Endocrine Response and Social Behaviour: Relationships between Steroid Hormones and Prosocial Cooperation in Prisoner's Dilemmas

by

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B.Sc. (Psychology), Laurentian University, 2010

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Arts

in the
Department of Psychology
Faculty of Arts and Social Sciences

SIMON FRASER UNIVERSITY

Spring 2014

Approval

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Degree: **Master of Arts (Psychology)**

Title: **Endocrine Response and Social Behaviour: Relationships between Steroid Hormones and Prosocial Cooperation in Prisoner's Dilemmas**

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Date Defended: January 22, 2014

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Abstract

Individuals of social species are faced with the problem of deciding which group members and circumstances warrant social cooperation when selfishness often leads to greater rewards. The cognitive processes used to resolve this problem have been shaped, alongside biological systems, by evolution. The hormones testosterone (T) and cortisol (C) are involved in aspects of social relationships and cognition, and are therefore potential modulators of these cooperative strategies. Two experiments were conducted to explore the relationship between these hormones and social cooperation, using the Prisoner's Dilemma and Public Goods Game to account for pair and group cooperation respectively. Salivary T and C concentrations were compared with game performance against predetermined opponent strategies, which ranged from very to not at all cooperative. Results did not confirm a relationship between baseline levels of T or C and social cooperation, nor did opponent strategy influence participants' T or C.

Keywords: Social cooperation; testosterone; cortisol; prisoner’s dilemma; public goods game

Acknowledgements

I would like to thank everyone who made this document possible. Thanks to my supervisor Dr. Neil Watson for encouragement and financial support; to my colleagues in the behavioural endocrinology lab for their contributions to the collection and analysis of the data; and to my friends and family for everything else.

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List of Acronyms

C	Cortisol
ELISA	Enzyme-linked immunosorbant assay
PD	Prisoner's Dilemma
PGG	Public Goods Game
T	Testosterone

Chapter 1.

Introduction

The research described here is aimed at elucidating aspects of the relationship between social cognition and hormones. Specifically, how people respond in social dilemmas is compared with profiles of the steroid hormones testosterone and cortisol, as well as several biometric and psychological variables known or expected to be associated with those hormones.

A social dilemma is a situation in which individual behaviour that exploits a partner or group to which one belongs results in greater personal benefit than cooperation with that group, despite maximal group benefit when all members cooperate. That is, there is an incentive for individuals to behave selfishly when other group members behave cooperatively or altruistically. The dynamics of optimal decision making in these kinds of scenarios are the principle concern of game theory, which is the application of mathematical models to describe the range of payoffs in well-defined situations of conflict (Myerson, 1997). There are extensive definitions and analyses of conflict scenarios within game theory, however only a few general concepts are necessary to understand for the purposes of the studies presented here. These concepts are described below in the descriptions of each game, with the exception of the notion of Nash equilibrium for non-cooperative games. In game theory, the Nash equilibrium is the optimum decision or strategy for a game in the sense that a player cannot gain from changing that decision or strategy when they take into account their opponents' decision. That is, the player cannot increase their likely payoff in the game under the assumption that their opponents' decision is random (Myerson, 1997).

1.1. Game Theory

Game theory emerged in the middle of the twentieth century as a way to mathematically characterize strategies of zero-sum games such as chess and poker. This approach was characterized in The Theory of Games and Economic Behavior by von Neumann and Morgenstern in 1944. The theory evolved later to include cooperative games and non-zero-sum games (Klarreich, 2007). This range of game types is broad enough that the theory has been fruitfully applied to different fields such as evolutionary biology, and economic and social decision making in humans (Maynard Smith, 1974; Sanfrey, 2007).

There are some assumptions that are made by game theory about how a rational agent should behave that are generally not observed in human players empirically. One of these assumptions is that players will make decisions in such a way as to maximize their own utility, even when that utility involves a cost or decrease in utility to one's opponents (other players). According to the theory, the most rational decision is reflected by a game's Nash equilibrium, which again is the strategy that, once employed, cannot be improved upon by a player unilaterally altering their behaviour. This assumption precludes the existence of many kinds of altruism that are actually typical of human behaviour in many of the games defined in game theory (Lee, 2008). The Nash equilibria and typical behaviour will be described below for the games employed here.

1.1.1. Prisoner's Dilemma

The prisoners' dilemma is a non-cooperative, symmetric, non-zero-sum, simultaneous game. This means that the players cannot make a binding agreement to cooperate (non-cooperative), that the payoffs are determined irrespective of the identity of a player (symmetric), that the total number of points allotted does not sum to zero (non-zero-sum), and that players are made aware of their opponent's decision at the same time (simultaneous). In the prisoners' dilemma, two players have a single choice to make, whether to cooperate with or defect against their opponent. As such, there are four possible payoffs for each player. They are the reward for mutual cooperation (R), defection when one's opponent cooperates, also called temptation to defect (T), the sucker's payoff for cooperating with a defector (S), and the punishment for mutual

defection (P). For the prisoners' dilemma to be a true social dilemma, the following condition for the values of each payoff must be met:

$$T > R > P > S$$

For the experiment described here, the following values were used: T = 5, R = 3, P = 1, and S = 0.

This ensures that the partnership collectively receives more points for mutual cooperation than any other combination, while the temptation to defect is the largest individual payoff. This is a definitional requirement for it to be a true social dilemma. The Nash equilibrium for a one-shot prisoners' dilemma is to defect, but the iterated version of the game is more complex, as players can modify their future choices based on their opponent's apparent strategy (Axelrod, 1980). In both the one-shot and iterated versions of the game, players make their decisions confidentially and are then made aware of their opponent's decision through the payoff. Therefore in the iterated version, players can adapt their future choices to their opponent's prior decisions to maximize their score, or utility.

1.1.2. Public Goods Game

The public goods game is also a non-cooperative, symmetric, non-zero-sum, simultaneous game, and can be likened to an *n*-person prisoners' dilemma. In this game, a group of players are each allotted a set number of points (or tokens, dollars, etc.). Players choose how many points to contribute to a public goods pot, and the sum of all contributions is multiplied by a number greater than one but less than the number of players. This final pot value is then equally divided and distributed between all players whose individual holdings grow accordingly. (Hauert et al., 2006). For the experiment described here, the number of points allotted each round was eight, and each pot was doubled before redistribution. So, for example, in a four-player game where one player contributed nothing while all three other players contributed their full amount, the pot size would be 24, which when doubled and equally distributed would mean that each player receives 12 points from the pot. In this case the "free rider", i.e. the player who contributed nothing, would have 20 points while each of the others would have 12. In the

case where all players contribute all their points, the total number of points held by the group would be 64 rather than 56 as in the previous example. The Nash equilibrium for a single-shot public goods game is to contribute nothing to the pot (Andreoni, 1988); however like the prisoners' dilemma the situation is more complex when the game is repeated over several rounds.

1.2. Hormones

There is a growing literature linking fluctuating levels of steroid hormones to social behaviours in humans (Archer, 2006; van Anders & Watson, 2006; McCall & Singer, 2012). Steroid hormones are lipophilic molecules that are synthesized through various enzymatic pathways, being ultimately derived from cholesterol. Steroid hormones in humans are classified into four distinct functional groups: progestogens, androgens, adrenocorticoids, and estrogens. These groups are classified based on the nuclear receptor proteins to which they bind and exert their effects on cells. These effects are primarily to modify gene expression, as the complex of hormone and its receptor act as a transcription factor. The result is to increase or decrease the mRNA and protein products of several genes, depending on cell type and steroid receptor cofactors, with many possible results including ultimately effects on behaviour. Another way that hormones can exert their influence is more directly through non-genomic effects (Falkenstein et al, 2000; Simoncini, 2003). These effects occur through the regulation and modulation of intracellular signalling pathways such as IP_3 and G-protein-coupled receptors pathways, and others.

1.2.1. Testosterone

Testosterone is the primary androgen in humans. It is synthesized in and released in large quantities by Leydig cells of the testes in males, and in smaller quantities from the adrenal cortex in both males and females. Testosterone is produced as a response to luteinizing hormone (LH) which is released into the bloodstream from the anterior pituitary gland. In turn, LH release is stimulated by the release of gonadotropin releasing hormone (GRH) from the hypothalamus, which is itself influenced by the presence of testosterone. This feedback system constitutes the

hypothalamic-pituitary-gonadal (HPG) axis. The primary target of testosterone is the nuclear bound androgen receptor (AR) protein (Lubahn et al., 1988; Rivier, 1991). Testosterone levels cycle over the course of a day, having a peak in the early morning and a low point in the late evening (Luboshitzky et al., 2001). It also varies seasonally with a peak in the late fall (Dabbs, 1990). There are also relative lifetime peaks in testosterone which correspond to physiological organizational effects. One of these peaks is perinatal, after which there is a sharp reduction in testosterone production until the second peak during puberty (Lutchmaya et al., 2004; Granger et al., 1999).

Exposure to testosterone *in utero* has organizational effects in the brain in many species, including humans (Guilette et al., 1995; Hines et al., 2003), and activational effects later in life. Organizational effects of hormones are relatively permanent changes that occur as a result of exposure to a hormone during a limited developmental time window, called a critical period. These effects are seen in peripheral organs such as the differentiation of reproductive tracts, and in the brain as changes to structures and subsequent responsiveness to biochemical signals. The latter effect can have a direct subsequent impact on some aspects of cognition such as spatial abilities (Falter et al., 2006). Activational effects are transient changes in structure and/or function that wax and wane in concert with fluctuations in hormone exposure, usually later in life. Organizational and activational effects can be closely interrelated, such as when a hormone influences the number of cells expressing a receptor during development, and those receptors are then differentially activated later in life based on the relative concentration of that hormone or other biochemical signals (Moore, 1991).

Testosterone has long been studied for its involvement with aggression and social dominance in males (Mazur & Booth, 1998; Archer, 2006), and has been previously investigated in scenarios that have been well defined in game theory. In the ultimatum game, high levels of testosterone cause men to make lower offers to their opponent, and to more frequently reject low offers made to them (Zak et al., 2009; Burnham, 2007). Another study demonstrated that in women, exogenous testosterone increased prosocial behaviour in the ultimatum game by causing them to keep their offers high (Eisenegger & Naef, 2011). It is interesting that while testosterone was associated with contradictory behaviours between the sexes on the same task, both were interpreted respectively as status-seeking behaviours. There has been no

observed relationship between testosterone and cooperation in a one-shot prisoner's dilemma (Sanchez-Pages & Turiegano, 2010); however as discussed below, there may be reason to expect that a relationship exists in an iterated version of the game in conjunction with participants' individual concentrations of cortisol.

There are additional reasons for thinking that testosterone should be related to response patterns in social dilemmas. For one, risk is an inherent component of iterated social dilemmas, in that one's opponents may perceive themselves as being exploited if the strategy is to defect. Hence defection is a gamble that could break a cooperative alliance. Risk taking appears to be associated with moderate circulating testosterone, while both extremely high and low levels are associated with risk aversion, at least in the kinds of economic decisions that are approximated in the present studies (Stanton et al., 2011). Another reason is that testosterone is involved in social aggression (Hermans et al., 2008). Social aggression (see Dual-Hormone Hypothesis below), especially reactive aggression in which players attempt to punish opponents who defect on a partnership or group, is expected to be a component of the social dilemmas described in the present studies.

1.2.1.1. Biometric Measures

There are several biometric variables that relate to testosterone during different periods of life. Three of these measures, second-to-fourth digit ratio (2D:4D), facial width-to-height ratio, and voice frequency are used in these studies because they have been proposed to reflect organizational aspects of testosterone exposure during development. These aspects in turn may reflect behaviours relevant to aggression, of which game theory decisions can be seen as a subset. For example, 2D:4D is a negative correlate of fetal exposure to testosterone (Putz et al., 2004), and has been implicated in aggressive decisions by males in a study on war games (McIntyre et al, 2007). Facial width-to-height ratio and voice frequency relate to adolescent exposure (Feinberg et al., 2008). These measures can be used as a proxy for participants' life history with regards to testosterone exposure, which could in turn provide insight into their current hormone profiles and response patterns in social dilemmas.

1.2.2. Cortisol

Cortisol is the primary glucocorticoid in humans. It is synthesized and released into the bloodstream from the middle layer (zona fasciculata) of the adrenal cortex in response to adreno-corticotropin hormone (ACTH) release from the anterior pituitary gland. The anterior pituitary is signalled through corticotropin releasing hormone (CRH) from the hypothalamus, which is ultimately governed by higher centres of the brain. The release of CRH and ACTH is itself modulated by cortisol; this multi-level system by which the brain governs the release of cortisol is known as the hypothalamic-pituitary-adrenal (HPA) axis. Cortisol has its effects on cells through its binding with the glucocorticoid receptor (GR) and, to a lesser extent the mineralocorticoid receptor (MR), proteins that homodimerize when bound to cortisol. The receptor proteins are found in the cytosol of cells when unbound to cortisol, but once they form a homodimer they are transported into the nucleus where they act as transcription factors for several genes, depending on cell type and the expression of regulatory proteins (Dickerson & Kemeny, 2004). Expression of GRs and MRs is prevalent in the limbic system, especially the hippocampus, as the integration site of neuroendocrine functions (Seckl et al, 1991; De Kloet et al, 2000).

Cortisol is most commonly referred to as the “stress hormone”, as it is released in relatively high concentrations when there is a perceived challenge or threat to homeostasis (Kirschbaum et al., 1995). Its function in this capacity is to help coordinate physiological resources to deal with the challenge. In this way it acts both to suppress immune responses and to increase glycogenolysis in order to provide an increase in glucose (Dickerson & Kemeny, 2004).

Like testosterone, basal cortisol levels fluctuate over the course of a day and over the course of a lifetime. There is a circadian pattern in the release of cortisol into the bloodstream, peaking in the early morning and reaching its lowest point in the late evening. In addition to its circadian variability, cortisol release shows infradian variation, due to pulsatile release with a period of 60-90 minutes (Young et al., 2004). On the scale of a lifetime, the first year of life corresponds with the highest concentrations of cortisol which then sharply decreases in the next year before slowly increasing again until adulthood. Although concentrations stabilize in adulthood, on average there is an

enduring circadian phase shift evident after midlife such that the daily peak and trough have earlier onsets (Kiess et al., 1995; Sherman et al., 1985). The production rate of cortisol has been measured at 27.3 ± 7.5 μmol/day (Esteban et al., 1991).

Beyond the physiological importance of cortisol, there are robust psychological effects as well. Cortisol has well established associations with depression (Vedhara et al., 2003; Tse & Bond, 2004, anxiety and post-traumatic stress disorder (Yehuda et al., 1990; Yehuda et al., 1993; Yehuda, 2001; Vedhara et al., 2003; Meewisse et al., 2007;), emotion, and several aspects of cognition, including social cognition. Chronically high levels of cortisol are associated with shrinkage of the dentate gyrus of the hippocampus, which can cause memory and spatial learning deficits, especially as a function of age (Lupien et al., 1994; Kirschbaum et al., 1996; Lupien et al.,1998). Conversely, increased cortisol levels can improve memory for emotional stimuli (Buchanan et al., 2001).

For the purposes of the present studies, the role of cortisol with respect to social cognition is the most relevant. There are several ways in which cortisol has been shown to influence, and in turn be influenced by, various aspects of social cognition. For example, beginning in early childhood, the type of social relationships a child develops has an impact on their basal cortisol levels, with socially rejected children showing higher basal cortisol than their accepted peers, and this can potentially negatively influence their temperament (Gunnar et al., 2002; Blackhart et al., 2007). In adolescents, low cortisol levels are found in males who show callous and unemotional personality traits when compared to normal controls (Loney et al., 2006). Sex differences in cortisol levels in response to stress have been reported, although they seem to depend on the type of stress. Men show an increase in cortisol when having to deal with social or achievement challenges, while women show an increase after social rejection (Kudielka & Kirschbaum, 2005). Most interesting for the present study, social memory (the ability to accurately and persistently identify other social agents and their behaviour) is decreased when subjects are socially stressed, associated with high cortisol levels (Takahashi, 2005). This could have implications for how participants respond to different game strategies. For example, high cortisol may be associated with low recall for an opponent's response pattern in the prisoner's dilemma or public goods game. However, it should be noted that for the studies listed above are largely correlative, and the possibility exists that causal relationship between cortisol and these behaviours works in

either direction.

1.2.3. Dual Hormone Hypothesis

There are sufficient reasons to expect testosterone and cortisol concentrations to have independent relationships with individual behaviour in social dilemmas, but more recently there have been proposals that these two steroids also act in concert to influence behaviour. This perspective is consistent with the observation that while the relationship between the HPG and HPA axes is complex, they are in general mutually inhibitory (Viau, 2002).

There are many behaviours and personality traits that are associated with different combinations of testosterone and cortisol concentrations. For example, social dominance in men is associated with high testosterone and low cortisol (Mehta & Josephs, 2010), which can be seen in response to competitive victory (Zilioli & Watson, 2012). The same combination of hormones is also associated with social aggression (Terburg et al., 2009; Montoya et al., 2012), which is predicted to play a role in relation to social dilemmas. However, these behaviours are not seen when both hormones are relatively high or low together. Finally, with respect to the relationship between emotional control and steroid hormone combination, reactive social aggression is highest in women who are high in both cortisol and testosterone, while men are more able to maintain emotional control when testosterone is high and cortisol low (Denson et al., 2012a; Denson et al., 2012b).

1.3. Psychological Measures

There are a number of psychological variables that have been or are expected to be related to behavioural and hormonal responses to social dilemmas. Individual traits that independently influence these responses provide additional explanatory robustness when interpreting subjects' performance. There are many such potential influences, but four in particular were selected for closer study based on their relevance to the social and hormonal measures used in the present studies. They are psychopathy, social phobia, pride, and narcissism.

1.3.1. Psychopathy

Psychopathy is an antisocial personality disorder made up of many individual characteristics including callousness, deceit, selfishness, impulsivity and aggression (Lalumiere et al., 2001). The causes of psychopathy are not fully understood, but it is more likely a phenotypic trait than the result of a developmental instability (Blair et al, 2006), although there is a developmental component. It is more prevalent in males than females and also more prevalent in criminal populations than non-criminal ones.

There are several reasons for considering psychopathy to be relevant with respect to social dilemmas and steroid hormones. As mentioned, there is a sex difference in the expression of psychopathic traits and there is evidence to suggest that testosterone is at least partially responsible (Cale et al., 2002; Stalenheim et al., 1998). In accordance with the dual hormone hypothesis, the ratio of testosterone to cortisol is high in those who score high in psychopathy (Glenn et al., 2011). There is also a sex difference in cortisol response to stress which is mediated by psychopathic traits, such that males who score high on the self-report psychopathy scale (SRPS) have a diminished cortisol response to stress compared to males who score low (O'Leary et al., 2007). The social aggression demonstrated by those with high scores on psychopathy could translate into altered response patterns in social dilemmas, especially between cooperative versus non-cooperative opponents. For example, traits such as selfishness and deceit could translate into patterns of consistent defection or free riding in the prisoner's dilemma and public goods game respectively. In fact, there is evidence that criminal psychopaths display reduced cooperative responses in the prisoner's dilemma (Mokros et al, 2008), so it is plausible to expect a graded degree of defection as a function of subjects' scores on the psychopathy scale.

1.3.2. Social Phobia

Social phobia is the fear of being negatively scrutinized or humiliated by others. (Mattick & Clark,1998). There are several biological markers in social phobia, including abnormalities of neurotransmitters and hormones (Bell et al., 1999; Hudson & Rapee, 2000). Cortisol is one such marker that is relevant for the studies described here. Although there is likely no difference in the baseline cortisol levels of social phobics

versus normal controls (Uhde et al., 1994), it has been reported that the maximum change in cortisol away from baseline does differ between those groups, with a greater increase for social phobics (Condren et al., 2002). That is, social phobics have a higher cortisol response to a psychological stressor than normal controls. The relevance of the cortisol-social phobia relationship to social dilemmas is that because social phobics fear scrutiny over casual behaviour, those who score high on a scale of social phobia are expected to show more cooperative behaviour in order to avoid negative judgement by their opponents.

1.3.3. Pride

Another psychological variable that might moderate the relationship between hormones and individual behaviour in social dilemmas is pride. Two facets of pride have been hypothesized, authentic and hubristic (Tracy & Robbins, 2007a). The function of pride between facets is similar, but the ultimate motivation behind the experience and expression of pride depends on whether it is authentic or hubristic. Authentic pride serves to signal to others about one's actual successes and indirectly about one's status, as well as to genuinely reinforce socially desirable behaviours. Hubristic pride serves the same functions, but can be interpreted to be a "cheaters" version, such that no actual accomplishments or high status are required (Tracy & Robins, 2007b). This interpretation of pride directly parallels the relationship between a cooperator and defector in social dilemmas, which is why they are of interest here.

1.3.4. Narcissism

Finally, a narcissism scale is used in the second study (public goods game) to complement the pride scales. Someone who scores high in narcissism is characterized by a "grandiose yet fragile sense of self and entitlement as well as a preoccupation with success and demands for admiration" (Ames et al., 2006). The narcissistic qualities that have the most relevance for social dilemmas are exploitation and lack of empathy (Ronningstam, 2010). Both separately and in combination, these qualities are expected to generate a response pattern of increased free riding relative to individuals who score low on narcissism. Those who score high on narcissism, like psychopaths, are prone to social aggression (Papps & O'Carroll, 1998). Additionally, there is a known sex

difference with risk taking (Cambell et al., 2004) which is of interest when considering individuals' hormone profiles and their relationship to response patterns in social dilemmas.

1.4. Hypotheses

Several predictions have already been alluded to with respect to game play and hormonal profiles, which can now be rephrased as formal hypotheses. First, it is expected that there will be a post-game increase in testosterone and cortisol in subjects assigned to the conditions with the less cooperative opponents compared to those in the conditions with the more cooperative opponents (experimental conditions are described below in Methods). Second, it is expected that subjects, especially males, with relatively elevated baseline testosterone and cortisol will defect or free-ride more frequently than those with lower baseline levels of those hormones, irrespective of condition. Third, it is expected that subjects, especially males, with lower 2D:4D and voice frequency, and higher facial width-to-height ratios will defect or free-ride more frequently than subjects with the reverse profiles. Finally, it is expected that subjects who score high in psychopathy, social phobia, and hubristic pride will defect or free-ride more frequently than subjects with the reverse profiles, and that those with high scores in authentic pride will cooperate more frequently than those with lower scores.

Chapter 2.

Methods

2.1. Participants

Participants for both studies consisted of undergraduate students from Simon Fraser University who were recruited from the Psychology Department's research participation system. The sample for both studies consisted principally of students enrolled in a first year psychology course. For study 1 there were an equal number of males (N=68) and females (N=68). Study 2 had a slightly unequal number of males (N=59) and females (N=61). All study sessions were conducted between 9:30am and 12:30pm to simultaneously control for circadian fluctuations in both cortisol and testosterone (Dickmeis T, 2009; Knutsson U, et al., 1997; Ankarberg C & Norjavaara E 1999; Diver MJ et al., 2003). This is a compromise solution to cortisol and testosterone circadian fluctuations because they vary out of sync with each other. Each session lasted approximately an hour.

2.2. Protocol

The sessions began with participants reading and signing the consent form (Appendix A), followed by a baseline saliva sample in which an oral swab (Salimetrics, Inc., State College, PA) was placed in the participants' mouth below the tongue for five minutes. Once the sample was collected participants played the game (either the Prisoner’s Dilemma for study 1, or the Public Goods Game for study 2). The games, including opponent strategies, were built by the author and played by participants on E-Prime version 2 (Psychology Software Tools, Inc., Sharpsburg, PA). This was followed by questionnaires including the Social Phobia Scale (Mattick, R. P., & Clarke, J. C., 1998; Appendix F), the 7-item Athentic and Hubristic Pride Scales (Tracy, J. L., &

Robins, R. W., 2007; Appendix G), the Levenson Self-Report Psychopathy Scale (Levenson, M. R., et al., 1995; Appendix E), and general demographics (Appendix C) for both studies. An additional questionnaire, the Narcissistic Personality Inventory-16, was included in study 2 (Ames, D., et al., 2006; Appendix H). A second saliva sample was collected 15-20 minutes after the end of the game, as well as a hand scan to measure 2D:4D, a portrait picture to measure facial masculinity and fluctuating asymmetry, and a voice recording of participants counting from 0 to 10 to measure their fundamental voice frequency.

2.2.1. Prisoner's Dilemma

Participants played 50 rounds of the Prisoner's Dilemma with payoff matrix values of 5 for the temptation to defect (defect/cooperate), 0 for the sucker's payoff (cooperate/defect), 3 for mutual cooperation, and 1 for mutual defection (Appendix D). Participants were led to believe that they were playing against human opponents, via the computer interface, but in reality they were matched against one of two preprogrammed strategies. After each round, participants were given feedback about whether their opponent cooperated or defected in that round, and what each player's payoff was. At the end of the experiment the participants were rewarded with a monetary sum equal to their final score multiplied by five cents. Based on the nature of the opponent strategies, the minimum payout was $2.70 and the maximum was $7.50. This reward was used as an incentive for participants to play the game using their optimal strategy. A random time interval between 0-15 seconds occurred between rounds to give the illusion that their opponent was considering their choice by weighing the previous round(s).

2.2.1.1. PD Experimental Conditions

There were two experimental conditions for the game, "friendly" and "provocative", with each participant assigned to only one of the conditions. These conditions corresponded with the programmed opponent strategy. The friendly condition was the "tit-for-tat" strategy in which the pre-programed "opponent" began the first round by cooperating and then subsequently played whatever the participant had played in the previous round. The provocative strategy was a variation of the "tit-for-tat" strategy in which the program usually mimicked the participant's previous decision, but occasionally

defected where it would otherwise have been expected to cooperate; this is also known as “naïve prober” (Mittal, S., & Deb, K., 2009). Participants who opted to defect in every round were excluded from analysis, since this pattern of response nullifies the differences between conditions. In other words, the conditions are indistinguishable when players opt for the all-defect strategy.

2.2.2. Public Goods Game

Participants were led to believe they were playing against three human opponents segregated in other lab rooms, but in fact played 20 rounds of the Public Goods Game against three preprogrammed opponent strategies. Players started each round with eight “points”. In each round, players could contribute as few or as many of these points as they wished to a communal “pot”. After each round, participants were given feedback about their opponents’ contribution to the public pot, as well as each of the other players’ payoffs for that round. A monetary incentive was invoked before play began to get participants to perform realistically (i.e. avoid automatic responses). In addition, a random interval of time between 0 and 15 seconds between each round elapsed to give the participant the illusion that the opponents were considering their decision.

2.2.2.1. PGG Experimental Conditions

There were four conditions for this experiment that corresponded with all combinations of cooperative and exploitative opponents. As in the prisoner's dilemma experiment, the opponents were all programmed in advance to produce cooperative or exploitative decisions. The four combinations of opponents were: 1) all friendly; 2) two friendly and one provocative; 3) one friendly and two provocative; and 4) all provocative. In order to give the illusion that the participants were playing against human players, the opponents randomly selected from a range of point values at the high or low end of the gradient depending on the conditions. The friendly strategies would consistently and randomly select between six to eight points, and the provocative strategies between zero and two points.

2.3. Salivary Hormones

Both studies involved saliva sample collection through oral swabs (Salimetrics Inc, State College PA). During sample collection, participants were instructed to place the swab below their tongue, without using their hands to avoid contamination, and hold it there for 5 minutes. A baseline sample was collected immediately prior to the beginning of each game, and a post-task sample was collected 15-20 minutes after the games were over. Once collected, the samples were placed in a cooler with an ice pack until they could be transferred to a freezer, where they were then stored at -20C until assayed. Saliva samples were analyzed in batches for testosterone and cortisol concentrations using the enzyme-linked immunosorbent assay (ELISA) technique (Engvall, E., & Perlmann, P., 1972).

2.3.1. ELISA

For both testosterone and cortisol, ELISA was performed using salivary assay kits provided by Salimetrics Inc. (State College, PA) in combination with a plate washer (ELx50 Microplate Strip Washer) and absorbance plate reader ELx808 (BioTek Industries Inc; Winooski, Vermont, USA).

The plates from the assay kits contain 96 wells, 94 of which are coated with antibodies that bind to the selected hormone analyte and two which contain no antibodies. The purpose of the two empty wells is to act as a safeguard against plate misreads, such that if any hormone analyte is detected in these wells then confidence in the accuracy of the other wells is challenged. Six of the wells are used to establish a standard curve based on samples of known concentration. This curve acts as a reference to which other wells are compared to establish their analyte concentrations. Control samples of known high and low hormone concentrations are also included in each run to calibrate the standard curve. The layout of both the testosterone and cortisol plates is illustrated in Appendix I.

All saliva samples, reagents, and plates were brought to room temperature gradually for three hours before being assayed according to the kit manufacturer's (Salimetrics Inc., State College, PA) protocols. Briefly, after the three hours, saliva

samples were centrifuged at 3000 rpm for 15 minutes. Next, 25µL of standards, controls, and saliva supernatant were individually pipetted into each well, followed by a mix of enzyme conjugate and assay diluent. For testosterone the ratio of enzyme conjugate to assay diluent was 1:1000 with 150µL being pipetted into each well using an electronic multichannel pipettor. For cortisol the ratio of enzyme conjugate to assay diluent was 1:1600 with 200µL being pipetted into each well using a Biohit Proline electronic multichannel pipettor (Helsinki). The enzyme conjugate was composed of horseradish peroxidase bound to the respective hormone. This hormone-protein complex competes with the free hormone in the standards, controls, and samples to bind to the antibodies in the wells. The plates were then mixed at 500 rpm for 5 minutes and left to incubate for 55 minutes. The plates were washed four times in the plate washer with wash buffer provided in each kit and then blotted, leaving only bound hormone analytes in the wells. Next, 200µL of tetramethylbenzidine (TMB) solution was added to each well. The TMB solution binds to the peroxidase, causing a blue (450nm) colour shift in the wells in proportion to the amount of peroxidase available, and thus in inverse proportion to the unconjugated testosterone in the sample. After 5 minutes of mixing at 500RPM and 25 minutes of incubation in the dark, 50µL of 3M stop solution (sulphuric acid) was added to each well, and mixed at 500 rpm for 3 minutes. Colour density for each well was read using the plate spectrophotometer (plate reader); comparison of these values to the derived standard curve was used to calculate the hormone concentrations in the samples.

There are several criteria for accepting hormone concentrations that are read in each plate. The first is that the standard curve is adequately calibrated by providing an R^2 value greater than 0.99. This value represents the coefficient of determination, a measure of how close standard values fit a theoretical curve. Second, measurement of the high and low control samples must closely approximate their known concentrations. Finally, the duplicate samples must each have a coefficient of variation (CV), which is the measured concentration difference between duplicate wells, below 15%. If all of these conditions are met then the average value for each duplicate sample pair can be used. Precision of measurement is also established within each study through intra- and inter-assay CVs. An intra-assay CV is the mean of all sample CVs and is generally acceptable when the value below 10%. The inter-assay CV is the mean of the high and

low controls from all plates within each study and is acceptable when the value is below 15% (Schultheiss, O.C., Stanton, S.J., 2009). All hormone concentrations are expressed in µg/dL.

2.4. Biometric Data Collection

2.4.1. 2D:4D

The hand scan was made using a Canon CanoScan LiDE 210 scanner at 300dpi. Second-to-fourth digit ratios (2D:4D) were established by taking an average of measures made by two research assistants using the program ImageJ (National Institute of Health, 2013) from the tip to the proximal skin crease at the base of the finger, next to the palm.

2.4.2. Facial Width:Height

Facial measurements were similarly established by taking an average of measures made by two research assistants, using tagged points on ImageJ, a method that has been described in previous studies (Scheib et al., 1999; Penton-Voak et al., 2001). Portrait pictures were taken for face measurements using a Canon PowerShot SX 130 IS camera with participants gazing directly into the lens with a neutral facial expression. All faces were scaled to an interpupillary distance of 100 pixels in Matlab prior to measurement. The measurement used in this study was the width-to-height ratio, which is the distance between the cheekbones divided by the distance between the nasion and prosthion. This measure has been associated with aggressive behaviour (Carre & McCormick, 2008).

2.4.3. Voice Fundamental Frequency

An external microphone was used to collect a sample of each participant counting from zero to ten after being instructed to speak in as normal and casual a way as possible. Voice frequency was calculated using the average of the fundamental frequency of the verbal utterance after the first and last utterances (zero and ten) were

removed to reduce variability. This measurement was made using the program Praat (Institute of Phonetic Sciences, University of Amsterdam).

2.5. Psychometric Data Collection

2.5.1. Psychopathy

The primary tool used to measure someone's degree of psychopathy in criminal populations is the Hare Psychopathy Checklist-Revised (Hare et al., 1991), but for research purposes on a non-institutionalized population, the Self-report Psychopathy Scale (SRPS) is often used, and was the measure used here (Levenson et al., 1995; Appendix E). The scale consists of 26 phrases rated on a 4-point scale from "strongly disagree" to "strongly agree". The SRPS is broken down into two components: primary and secondary psychopathy. Primary psychopathy relates to callousness, manipulation, and selfishness, while secondary psychopathy is associated with antisocial and socially impulsive behaviour.

2.5.2. Social Phobia

For this experiment, the tool used to measure social phobia is the Social Phobia Scale (Mattick & Clark, 1997). The scale consists of 20 phrases rated on a 5-point Likert scale, where participants are asked to "indicate the degree to which [they] feel the statement is characteristic or true of [them]" (Appendix F).

2.5.3. Pride

For these studies, the pride scales developed and validated by Tracy and Robins (2007a) called the 7-Item Authentic and Hubristic Pride Scales were used. Each type of pride is measured by 7 items for a total of 14 items. These items are descriptive words that subjects score on a 5-point Likert scale with respect to how strongly they identify with the items (Appenix G).

2.5.4. Narcissism

The tool used to measure narcissism is the Narcissism Personality Inventory (NPI-16), a sixteen question self-report (Appendix H) that has been shown to be valid when compared to the longer NPI-40 (Ames et al., 2006). Narcissism acts as a barrier to forgiveness for social transgressions, and is predicted to drive subjects high in narcissism towards defecting more frequently (Exline et al., 2004).

Chapter 3.

Results

3.1. Statistical Analyses

All analyses were conducted using SPSS (Version 18.0. Chicago: SPSS Inc.) the general linear model for linear regression, logistic regression, ANOVA, and t-tests. Bonferonni correction was used to adjust for family-wise error where applicable, as described below. Unless otherwise specified, statistical significance (i.e. the decision to reject the null hypothesis) was set with an alpha of 0.05. The dependent variables described below include the change in absolute values of hormone concentrations for testosterone and cortisol, and the behavioural measures of first move and number of cooperations. For the game-related behavioural measures, the first move is straightforward but differs between the two studies in that it is a binary measure for the Prisoner's Dilemma and a continuous variable with a range of values from zero to eight in the Public Goods Game. The amount of cooperations was expressed as a proportion of cooperative responses in the Prisoner's Dilemma, but is reflected in the Public Goods Game as an average of the subjects' responses in all rounds.

3.2. Prisoner’s Dilemma

All directly measured (not calculated) independent variables were normally distributed, with skewness and kurtosis values in the acceptable range ($p<0.05$), with a few numbered exceptions listed below.

1. Both pre-and post-task cortisol measures were positively skewed ($D_{123}=2.437$, $p<0.05$; $D_{125}=4.195$, $p<0.05$). This is typical for measures of cortisol (Polk et al., 2005; Zoccola et al., 2010), but for the sake of statistical analysis only the log transformed

measures of cortisol were used.

2. The first measure of psychopathy on the Levenson scales was positively skewed (D_{133}=0.992, p<0.05). The values were transformed by adding a constant of the one plus the absolute value of lowest score, and then taking the square root (Coolican, 2009). The resulting variable was normally distributed.

3. The measure of hubristic pride showed a floor effect, possibly due to the undesirability of perceived negative self-assessment. Therefore, non-parametric tests were used for this variable.

4. Social phobia was positively skewed (D_{134}=0.774, p<0.05). The values were transformed by taking the square root, and the resulting variable was normally distributed.

Outliers above three standard deviations for each variable, and subjects whose mean reaction times were below 300ms and whose responses were unvaried, were excluded from game-related analyses. Unvarying very low average response reaction times presumably reflect a lack of processing and/or response to the opponent's moves; such responses were likely not influenced by the game incentives. An example might be a subject who is attempting to get through the trials by pressing the same key repeatedly. Once these cases were removed, each variable was normally distributed.

3.2.1. Tit-for-Tat versus Naïve Prober

The first set of tests was related to the influence of the experimental conditions on the change in salivary hormone concentrations. Males and females were considered separately for testosterone changes and the interaction between change in testosterone and change in cortisol, but together for change in cortisol alone because there was no sex difference in baseline cortisol concentrations (t_{122}=1.754, p=0.082). This yielded 3 sets of t-tests:

1. Change in cortisol concentrations: There was no statistically significant difference in the fluctuation of cortisol concentrations between the two experimental conditions (t_{115}=-0.564, p=0.574).

2. Change in testosterone concentrations: There were no statistically significant differences in the fluctuation of testosterone concentrations between the two conditions either males (t_{63}=1.483, p=0.143) or females (t_{65}=0.233, p=0.816).

3. Interaction between changes in both cortisol and testosterone: There were no statistically significant differences between conditions with respect to this interaction for either males (t_{51}=-0.67, p=0.506) or females (t_{62}=0.362, p=0.719).

3.2.2. Baseline Hormone Profiles and Behaviour Patterns

The next set of tests was related to the relationship between baseline measures of testosterone and cortisol with two dependent measures of behavioural response in the Prisoner's Dilemma. Males and females differed on baseline testosterone (t_{131}=18.73, p>0.01, SEM=6.174, *d*=3.27*,* observed power=*1*; Figure 1) but not cortisol. The two behavioural measures were the choice of first move, and the total number of cooperations in all fifty rounds. Once again for this set of hypotheses, males and females were considered separately for testosterone and the testosterone-cortisol interaction, and together for cortisol. Additionally, while both conditions were considered together for the tests involving the first move, the conditions were considered separately for the total number of cooperations, as the means for this variable were significantly different (t_{133}=4.89, p<0.01, SEM=2.552, *d=0.85,* observed power=0.998; Figure 2) due to the provocative nature of the response pattern in the second condition.

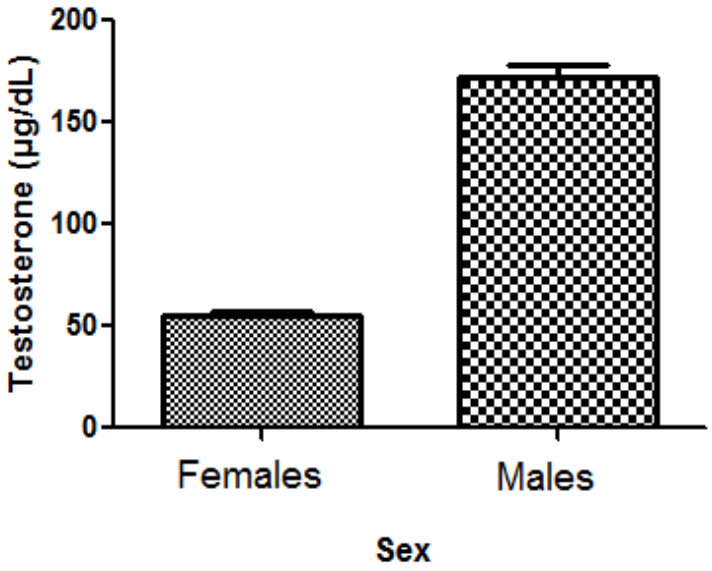

Figure 1 **Sex difference in baseline testosterone**

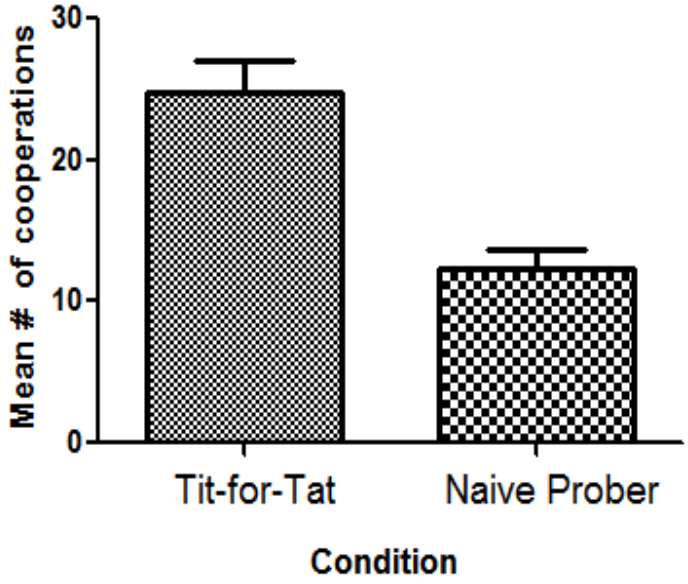

Figure 2 **Mean number of cooperations in each condition**

A stepwise binary logistic regression model was used to determine what the effects of these baseline hormone levels were on participants' choice of first move in the Prisoner's Dilemma. The first step included cortisol and testosterone concentrations as predictor variables, and the second step added the interaction between the two hormones. The model as a whole and each variable within it failed to achieve statistical significance in predicting the first move choice for either sex. A linear regression model was used with the proportion of cooperations substituted for the outcome variable. This model and each independent variable also failed to predict the outcome variable.

3.2.3. Biometrics

Next the three biometric measurements were explored in order to determine their impact on cooperative behaviour. As expected, 2D:4D was significantly different between males and females for both the left and right hands (t_{130}=-3.983, p<0.001, SEM=0.006, *d*=0.70, observed power=0.977; t_{128}=-4.121, p<0.001, SEM=0.006, *d*=0.73*,* observed power=0.984; Figure 3), as was voice frequency (t_{127}=-30.101, p<0.001, Figure 4), but not facial width-to-height ratio. Therefore, the first two measures were split by sex for all subsequent analysis.

Binary logistic analyses were performed on all biometric variables with the first move as the outcome variable. None of these tests yielded statistically significant results. Linear regression analyses were performed with the proportion of cooperations as the outcome variable, but none of these tests yielded significant results even after splitting the data by condition to account for the difference in cooperation frequencies between them (Figure 2). Finally, a t-test revealed that in the tit-for-tat condition, females cooperated less than males did (t_{69}=2.611, p=0.011, SEM=4.048, *d*=0.63, observed power=0.737*;* Figure 5).

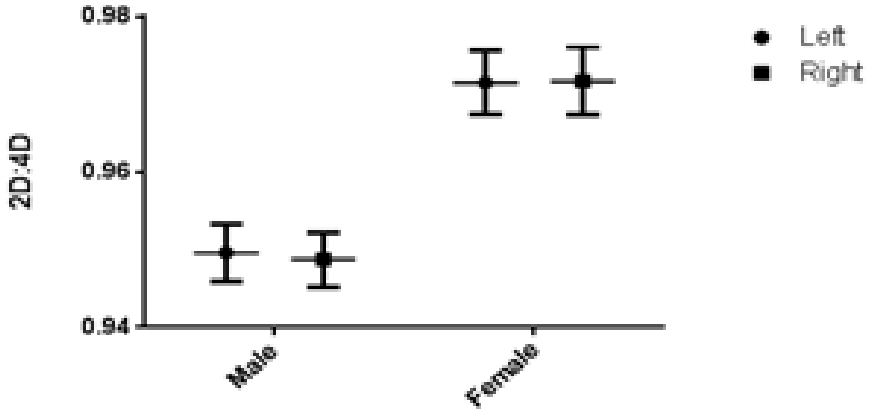

Figure 3 Sex differences in 2D:4D

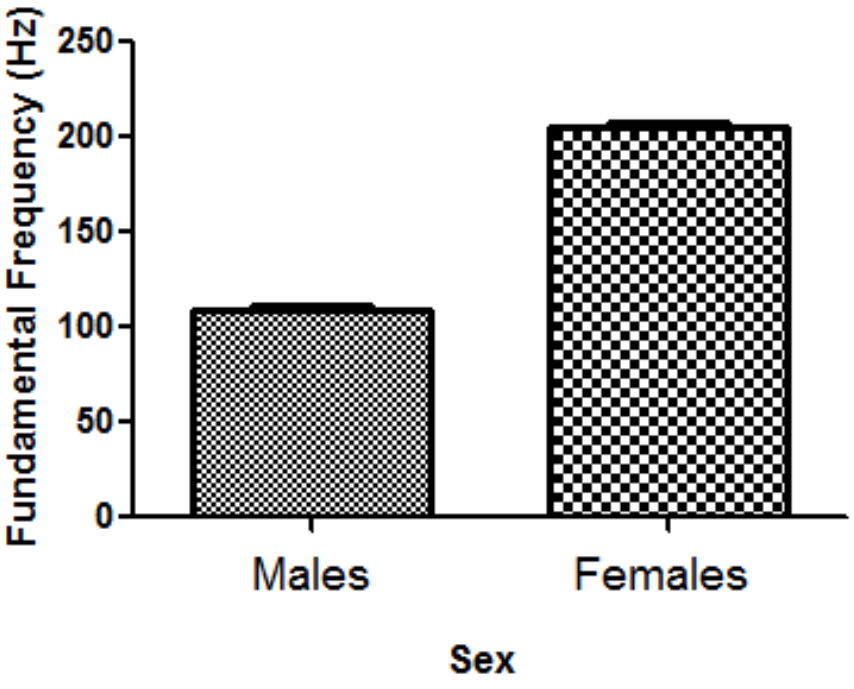

Figure 4 Sex difference in voice pitch

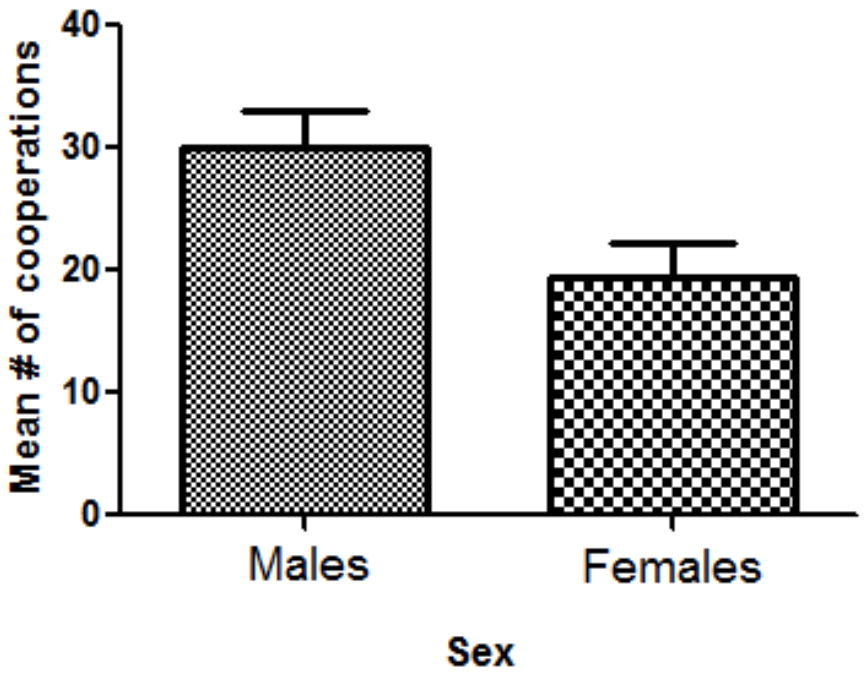

Figure 5 Sex difference in number of cooperations in against tit-for-tat

3.2.4. Psychometrics

There were no sex differences for any other psychometrics measures with the possible exception of Levenson's first measure of psychopathy (t_{134}=2.028, p=0.045). However, this difference was not significant following a Bonferroni correction for the four tests run (α=0.05/4=0.0125).

Binary logistic analyses were performed on all psychometric variables with the first move as the outcome variable. There was no significant difference on any variables when the sexes were analyzed together, but when males and females was analyzed separately there was a significant effect of authentic pride on the choice of first move for females. Females with higher scores for pride chose to cooperate more often (B=0.185, p=0.005, SEM=0.066; Figure 6). This was not the case for males. None of the other psychometric variables were significant in predicting the first move. In a linear regression model for all four normally distributed psychometric variables with the proportion of cooperations as the outcome variable, Levenson's first measure of psychopathy had a

trend towards statistical significance after Bonferonni correction (t_{129}=2.368, p=0.019), although the model itself was not significant. As mentioned, hubristic pride was not normally distributed. Non-parametric tests found no significant differences in hubristic pride between those who chose to cooperate and those who chose to defect as their first move.

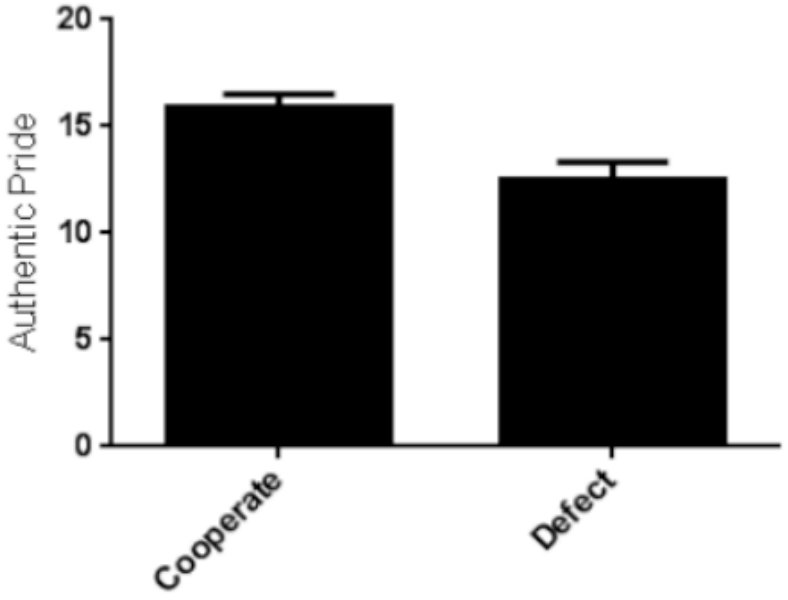

Figure 6 Female authentic pride scores for each choice of first move

3.3. Public Goods Game

As in the Prisoner's Dilemma, all directly measured independent variables were normally distributed after outliers were removed, with skewness and kurtosis values in the acceptable range (p<0.05), with a few corrected exceptions listed below.

1. Both pre-and post-task cortisol measures were positively skewed (D_{105}=2.15, p<0.05; D_{103}=2.479, p<0.05). Therefore normally distributed log transformed measures of cortisol were used. A log transform was applied for cortisol as it is commonly applied in the literature.

2. Social phobia was positively skewed (D_{113}=0.918, p<0.05) even after the

removal of outliers, so a square root transformation was used to normalize the variable.

3. Hubristic pride showed a floor effect, probably for the same reason as in the Prisoner's Dilemma. Therefore, non-parametric tests were used for this variable.

All other criteria for the use of data in the following analyses were the same as in the Prisoner's Dilemma study.

3.3.1. Experimental Conditions' Effect on Hormone Levels

A multivariate analysis of variance (MANOVA) was used to determine whether there was an effect exerted by the experimental manipulation of conditions (opponents' frequencies of defections) on the change in hormones. There were no significant differences between the conditions for either testosterone or cortisol ($F=0.466$, $p=0.831$), but there appeared to be a potential difference between the first two conditions and the last two (low vs high opponent defections) on the change in testosterone in males. However, this observation did not yield any significant results when the first and last two groups were collapsed, or when the most cooperative group was compared to the least cooperative.

3.3.2. Baseline Hormone Profiles and Behaviour Pattern

Two linear regression models were used to test the effect of baseline hormone profiles, one with the first move as the outcome variable and the other with the average contribution as the outcome variable. In the latter model, the average contribution variable was split by condition because of the difference between opponent contributions between conditions. Neither model, nor any of the individual independent variables (testosterone, cortisol, or the interaction between these hormones), achieved statistical significance in predicting the outcome variables.

3.3.3. Biometrics

Biometric variables were analyzed for their contribution to the behavioural measures of first move and average contribution, using a multiple linear regression model with all biometrics as independent variables for each dependent variable. Neither

model was significant in predicting the behavioural measures, but when the conditions were split into low (conditions 1 and 2) and high (conditions 3 and 4) categories with respect to the opponents' tendency to defect, there was a trend towards significance for males' left second-to-fourth digit ratio as a correlate of average contribution ($p=0.089$ and $p=0.097$ for low and high opponent defections respectively). No other correlations were close to significance.

3.3.4. Psychometrics

As in the Prisoner's Dilemma, the effect of the psychometric measurements was analyzed as a group in relation to the two dependent variables of first move and the average contribution. All normally distributed psychometric variables were significantly correlated with each other after Bonferonni correction ($p<0.01$) except for Levenson's second measure of psychopathy with narcissism ($p=0.453$), and the first measure of psychopathy with authentic pride ($p=0.030$) and with narcissism ($p=0.027$). However, none of the variables were significant in predicting the first move, or the average contribution in multiple linear regression models. The possible exception is authentic pride in the condition with the third most frequently defecting opponents. However the model itself was not significant, the correlation did not appear significant in any other condition, and the p-value was on the cusp of acceptability after Bonferonni correction ($p=0.01$). It was decided that this was a spurious correlation, and the null hypothesis was retained. As already mentioned, hubristic pride was not normally distributed and showed a floor effect, and was therefore excluded from analyses.

These results generally did not support the primary hypotheses of the two studies regarding the influence of opponent strategy on hormone profiles, and the effect of baseline hormones on behaviour in economic games. However, some secondary variables that are associated with the influence of hormones developmentally were found to be significant or near significance in predicting behaviour in both the Prisoner's Dilemma and the Public Goods Game. These findings, as discussed below, can be considered a source of direction for future investigation of the relationship between hormones and behaviour in the context of game theory.

Chapter 4.

Discussion

The majority of the hypotheses described for these studies were not validated. This was especially true for the second study using the public goods game, where none of the analyses yielded results that were predicted *a priori*. This section will address several issues that emerge from the results presented above. First, the positive results will be interpreted and contextualized. Second, the possible reasons for unexpected negative results (results that did not conform to *a priori* hypotheses) will be explored. Third, the difference between results derived from parallel analyses between the two studies will be explored. Finally, the possible ecological implication and directions for future research will be discussed.

4.1. Positive Results

4.1.1. Prisoner's Dilemma

In the prisoner's dilemma, males and females differed in the proportion of cooperations with their opponents when the opponent played a tit-for-tat strategy, but not when the opponent played as a naive prober. The first case is consistent with very early research using the prisoner's dilemma (Rapaport & Chammah, 1965). Another result that emerged from this study is that on average, females who chose to cooperate on their first move had higher scores on authentic pride compared to those who chose to defect. The differences could be a result of differing evolutionary strategies (Buss & Schmitd, 1993), but unfortunately, because the sex of the "opponent" was never specified to participants, interpretations that involve the possibility that these effects are a result of sexual strategy are precluded.

4.1.2. Public Goods Game

As there were no statistically significant relationships observed that would have validated any of the hypotheses outlined for the public goods game, only the absence of these relationships needs explanation, which is described below.

4.2. Negative Results

4.2.1. Hormones

Neither testosterone nor cortisol showed any significant changes pre- and post-game in either experiment as a result of the differential exposure to opponent strategies. Additionally, the baseline values of these hormones failed to predict what was expected to be differences in response patterns within and between experimental conditions. There are several possible explanations for this pattern of results. The default explanation is that there is simply no relationship between these hormones and social cooperation as measured by these sorts of games. Another possibility is that the operational definition of social cooperation used here is insufficient to encompass more ecologically valid behavioural constructs. Monetary incentives are an important aspect of social cooperation in natural contexts, but at least part of the reason why no hormonal changes were observed could be because either the incentive was too small to evoke any meaningful effort from participants, or because the game scenario was too far removed from an actual social interaction. The first possibility could be remedied in future research by offering higher incentives. The second possibility is more difficult to address, since the game is analogous to many real world scenarios involving dichotomous cooperate/defect choices (Axelrod, 1984), but one way would be to associate the choice with a realistic narrative. However, engaging with a live human opponent with more tangible decision outcomes might be a way to address the issue of ecological validity. Finally, it could be that the test measures were appropriate, but that the effects of these hormones is so subtle that the behavioural measures were not sensitive enough to pick them up, or that the context in which the relationship would emerge is more narrow than measured here.

4.2.2. Biometrics

In both studies, it was expected that 2D:4D, voice pitch, and the facial width-to-height ratio would be associated with the participants' responses, by virtue of their hypothesized relationship to developmental hormone exposure, but this pattern was not observed. A few possibilities could account for the lack of relationship observed between these variables. One is that while the biometric variables reflect *organizational* effects of testosterone, the behaviours measured in both experiments may relate more closely to the *activational* effects of testosterone (Falter et al., 2006). Another possibility is that behavioural effects of testosterone are highly contextual and that the games used in these experiments were not sensitive enough to pick them up. Finally, it could be that the nature of the experiment was too transparently artificial for participants, and therefore did not evoke the behaviours that would reflect a relationship with these biometrics in a more ecologically valid context. A small number of subjects alluded to this kind of suspicion in written open feedback after the experiment, but because feedback about suspicion was not directly asked of participants, it could not be thoroughly analyzed.

4.2.3. Psychometrics

With only one exception (authentic pride in the Prisoner's Dilemma), none of the psychometric variables reached statistical significance in predicting the first move or the amount or magnitude of cooperations in either experiment. The default and simplest explanation is that no relationships exist between these variables and the kind of social cooperation measured by these games. However, other possibilities exist which are similar to the ones described for the biometric variables. Self-report measures were unique to the psychometric variables. This constitutes a plausible reason for why hubristic pride scores were not normally distributed; participants may have not wanted to admit to possessing what is perceived as negative personality traits. Self-reports introduce an element of subjectivity to the measures, making them potentially vulnerable error through cognitive biases (Kahneman & Tversky, 1996) like the self-serving bias alluded to above.

4.3. Differences between PD and PGG

The effect of authentic pride was the most prominent difference between the prisoner's dilemma and public goods game results, in that the former showed an effect on females' choice of first move while the latter did not. The most salient candidate explanation for this difference is that it was a result of the difference in the type of response that each game required. The dichotomous choice in the prisoner's dilemma leaves no room for ambiguity about the strategy or intention of the participants and creates either a floor or ceiling effect relative to the spectrum of available choices in the public goods game. This is not a full explanation, though. It would be necessary to run a within-subjects experiment using both of the games to establish whether or not there is a pattern to choice-flipping between the prisoner's dilemma and public goods game that is being driven by authentic pride in females.

4.4. Ecological Implications

The implications for real world contexts can only be established for the observations that actually demonstrated statistical significance. Therefore this section will ignore all of the above speculation about why various *a priori* hypothesis tests yielded negative outcomes and instead focus solely on the positive results. The most notable positive result was the observed relationship between authentic pride in females and their first choice in the prisoner's dilemma. Why should women with high scores in authentic pride choose to cooperate while women with low scores choose to defect? And why should this effect only exist for women? There are two perspectives that may illuminate these results. One is to view this relationship from an evolutionary point of view, and the other from a developmental point of view.

The evolutionary possibility could be a result of sexual selection. Women could have been selected for on the basis on higher levels of cooperation due to cooperative behaviours being intrinsic to nurturing, but this idea needs further investigation to establish whether or not this increased cooperation in females with high authentic pride is differentially directed at males and other females. It would, however, account for why hubristic pride did not show the same results, as hubristic pride can be interpreted as the

“cheaters” version of pride as already mentioned above. The other possibility is that it is a result of developmental differences between males and females. In this interpretation, females may be rewarded for defecting in social encounters more frequently than males are which would encourage and perpetuate that behaviour. While there is no direct evidence that this is the case, there are known differences in the way that men and women approach social relationships (Vigil, 2007). The evolutionary and developmental perspectives are not mutually exclusive. In fact there is every reason to believe that they are highly interrelated, and the findings here may be a step in providing an explanation, or at least a research direction, for a mechanism that establishes or maintains these differences.

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Appendix A.

Consent Form

Testosterone and cortisol fluctuation and behavioural effects in the Prisoner's Dilemma

Application number: 2011s0507

Behavioral Neuroendocrinology Laboratory

Department of Psychology

Hormones and competition

CONSENT FORM

You are being invited to participate in a research study in Behavioral Neuroscience. This study is being conducted by Evan Caldbick and Samuele Zilioli, from the Behavioral Neuroendocrinology Laboratory of the Psychology Department at Simon Fraser University. The study is being conducted as part of the graduate students' project.

There are no known risks if you decide to participate in this research study. There are no costs to you for participating in the study. The information you provide will help us to clarify the role of hormones in competition settings. The information collected may not benefit you directly, but the information learned in this study should provide more general benefits.

In this study you will be asked to provide four saliva samples that are necessary to detect your hormone levels. You will also be asked to pose for two photographs, one of your face and one of your hands, and to provide a brief voice recording. These measurements are related to previous hormone exposure. You are going to be asked to compete against another person in a contest called the Prisoner's Dilemma. An identification number will be used to identify the results of your tests. In case data is published, no individual information will be disclosed.

All data will be kept in digital format and locked filing cabinet in our research laboratory (7401 RCB) at SFU Burnaby. Only the study researchers named in this document will have access to the cabinet. Each participant will be identified with an ID number, the code to which will also be stored in a locked cabinet. We are going to retain the data for a period of 3 years at which time it will be destroyed. Saliva samples will be destroyed as soon as possible after testing, and that they will only be used for measuring hormone concentrations for this study.

In exchange for your participation in this study, you will receive course credit as part of an introductory psychology course. Besides, your level of performance will determine the value of a monetary reward at the end of the experiment.

Your participation in this study is voluntary. If you choose to participate, please sign below and follow carefully the research assistances instructions during the experiment. When the tasks are done if you have any questions about the study, please contact Samuele Zilioli from the Behavioral Neuroendocrinology Laboratory of Department of Psychology at Simon Fraser University (mailing address: 8888 University Drive, Burnaby, BC V5A 1S6; phone number: [redacted] or [redacted]; email: [redacted]). Feel free to contact him also if you are interested in obtaining research results.If you have any questions or concerns about being in this study, you may contact Dr. Neil Watson, supervisor of the Behavioural Endocrinology Lab, at [redacted] or [redacted] primarily, or Dr. Hal Weinberg, Director, Office of Research Ethics at [redacted] or [redacted] as a secondary contact.

The participant shall fill in this area. Please print legibly.

Participant Last Name: _____

Participant First Name: _____

Participants Signature:

_____

Participants Identification Number (to be filled by the research assistant):

_____

Date (Use MM/DD/YY format):

_____

Appendix B.

Debriefing Form

Application number: 2010s0326

Behavioral Neuroendocrinology Laboratory

Department of Psychology

DEBRIEFING FORM

Prisoner Dilemma and Testosterone

Dear Participant,

The purpose of the study is to investigate how hormones, specifically Testosterone, modulate cooperative behavior in men and women. We hypothesized a higher ratio of defection/cooperation in subject with higher levels of Testosterone. We also expect this finding to be moderated by 2d:4d ratio, which is a proxy of fetal exposure to androgens and, therefore, responsible for brain masculinization.

If you have any concerns about your participation or the data you provided in light of this disclosure, please discuss this with us. We will be happy to provide any information we can to help answer questions you have about this study.

If your concerns are such that you would now like to have your data withdrawn, and the data is identifiable, we will do so.

If you have questions about your participation in the study, please contact Evan Caldbick from the Behavioral Neuroendocrinology Laboratory of Department of Psychology at Simon Fraser University (mailing address: 8888 University Drive, Burnaby, BC V5A 1S6; phone number: [redacted] or [redacted]; email: [redacted]).

If you have questions about your rights as a research participant, you may contact Dr. Hal Weinberg, Director, Office of Research Ethics at [redacted] or [redacted].

Please again accept our appreciation for your participation in this study.

Participant Last Name: _____

Participant First Name: _____

Participants Signature:

_____

Participants Identification Number (to be filled by the research assistant):

_____

Date (Use MM/DD/YY format):

_____

Appendix C.

Demographics Questionnaire

Date _____

Participant Identification Number_____

Questionnaire

Please provide a brief statement about your perception of the experiment:

_____

Have you ever heard about the Prisoner's Dilemma before today?: YES NO

If YES, have you ever played it before today?: YES NO

Please answer the following questions to the best of your ability. Your responses are strictly confidential and will be used for research purposes only. Your responses will be identified only by a confidential participation number.

1. Age: _____
2. Have you experienced any gum bleeding over the past days? YES NO
3. Have you experienced any other oral infections and/or oral lacerations over the past days? YES NO
4. How many hours ago has it been since you consumed caffeine (coffee, tea, soda, chocolate)? _____
5. Do you have a diagnosed endocrine disorder? YES NO.

5a. If Yes, which? _____

6. Do you use recreational drugs (e.g., marijuana, Ecstasy, speed, cocaine, heroin)? YES NO
7. Do you smoke? YES NO

8. Do you take anabolic steroids? YES NO
9. What is your occupation? _____
10. What is your weekly estimated physical activity?:

    _____ less than 1h

    _____ 1-4h

    _____ more than 4h

11. Are you currently taking any prescription or non-prescription medications or other hormone supplements? (Please circle one)

    NO, I am not taking any medication.

    YES (please list the medications you are taking):

    _____

12. What is the highest level of education you completed? (Please circle one)

    _____High school graduate

    _____At least one year of college, university, or specialized training

    _____College or university graduate

13. What is your sexual orientation?

    _____Homosexual

    _____Heterosexual

    _____Bisexual

14. Do you have any oral health problems or injuries? YES NO

15. At present, do you have any type of infection (e.g., flu) or physical condition that might later your hormone (e.g., PCOS)? YES NO

16. Relationship status (please circle all that apply):

_____Single

_____Dating one person and not in a long-term relationship

_____Dating more than one person and not in a long-term relationship

_____In a long-term relationship with one person for less than a year

_____In a long-term relationship with one person for more than a year

_____Married/Common-law

_____Divorced/Separated

17. How many sexual partners have you had? _____

18. Have you had sexual intercourse in the last 24 hours? YES NO

19. Please indicate the hand (left or right) you typically use in activities such as writing, brushing you teeth, holding a glass, etc.. _____

20. How often do you masturbate?

_____less than once/month

_____once/month

_____2-3 times/months

_____once/week

_____2-4 times/week

_____once/day

_____more than once a day

21. What is your weight (please indicate kg or lbs): _____

22. What is your height (please indicate, cm, inches, feet): _____

23. What is your ethnicity? (circle): Caucasian Asian

Other:_____

24. Do you have any siblings? YES NO

a. If YES, please complete the following chart (put an arrow besides your row):

Sex	Birthdate	Same Mother as You	Same Father as You

25. What religion do you identify with, if any?: _____

26. How religious do you consider yourself?(circle a #): not 1 2 3 4 5 very

27. How long have you lived in Canada?

a. All my life

b. For this long:_____

Sleep/Week Cycle (please indicate am/pm)

1. What time do you normally wake up on weekdays?_____
2. What time do you normally wake up weekends? _____
3. What time do you normally go to sleep on weekdays? _____
4. What time do you normally go to sleep weekends? _____
5. What time did you go to sleep last night? _____

6. What time did you get up this morning?

   _____

7. If you did not have to wake up because of external circumstances like school or work, when would you most prefer to wake up? (please check one)

   _____ Before 6:30 am

   _____6:35 am-7:30 am

   _____7:35 am-9:00 am

   _____9:05 am-10:30 am

   _____10:35 am-12:00 pm

   _____12:05 am-1:30 pm

   _____after 1:35 pm

Women Only:

1. What is the normal length of your menstrual cycle, from the first day of one menstrual period to the first day of the next menstrual period? (please circle one)

a. 23 days less

b. 24-26 days

c. 27-30 days

d. 31-34 days

e. 35 days or more

2. How regular are your menstrual cycles in their time of onset? (Please circle one)

a. perfectly regular
b. varies by 1-2 days
c. varies by 3-4 days
d. varies by 5-6 days
e. varies by 7 days or more
f. completely unpredictable

3. Are you pregnant or breast-feeding an infant at present? YES NO
4. Do you ever go through long periods of time without having menstrual periods (for reasons other than pregnancy)? YES NO

   4a. If YES, has this happened in the last 12 months? YES NO

5. Are you currently menstruating? YES NO

   5a. If YES, what date did you current (most recent) period begin? _____

   5b. If YES to 5, what day are you at? (Please be as accurate as possible) _____

   5c. If NO, when was the beginning of your last period? _____

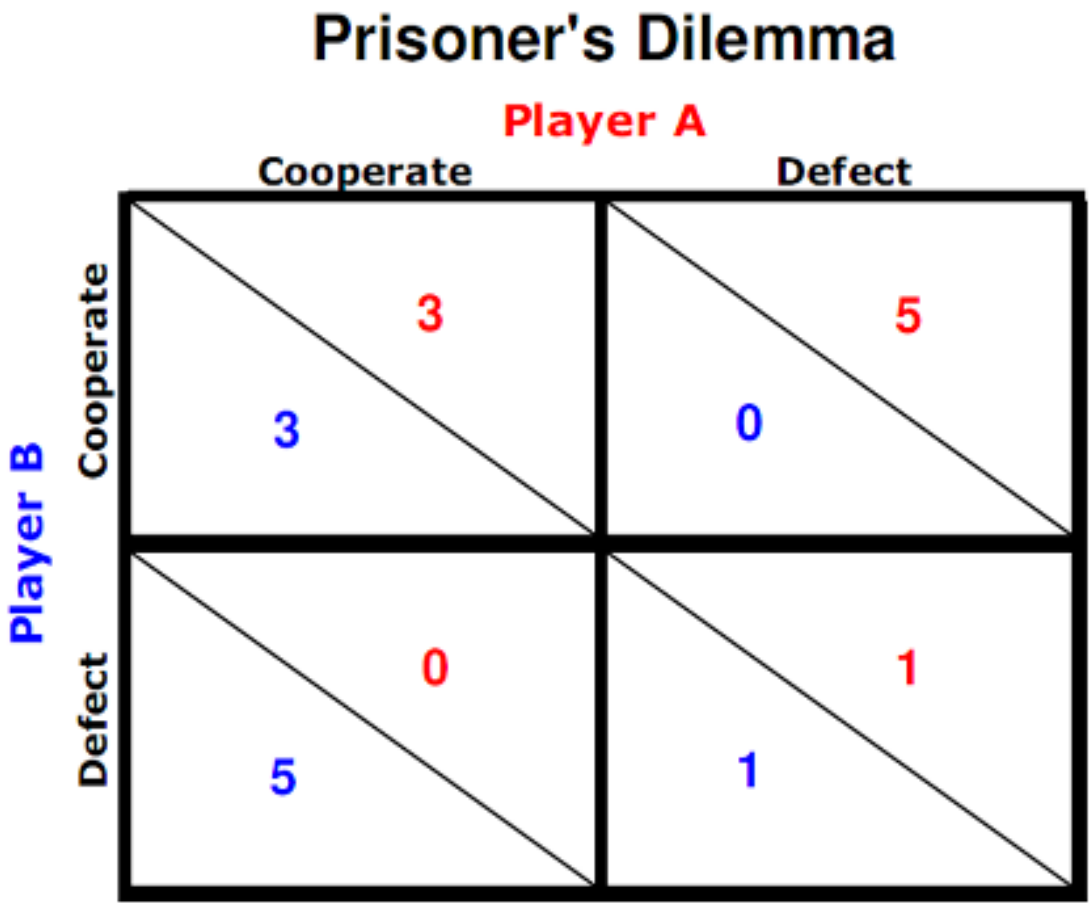
6. If you do not menstruate in general (e.g., post-menopausal woman), why?

a. I am a post-menopausal woman
b. I have a clinical condition such that I do not menstruate
c. I am taking hormonal contraceptives that prevent menstruation
d. Another reason: _____

7. Have you used hormonal contraceptives within the last three months? YES NO
8. What age did you have your menarche (first menstrual cycle)? Be as precise as possible. _____

Appendix D.

Prisoner's Dilemma Payoff Matrix



Appendix E.

Levenson Psychopathy Scale

Items and Factor Loadings in the Primary and Secondary Psychopathy Scales

Item
Primary Psychopathy
1. Success is based on survival of the fittest; I am not concerned about the losers.
2. For me, what's right is whatever I can get away with.
3. In today's world, I feel justified in doing anything I can get away with to succeed.
4. My main purpose in life is getting as many goodies as I can.
5. Making a lot of money is my most important goal.
6. I let others worry about higher values; my main concern is with the bottom line.
7. People who are stupid enough to get ripped off usually deserve it.
8. Looking out for myself is my top priority.
9. I tell other people what they want to hear so that they will do what I want them to do.
10. I would be upset if my success came at someone else's expense.
11. I often admire a really clever scam.
12. I make a point of trying not to hurt others in pursuit of my goals.
13. I enjoy manipulating other people's feelings.
14. I feel bad if my words or actions cause someone else to feel emotional pain.
15. Even if I were trying very hard to sell something, I wouldn't lie about it.
16. Cheating is not justified because it is unfair to others.
Secondary Psychopathy
1. I find myself in the same kinds of trouble, time after time.
2. I am often bored.
3. I find that I am able to pursue one goal for a long time.
4. I don't plan anything very far in advance.
5. I quickly lose interest in tasks I start.
6. Most of my problems are due to the fact that other people just don't understand me.
7. Before I do anything, I carefully consider the possible consequences.
8. I have been in a lot of shouting matches with other people.
9. When I get frustrated, I often "let off steam" by blowing my top.
10. Love is overrated.

Appendix F.

Social Phobia Scale

	Item content
1.	I become anxious if I have to write in front of other people
2.	I become self-conscious when using public toilets
3.	I can suddenly become aware of my own voice and of others listening to me
4.	I get nervous that people are staring at me as I walk down the street
5.	I fear I may blush when I am with others
6.	I feel self-conscious if I have to enter a room where others are already seated
7.	I worry about shaking or trembling when I'm watched by other people
8.	I would get tense if I had to sit facing other people on a bus or a train
9.	I get panicky that others might see me to be faint, sick or ill
10.	I would find it difficult to drink something if in a group of people
11.	It would make me feel self-conscious to eat in front of a stranger at a restaurant
12.	I am worried people will think my behaviour odd
13.	I would get tense if I had to carry a tray across a crowded cafeteria
14.	I worry I'll lose control of myself in front of other people
15.	I worry I might do something to attract the attention of others
16.	When in an elevator I am tense if people look at me
17.	I can feel conspicuous standing in a queue
18.	I get tense when I speak in front of other people
19.	I worry my head will shake or nod in front of others
20.	I feel awkward and tense if I know people are watching me

Appendix G.

Pride Scales

Below are a number of words and phrases that describe different feelings and emotions. Read each item and then indicate the extent to which you generally feel this way (i.e., how you feel on the average) using the scale shown below:

Authentic Pride Items

1.accomplished

2.like I am achieving

3.confident

4.fulfilled

5.productive

6.like I have self-worth

7.successful

Hubristic Pride Items

1.arrogant

2.conceited

3.egotistical

4.pompous

5.smug

6.snobbish

7.stuck-up

Appendix H.

Narcissism Scale

16-item pair measure of narcissism

Narcissistic response	Non-narcissistic response
I know that I am good because everybody keeps telling me so	When people compliment me I sometimes get embarrassed
I like to be the center of attention	I prefer to blend in with the crowd
I think I am a special person	I am no better or nor worse than most people
I like having authority over people	I don't mind following orders
I find it easy to manipulate people	I don't like it when I find myself manipulating people
I insist upon getting the respect that is due me	I usually get the respect that I deserve
I am apt to show off if I get the chance	I try not to be a show off
I always know what I am doing	Sometimes I am not sure of what I am doing
Everybody likes to hear my stories	Sometimes I tell good stories
I expect a great deal from other people	I like to do things for other people
I really like to be the center of attention	It makes me uncomfortable to be the center of attention
People always seem to recognize my authority	Being an authority doesn't mean that much to me
I am going to be a great person	I hope I am going to be successful
I can make anybody believe anything I want them to	People sometimes believe what I tell them
I am more capable than other people	There is a lot that I can learn from other people
I am an extraordinary person	I am much like everybody else

Appendix I.

ELISA Plate Layout

Std 1	Std 1	High Cont.	High Cont.	Sample 7	Sample 7	Sample 15	Sample 15	Sample 23	Sample 23	Sample 31	Sample 31
Std 2	Std 2	Low Cont.	Low Cont.	Sample 8	Sample 8	Sample 16	Sample 16	Sample 24	Sample 24	Sample 32	Sample 32
Std 3	Std 3	Sample 1	Sample 1	Sample 9	Sample 9	Sample 17	Sample 17	Sample 25	Sample 25	Sample 33	Sample 33
Std 4	Std 4	Sample 2	Sample 2	Sample 10	Sample 10	Sample 18	Sample 18	Sample 26	Sample 26	Sample 34	Sample 34
Std 5	Std 5	Sample 3	Sample 3	Sample 11	Sample 11	Sample 19	Sample 19	Sample 27	Sample 27	Sample 35	Sample 35
Std 6	Std 6	Sample 4	Sample 4	Sample 12	Sample 12	Sample 20	Sample 20	Sample 28	Sample 28	Sample 36	Sample 36
Zero	Zero	Sample 5	Sample 5	Sample 13	Sample 13	Sample 21	Sample 21	Sample 29	Sample 29	Sample 37	Sample 37
NSB	NSB	Sample 6	Sample 6	Sample 14	Sample 14	Sample 22	Sample 22	Sample 30	Sample 30	Sample 38	Sample 38

Appendix J.

Research Ethics Approval

SFU SIMON FRASER UNIVERSITY
THINKING OF THE WORLD

H. Weinberg, Ph.D.
Director, Office of Research Ethics
Simon Fraser University

8888 University Drive
Multi-Tenant Facility
Burnaby, B.C. Canada , V4A 1S6
778 782 6593

Minimal Risk Expedited Approval

Date	File	Approval	Principal Investigator
4 Jan. 2012	[2011s0507]	Approved	Caldbick, Evan

Title	Start Date	End Date
Testosterone and cortisol fluctuation and behavioural effects in the Prisoner's Dilemma	4 Jan. 2011	4 Jan. 2014

SFU Position	Department / School	Supervisor
Graduate Student	Psychology	Watson, Neil

Hello Evan,

Your application has been categorized as 'Minimal Risk' and approved by the Director, Office of Research Ethics on behalf of the Research Ethics Board, in accordance with University Policy r20.01 (http://www.sfu.ca/policies/research/r20.01.htm)

The Research Ethics Board reviews and may amend decisions made independently by the Director, Chair or Deputy Chair at the regular monthly meeting of the Board.

Please acknowledge receipt of this Notification of Status by email to dore@sfu.ca and Include the file number as shown above as the first item in the Subject Line.

You should get a letter shortly. Note: All letters are sent to the PI addressed to the Department, School or Faculty for Faculty and Graduate Students. Letters to Undergraduate Students are sent to their Faculty Supervisor.

Good luck with the project,

Hal Weinberg, Director