53$, $p < 0.01$.

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 (within-subject factor, sample time; between-subject factors, competition outcome and) ANOVA was conducted 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 ($F_{1,71} = 12.35$, $p < 0.001$ 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’ 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’ 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; $M = -24.57$, women; $M = -4.14$, $t_{73} = 2.50$, $p = 0.015$). The 'time by by outcome' interaction was not significant ($F_{1, 71} = 1.65$, $p = 0.20$).

Behavioural Responses to 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 interaction ($F_{1, 95} = 2.24$, $p = 0.14$) on aggressive responses. There was no main effect of either or competition outcome, or interaction of the two factors, for reward responses or for protection responses on the PSAP (all $ps > 0.43$).

Relationship 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. 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 aggressive behaviour ($R^2_{\text{change}} = 0.07$, $F_{2, 33} = 1.18$, $p = 0.32$). The two-way and three-way

interactions did not predict aggressive behaviour (all $ps > 0.25$). 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 ($R^2_{\text{change}} = 0.22$, $F_{2,21} = 3.40$, $p = 0.05$), indicating that post competition testosterone concentrations (controlling for pre-competition testosterone) were positively correlated with 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 $ps > 0.25$)².

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 & 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, post-competition testosterone concentrations (controlling for pre-competition testosterone) explained 42% of unique variance in aggressive behaviour (step 2; $R^2_{\text{change}} = 0.42$, $F_{1,9} = 8.59$, $p = 0.02$; see Figure 5), and the post-

² Examination of predictor variables indicated that all were relatively normally distributed. Also, examination of regression residuals showed no major violations of the assumptions of independence, homoscedasticity, or normality.

competition testosterone by trait dominance interaction did not explain any additional variance in aggressive behaviour (step 3; $R^2_{\text{change}} = 0.003$, $F_{1,8} = 0.6$, $p = 0.82$).

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 post-competition testosterone concentrations (step 2: $R^2_{\text{change}} = 0.07$, $F_{1,9} = 0.77$, $p = 0.40$). The interaction between post-competition testosterone concentrations and trait dominance explained 38% of unique variance in aggressive behaviour (step 3; $R^2_{\text{change}} = 0.38$, $F_{1,8} = 6.74$, $p = 0.03$). Predicted aggression scores were computed by including high and low (Mean \pm 1 S.D.) post-competition testosterone concentrations and trait dominance scores into the regression equation (see Figure 6). Simple slope analyses were conducted using a computer software program (www.quantpsy.org) developed by Preacher and colleagues (2006). Post-competition testosterone concentrations were positively related to aggressive behaviour in men with high trait dominance ($b = 0.896$, $t_8 = 2.42$, $p = 0.038$) but not related in men with low trait dominance ($b = -0.770$, $t_8 = -1.52$, $p = 0.16$). No significant main effects or interactions were found when the same analysis (i.e., separate analysis for winners and losers) was performed on women ($ps > 0.17$).

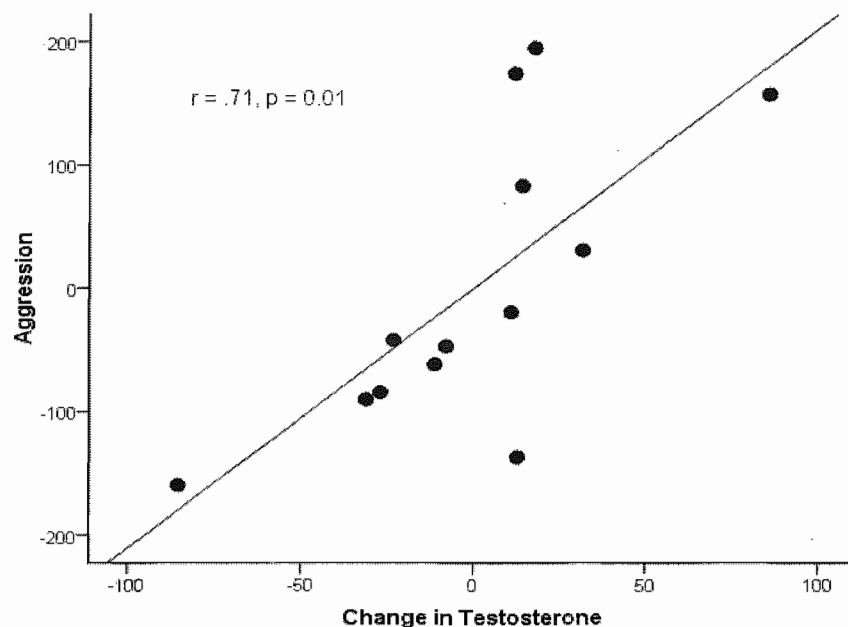


Figure 5. Change in testosterone concentrations and aggressive behaviour among men assigned to the loss condition. A partial regression plot (pre competition testosterone controlled), showing a positive correlation between change in testosterone and aggressive behaviour. Both variables in the partial regression plot are residuals ($n = 13$ men). partial- $r = .71$, $p < 0.01$.

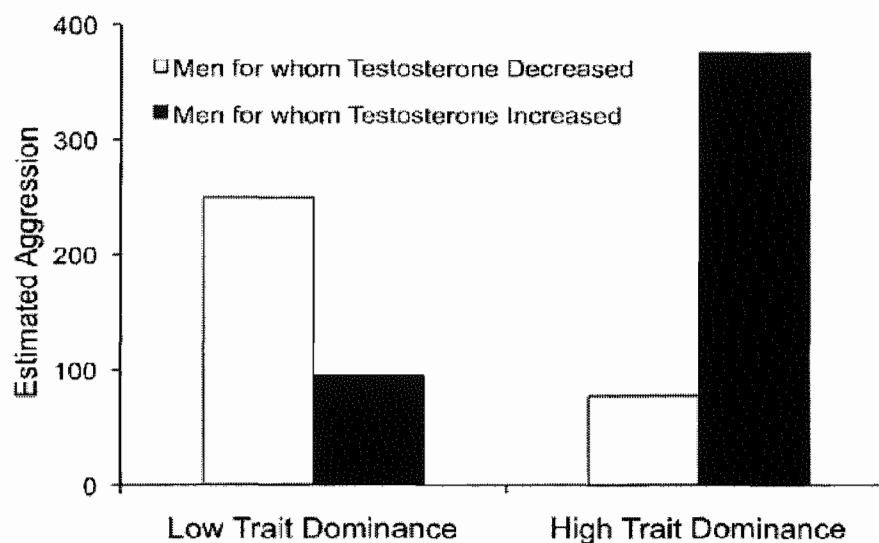


Figure 6. The plot of the interaction between trait dominance and change in testosterone concentrations (using ± 1 S.D. of the mean) predicting aggressive behaviour among men assigned to the win condition ($n = 14$).

Mediation Analysis

An association between trait and state variables and the PSAP measures was observed among men assigned to the loss condition (see Table 6). That is, there were strong associations between change in testosterone concentrations and aggression and reward responses ($r = 0.71$ and $r = -0.61$, respectively).

Table 6.

Correlations between baseline testosterone concentrations, change in testosterone concentrations, trait dominance, and Point Subtraction Aggression Paradigm (PSAP) responses. Correlations for women are inside parentheses.

	Reward	Aggression	Protection
Win Condition			
Baseline testosterone (pg/mL)	-.13 (.40)	.26 (-.26)	.05 (-.51*)
Testosterone change	-.10 (.04)	.28 (-.13)	.33 (-.03)
Trait dominance	.05 (-.06)	.21 (-.12)	.13 (.17)
Loss Condition			
Baseline testosterone (pg/mL)	-.29 (.39)	.34 (-.20)	-.04 (-.17)
Testosterone change	-.61* (-.10)	.71** (-.09)	.34 (.01)
Trait dominance	-.05 (-.29)	-.05 (.33)	-.15 (.07)

* $p < 0.05$, ** $p < 0.01$

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, $p = 0.01$.

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.

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 & 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 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 & 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 & Rhode, 2002; Mehta & 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.

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 & 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 & France, 2001; Sellers et al., 2007) and between implicit dominance (p Power) and testosterone concentrations (Schultheiss et al., 1999).

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 & 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. Others have found that a loss of status (defined as losing a competition) is associated with poor performance among high testosterone individuals (Josephs, Newman, Brown, & Beer, 2003; Josephs et al., 2006; Newman, Josephs, & Guinn-Sellers, 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 & 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.

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 & 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, Parrot, & Frey, 2003; Archer, 2004). Sex differences are not always found for behavioural measures of aggression (e.g., Moe, King, & Bailly, 2004), and there is some evidence to suggest that women make use

of indirect forms of aggressive behaviour more frequently than do men (Hess & Hagan, 2006).

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, Landys, & Wingfield, 2007) and Biosocial Model of Status (Mazur, 1985; Mazur & Booth, 1998). 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.

Rationale for Study 3

An interesting finding that emerged from Studies 1 and 2 was that participants engaged in a high level of aggressive behaviour at the expense of extrinsic reward. Specifically, aggressive behaviour on the PSAP was negatively correlated with total points earned during the task, indicating that participants sacrificed financial reward to punish their partner. The best strategy on the PSAP is to simply select the point reward response during the task, as this behavioural response is highly correlated with total points earned ($r_s > .85$). So, why did men engage in such behaviour if it came at a cost to external reward (i.e., point earned, which translates into money)?

Given that men engage in costly aggressive behaviour, there must be some kind of incentive for behaving aggressively on the PSAP. Perhaps the intrinsically rewarding nature of retaliation (i.e., reactive aggression) is sufficient to outweigh the financial costs of such behaviour. In fact, experiments with animal models indicate that animals will form a preference for locations that were paired with male-to-male aggressive interactions (Meisel & Joppa, 1994; Martinez, Guillen-Salazar, Salvador, & Simon, 1995; Farrell & Wilczynski, 2006), and that animals will work vigorously to gain access to aggressive interactions (Fish, DeBold, & Miczek, 2005; Couppis & Kennedy, 2008) suggesting that such behaviour is rewarding. Similarly, a recent imaging experiment in humans indicates that individual differences in the desire to punish unfair players (at a cost to oneself) was associated with activation of the striatum, a brain structure critically involved in processing reward (de Quervain, Fishbacher, Treyer, Schellhammer, Schnyder, Buck, & Fehr, 2004).

To examine the motivational factors underlying aggressive behaviour during the PSAP, I created four versions of the PSAP that differed in the extent to which participants were provoked (e.g., provoked or not) and the extent to which they were able to keep the points that they stole (e.g., rewarded for aggression or not). After participants performed the PSAP, they were asked to rate the extent to which they enjoyed the task (i.e., a measure of intrinsic reward) and also to choose between a competitive versus non-competitive task for the final part of the study. One question addressed by this experiment was whether the intrinsic reward value of the PSAP differed as a function of whether participants used aggression in response to provocation and/or the opportunity to gain points from stealing. Also, would individual differences in aggressive behaviour be associated with the extent to which participants enjoyed the task? If so, would this relationship hold across each of the four versions of the PSAP?

Another goal was to determine whether testosterone concentrations would increase as a function of whether participants were provoked during the task and/or whether participants were able to keep points that they stole. Also, this experiment examined whether the positive relationship between testosterone dynamics and aggressive behaviour previously observed (Study 1) would extend beyond the condition in which participants are provoked and do not get to keep points that they steal (i.e., reactive aggression). In other words, is the relationship between testosterone dynamics and aggressive behaviour specific to reactive aggression, or does it extend to proactive forms of aggression?

CHAPTER 4: MOTIVATIONAL AND SITUATIONAL FACTORS AND THE RELATIONSHIP BETWEEN TESTOSTERONE DYNAMICS AND HUMAN AGGRESSION DURING COMPETITION

Note: This section is based on the following article, with permission: Carré, J.M., Gilchrist, J., Morrissey, M.D., & McCormick, C.M. (in press). Motivational and situational factors and the relationship between testosterone dynamics and human aggression during competition. *Biological Psychology*.

Abstract

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 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.

Introduction

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 & 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, 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 & Coie, 1987; Crick & 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, mating opportunities), and does not typically involve physiological arousal (Dodge & Coie, 1987; Crick & 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 points are 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. However, 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 & 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, Schmittberger, & Schwarze, 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 given to the proposer (Camerer & Thaler, 1995). This behaviour, which comes at the expense of extrinsic reward, may function to prevent unfair allocations in future social interactions (Fehr & Gächter, 2000; Fehr & Gächter, 2002; Nowak, Page, & Sigmund, 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. This 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 & McCormick, 2008). A number of experiments with animal models indicate that testosterone has rewarding properties (see Frye, 2007 and Wood, 2008 for reviews). For example, male hamsters self-administer testosterone (Johnson & Wood, 2001; Wood, Johnson, Chu, Schad, & Self, 2004), and male rats develop a preference for locations that were previously paired with testosterone injections versus locations paired with saline injections (Alexander, Packard, & Hines, 1994; Packard, Cornell, & Alexander, 1997). Thus, an increase in testosterone may contribute to the intrinsically rewarding nature of reactive aggression.

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 by 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 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 (Carré & McCormick, 2008), 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 were limited to the condition in which there was provocation and the aggression was costly.

Methods

Participants

The participants were 151 undergraduate men recruited from Brock University (M age = 19.78, SD = 1.93). The majority of participants self-identified as Caucasian (84.1%). Participants were instructed not to eat one hour prior to arriving in the laboratory for testing. Eight participants reported taking prescription medication (e.g., SSRIs, glucocorticoids, thyroxin, Ritalin) and were removed from the analyses. Behavioural data

from four participants were lost due to computer malfunction. Thus, the final sample consisted of 139 male participants.

Measures

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, points are taken from participants 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 & McCormick, 2008; Carré et al., 2009), it can be inferred that participants are stealing points to ‘punish’ their partner. 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 & Richardson, 1994, p. 7). 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 & 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 four experimental conditions in which the PSAP was modified to differ in the extent of provocation and external reward received for aggression (See Table 7 for a breakdown of conditions). (1) *Provoked/Not Rewarded*: In this condition, similar to our previous studies, participants were provoked (have points stolen) by their fictitious partner and were told that they could steal points from their opponent, but that they had been randomly assigned to the experimental condition in which they did not get to keep stolen points whereas the opponent did. (2) *Not Provoked/Not Rewarded*: In this condition, participants were never provoked during the task and did not get to keep the points that they stole from their partner. (3) *Provoked/Rewarded*: In this condition, participants were provoked during the task and were told that any points stolen from their partner would be added to their own point counter. (4) *Not Provoked/Rewarded*: Participants in this condition were never provoked and were told that any points stolen from their partner would be added to their own point counter. As in our previous studies (Carré & 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 one 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 seconds and a maximum of 90 seconds after which the random point subtractions would continue to occur every 12 to 45 seconds. 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 to 45 seconds in the absence of any Button 2 or Button 3 selections. For conditions not involving provocation, participants never had points stolen from them.

Table 7.

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)

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 minutes. 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%.

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-minute practice session to become familiar with the response options. Next, participants played three 10-minute sessions of the PSAP. After the second session (i.e., approximately 24 minutes 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 analyses³. 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 minutes 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 minutes) 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 Figure 7 for an overview of the procedure).

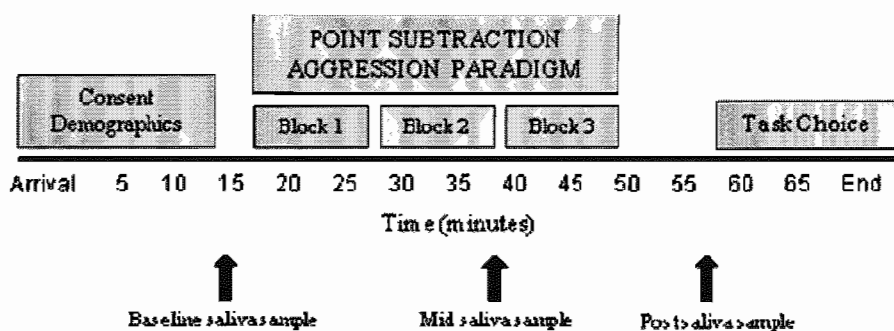


Figure 7. Timeline of experimental procedures.

³ Independent samples t-tests were performed to see whether individuals who were suspicious about whether they were actually playing against another person differed on any of the variables from individuals who were not suspicious. There were no significant differences on any of the variables.

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 (from zero) 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).

Results

Descriptive Statistics

Descriptive statistics for age, baseline-, mid-, and post- PSAP testosterone concentrations across experimental conditions are presented in Table 8. 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.

Table 8.

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

	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 ^{a*}	87.00 (6.76)	103.99 (6.98)	85.33 (8.47)	98.07 (7.98)
Mid testosterone ^a	94.34 (6.58)	109.00 (8.99)	83.93 (6.07)	92.70 (8.26)
Post testosterone ^a	88.05 (6.11)	103.33 (7.88)	85.29 (7.43)	92.69 (7.98)

* $p = 0.05$ main effect of provocation

^a Testosterone concentrations are measured in pg/mL

Aggression presses and points earned 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 Figure 8). 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 Provocation by 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.

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. Men in the Provoked/Not Rewarded condition were more likely to choose the competitive versus non-competitive task than all 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 men in the Not Provoked/Rewarded condition ($p = 0.02$). Chi square analyses were used to examine whether preference to choose the competitive task was significant in each condition. 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 Figure 8).

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 ($r = -0.07, p = 0.69$).

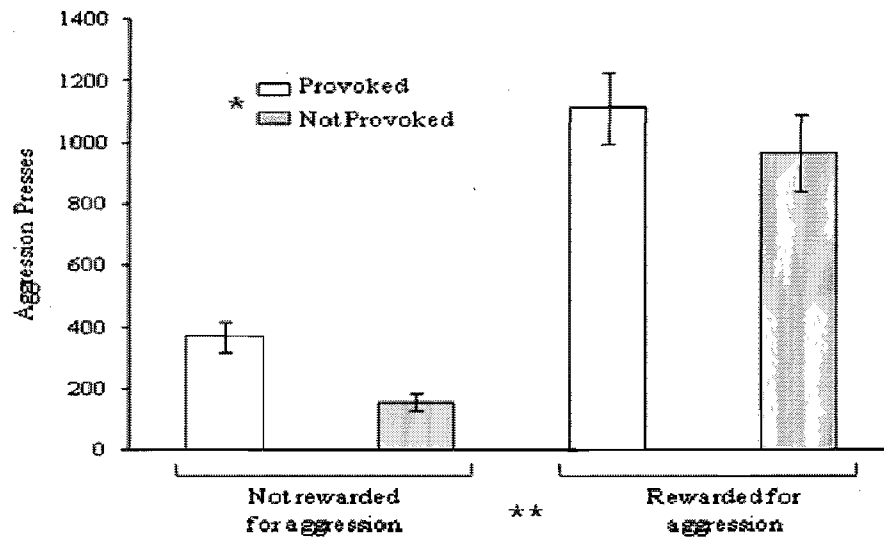


Figure 8. Mean (SEM) aggression presses as a function of Reward and of Provocation. *main effect of Provocation ($p = 0.04$). **main effect of Reward ($p < 0.001$).

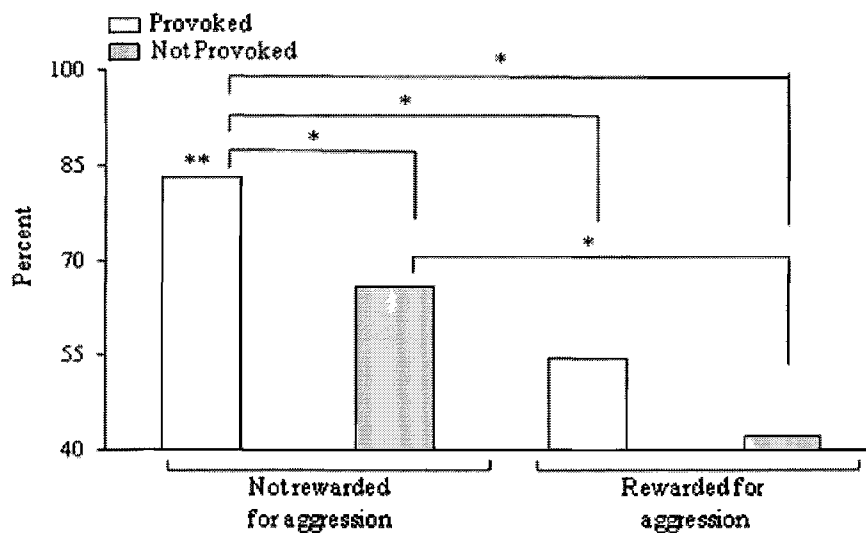


Figure 9. Percentage of men who chose the competitive versus the non-competitive task in each experimental condition. * significant group differences in percent choosing the competitive task ($ps < 0.04$). ** significant preference for the competitive task within a condition ($p < 0.001$).

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 main effect of Reward and the interaction of the two factors were not significant ($p = 0.13$, and $p = 0.90$) (see Figure 10). 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 9 for other correlations).

Table 9.

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

	Experimental Conditions			
	Provoked/Not Rewarded	Not Provoked/Not Rewarded	Provoked/Rewarded	Not Provoked/Rewarded
Pre testosterone (pg/mL)	-.15	.22	-.08	.06
Change in testosterone (pre- to mid- PSAP)	.34*	.03	.21	-.01
Change in testosterone (pre- to post- PSAP)	.10	.12	-.01	.02
Task enjoyment	.41*	.10	-.20	.15

* $p = 0.05$ main effect of provocation

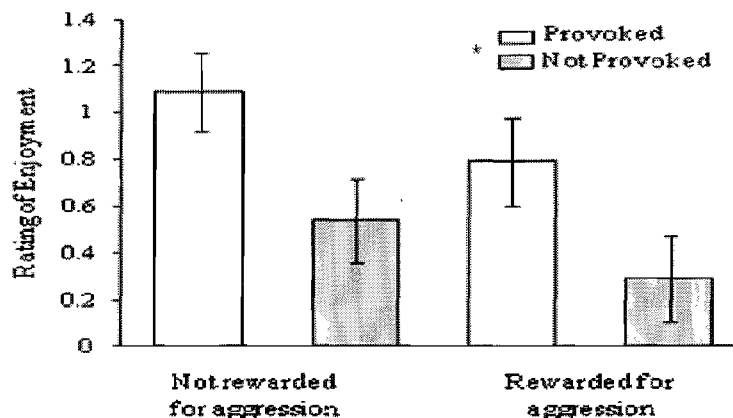


Figure 10. Mean (SEM) ratings of enjoyment of the Point Subtraction Aggression Paradigm (PSAP) as a function of Reward and of Provocation. *main effect of Provocation ($p < 0.01$).

Relationship between testosterone dynamics and aggression

Three participants who had change in testosterone scores greater than 3 standard deviations from the mean were removed from all subsequent analyses involving testosterone dynamics. No main effects of Reward or Provocation were evident when an 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 (M increase = 14.58% , $t_{34} = 2.23$, $p = 0.03$) (see Figure 11). Also, for men in this condition, the change in salivary testosterone concentrations from baseline to mid-PSAP and aggressive behaviour was significant ($r = 0.34$, $p = 0.049$) (see Figure 12). For the other conditions, no correlation was significant (see Table 9).

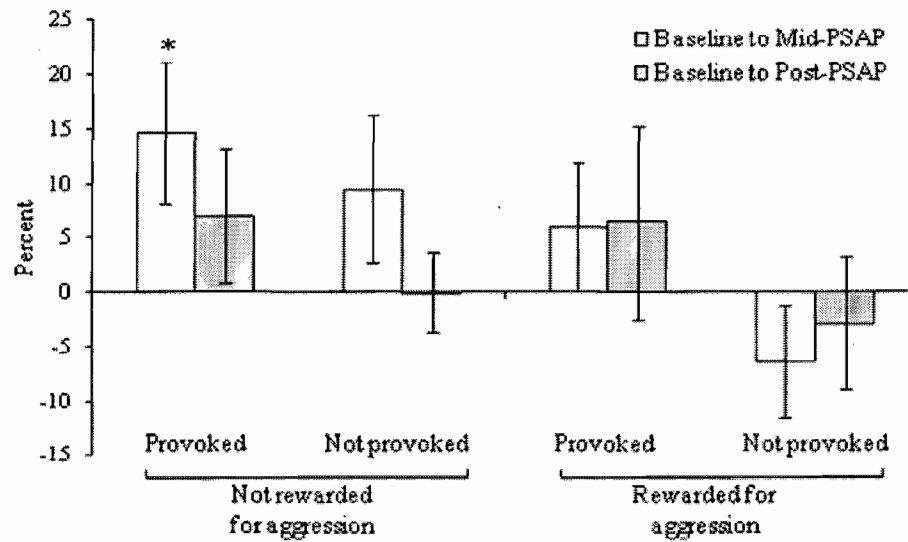


Figure 11. Mean (SEM) percent change in testosterone from baseline to mid- PSAP and from baseline to post- PSAP as a function of Reward and of Provocation. #Significant increase in testosterone within a condition ($p = 0.03$).

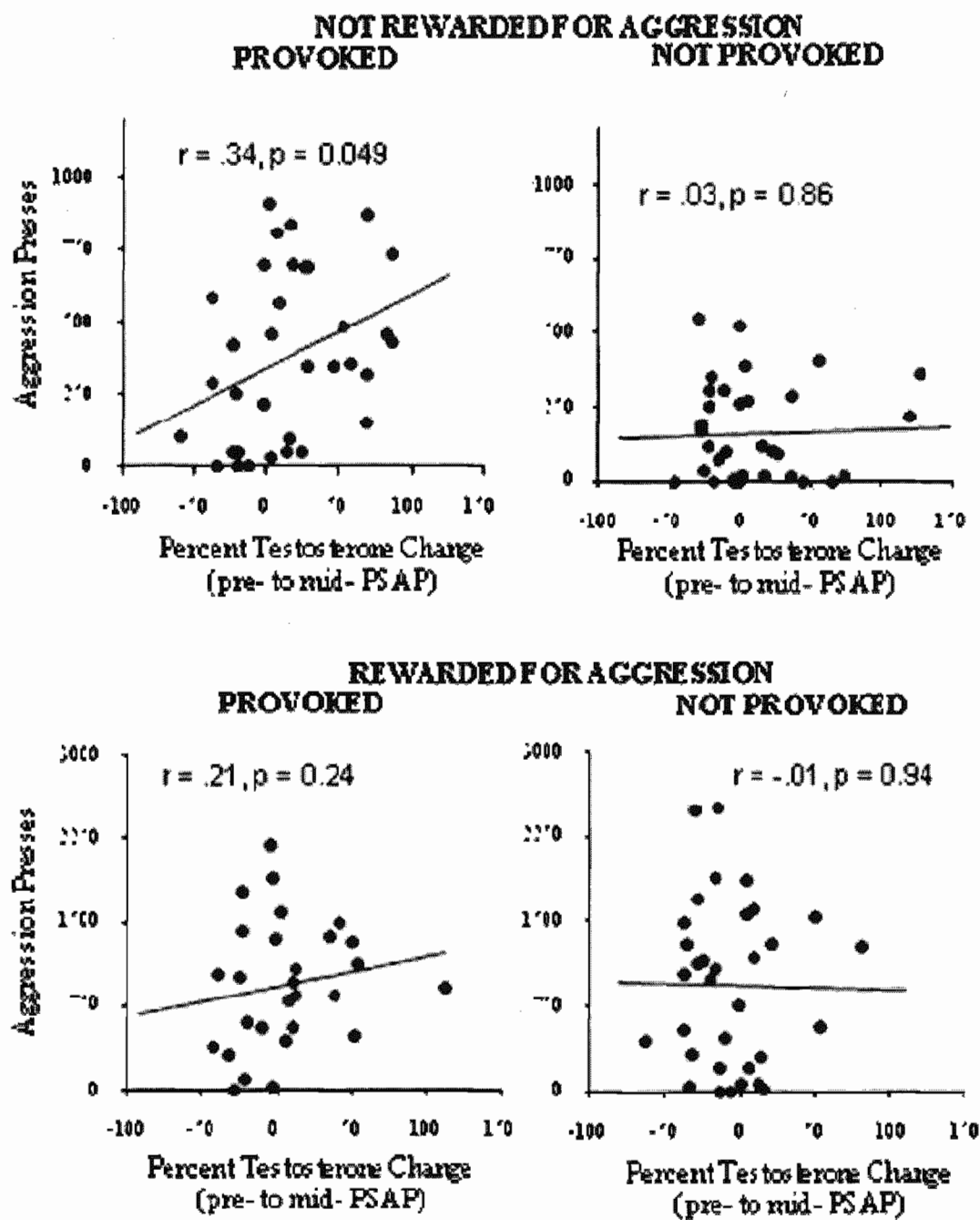


Figure 12. Relationship between percentage change in testosterone (baseline to mid-PSAP) and aggression presses for each experimental condition.

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 ($\chi^2 (2, n = 32) = 18.97, p < 0.001$), 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 ($M = 17.30\%$) and were more aggressive ($M = 1200.78$) than individuals who chose the non-competitive task ($M = -16.70\%$ and 800.43 , respectively).

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 &

Gächter, 2000; Fehr & Gächter, 2002; de Quervain et al., 2004; Carré & 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 without 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 consistent with our previous study that involved the reactive aggression condition in which 71 percent of men chose a competitive versus a non-competitive option after the PSAP task (Carré & 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 and colleagues (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, Seymore, O'Doherty, Stephan, Dolan, & Frith, 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 the extrinsic cost of reactive aggression may be offset by its intrinsic reward value related to retaliation.

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 & 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 & 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 & 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 & Coie, 1987; Crick & 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 defence and/or establishment of social dominance, but were not associated with maladaptive forms of escalated aggression (Higley, Mehlman, Poland, Taub, Vickers, Suomi, & Linnoila, 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, Tybur, Gangestad, Perea, Shapiro, & Kenrick, 2009). We have proposed that what may appear to be irrational economic behaviour on the PSAP, such as 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 & Marler, 2005; Meisel & Joppa, 1994; Martínez, Guillen-Salazar, Salvador, & Simon, 1995; Farrell & 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 & Josephs,

2006; Klimesmith et al., 2006; Carré & 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 & 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 reported that individuals who engaged in high levels of unprovoked aggression scored significantly higher on measures of psychopathy and personality disorders (Nouvion, Cherek, Lane, Tcheremissine, & Liewing, 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. 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.

CHAPTER 5 - GENERAL DISCUSSION

“Research into the endocrine effects of competition is situated in an evolutionary context, and authors mainly interpret their findings in evolutionary terms. However, the functions served by the increased T remain to be empirically established” (van Anders & Watson, 2006, p. 220).

Testosterone concentrations are highly responsive to human competitive interactions (see Mazur & Booth, 1998; Archer, 2006 for reviews). These findings have mainly been interpreted from a functional perspective whereby a rise in testosterone during competition serves to modulate ongoing and/or future social behaviour. However, few studies have empirically tested this assumption. The main goal of the studies reported in this dissertation was to fill this gap in the literature by examining the extent to which competition-induced fluctuations in testosterone would be associated with ongoing and/or future competitive and aggressive behaviour in humans. Results from these studies provide some of the first empirical evidence concerning the potential functional role of testosterone dynamics within the context of human competition (see Table 10 for a summary of the findings). Briefly, testosterone concentrations increased in response to aggressive interactions (Study 1 and Study 3, reactive condition); men for whom testosterone increased during competition were more willing to engage in a second competition (Study 1 and Study 3, proactive condition); a competition-induced rise in testosterone predicted future aggressive behaviour in men but not women (Study 2); aggressive responses associated with higher testosterone were made at a cost to extrinsic reward (Studies 1-3); and aggressive behaviour was positively correlated with the extent to which men enjoyed the experimental task (Study 3, reactive condition).

In Study 1, baseline testosterone concentrations were not associated with aggression, but aggressive behaviour was positively correlated with an increase in testosterone concentrations during the PSAP. Recent studies indicate that steroid hormones rapidly modulate behaviour in animal models (Aikey et al., 2002; Ramage-Healey and Bass, 2006; Trainor et al., 2007; 2008), suggesting that fluctuations in testosterone may influence ongoing behaviour, likely through non-genomic mechanisms (see Michels & Hoppe, 2008; Foradori et al., 2008 for reviews). Changes in testosterone concentrations may not necessarily activate aggressive behaviour *per se*, but instead, may contribute to the persistence of aggression. Wingfield (1994) found that during the breeding season, free-living male song sparrows demonstrated an increase in testosterone in response to a simulated territorial intrusion, and this was associated with enhanced aggressive displays (e.g., singing, patrolling the territory, and attacking the intruder), which continued to persist for up to 24 hours after the removal of the stimulus intruder. Castrated male song sparrows responded to the territorial intrusion with aggressive displays, but in this case, aggressive behaviour ceased immediately after the stimulus intruder was removed. Persistent aggressive behaviour (i.e., behaviour that persists even after the stimulus intruder is removed) was restored in castrated male song sparrows that received testosterone implants. These data indicate that testosterone may not be required for the activation of aggression, but that an increase in testosterone during a competitive interaction may serve to maintain elevated levels of aggressive behaviour.

Table 10.

Summary of the findings

Study 1	Study 2	Study 3
-Basal testosterone was not associated with aggression	-Basal testosterone was not associated with aggression	-Basal testosterone was not associated with aggression
-Mean increase in testosterone from pre- to post- PSAP	-Mean decrease in testosterone from pre- to post- NTT	-Mean increase in testosterone from pre- to mid- PSAP (reactive condition only)
-Aggressive behaviour was negatively correlated with points earned	-Aggressive behaviour was negatively correlated with points earned	-Aggressive behaviour was negatively correlated with points earned (reactive and control conditions)
-Aggressive behaviour was positively correlated with pre- to post- PSAP increase in testosterone	-Men had higher trait dominance scores and were more aggressive than women	-Aggressive behaviour was positively correlated with pre- to mid- PSAP increase in testosterone (reactive condition only)
-Aggressive behaviour predicted willingness to choose a non-competitive task -Increase in testosterone during PSAP predicted willingness to choose a competitive task	-For men assigned to the loss condition, change in testosterone during the NTT was positively correlated with subsequent aggressive behaviour	-Individuals assigned to the reactive condition enjoyed the PSAP the most and were more likely to choose the competitive task.
	-For men assigned to the win condition, change in testosterone during the NTT was positively correlated with subsequent aggressive behaviour, but only in men with relatively high trait dominance scores	-Individual differences in aggressive behaviour were positively correlated with the extent to which men reported enjoying the task (reactive condition only)

The finding that changes in testosterone during the PSAP predicted subsequent choice of a competitive versus non-competitive task (Study 1) is consistent with theoretical models concerning the bidirectional relationship between testosterone and human competitive behaviour (see Mazur, 1976; 1985; Mazur & Booth, 1998 for reviews). This finding is also consistent with a recent study indicating that testosterone dynamics during competition predicted subsequent willingness to compete (Mehta & Josephs, 2006). However, this effect was only observed among individuals who had lost a previous competitive interaction. In Study 1, the extent to which participants believed they earned more points than their opponent (i.e., subjective winner/loser) did not influence the relationship between testosterone dynamics and subsequent choice. One important difference is that participants in the Mehta and Josephs (2006) study were experimentally assigned to a win or lose condition, whereas participants in Study 1 were not aware of the objective outcome of the interaction. Perhaps the objective outcome of the competitive interaction is the key factor influencing the extent to which testosterone dynamics predict subsequent behaviour.

Results from Study 2 indicated that competition-induced fluctuations in testosterone predicted subsequent aggressive behaviour in men, but not women. This is the first report indicating that testosterone responses to competition influence subsequent human aggression. This finding is consistent with recent studies in animal models indicating that a rise in testosterone during competition is related to subsequent aggressive behaviour (e.g., mice, Trainor et al., 2004; Gleason et al., 2009; fish, Oliveira et al., 2009). The results are also consistent with the idea that the outcome of a

competitive interaction influences the relationship between change in testosterone and subsequent behaviour (Mehta & Josephs, 2006). More specifically, the relationship between change in testosterone and aggressive behaviour was much stronger among men assigned to the loss condition ($r = .71$) relative to men assigned to the win condition ($r = .28$). For men assigned to the win condition, a rise in testosterone alone was not sufficient to influence subsequent aggressive behaviour. For these men, a rise in testosterone was positively correlated with subsequent aggressive behaviour, but only among those with high trait dominance scores. However, it should be noted that although the relationship between change in testosterone and aggressive behaviour was much stronger in losers, there was no interaction between outcome and change in testosterone, and as a result, this finding should be interpreted with caution.

In addition to the relationships observed between individual differences in changes in testosterone and aggressive/competitive behaviour, one interesting behavioural result that emerged in all three studies was that participants engaged in aggressive behaviour at a cost to extrinsic reward. This finding is similar to results obtained from studies in behavioural economics paradigms (e.g., ultimatum game, third party punishment game), whereby participants punish others for unfair behaviour at a significant economic cost to themselves (Gächter & Fehr, 2000; 2002; de Quervain et al., 2004). These findings suggest that the costly aggressive behaviour must be intrinsically rewarding. Results from Study 3 were consistent with this hypothesis, indicating that individuals who were provoked, but did not receive reward for aggression enjoyed the task the most, and were more likely to choose a subsequent competitive versus non-competitive task. Also, individual differences in costly aggressive behaviour among men

who were provoked but did not receive reward for aggression were positively correlated with the extent to which they enjoyed the task and with changes in testosterone during the PSAP. These results are consistent with observations that animals will form a preference for locations previously associated with aggressive interactions (Meisel & Joppa, 1994; Martinez et al., 1995), will work vigorously to gain access to aggressive interactions (Couppis & Kennedy, 2008; DeBold et al., 2002; Ferrari et al., 2003), and also experience an increase in testosterone following a successful aggressive interaction (Oyegbile & Marler, 2005).

What are the neural structures through which testosterone influences aggressive behaviour? Recently, using fMRI, several studies have found that individual differences in endogenous testosterone concentrations are positively correlated with amygdala responses to angry faces (Derntl, Windischberger, Robinson, Kryspin-Exner, Gur, Moser, & Habel, 2009; Manuck et al., 2009; Hermans et al., 2008). Also, recent experiments indicate that exogenous testosterone administration produces an increase in amygdala reactivity to angry faces (Hermans et al., 2008; van Wingen, Zylick, Pieters, Mattern, Verkes, Buitelaar, & Fernandez, 2008). These findings are particularly intriguing given that reactively aggressive individuals (i.e., individuals diagnosed with intermittent explosive disorder) also demonstrate exaggerated amygdala reactivity to angry faces (Coccaro, McCloskey, Fitzgerald, & Phan, 2007). To the extent that increased amygdala reactivity to angry faces is a marker of propensity for aggressive behaviour – these findings suggest that individual differences in testosterone concentrations may bias amygdala reactivity to signals of threat (i.e., angry faces), and that such a pattern of neural activity may be associated with one's likelihood of behaving aggressively in

response to provocation. It will be important to examine whether amygdala responses to angry faces predict individual differences in aggressive behaviour as measured in laboratory tasks such as the TAP or the PSAP.

In a more direct examination of the neural structures through which testosterone influences aggressive behaviour, Mehta and Beer (in press) reported that the association between testosterone concentrations and aggressive behaviour (using rejection of unfair offers in the Ultimatum Game as a putative index of aggression) was statistically mediated by activity in the medial OFC. That is, individuals with elevated baseline testosterone concentrations demonstrated reduced activation in bilateral medial OFC during the Ultimatum Game and this was associated with more aggressive behaviour (i.e., rejection of unfair offers). It will be important to extend this research by examining the extent to which competition-induced fluctuations in testosterone concentrations influence the activation of the neural circuitry subserving aggressive behaviour.

Acute fluctuations in testosterone may also, through its effects on the meso-limbic dopamine system, reinforce learning associated with aggressive behaviour (Oyegbile & Marler, 2005; Marler, Oyegbile, Plavicki, & Trainor, 2005; Gleason et al., 2009). This possibility is supported by data indicating that animals demonstrate a preference for locations previously paired with testosterone administrations (Alexander et al., 1994; Packard et al., 1997) and with successful aggression interactions (Meisel & Joppa, 1994; Martinez et al., 1995; Farrell & Wilczynski, 2006). Preferences for these locations can be blocked by a dopamine receptor antagonist (Couppis & Kennedy, 2008; Packard, Schroeder, & Alexander, 1998; Schroeder & Packard, 2000), suggesting that a rise in testosterone in response to an aggressive interaction may facilitate learning associated

with aggressive interactions through its effects on the mesocorticolimbic dopamine system.

One limitation to the current studies is that in contrast to experimental evidence in animal research (e.g., Trainor et al., 2004; Gleason et al., 2009; Oliveira et al., 2009), the studies reported in this dissertation did not involve direct manipulation of testosterone concentrations, and thus, the results are correlational. For instance, it may be that some third factor not measured in these studies influenced both testosterone dynamics and aggressive behaviour. Thus, it will be important for future studies to use pharmacological techniques to test whether testosterone plays a causal role in shaping social behaviour in humans. As discussed previously, this experimental approach has found that acutely elevating testosterone concentrations modulates a number of behaviours that may be relevant within the context of human competition (see van Honk, Harmon-Jones, Morgan, & Schutter, 2010).

Another limitation is that it is unclear whether the relationship observed between testosterone dynamics and competitive/aggressive behaviour is mediated via androgen and/or estrogen receptor pathways. Clearly, studies in animal models will certainly be important to our understanding of the biological pathways through which testosterone dynamics may influence social behaviour (see Trainor et al., 2004). Nonetheless, future studies in human neuroendocrinology may examine the extent to which testosterone-behaviour relationships are influenced by variability in the promoter region of the gene coding for the androgen receptor (AR). *In vitro* work has demonstrated that variability in the number of CAG repeat sequences in the promoter region of the AR, is directly associated with the trans-activation potential of the AR (Chamberlain, Driver, &

Miesfeld, 1994). Generally speaking, a greater number of CAG repeat sequences confer a less efficient AR. If the androgen receptor is critically involved in mediating the effects of testosterone on aggressive behaviour (as in Trainor et al., 2004; Raskin et al., 2009), one may predict that fewer CAG repeats would be associated with more aggressive behaviour. Consistent with this prediction, a recent study reported that men convicted of murder had fewer CAG repeats (i.e., more efficient AR) than did age-matched controls (Rajender, Pandu, Sharma, Gandhi, Singh, & Thangaraj, 2008). Few studies have examined the potential interactive effects of current testosterone concentrations and CAG length variation of the AR on human social behaviour. One study reported that fewer CAG repeats (i.e., more efficient AR) were associated with elevated scores on a depression scale, but only among men who also had low baseline testosterone concentrations (Seidman, Araujo, Roose, & McKinley, 2001). Moreover, Manuck and colleagues (2009) recently found a positive correlation between baseline testosterone concentrations and ventral amygdala responses to threatening faces, but only among men with relatively fewer CAG repeats. Another study reported that individual differences in CAG-repeat length predicted salivary testosterone responses among men interacting with attractive women (Roney, Simmons, & Lukazewski, 2009). Specifically, the authors found that men with fewer AR CAG repeats (i.e., more efficient receptors), demonstrated a larger increase in testosterone during brief interactions with women (Roney et al., 2009). These studies demonstrate the importance of considering both hormone and receptor polymorphisms when attempting to uncover neuro-endocrine correlates of complex human social behaviour.

Although I found no evidence for a relationship between baseline testosterone concentrations and aggressive behaviour (Studies 1-3), it is possible that other biological factors may moderate the association between baseline testosterone and aggression. In particular, recent studies have reported that individual differences in baseline cortisol concentrations interact with baseline testosterone concentrations to predict social behaviour in humans (Popma et al., 2007; Mehta & Josephs, unpublished). Popma and colleagues (2007) found that baseline testosterone concentrations predicted aggressive behaviour in adolescent males, but only among those with low baseline cortisol concentrations. Also, Mehta and Josephs (unpublished) found that individual differences in baseline testosterone concentrations predicted willingness to compete and leadership behaviour, but only among individuals with relatively low baseline cortisol concentrations. Thus, it appears that a combination of high baseline testosterone concentrations and low baseline cortisol concentrations is associated with aggressive, competitive, and leadership behaviours (see van Honk et al., 2010).

Summary

To conclude, the findings reported in this dissertation make an important contribution to the growing body of literature on the relationship between competition-induced fluctuations in testosterone and future competitive/aggressive behaviour in humans. It will be important to examine the extent to which competition-induced changes in testosterone and/or testosterone responses to social interactions with potential mates (e.g., Roney et al., 2003; 2007; 2009) modulate other forms of human social behaviour (e.g., risk-taking, mate-seeking, leadership behaviour). I believe that future research that combines techniques from genetics (e.g., androgen receptor polymorphism), brain

imaging (e.g., fMRI, PET), and pharmacology (e.g., exogenous hormone administration) will be critical to our understanding of the mechanisms through which socially-induced fluctuations in testosterone modulate individual differences in human social behaviour (see Hariri, 2009 for a discussion of this approach).

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APPENDIX A

DATE: August 15, 2007

FILE: 06-367 CARRE

TITLE: Relationship between salivary testosterone and strategic decision making

DECISION: Accepted as Clarified.

This project has received ethics clearance for the period of August 15, 2007 to December, 2007 subject to full REB ratification at the Research Ethics Board's next scheduled meeting. The clearance period may be extended upon request. *The study may now proceed.*

Please note that the Research Ethics Board (REB) requires that you adhere to the protocol as last reviewed and cleared by the REB. During the course of research no deviations from, or changes to, the protocol, recruitment, or consent form may be initiated without prior written clearance from the REB. The Board must provide clearance for any modifications before they can be implemented. If you wish to modify your research project, please refer to <http://www.brocku.ca/researchservices/forms> to complete the appropriate form **Revision or Modification to an Ongoing Application**.

Adverse or unexpected events must be reported to the REB as soon as possible with an indication of how these events affect, in the view of the Principal Investigator, the safety of the participants and the continuation of the protocol.

If research participants are in the care of a health facility, at a school, or other institution or community organization, it is the responsibility of the Principal Investigator to ensure that the ethical guidelines and clearance of those facilities or institutions are obtained and filed with the REB prior to the initiation of any research protocols.

The Tri-Council Policy Statement requires that ongoing research be monitored. A Final Report is required for all projects upon completion of the project. Researchers with projects lasting more than one year are required to submit a Continuing Review Report annually. The Office of Research Services will contact you when this form *Continuing Review/Final Report* is required.

Please quote your REB file number on all future correspondence.

MM/bb

Brenda Brewster, Research Ethics Assistant
Office of Research Ethics, MC D250A
Brock University
Office of Research Services

APPENDIX B

Date: August 2007

Project Title: Relationship between salivary testosterone and strategic decision-making.

Principal Investigator

Justin Carré, PhD Candidate
Psychology
Brock University
905-688-5550 ext 3034
justin.carre@brocku.ca

Faculty Supervisor

Cheryl McCormick, PhD
Psychology
Brock University
905-688-5550 ext 3700
cmccormi@brocku.ca

INVITATION

You are invited to participate in a study that involves research. The purpose of this study is to investigate the influence of testosterone on decision-making processes.

WHAT'S INVOLVED

As a participant, you will be asked to provide the researcher with two saliva samples (1 – 2 mL) to later be assessed for testosterone. Furthermore, you will be competing against another individual at a task that involves strategic thinking. You will have the opportunity to make between 7-10 dollars at this task depending on the type of strategy that you use. After completing this task, there will be approximately 10 minutes left in the experiment and you will be given the opportunity to choose from a series of tasks how you would like to spend this time. Participation will take approximately 1 hour and 15 minutes of your time.

POTENTIAL BENEFITS AND RISKS

Possible benefits of participation include earning money based on strategic decision-making. Also, participation in this task may benefit the scientific community by adding to the developing knowledge on the relationship between testosterone and strategic decision-making.

CONFIDENTIALITY

All information you provide is considered confidential; your name will not be included or, in any other way, associated with the data collected in the study. Furthermore, because our interest is in the average responses of the entire group of participants, you will not be identified individually in any way in written reports of this research. Data collected during this study will be stored in a locked file cabinet in Dr. Cheryl McCormick laboratory). Data will be kept for 5 years after which time all data will be shredded and disposed. Access to this data will be restricted to Justin Carré and Dr. Cheryl McCormick.

VOLUNTARY PARTICIPATION

Participation in this study is voluntary. If you wish, you may decline to answer any questions or participate in any component of the study. Further, you may decide to

withdraw from this study at any time and may do so without any penalty or loss of benefits to which you are entitled.

PUBLICATION OF RESULTS

Results of this study may be published in professional journals and presented at conferences. Feedback about this study will be available from Justin Carré. If you wish to learn about the results of the study, you may contact him at justin.carre@brocku.ca

CONTACT INFORMATION AND ETHICS CLEARANCE

If you have any questions about this study or require further information, please contact the Principal Investigator or the Faculty Supervisor (where applicable) using the contact information provided above. This study has been reviewed and received ethics clearance through the Research Ethics Board at Brock University (insert file #). If you have any comments or concerns about your rights as a research participant, please contact the Research Ethics Office at (905) 688-5550 Ext. 3035, reb@brocku.ca.

Thank you for your assistance in this project. Please keep a copy of this form for your records.

CONSENT FORM

I agree to participate in this study described above. I have made this decision based on the information I have read in the Information-Consent Letter. I have had the opportunity to receive any additional details I wanted about the study and understand that I may ask questions in the future. I understand that I may withdraw this consent at any time.

Name: _____

Signature: _____ Date: _____

This study is supported by a National Science and Engineering Research Council (NSERC) grant to Dr. Cheryl McCormick as well as by an NSERC Doctoral Fellowship to Justin Carré

APPENDIX C

Dear Participant,

Thank you for participating in the experiment entitled "Relationship between salivary testosterone and strategic decision-making". Your participation is greatly appreciated.

Although you were led to believe that the main purpose of the task was to measure the relationship between testosterone and decision-making strategy, we were primarily interested in the relationship between testosterone and aggressive behaviour.

The task that you performed was designed to assess the amount of point subtractions that you delivered to your 'competitor' throughout the sessions. You were not actually competing against another individual, but rather, points were randomly taken from your counter by a computer designed to provoke you every 6-120 seconds.

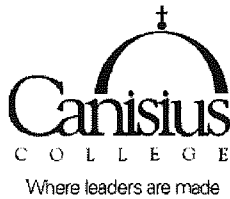
We apologize for deceiving you; however, this deception was crucial in order to get a valid measure of aggressive responding. If you are unhappy with the deception and wish to have your name removed from the data set, please contact Justin Carré.

Thank-you once again for your participation in this study,

Sincerely,

Justin Carré
Graduate Student
Psychology
Brock University
justin.carre@brocku.ca

APPENDIX D



Institutional Review Board for Research on Human Subjects
KAC 211 | phone 716-888-2964 | fax 716-888-3219 | email mdolan@canisius.edu

November 6, 2007

Dr. Susan K. Putnam, Associate Professor of Psychology

Re: "Influence of digit ratio, acute changes in testosterone and trait dominance on a laboratory measure of aggressive behavior" IRB 2007-03 EX.

Dear Dr. Putman:

Canisius College's Institutional Review Board has completed its review of the above named project. The proposal was approved as submitted on October 16, 2007 and you are authorized to use human subjects in the manner specified until November 6, 2008. At the end of that time, if your project is not complete, you need to submit a request for an extension and a progress report to continue beyond that date. If it becomes necessary to make changes, please submit them for review and inclusion in your project file.

As indicated in the cover:

- Participation is voluntary.
- Responses will be kept strictly confidential and no association between individuals and responses will be reported

In addition, please include that the survey was approved by the Canisius College IRB and any questions regarding your rights as a research participant can be directed to Michael Dolan, Chair, Canisius College IRB, mdolan@canisius.edu or 716-888-2964.

Good luck with your project and feel free to contact me if you have any questions.

Sincerely,

Michael G. Dolan
Chair, IRB

APPENDIX E

Project Title: Digit lengths, hormone levels, and personality: Relationship to strategic decision-making and cognitive function.

<u>Principal Investigator</u>	<u>Graduate Student</u>	<u>Faculty Supervisor</u>
Susan Putnam, PhD	Justin Carré, PhD Candidate	Cheryl McCormick, PhD
Psychology	Psychology	Psychology
Canisius College	Brock University	Brock University
716-888-2895	905-688-5550 x 3034	905-688-5550 x 3700
putnams@canisius.edu	justin.carre@brocku.ca	cmccormick@brocku.ca

INVITATION

You are invited to participate in a study examining the relationship between digit lengths, hormones, and personality with cognitive functions and decision-making. The purpose of this study is to investigate how individual differences in personality, hormone levels, and digit lengths predict decision-making processes.

WHAT'S INVOLVED

As a participant, you will be asked to do the following:

- Provide 3 saliva samples (1 – 2 mL)
- Answer a brief questionnaire (10 items)
- Have both of your hands scanned via digital scanner
- Have your picture taken
- Compete with another individual at a series of puzzles
- Play a computer game where you can earn money (between 5-7 dollars)

POTENTIAL BENEFITS AND RISKS

Earn course credit. You will also have the opportunity to earn money based on strategic decision-making. Also, participation in this task may benefit the scientific community by adding to the developing knowledge on the relationship between individual differences in hormone systems and strategic decision-making.

CONFIDENTIALITY

All information you provide is considered confidential; your name will not be included or, in any other way, associated with the data collected in the study. Furthermore, because our interest is in the average responses of the entire group of participants, you will not be identified individually in any way in written reports of this research. Data collected during this study will be stored in a locked file cabinet in Dr. Cheryl McCormick laboratory. Data will be kept for 5 years after which time all data will be shredded and disposed. Access to this data will be restricted to Dr. Susan Putnam, Justin Carré and Dr. Cheryl McCormick.

VOLUNTARY PARTICIPATION

Participation in this study is voluntary. If you wish, you may decline to answer any questions or participate in any component of the study. Further, you may decide to withdraw from this study at any time and may do so without any penalty or loss of benefits to which you are entitled.

PUBLICATION OF RESULTS

Results of this study may be published in professional journals and presented at conferences. Feedback about this study will be available from Justin Carré. If you wish to learn about the results of the study, you may contact him at justin.carre@brocku.ca

CONSENT FORM

I agree to participate in this study described above. I have made this decision based on the information I have read in the Information-Consent Letter. I have had the opportunity to receive any additional details I wanted about the study and understand that I may ask questions in the future. I understand that I may withdraw this consent at any time.

Name: _____

Signature: _____ Date: _____

This study is supported by a National Science and Engineering Research Council (NSERC) grant to Dr. Cheryl McCormick as well as by an NSERC Doctoral Fellowship to Justin Carré

APPENDIX F

Very Inaccurate	Moderately Inaccurate	Neither Inaccurate Nor Accurate	Moderately Accurate	Very Accurate
-2	-1	0	1	2
1) Like having authority over others				
-2	-1	0	1	2
2) See myself as a good leader				
-2	-1	0	1	2
3) Am not highly motivated to succeed				
-2	-1	0	1	2
4) Try to lead others				
-2	-1	0	1	2
5) Dislike taking responsibility for making decisions				
-2	-1	0	1	2
6) Want to be in charge				
-2	-1	0	1	2
7) Have a strong need for power				
-2	-1	0	1	2
8) Dislike having authority over others				
-2	-1	0	1	2
9) Find it easy to manipulate others				
-2	-1	0	1	2
10) Wait for others to lead the way				
-2	-1	0	1	2

Appendix G

Number Tracking Test

This test requires you to connect consecutive numbers with lines as fast as possible. The next consecutive number is **ALWAYS ADJACENT** to the number you have currently arrived at. It may be located above, below, to the right of, to the left of or diagonally to the current number. Sometimes you may have to cross a line to connect two consecutive numbers. Here is an example:

16	4	5	8	9
15	1	3	6	10
14	2	9	7	12
16	13	8	10	13
15	12	11	13	15

The start number (1) and the final number (a number between 50 and 99) are highlighted. You always start at the highlighted number 1 and work your way through the numbers with one uninterrupted line. If you have taken a wrong turn somewhere, trace the line back to the last correct number and continue from there. The task is made more difficult (a) by distractor numbers surrounding consecutive numbers and (b) by highlighted distractor numbers that look like final numbers. However, there is only one possible path from the starting number to the final number and only one valid final number.

Try to track the numbers with your pen in the following exercise. Hold the pen closer to its rear end so your hand doesn't block your sight on the neighbouring numbers. Make sure that you cross each number while drawing the line.

Appendix H

We thank you very much for taking part in our study entitled “Influence of digit ratio, acute changes in testosterone and trait dominance on a laboratory measure of aggressive behavior”.

Our primary research goal was to examine whether competition-induced changes in testosterone levels would predict aggressive behavior. At the start of the experiment, you competed with another individual at a series of number tracing puzzles. The outcome of the contest was rigged, such that one individual was given several easy puzzles, while the other was given several hard puzzles. The goal of this part of the experiment was to experimentally create a ‘winner’ and ‘loser’ in the laboratory. Furthermore, we were interested in examining testosterone responses to the competitive interaction.

You also performed a computer task where the main goal was to gain as many points as possible, which would later be exchangeable for money. For this game, you were actually playing against the computer, which was designed to ‘steal’ points from you periodically throughout the task. This manipulation served as a provocation, and we were interested in examining your behavior in response to such provocations. The number of times that you selected button 2 (steal button) served as our primary measure of aggressive behavior. Also, you were told that you could earn money based on your performance at this task. We gave this instruction to motivate you to try hard at this task. In actuality, we gave everyone \$5 regardless of actual performance.

For this experiment, we also took digital scans of your hands. The relative length of your second (index finger) to fourth (ring finger) has been hypothesized to reflect early exposure to testosterone. A lower ratio (longer ring finger relative to index finger) is presumed to reflect greater exposure to testosterone. Our goal in this experiment was to investigate whether a lower digit ratio was related to higher aggressive behavior on the computer task.

Lastly, we also took photographs of you during the experiment. Just as a reminder, none of the photographs will be linked to your name. Your pictures will later be rated by students from Brock University for various characteristics such as; dominance, masculinity, attractiveness, etc.. We will then examine whether these ratings are related to your testosterone levels, digit ratios, and aggressive behavior.

We thank you once again for participating in this study. Results from this study will go along way in identifying variables that interact to predict human aggression. If you have any questions and/or concerns about the study, please feel free to contact me. Also, if you are interested in the results of the study, send me an email and I will surely provide you with a breakdown of the results.

Sincerely – Justin Carré (justin.carre@brocku.ca)

APPENDIX I

DATE: September 18, 2008
FILE: 06-367 - CARRE
TITLE: Relationship between salivary testosterone and strategic decision making
DECISION: Modification accepted

The Research Ethics Board finds that your *modification request* to an ongoing project involving human participants conforms to the Brock University guidelines set out for ethical research.

MM/an

Research Ethics Office
Brock University

Office of Research Services, MC D250A

APPENDIX J

Date: September 2008

Project Title: Relationship between hormone levels and strategic decision-making.

Principal Investigator

Justin Carré, PhD Candidate
Psychology
Brock University
905-688-5550 ext 3034
justin.carre@brocku.ca

Faculty Supervisor

Cheryl McCormick, PhD
Psychology
Brock University
905-688-5550 ext 3700
cmccormi@brocku.ca

INVITATION

You are invited to participate in a study involving hormones and decision-making. The purpose of this study is to investigate how individual differences in hormone levels predict the types of strategies and decision-making that people use while playing a computer game

WHAT'S INVOLVED

As a participant, you will be asked to provide the researcher with three saliva samples (1 – 2 mL) to later be assessed for hormone levels. Saliva samples will be collected non-invasively through passive drool into a small vial. Furthermore, you will be competing against another individual at a task that involves strategic thinking. You have the opportunity to make between 5-10 dollars at this task. After completing this task, there will be another 10 minutes session in which you will be given the opportunity to play another similar computer game. Participation will take approximately 1 hour and 15 minutes of your time.

POTENTIAL BENEFITS AND RISKS

Earn money based on strategic decision-making. Also, participation in this task may benefit the scientific community by adding to the developing knowledge on the relationship between individual differences in hormonal systems and strategic decision-making.

CONFIDENTIALITY

All information you provide is considered confidential; your name will not be included or, in any other way, associated with the data collected in the study. Furthermore, because our interest is in the average responses of the entire group of participants, you will not be identified individually in any way in written reports of this research. Data collected during this study will be stored in a locked file cabinet in Dr. Cheryl McCormick's laboratory. Data will be kept for 5 years after which time all data will be shredded and disposed. Access to this data will be restricted to Justin Carré, Jenna Gilchrist (undergraduate thesis student) and Dr. Cheryl McCormick.

VOLUNTARY PARTICIPATION

Participation in this study is voluntary. If you wish, you may decline to answer any questions or participate in any component of the study. Further, you may decide to withdraw from this study at any time and may do so without any penalty or loss of benefits to which you are entitled.

PUBLICATION OF RESULTS

Results of this study may be published in professional journals and presented at conferences. Feedback about this study will be available from Justin Carré. If you wish to learn about the results of the study, you may contact him at justin.carre@brocku.ca

CONTACT INFORMATION AND ETHICS CLEARANCE

If you have any questions about this study or require further information, please contact the Principal Investigator or the Faculty Supervisor (where applicable) using the contact information provided above. This study has been reviewed and received ethics clearance through the Research Ethics Board at Brock University (#06-367). If you have any comments or concerns about your rights as a research participant, please contact the Research Ethics Office at (905) 688-5550 Ext. 3035, reb@brocku.ca.

Thank you for your assistance in this project. Please keep a copy of this form for your records.

CONSENT FORM

I agree to participate in this study described above. I have made this decision based on the information I have read in the Information-Consent Letter. I have had the opportunity to receive any additional details I wanted about the study and understand that I may ask questions in the future. I understand that I may withdraw this consent at any time.

Name: _____

Signature: _____ Date: _____

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Appendix K

Thank you for participating in the experiment entitled “Relationship between salivary testosterone and strategic decision-making”. Your participation is greatly appreciated.

Although you were led to believe that the main purpose of the task was to measure the relationship between testosterone and decision-making strategy, we were primarily interested in the relationship between testosterone and aggressive behaviour.

The task that you performed was designed to assess the amount of point subtractions that you delivered to your ‘competitor’ throughout the sessions. You were not actually competing against another individual, but rather, points were randomly taken from your counter by a computer designed to provoke you every 6-120 seconds.

We apologize for deceiving you; however, this deception was crucial in order to get a valid measure of aggressive responding. If you are unhappy with the deception and wish to have your name removed from the data set, please contact Justin Carré.

Thank-you once again for your participation in this study,

Sincerely,

Justin Carré
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