When a boy meets a girl

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	Prof. dr. M. van Vugt

Contents

Chapter 1

An introduction into social hormones

"I grew up with a lot of boys. I probably have a lot of testosterone for a woman."

-Cameron Diez

"What basically happens is your hormones get out of whack. Because of the stress in your life your body says, 'I need more hormones.' So, your hormones are trying to produce and produce and produce, and it's even more stressful and it is this wicked cycle."

-Marie Osmond

"I'm a bit of a slag... Some people don't think it's very nice, but I don't care... I've got hormones, and sex is there, so why not? Sex is good. Everybody does it, and everybody should!"

-Robbie Williams

"He's a guy. They don't talk, they fight. It's all that crazy testosterone."

-Kim Catrall

"I like there to be some testosterone in rock, and it's like I'm the one in the dress who has to provide it."

-Courtney Love

These quotes found on the internet show that there exists in society a wide understanding of the impact of hormones on human behaviour. Although many of these quotes underscore the idea that famous people are not scientists, the scientific literature has demonstrated many times that hormones and human behaviour are intertwined. Indeed, many studies from the last three decades have found that many hormones can affect human social functioning in many ways. Hormones have been found to be important in domains such as sexuality, emotion recognition, stress, competition, risk taking, and trust. Many studies have consistently shown that the release of hormones can explain in a unique way human behaviour and can provide insight in the functioning of social behaviour. This dissertation focuses on the hormonal responses of men to a number of social situations relevant for mating. Although there are other hormones that might play a role in such situations, this dissertation focuses on the role of cortisol and testosterone.

In the present chapter, I will explain how and where testosterone and cortisol are secreted. Following this, I will postulate a hypothetical biological mechanism through which the release of testosterone and cortisol can affect male behaviour in situations relevant for mating. Finally, I will present a short overview of how previous studies have linked cortisol and testosterone to social behaviour and will explain the most influential theories that explain the link between these hormones and behaviour.

1. Testosterone

1.1 What is testosterone?

Testosterone ($C_{19}H_{28}O_2$) is a hormone produced by the testes and in small amounts by the adrenal cortex and ovaries. Both men and women produce testosterone, although women produce very small amounts of testosterone. Testosterone is created by converting cholesterol through different steps into several types of androgens, including testosterone. Testosterone is a steroid hormone, and this means that it is lipid dissolvable and can therefore diffuse across cell membranes and capillary walls of blood vessels. In the blood most testosterone is bound to large proteins and inactive. However, the more important form of testosterone is the free unbound form, because only unbound testosterone is biologically active and can diffuse across capillary walls and bind to androgen receptors. The studies described in this dissertation have only measured unbound testosterone.

How is testosterone secreted? In men, the testes secrete testosterone in the blood stream through activation of the hypothalamus-pituitary-gonadal (HPG) axis. Neural cells in the hypothalamus secrete gonadotropin-releasing hormone (GnRH), which then passes into portal blood vessels that traverse the pituitary stalk and then enter the anterior pituitary gland. Here GnRH interacts with membrane receptors in the endocrine cells (gonadotropes), thereby stimulating the release into the blood of luteinizing hormone (LH) as well as follicle stimulating hormone (FSH). In the testes, FSH stimulates spermatogenesis in Sertoli cells, and LH stimulates the Leydig cells to produce testosterone. The secretion of GnRH usually occurs in a brief burst of action potentials approximately every 2 hours. Testosterone levels are highest when waking up and start declining throughout the day. At around 20.00h testosterone levels are lowest and start to rise throughout the evening and night until the next morning (Gupta et al., 2000). In Western society, testosterone levels steadily decline as men get older (Harman et al., 2001), although among some cultures this decline in testosterone levels is absent, for example, among the Tamang agropastoralists from central Nepal and Ache foragers from southern Paraguay (Ellison et al., 2002).

Like many other hormones, the production of testosterone is regulated by a negative feedback system to maintain a stable level of this hormone in the blood. The presence of testosterone mainly reduces LH secretion by inhibiting the frequency of GnRH bursts, which results in the secretion of less gonadotropins (LH and FSH), but it also acts directly on the anterior pituitary to cause less LH secretion (for a complete description of the physiology and function of testosterone see Nelson, 2005).

1.2 General functions of testosterone

Hormones form part of the body's communication system, since processes in the organism are regulated through changes in hormonal concentrations. Testosterone is no exception, and it has been known since the time of Aristotle in the fourth century BC that castration, i.e. manipulation of testosterone levels, can have a profound impact on physical appearance and behaviour (Wilson and Roehrborn, 1999). The main functions of testosterone are its masculinising effects which can be separated into anabolic and androgenic effects. Anabolic effects include an increases in muscle strength and growth and increases in bone mass. Androgenic effects include the maturation of the sex organs, hair growth and deepening of the voice.

But testosterone is important across the human life span. In fact, in the beginning of life testosterone differentiates the gonads of the human embryo into male genitals. Or in other words, testosterone turns the embryo male and the absence of testosterone turns the embryo female. During this crucial time of development, the exposure to prenatal testosterone proliferates the development of male structures and also causes masculinization of the central nervous system (Morris et al., 2004). Due to its big impact on fetal brain structures it has been hypothesized that the grade of exposure to prenatal testosterone influences personality traits (Austin et al., 2002). Chapter 6 in this dissertation investigated if this exposure of testosterone early in life also has consequences for personality traits later in life.

But also in adult life testosterone has a crucial function, as it regulates sexuality in both men and women. Research has shown that testosterone administration to women stimulates their sexual desire (Tuiten et al., 2000). Furthermore, studies in clinical settings have shown that when testosterone is administered to hypogonadal men (men who produce less testosterone than normal) their libido and sexual function increases (Shah and Montoya, 2007). In contrast, depriving healthy men of normal testosterone levels through medication causes a drop in sexual desire and sexual intercourse (Bagatell et al., 1994).

Apart from these functions, testosterone can also have more complex psychological effects on the organism. The administration of testosterone to women increases their risk taking behaviour (van Honk et al., 2004) and threat recognition (van Honk and Schutter, 2007). Testosterone administration to healthy men reduces fatigue-inertia and can slightly increase anger and hostility (O'Connor et al., 2004). Additionally, testosterone has rewarding properties, as it has been shown that mice actually prefer to be in places where they previously received testosterone administration (Arnedo et al., 2002). Indeed, there is also evidence that testosterone administration can cause dependence. The use and dependence of anabolic–androgenic steroids by athletes to increase their muscle mass and lower body fat is wide-spread worldwide (Kanayama et al., 2010).

1.3 The challenge hypothesis: Parental effort vs. Mating effort

Testosterone can have many complex functions in the organism, but it is not a goal of this dissertation to study its many functions. Instead, this dissertation focuses on the interaction between testosterone levels and behaviour relevant for human mating among young male adults. There is an overarching theory that helps explain the nature of the relationship between fluctuating testosterone levels and human mating. This theory is called the challenge hypothesis (Wingfield et al., 1990), and it has been important for behavioural endocrinology since it was first formulated (Moore, 2007). This hypothesis was first formulated to explain the rise and fall of testosterone concentrations among several species of monogamous birds. It had been observed that male birds experience an increase in testosterone levels during the breeding season when fighting among males over receptive females is common, whereas they experience a decrease in their testosterone levels when they are caring for their young (Wingfield et al., 1990). The challenge hypothesis states that testosterone levels rise during challenges in contexts that are relevant for reproduction, such as inter-male competition over receptive females. On the contrary, when males are required to care for offspring testosterone levels tend to be low. More recently, the challenge hypothesis has been extended to research on humans, now also incorporating challenges facing human males such as social status disputes and reactions towards sexual stimuli (Archer, 2006).

In humans, there are many indirect findings in support of this hypothesis. For example, men show an increase in testosterone levels after engaging in sexual intercourse (Dabbs and Mohammed, 1992), after any sexual activity resulting in an orgasm (Knussman et al., 1986) and even after watching erotic videos (Hellhammer et al., 1985; Stoléru et al., 1993). On the other hand, it has been found that testosterone levels are lower in contexts that require parenting effort rather than mating effort. For example, testosterone levels are lower when men are in a committed romantic relationship (Burnham et al., 2003; Gray et al., 2004), married men have lower testosterone levels than unmarried men (Mazur and Michalek, 1998; Gray et al., 2002), and testosterone decreases when they become fathers (Storey et al., 2000; Berg and Wynne-Edwards, 2002).

The challenge hypothesis can also be applied to situations indirectly relevant for reproductive success. Such a situation might be competition with another male, as the outcome of such a competition can affect the status, and thus the mating success of the winner as well as the loser. Therefore, according to the challenge hypothesis, in reaction to a challenging and evolving competition, testosterone levels should rise throughout the competition. Indeed, many different studies have found that testosterone is released during human physical and non-physical competition (for a review see Salvador and Costa, 2009).

The major goal of this dissertation was to test the predictions made by the challenge hypothesis. To do so I did not only study the more obvious social situations relevant for reproductive success such as contact with a potential mate (chapter 2,4,5) but I also studied intra-sexual competition (see chapter 3) and dominance as a personality trait (see chapter 6).

1.4 A hypothetical mechanism of how testosterone can affect behaviour

If testosterone can affect human behaviour and psychology what would be the physiological mechanism behind this? This is a difficult question to answer since there are many steps involved going from a stimulus that provokes a release of testosterone, to a change in the central nervous system (CNS), which finally changes behaviour. Furthermore, unlike non-human animal studies, it is more difficult to study these processes in CNS since it is obvious that participation in an experiment may not cause any psychological or physiological harm to human subjects. Notwithstanding this limitation, I have tried to formulate the hypothetical mechanism implicitly assumed in many studies on testosterone (see Figure 1).

In response to a stimulus, such as a social interaction with a woman, activity in the CNS changes due to, for example, the perception of an opportunity for courtship. This change in CNS activity then activates the hypothalamus-pituitary-gonadal axis which stimulates the release of testosterone.

After testosterone is secreted, it can have fast effects (sec-min) or slow effects (min-hours). The slow route for testosterone to exert its effects is through the classical or genomic pathway. Genomic mechanisms involve the activation of intracellular androgen receptors that modulate nuclear transcription after translocation of steroid–receptor complexes into the nucleus, typically taking days or hours to exert an influence (Schmidt et al., 2000). By contrast, the non-genomic route can affect an organism rapidly through testosterone binding to extracellular androgen receptors that can raise the intracellular calcium concentration, change membrane fluidity and activate second messenger pathways (Foradori et al., 2008). Through these changes the activity of the CNS is modulated, thereby leading to a change in behaviour.

Although the studies described in this dissertation cannot distinguish through which route testosterone has its effects, I speculate that the fast pathway is the most important one, as the studies presented in this dissertation have investigated changes in testosterone levels and behaviour over a period of minutes.

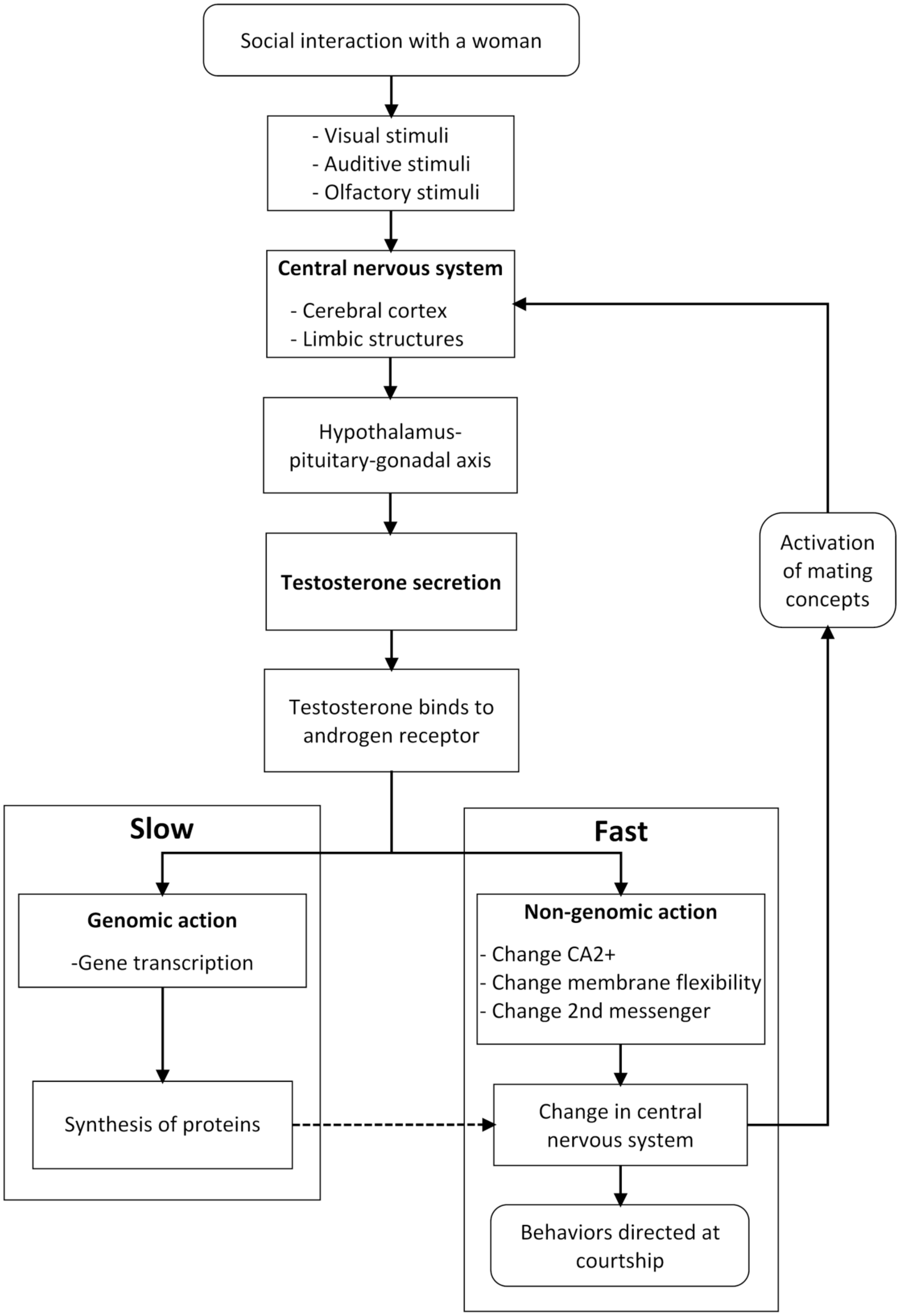

Figure 1: A hypothetical mechanism of how male testosterone release during a social interaction with a woman can change male behaviour and psychology.

2 Cortisol

2.1 What is cortisol

While most literature on the role of hormones and human mating has focused on testosterone, in the present dissertation I also examined the role of cortisol. Cortisol ($C_{21}H_{30}O_5$) is, like testosterone, a steroid hormone and is secreted by the adrenal cortex. Both men and women produce roughly similar quantities of cortisol throughout the day. This hormone is secreted through activation of the hypothalamus-pituitary-adrenal axis. The cells in the hypothalamus secrete corticotrophin releasing hormone (CRH) which then stimulates the pituitary to release adrenocorticotropic hormone (ACTH) into the blood. ACTH then travels through the blood to the adrenal cortex where it stimulates the release of cortisol. The production of cortisol is regulated by a negative feedback system, thereby, ensuring constant levels of this hormone in the blood. High cortisol concentrations slow down the secretion of cortisol by reducing the secretion of CRH in the hypothalamus. Cortisol levels follow a circadian rhythm. Levels are highest 30 minutes after waking up and then steadily decline throughout the day (Fries et al. 2009).

The adrenal cortex synthesizes cortisol by converting cholesterol into pregnenolone and though its derivates finally into cortisol. In the blood most cortisol is bound to large proteins (corticosteroid-binding globulin), however, the more important form of cortisol is the free unbound form, since only unbound cortisol can diffuse across capillary walls and is therefore biologically active.

2.2 General functions of cortisol

Cortisol regulates many different biological processes in the organism. The most important function attributed to cortisol is that it reigns in the stress response. As it suppresses the immune system, synthetic forms of cortisol are also used for the treatment of diseases associated with an overreaction of the immune system (for a more extensive discussion of the functions of cortisol please read Sapolsky et al., 2000).

As early as in the 1950's cortisol has been associated with the stress response, showing sharp increases of this hormone in reaction to non-specific psychological or physiological stressors (Selye, 1956). Later studies have focused on the exact nature of these stressors and found that cortisol is especially secreted when the physical well-being is threatened, e.g. when jumping out of an airplane (Chatterton et al., 1997). In addition to physically threatening contexts, it has also been shown that cortisol responses are elicited when the psychological well-being is threatened (for a review see (Dickerson and Kemeny, 2004). Such responses have been interpreted from the perspective of social self-preservation theory, which predicts that cortisol levels increase when individuals are motivated to maintain their social status or acceptance. Evidence for this theory is provided by studies showing that cortisol levels increase in situations where one's self-identity can be negatively judged by others (Seeman et al., 1995), and when the outcome of a negative situation is beyond one's control (e.g. Peters et al., 1998). In the laboratory, it has been replicated many times that exposure to psychosocial stress by, for example, performing a public speaking task, provokes an increase in cortisol levels (Kirschbaum et al., 1993; Almela et al., 2011a; Almela et al. 2011b).

The secretion of cortisol in response to stress has an adaptive function, as it diverts energy to exercising muscles, enhances cardiovascular tone, and suppresses unessential processes, such as digestion, growth, and reproduction (Sapolsky et al., 2000). However, exposure to physical or psychological stressors for a long period of time may cause chronically elevated cortisol levels that can have adverse effects on health, as it worsens various disorders, such as myopathy, adult-onset diabetes, hypertension, amenorrhea, and impotency (e.g. Munck et al., 1984; McEwen, 2008).

2.3 Cortisol: not only related to negative situations

Many scientists view the release of cortisol as a coping mechanism to aversive psychological or physical conditions. However, there is also a substantial amount of research that suggests that cortisol may have other distinct functions. For example, in the non-human animal literature, it has been shown that corticosterone (the non-human version of cortisol) facilitates pair bonding in male prairie voles but not in females (DeVries et al., 1996). Other studies have consistently found that corticosterone levels increase after copulation in a wide range of species, including stallions, bulls, pigs (Borg et al., 1991; Rabb et al., 1989), rats (Retana-Marquez et al., 1998) and mice (Bronson and Desjardins, 1982). Nevertheless, it has been reported that corticosterone levels in male rats may increase up to two fold after exposure to physical or non-physical contact with a receptive or non-receptive female (Bonilla-Jaime et al., 2006). In humans, the effect of cortisol on male sexual functioning is less clear. For example, some studies have found that cortisol levels do not change after watching erotic videos (Rowland et al., 1987; Carani et al., 1990; Exton et al., 2000), while another study has found that cortisol levels decrease after watching such videos (Uckert et al., 2003). Furthermore, chronically elevated cortisol levels, such as those caused by Cushing's Syndrome, tend to decrease sexual functioning (Starkman and Schteingart, 1981), whereas the administration of adrenocorticotropic hormone (which stimulates cortisol secretion) to patients with erectile dysfunction increases their sexual performance (Isidori et al., 1984).

This dissertation investigated if cortisol has also a function in social situations relevant for human mating. To do so, I studied in chapter 4 if social contact between a man and woman produces a change in male cortisol levels, and I investigated if this change in male cortisol levels was moderated by the perceived attractiveness of the woman with whom they had contact.

2.4 A hypothetical mechanism of how cortisol can affect behaviour

If cortisol can affect human behaviour and psychology, what would be the physiological mechanism behind this? As with the hormone testosterone, I have tried to formulate the hypothetical mechanism implicitly assumed in studies on cortisol and social behaviour (see Figure 2). In response to a stimulus, such as a social interaction with an attractive woman, activity in the CNS changes, due to, for example, the perception of an opportunity for courtship. This change in CNS activity then activates the hypothalamus-pituitary-adrenal axis which stimulates the release of cortisol.

Like testosterone, cortisol can have fast effects (sec-min) effects or slow effects (min-hours). The slow route for cortisol to exert its effects is through the classical or genomic pathway. Genomic mechanisms involve the activation of two different types of intracellular receptors: glucocorticoid receptors, which have a low affinity to cortisol, or mineralocorticoid receptors, which have a high affinity to cortisol. After receptor activation, steroid–receptor complexes are translocated into the nucleus to modulate nuclear transcription, typically taking days or hours to exert an influence (Schmidt et al., 2000).

By contrast, the non-genomic route can affect an organism rapidly through cortisol binding to extracellular receptors that can facilitate long term potentiation between neurons, and enhance the probability of glutamate release and the generation of action potentials postsynaptically (de Kloet et al., 2008). Through these changes the activity of the CNS is modulated, thereby leading to a change in behaviour. See Figure 2 for a hypothetical mechanism of how cortisol release can affect human behaviour (for a more complete description of this hormone and of how it exerts its effect see Nelson, 2005).

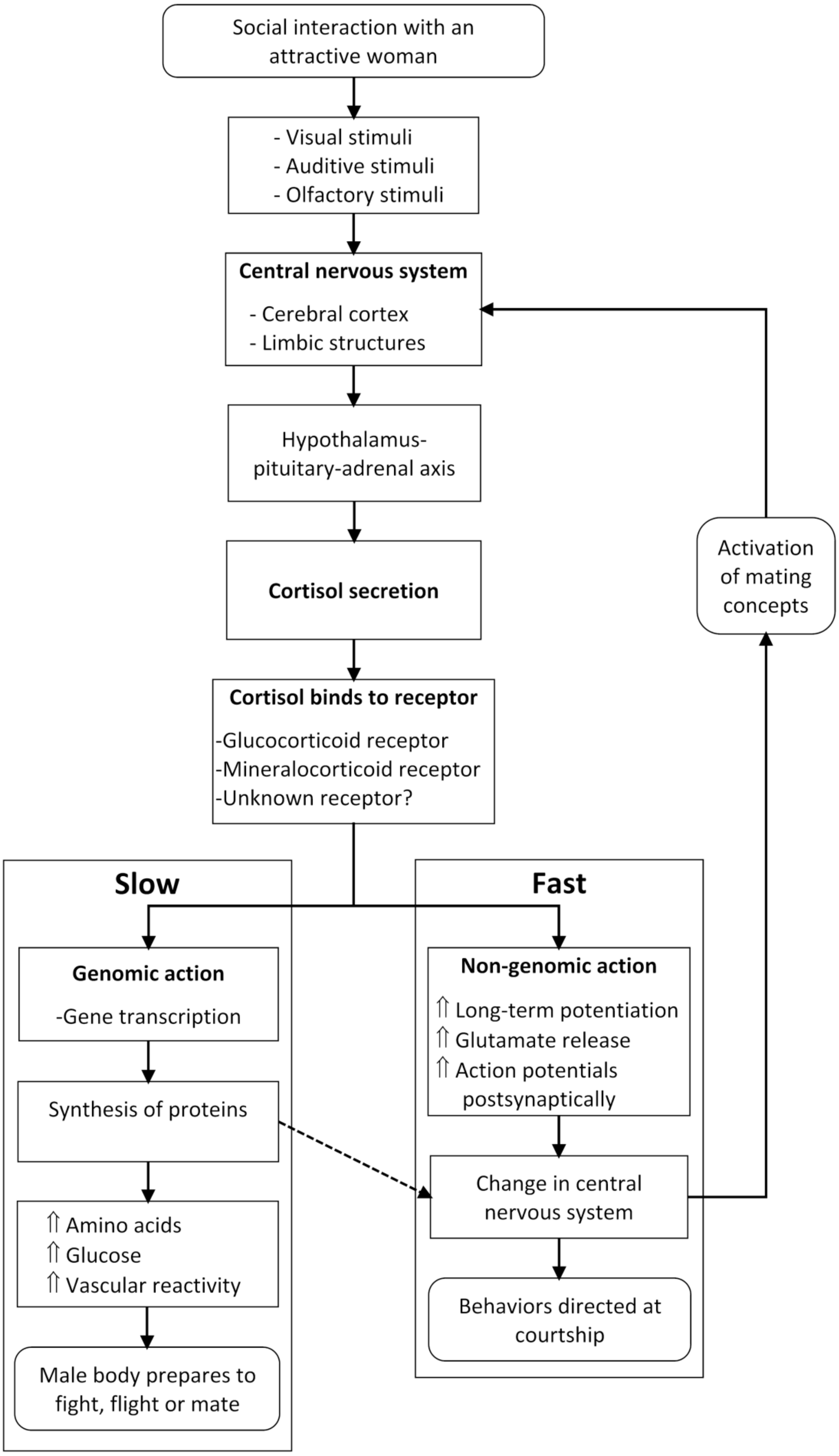

Figure 2: A hypothetical mechanism of how male cortisol release during a social interaction with a woman can change male behaviour.

3 Dissertation Outline

In chapter 2, I investigated if social contact with young women affects the release of testosterone in young men, and hypothesized that dominance as a personality trait moderates this potential change in testosterone levels. To study this, I used a similar paradigm as used by Roney et al. (2003). Some deception is included in this paradigm, because I wanted to avoid any unnatural or awkward social situation between interaction partners. In this paradigm, participants were not told that they were going to interact with another person. Instead, they were brought to a room where they were told to wait so that the experimenter could fetch the correct version of a puzzle for them. In this same room, a female or male confederate of the experimenter was also present. Participants and confederates were left alone to wait for approximately 5 min. This short period served as the contact period. Before and after the contact period participants provided a saliva sample for the measurement of their testosterone level. Participants were fully debriefed about the true nature of the experiment at the end of the study. By using this paradigm, I tried to create an everyday waiting room situation where social contact may occur.

In chapter 3, I investigated if competition between men creates an increase in testosterone levels among competitors. More specifically, I tried to explain why some might increase their testosterone levels and others not. Therefore, I studied not only the effects of winning and losing, but also studied the psychological state of the competitors. As a paradigm I developed a computer task on which participants had to compete. During this task, two participants were seated opposite to each other at the same table, each behind their own computer screen. The task contained questions used in intelligence tests and the outcome was fixed by the experimenter. With this paradigm I intended to create a controlled competitive situation that reflects male intra-sexual competition.

In chapter 4, I used the same paradigm as used in chapter 2, but this time I measured the hormone cortisol. I hypothesized that contact with a woman also produces a change in cortisol levels. But because the release of cortisol has been linked to stressful and challenging situations (see chapter 1), I also studied if the release of cortisol depended on how participants perceived the interaction period. Specifically, I investigated if the participants' perceived attractiveness of the woman with whom they interacted moderated a change in cortisol levels.

In chapter 5, I combined the paradigms used in chapter 2 (social contact) and 3 (competition). This time, I investigated if the release of male testosterone due to intra-sexual competition also prepares men for mate attraction. To do so, I took the testosterone change produced by the competitive computer task, and related this to the behaviour of the participants displayed during contact with a woman. Because the social contact period occurred shortly after the competition, some participants actually had elevated testosterone levels, while others had less of an increase or even a decrease. This variation in male testosterone responses gave me the opportunity to test the hypothesis that increased testosterone levels stimulate behaviours relevant for human mating, such as courtship.

In chapter 6, I investigated indirectly if the exposure to prenatal testosterone has an effect on male personality later in life. During fetal development, human brain structures are formed, and exposure of testosterone in this crucial phase masculinizes the central nervous system. Therefore, fetal testosterone exposure may affect the development of certain personality traits. I specifically investigated if this exposure to prenatal testosterone affected dominance as a personality trait, since previous studies have shown that dominance is related to testosterone levels (see chapter 2). I used the same questionnaire as in chapter 2 to measure sociable and aggressive dominance, and I obtained an indicator of prenatal testosterone exposure by measuring the ratio between the middle and ring finger (2D:4D). Finally, chapter 7 discusses the main findings of the empirical chapters and will give a new direction to future studies.

4 Hypotheses

The overview of the literature presented in this first chapter has shown that hormones and social behaviour are intertwined. The next five empirical chapters have studied testosterone and cortisol in contexts relevant for male mating. The hypotheses I tested in these empirical chapters are the following:

Chapter 2 The presence of a woman increases testosterone in dominant men.

Chapter 3 Male testosterone responses to competition with other men is moderated by their own and their opponent's psychological state.

Chapter 4 Contact with attractive women affects the release of cortisol in men.

Chapter 5 Testosterone stimulates male affiliative behaviour during contact with women.

Chapter 6 The relationship between 2D:4D in men and dominance as a personality trait depends on the type of dominance measured.

Chapter 2

Testosterone release in men during interactions with women

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The presence of a woman increases testosterone in aggressive dominant men

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ABSTRACT

In line with the challenge hypothesis, this study investigated the effects of the presence of a woman on the testosterone (T) levels of young men. An informal contact with a woman of approximately 5 min resulted in an increase in salivary T among men. These effects occurred particularly in men with an aggressive dominant personality. In addition, higher salivary T levels were related to a more aggressively dominant personality, being sexual inactive for a month or more, and not being involved in a committed, romantic relationship. The most important findings of this study are that the short presence of a woman induces specific hormonal reactions in men, and that these effects are stronger for aggressively dominant men.

Introduction

The challenge hypothesis (Wingfield et al., 1990) has had a big impact on behavioral endocrinology since it was first formulated (Moore, 2007). This hypothesis intends to explain the relationship between testosterone (T) and behavior in monogamous birds, and states that T levels rise during challenges in contexts that are relevant for reproduction, such as inter-male competition over receptive females. On the contrary, when males are required to care for offspring T levels tend to be low. More recently, the challenge hypothesis has been extended to research on humans, now also incorporating challenges facing human males such as social status disputes and reactions towards sexual stimuli (Archer, 2006).

In humans, indirect findings supporting this hypothesis range from men showing T increases after engaging in sexual intercourse (Dabbs and Mohammed, 1992), after any sexual activity resulting in an orgasm (Knussman et al., 1986) and even after watching erotic videos (Hellhammer et al., 1985; Stoléru et al., 1993). On the other hand, it has been found that T levels are lower in contexts that require parenting effort rather than mating effort. For example, men with lower T levels feel more sympathy in response to infant cries (Fleming et al., 2002), and men who express more need to comfort a crying baby actually decrease their T levels (Storey et al., 2000). Furthermore, men who are in committed relationships have lower T levels than uncommitted men (Burnham et al., 2003; Gray et al., 2004) and married men have lower T levels than unmarried men (Gray et al., 2002). In fact, T seems to decline when men marry (Mazur and Michalek, 1998) and when they become fathers (Storey et al., 2000; Berg and Wynne-Edwards, 2002).

Much more direct evidence comes from a study that examined if contact with a potential mate induces in men a mating response, consisting of a reactive increase in sex hormone levels accompanied by courtship behaviors (Roney et al., 2003). Although in this study the authors did find a significant increase in T levels after contact with a woman, and not after contact with a man, the difference in change between both conditions was not significant. Furthermore, Roney et al. (2003) examined if sexual experience acted as a potential moderator of the T change in men when in contact with a woman. This was in line with the animal literature, since in animals sexual experience seems to moderate the release of T after the presence of a female and after sexual contact (Kamel et al., 1975; Bonilla-Jaime et al., 2006). Roney et al. (2003) did find some limited evidence, in the sense that changes in T levels were close to zero among men with little sexual experience. In a follow up study, using a larger sample of men Roney et al. (2007), found more unequivocal evidence for an increase of T when in contact with a young woman. The number of previous sex partners did not influence this T increase, although this could only be tested in a sub sample consisting of men who were in a relationship.

Individual differences in T responses to potential mates have not been studied in much detail. Here we propose that differences in dominance may lead to different hormonal responses to interactions with women. This is because individuals high in dominance are expected to display relatively more dominant behavior when in challenging situations. Contact with a potential mate introduces challenge and might especially increase T levels in individuals high in dominance. This anticipating effect may occur because T plays a key roll in processes concerning the attainment or struggle for dominance. T is related to achieving status (Booth et al., 1989; Mazur et al., 1992),

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to a dominant or vigilant response towards angry faces (van Honk et al., 2000), to competition (Suay et al., 1999; Salvador et al., 2003; Salvador, 2005), and to dominance (for a review see Archer, 2006). Competing, being vigilant, achieving status or being dominant can be viewed as being evolutionary adaptive in terms of gathering critical resources such as food, shelter and potential mates (Mazur and Booth, 1998). Although there are many possible ways of defining dominance (Mazur and Booth, 1998), according to Kalma et al. (1993) two different dominance personality types can be distinguished: sociable dominance and aggressive dominance. Kalma et al. (1993) showed that both observational and self report data indicate that the two types of dominance are associated with the use of power strategies to influence others. However, aggressive dominant men tend to use a mix between "stating what one wants" and Machiavellian tactics, whereas sociably dominant men tend to use more reasoning strategies to influence people.

Bearing all this in mind, the aim of this study was to investigate the T responses of men when they come into contact with a potential mate. Building directly on the study of Roney et al. (2003), an informal contact was staged in which male participants had to wait in a waiting room situation with either a female confederate (experimental condition) or a male confederate (control condition). Salivary T levels were measured before and after the contact period. In addition to examining the main effect of being exposed to a woman we also examined the role of several potential moderators. First, we included sexual experience by using the following variables: number of sex partners, last time of sexual contact, and involvement in a committed romantic relationship. We expected that more sexual experience is associated with higher initial T levels and with stronger increases in the T response. Second, we included a questionnaire measuring sociable and aggressive dominance. We predicted that individuals high in either type of dominance would show a more pronounced hormonal change when meeting a potential mate and have higher T levels. In this study, we only considered dominance related to power relations and not phenomena like eminence or prestige, which refer to social status that is earned through accomplishments and that is bestowed freely (Kemper, 1990; Johnson et al., 2007).

Method

Participants and stimulus persons

Sixty-three male students were recruited from different cafeterias of the University of Groningen and Hanze College in Groningen. A male and female recruiter approached men and asked them if they would like to participate in a study at the faculty of psychology. Participants were paid 5 euros for their participation. Ages of the participants ranged from 18 to 27 years ($M=21.8$, $SD=2.1$). The data of four participants were removed because they indicated to have a gay or bisexual orientation.

Participants came into contact with a confederate who was either a man (control condition) or a woman (experimental condition). In order to achieve this, three men and three women played the role of stimulus person. At face value, female stimulus persons were chosen on the basis of being moderately attractive for the student population (in the experiment this was later validated, see 3.1). Ages of the female stimulus persons were 20, 23, and 23 years and for the men the ages were 21, 23, and 25 years.

Procedure

Upon arrival at the faculty the participants were told by the experimenter that they were about to participate in a study on the link between personality and physiological reactions. Next, to habituate the participants to the experimental setting, they filled in a general background questionnaire, signed an informed consent, and answered several questions that were not related to this study. After this, half of the participants were randomly assigned to have contact with a man (control condition) and the other half to have contact with a woman (experimental condition). The contact procedure was partly taken from Roney et al. (2003).

Next, the participants provided their first saliva sample to measure T. As a bogus task, the participants were then brought to another room to solve a puzzle (the type of puzzle was a sudoku). In this room another participant appeared to solve a similar puzzle, but this participant was actually a confederate of the experimenter and functioned as a stimulus person. The experimenter then made the excuse that he did not have the correct puzzle for the participant. The participant and stimulus person were then asked to wait, so the experimenter could get the correct puzzle. The experimenter left and the participant and the stimulus person were left alone to wait together for 5 min. All stimulus persons received the instructions to engage in friendly conversation in a natural manner, were instructed to act as if they were participants in the same study, and were tolled to allow long pauses if the subjects elected not to talk. These instructions were given to avoid a competitive interaction among participants and stimulus persons.

After 5 min, the experimenter returned with the correct puzzle. The participant received the instruction to solve the puzzle in a relaxed manner. Then the stimulus person left the room with the experimenter. After trying to solve the puzzle for 15 min, the experimenter returned to collect the puzzle from the participant. He then asked the participant to provide a second saliva sample, for the purpose of determining a change in their T level. After this, the participant filled in several questionnaires and rated the attractiveness of the female stimulus person.

Finally, the participants were debriefed, received five euros, and a letter with a detailed description of the true purpose of the study. The session took about 60 min to complete and participants were tested from nine o'clock in the morning to four o'clock in the afternoon.

Questionnaires and scales

At the end of the study the participants filled in two questionnaires measuring sociable and aggressive dominance, consisting of eight items for the sociable dominance scale and seven items for the aggressive dominance scale (Kalma et al., 1993). A Cronbach Alpha of 0.79 has been reported for the sociable dominance scale and an Alpha of 0.68 for the aggressive dominance scale (Kalma et al., 1993). The original Dutch versions of the questionnaires were used (Kalma et al., 1993). Examples of the items for sociable dominance are: *No doubt I'll make a good leader*, *I like taking responsibility*, and *People turn to me for decisions*. Examples of the aggressive dominance scale are: *I make smart, sarcastic remarks to people when they deserve it, I think it is important that my opinion prevails,* and *while telling a lie, I can look anyone in the eye.* For every item in the two questionnaires, the participants rated to what extent they agreed with the statements on a scale from 1 (strongly disagree) to 6 (strongly agree).

After being presented with the dominance scales, the participants were asked how many sexual partners they have had (open end), if they were involved in a committed romantic relationship (yes or no), when the last time was when they engaged in sexual activity ranging from 1 = a few days ago to 6 = more than a year (or 7 = I never had sexual contact), and their sexual orientation (heterosexual, homosexual, or bisexual). Participants also could choose not to answer all these questions by filling in 'private'. Next, they rated how attractive they thought the female stimulus person was from 1 = very unattractive to 7 = very attractive.

Finally, participants were asked what they thought was the true purpose of the study. None of the participants included in their answer that the stimulus persons were part of the experiment.

Hormonal assays

Participants provided two saliva samples by depositing 5 ml of saliva into plastic vials. The samples were frozen at −20 °C and shipped to the endocrinology laboratory at the University Medical Center Utrecht. We chose 20 min as the interval between the two saliva samples because psychological stimulation needs some time to affect T levels (Hellhammer et al., 1985).

The saliva samples were tested using a radio-immunoassay. T in saliva was measured after diethyl-ether extraction, using an in house competitive radio-immunoassay employing a polyclonal anti-T-antibody. The lower limit of detection was 10 pmol/L. Inter-assay coefficient of variation ranged from 8–13% (range 40–500 pmol/L) and the intra-assay coefficient of variation ranged from 5–7%.

For calculating a T change, the data of one participant were removed because the second saliva sample did not contain enough saliva to measure T.

Statistical analysis

We first performed several independent *t*-tests to assess if the random distribution of the participants among conditions created any differences between the experimental and the control group. A Spearman correlation was used to look at the possible influence of time of saliva sample with baseline T.

To examine if there was an increase of the salivary T level in response to contact with a woman, we executed an ANCOVA with Repeated Measures with moment of collecting the saliva sample as within-subject variable and sex of the stimulus person as between-subject variable. As a covariate we included being in a relationship (see 3.1). Post hoc, paired *t*-tests were used to assess differences with baseline T.

Regression analyses were used to investigate the moderating effects of attractiveness of the stimulus person, sexual experience and dominance on the T change in the female condition. Independent *t*-tests were performed to investigate differences in baseline T for sexual experience and dominance. For this purpose we divided our sample in being sexual active or inactive in the last month and we compared participants low (below the mean) and high (above the mean) for both sociable and aggressive dominance.

No violation of the normality assumption was found in the T values, therefore there was no need to transform them. A value of $p<0.05$ (two-tailed) was considered statistically significant. Statistical tests were performed with SPSS version 13.0 and effect sizes were calculated with G*Power 3 (Faul et al., 2007). Cohen's d, f^2, and d_z are reported for the effect sizes and when not otherwise specified values are Mean ± SEM.

Results

Preliminary analysis

The data from 59 participants were used for the statistical analysis, of whom 29 participants had contact with a man (28 when analyzing the T change, see 2.4) and 30 participants had contact with a woman. There were no differences between conditions for the following variables: age, housing condition, educational level, last time of sex, number of sex partners, sociable dominance, and aggressive dominance ($p \geq 0.149$). However, we did find that by chance we had more participants with a committed romantic relationship in the control condition ($n=23$) than in the experimental condition ($n=12$), t $(57)=-2.9$, $p=0.005$. We therefore controlled for this variable by including it as a covariate in our analysis to examine a possible T change.

The participants rated the female stimulus persons on average a 4.2 ± 0.2, meaning they thought the female stimulus persons were moderately attractive. Finally, in our sample there did not appear to be a significant relation between time of collecting the saliva sample and baseline T, $r=-0.14$, ns.

Main effect of the testosterone change

There was a significant interaction between the sex of the stimulus persons and moment of collecting the saliva sample, $F(1,55)=4.02$, $p=0.050$. An inspection of Fig. 1 reveals that men showed an increase in their salivary T level when they had been in contact with a woman. The participants who had contact with a woman had an average increase in their salivary T level of +7.8%, paired-$t(29)=2.69$, $p=0.012$, $d_z=0.49$. Participants who had contact with a man had on average a decrease in their salivary T level of −0.5%, paired-$t(27)=0.63$, $p=$ns, $d_z=0.12$. Finally, there were no baseline differences in T level between the male and female condition, $t(57)=-1.09$, $p=$ns, $d=0.28$. We also examined if the increase in T depended on the perceived attractiveness of the female stimulus person. No significant effect was found, $\beta=0.04$, $p=$ns. Thus, the T increase was not influenced by the perceived attractiveness of the female stimulus person.

Sexual experience

There was no relation between T change in the female condition and number of sex partners, $\beta=-0.092$, $p=$ns, nor with last time of having sex, $\beta=-0.093$, $p=$ns. The T increase during contact with a woman did not differ between men with a relationship (27.7 ± 14.8, $n=7$,) and men without a relationship (21.8 ± 10.4, $n=23$), $t(28)=0.29$, $p=$ns, $d=0.13$. Furthermore, the T increase did not differ between

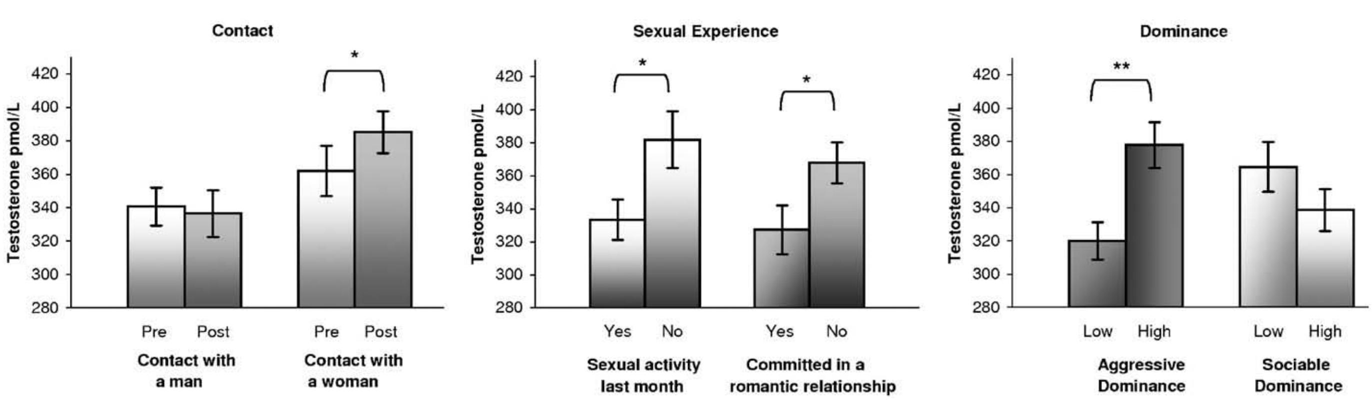

Fig. 1. Salivary testosterone concentrations depicted by contact with a man ($n=28$) or contact with a woman ($n=30$). Baseline testosterone levels are reported for men with a relationship ($n=24$) or without one ($n=35$), and for men who were sexually active in the last month ($n=31$) or inactive ($n=22$). Also depicted are men low ($n=27$) or high ($n=32$) in aggressive dominance, and for men low ($n=29$) or high ($n=30$) in sociable dominance. Values are Mean ± SEM. *$p<0.05$, **$p<0.01$.

those who had been sexually active (36.8±15.9, $n=13$) or sexually inactive (18.0±9.0, $n=14$) in the last month, $t(25)=1.0$, $p=0.306$, $d=0.40$. Only one participant in the condition of contact with a female was a virgin, and was therefore excluded from this last analysis; however, including him did not change p to significance.

The results did show that participants who were not sexually active in the last month had higher baseline T levels compared to men who were sexually active in the last month, $t(51)=-2.36$, $p=0.022$, $d=0.65$ (see Fig. 1). There were four virgins in our total sample and they were excluded from this last analysis, although including them did not change the p level to significance. Additionally, men who were involved in a committed, romantic relationship had lower salivary T levels, $t(57)=-2.10$, $p=0.041$, $d=0.68$ (see Fig. 1). However, sexual activity in the last month (virgins included) and being in a relationship were heavily correlated, Spearman's rho=0.75, $p\leq0.001$. When added together in the same multiple regression using the enter method we found a significant model, $F(2,54)=3.3$, $p=0.044$, adjusted R square=0.08, $f^2=0.12$. Although not significant, participants who did not have sexual contact in the last month had somewhat higher T baseline levels, $\beta=0.27$, $p=0.170$. Being in a relationship was not related to baseline T, $\beta=0.07$, $p=0.711$. These data suggest that most important was sexual activity in the last month, whereas being in a relationship was of no importance.

Dominance

Sociable dominance did not predict a T change in the female condition, $\beta=0.21$, $p=$ns. However, aggressive dominance marginally predicted a T change, $\beta=0.35$, $p=0.058$. The more the participants had an aggressive dominant personality, the greater their T change was during contact with the female stimulus person. Since baseline T was related to aggressive dominance (see below) we included baseline T as a predictor together with aggressive dominance. When added together in the same multiple regression using the enter method we found a significant model, $F(2,27)=6.1$, $p=0.006$, adjusted R square= 0.26, $f^2=0.45$. As participants scored higher on the aggressive dominance scale, their T levels increased more, $\beta=0.50$, $p=0.006$. As participants had a higher baseline T level, the increase in T was lower, $\beta=-0.46$, $p=0.011$.

Finally, the results showed that participants scoring above the mean of the aggressive dominance scale had higher baseline T levels than persons scoring below the mean, $t(57)=-3.2$, $p=0.003$, $d=0.84$, whereas for sociable dominance no effects were found, $t(57)=1.3$, $p=$ns, $d=0.35$ (see Fig. 1).

Discussion

Originally the challenge hypothesis was formulated to explain the relationship between T and behavior in monogamous birds (Wingfield et al., 1990). However, the main results of the present research were in line with predictions from the challenge hypothesis when applied to humans (Archer, 2006). Participants showed an increase in their salivary T level after exposure to a woman and not after exposure to a man. Thus, we did not find evidence for a competitive inter-male interaction in our control condition since for this condition no T changes were found. However, the use of other control groups can be of interest, for example contact with a considerably older woman. Our results are similar to that obtained in an earlier study (Roney et al., 2007), with the difference that we already found a T increase after only 5 min of exposure to a woman, while Roney et al. (2007) found effects after 15 min of exposure.

One of the ultimate functions of T may be to attract mates, since it has been speculated that T could have the proximate function of promoting dominant behavior intended to achieve or maintain high status (Mazur and Booth, 1998) which might increase one's desirability as a sexual partner. This hypothesis is supported by evidence that dominance behaviors of men increases their sexual attractiveness and desirability as a date (Sadalla et al., 1987), and by research showing that men who exhibit more dominant-like behavior make more frequent successful contact with women in bars (Renninger et al., 2004).

The female stimulus persons probably represented the type of women with whom the participants normally form sexual relationships, since the female stimulus persons were rated as moderately attractive, and both participants and stimulus persons were students of approximately the same age. If this reasoning is correct and the hormonal changes are part of a response to a potential partner, it is possible that this response depends on the attractiveness of the woman in question. However, the present results did not show evidence for this. It is possible that the stimulus persons did not differ enough in attractiveness to moderate the T increase or that the increase in T described here is an automatic process which is not influenced by conscious judgments of attractiveness.

While we expected on the basis of the animal literature (Kamel et al., 1975; Bonilla-Jaime et al., 2006) that sexual experience would moderate the hormonal reactions of men to the presence of a woman, we did not find clear evidence for this. However, tentative evidence was found for a higher increase in T during contact with a woman when being sexually active in the last month or more. This promising result did not reach significant levels most likely due to a type II error, since the group sizes were small (Cohen, 1992). Possibly, moderation by sexual experience is more difficult to detect in humans than in animals, since in humans their complex personal experiences may obscure any effect. Perhaps research with more participants and more detailed information regarding the sexual experience will find more unequivocal evidence for moderation of sexual experience on a T response to women.

There were various relationships between baseline salivary T and sexual experience. We found that men who had not been sexually active in the past month or longer had higher T levels. It is possible that a lack of sexual contact in the long term induces a rise of baseline T in the male body, thereby causing a stronger motivation and preparation to engage in mate attraction. Following this reasoning, one of the evolutionary functions of high T may be promoting sexual contact. As previous research did (Burnham et al., 2003; Gray et al., 2004), we also found that men who were involved in a committed, romantic relationship had lower T. This result supports the view that men involved in committed, romantic relationships may be less engaged in seeking mating opportunities. However, when including sexual experience it appeared that lower T levels among committed men were actually driven by recent sexual activity. All the men in our study with a committed romantic relationship had had sexual contact in the last month, and it was therefore probably the lack of sexual contact that induced higher T levels among non-committed men.

The present study is the first study to show that personality differences in dominance influence an increase in T when meeting a woman. We found that only aggressive dominance and not sociable dominance moderated this increase in T. The more the participants had an aggressively dominant personality the more their salivary T increased during contact with a woman. Our study cannot give a definite answer to the important question of whether high T causes dominance or dominance causes high T. But we would like to suggest that aggressively dominant men may have more extreme hormonal reactions when they come into contact with potential partners, i.e. they possibly seek more short term mating opportunities. This reasoning is in line with studies investigating the positive relation between antisocial behavior and short term mating (Ellis, 1988; Charles and Egan, 2005), and with findings that men with higher T are less likely to marry and have a greater likelihood to divorce (Booth and Dabbs, 1993). In addition, high baseline T levels were associated with a lesser T increase. Perhaps those men with high baseline T levels are close to their optimal T level for successful mate attraction. Another physiological possibility is that those men had a lesser increase because negative feedback from their hypothalamic–pituitary–gonadal axis was more sensitive in signaling a decrease of T, due to already high T levels.

We also showed that men with high baseline T were more aggressively dominant. These results are supported by other studies finding that dominance and T are linked. A review by Archer (2006) showed a solid relation between dominance and T with a mean weighted r value of 0.27 ($n = 11$, excluding two studies as outliers). A recent study found that T levels are actually negatively related to prestige (Johnson et al., 2007). Examination of the scales we used revealed that only one item could be related to prestige (for the items see Kalma et al., 1993), and we therefore view our dominance scales as assessing different characteristics than obtained prestige. Our study did not detect a link between T and sociable dominance, while some previous studies did show such a relationship. T and social dominance (i.e. sociable dominance) have been found to be related among boys (Schaal et al., 1996; Tremblay et al., 1998) and among prisoners (Ehrenkranz et al., 1974). The discrepancy between these findings and those of the present research may be due to differences in measuring social dominance. To determine social dominance, this study used a self reporting questionnaire, while the other studies used ratings of toughness and leadership by unfamiliar peers after 3 h interaction (Schaal et al., 1996; Tremblay et al., 1998), and recognition as socially dominant by inmates and prison staff (Ehrenkranz et al., 1974). There is some evidence that self report can yield lower effect sizes in T studies when comparing it to behavioral measures (for a review see Archer et al., 2005) and therefore it is possible that our study did not provide enough power to detect an effect.

Most findings from this study lend support for evolutionary theorizing. Independently building upon previous findings, we showed that T levels increased in men after contact with women. This increase is probably an important mechanism through which men acquire partners. At the same time, this T response seemed to be moderated by individual differences in aggressive dominant personality. Results from this study fit into theorizing viewing an increase in T as an evolved human response, activating receptors in organs and the nervous system to prepare the human body for mate attraction. Potentially interesting for further research are measuring other types of dominance like prestige or eminence as well as measuring the influence of status disputes on T.

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Chapter 3

Competition between men and the release of testosterone

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Testosterone responses to competition: The opponent's psychological state makes it challenging

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ABSTRACT

Testosterone (T) increases after competition have typically been attributed to winning, yet there is also evidence that being victorious is not in itself sufficient to provoke a T response. Instead, it has been proposed that T responses are moderated by psychological processes. Here, we investigated whether the opponent's psychological state affected hormonal changes in men competing face to face on a rigged computer task. The results show that, irrespective of outcome, the competition led to increases in heart rate and T levels. We found that the T levels of the participants increased more when their opponents had high self-efficacy and that T levels were not influenced by participants' own psychological state. Furthermore, the T levels of losers, but not winners, increased more when their opponent judged the competition to have low importance. The findings from this study are consistent with the challenge hypothesis. Both winners and losers were being challenged to compete for social status; therefore their T responses did not differ. In addition, the psychological state of the opponent makes a competition challenging and subsequently triggers T responses.

1. Introduction

Changes in testosterone (T) during competitive interactions have attracted a lot of attention in behavioural and endocrinological research (Salvador, 2005). Two main hypotheses have been proposed to explain the function of T in competition. These are the biosocial theory of status (Mazur, 1985; Mazur and Booth, 1998) and the challenge hypothesis (Wingfield et al., 1990; Archer, 2006).

According to the biosocial theory of status, the relationship between status and T is reciprocal. The model predicts that in physical or non-physical competition, winning and thereby gaining status causes an increase in T, while losing decreases T levels. Some studies have found support for these predictions in humans (Mazur and Lamb, 1980; Elias, 1981; Booth et al., 1989; Gladue et al., 1989; Mazur et al., 1992; McCaul et al., 1992), while others have found no different T change between winners and losers (Salvador et al., 1987; Gonzalez-Bono et al., 1999; Suay et al., 1999; Gonzalez-Bono et al., 2000; Filaire et al., 2001; Mehta and Josephs, 2006). Because of this mixed support it has been proposed that winning or losing is not in itself enough to cause T levels to shift, but that T responses in reaction to competition are moderated by psychological processes (Salvador, 2005; Salvador and Costa, 2009). In support of this it has been shown that a high motivation to win is positively related to T changes during competition (Suay et al., 1999) and a high power motivation predicts T increases among winners and decreases among losers (Schultheiss et al., 2005). Furthermore, it has been found that among winners a positive mood accompanies a T increase (Booth et al., 1989) and similarly, it has been shown that men who increase their T levels during a competition express a desire to compete again after social defeat but not after victory (Mehta and Josephs, 2006; Carré and McCormick, 2008).

From an evolutionary perspective, the challenge hypothesis (Wingfield et al., 1990; Archer, 2006) predicts that T levels should increase in challenging contexts that are relevant for reproduction. This hypothesis was originally focused on birds (Wingfield et al., 1990) but has also been applied to humans (Archer, 2006). Recent studies have found direct support for this hypothesis, showing that an informal encounter with a potential mate induces a T rise in men after 15 min of contact (Roney et al., 2007) or even as little as 5 min (van der Meij et al., 2008). The challenge hypothesis also predicts that T increases throughout a competitive interaction and may in the long-term cause a further rise of T in the winner of the competition. The outcome of such an interaction can be relevant for reproductive success, since it could affect the status, and thus the mating success of the winner. Therefore, according to the challenge

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hypothesis, in reaction to a challenging and evolving competition, T should first rise throughout the competition for both winners and losers and, only when considering a long-time interval, further increase among the winners.

Several non-human studies have looked at the impact of the opponent on T changes during competition. For example, cichlid fish (*Oreochromis mossambicus*) and Japanese quail (*Coturnix japonica*) do not increase their T levels when fighting against a mirror image of themselves but they do respond with increased androgen levels when fighting a real opponent (Oliveira et al., 2005; Hirschenhauser et al., 2008, 2004). To explain these findings it has been proposed that to mount a T response, information or feedback from the fighting ability of the opponent are necessary components (Hirschenhauser et al., 2008). In the experiment reported here, we tested this hypothesis in humans. Our aim was to investigate whether the characteristics of the opponent are a crucial component in provoking a T increase.

Possible psychological processes of special significance include the motivation and perceived self-efficacy of the opponent. Perceived self-efficacy refers to beliefs in one's capabilities to organize and execute the courses of action required to manage prospective situations (Bandura, 1995). An opponent who has a strong sense of efficacy exerts greater effort to master a challenge (Bandura, 1982), and may more easily provoke a competitive interaction and augment T levels in the individual with whom it is interacting. We therefore predicted that T increases during a non-physical contest in men are enhanced when the opponent reports a high self-efficacy, expects to win and perceives the competition as important. According to the biosocial theory of status, these moderating effects could depend on the outcome of the competition. However, based on the challenge hypothesis, we expected that these moderating effects would be similar for winners and losers, as this hypothesis states that the competitive interaction in itself is relevant, and only in the long-term the outcome can be relevant for T levels.

We performed an experiment in which pairs of men engaged face to face in a competitive computer task. This task was designed to intensify the competitive nature of the interaction and to be sensitive to changes in social status. The outcome of the competition was rigged, so that we could assess the direct effect of winning or losing without any confounding influence of the participants' true abilities. The psychological effects produced by the competition were analyzed by measuring mood changes and situational appraisal. To investigate the physiological reaction to the competition we recorded heart rate and collected saliva samples to measure T.

2. Methods

2.1. Participants

Eighty-four male students, aged 18–29 years (21.2 ± 0.31), participated in this study in exchange for €10. We assessed participants' body mass and measured subjective socio-economic status (Adler et al., 2000) to provide some general characteristics of our sample. The participants had a mean body mass index of 23.4 (± 0.44) and they reported a mean subjective socio-economic status of 6.6 (± 0.09). The participants were recruited from cafeterias and classrooms of the University of Valencia. All were first interviewed and asked to complete a questionnaire, on the basis of which we excluded those enrolled in a psychology degree, smoking more than 5 cigarettes a day, or reporting a serious medical or psychological problem or drug abuse. Participants were also excluded if they were using any medication directly related to cardiac, emotional or cognitive function, or one that was able to influence hormonal levels, such as glucocorticoids or β-blockers.

Up until 1 day before the experiment, the participants were asked to maintain their typical habits, including sleeping for as long as usual. Additionally, they were instructed to refrain from alcohol consumption and any heavy physical activity the day before the session, and during 2 h immediately beforehand to drink only water and avoid any stimulants, such as coffee, cola, caffeine, tea or chocolate. All the participants received verbal information about the study and signed an informed consent form. This study was approved by the ethical committee of the Faculty of Psychology (University of Valencia).

2.2. The competition

Each participant competed with another participant on a computer task. Unknown to them, the outcome of this task was actually manipulated by the experimenter, with participants randomly assigned to the winner or loser conditions. The participants were told that the test used in this experiment was an important test that was commonly used by companies and psychologists to assess if a person is intelligent or not. To intensify the competition, the participants were informed that the winner of the competition would receive €10 and the loser €5, but at the end of the study they all received €10, since the result was manipulated.

The competitive task consisted of items similar to those used in intelligence tests. To familiarise themselves with the task, the participants first completed a practice session with feedback indicating the correct answer. During the subsequent task, they were simultaneously presented with the same item and within 30 s had to choose the correct answer from four, five or six possibilities. They were informed that they would win an item if they were the first to enter the correct answer, but in reality the computer task determined for every item which of the contestants won and lost. During the task the participants were seated roughly 1 m apart on opposite sides of the same table, each behind their own computer screen and facing their opponent. The experimenter remained clearly visible to the participants and observed the progress of the task.

There were 27 items in all, divided into three sets of nine items each (visual–spatial, mathematics and analogies) and taking a total of 18 min to complete. After contesting a given item, the message "*you win!*" appeared on the winner's screen, while the loser's screen showed "*you lose!*", and the loser's specific buzzer was loudly heard. The participant with the most wins at the end of the competition was declared the overall winner. During the first part the participants in the loser condition won five items, for the second part they won only two items and in the last part they did not win any items at all. Both contestants could constantly see their score and that of their opponent in the right corner of their screen. After the first part of the competition the experimenter encouraged the participants by telling them "*the both of you are doing really well*". After the second part the experimenter commented to the winner "*you are doing really well*" and to the loser "*you can still beat him*". At the end of the task their screen showed them a message with their end score, together with a statement of whether they had lost or won and the amount of money they could expect to receive (€10 for the winner, €5 for the loser).

2.3. Procedure

Upon arrival at the laboratory the participants were greeted by the male experimenter and were briefed on the general procedure of the study. Unknown to themselves, half of the participants were randomly assigned to the loser condition and the other half to the winner condition. They filled in an informed consent form, their height and weight was measured and a heart-rate monitor was put on. All participants were alone in a separate room when they filled in the questionnaires of this study to avoid any social influence of their opponent while answering the questionnaires.

Ten minutes after arrival at the laboratory the participants provided their first saliva sample (T1) for the measurement of their basal T level. Immediately after this, they were seated at opposite sides of the same table and individually practiced on the computer task (duration 10 min). Next, they went to a separate room where they filled in a questionnaire concerning their psychological state and a questionnaire measuring their mood (duration 5 min). Then the competitive task took place (duration 18 min).

After the competition they each went to a separate room and filled in questionnaires concerning their mood and situational appraisal (duration 10 min). After these questionnaires (10 min after the competition and approximately 45 min after T1), the participants provided a second saliva sample (T2). Finally, they were debriefed about the true nature of the experiment and each received €10. The whole procedure lasted 1 h and sessions were held from 16.00 to 19.00 h to control for circadian fluctuations in T (Dabbs, 1990).

2.4. Questionnaires and scales

2.4.1. Psychological state

Before the computer task, the self-efficacy (Bandura, 1997) of the participants was measured. This study operationalised self-efficacy with the following two items, both on a scale from 1 (none) to 100 (very much): (i) What do you think is your capacity to win this competition? (ii) How much confidence do you have that you will win this competition? The scores on both items were averaged and had a Cronbach's alpha of 0.88. Motivation was measured by asking (again on a scale from 1 to 100): How important is it for you to win this competition? Finally, they were asked about their expectancy: do you expect a victory (1) or a defeat (2)?

2.4.2. Situational appraisal

After the competition participants completed five questions regarding the perception of the competition. They were asked about their perceived frustration, effort, importance, difficulty and stress (e.g. *How much effort did the task require?*). These questions were formulated based on a previous study by Baggert et al. (1996). Participants answered each question on a 5-point Likert scale (1 = not at all, 5 = extremely).

2.4.3. Mood

We measured the positive and negative mood of the participants before and after the competition by using the Spanish version (Sandín et al., 1999) of the PANAS questionnaire (Watson et al., 1988). The scale consisted of 10 items describing positive mood (e.g. enthusiastic, activated) and ten describing negative mood (e.g. ashamed, irritable), for each of which the participants were required to indicate the extent to which it corresponded with their current mood. For negative feelings we found a Cronbach's alpha of 0.87 before the competition and an alpha of 0.80 afterwards; for positive feelings the figures were 0.85 beforehand and 0.89 afterwards.

2.5. Heart rate

During the session the heart rate of the participants was recorded at 5-s intervals using a Polar heart-rate monitor. This technique provides a valid measure of heart rate (Goodie et al., 2000). Artefacts were manually removed from the heart-rate register. To analyze these data, we divided the heart-rate register into five phases: baseline, the first, middle and last parts of the competition and a recuperation phase. Not all phases were of equal length, so we took from each phase the middle 3 min and used these to calculate an average heart rate for the phase. Five participants were excluded from this analysis: three had an incomplete heart-rate register and two outliers whose heart-rate average differed by more than three standard deviations from the mean.

2.6. Hormonal assays

Participants provided two saliva samples by depositing 5 ml of saliva into plastic vials. The samples were frozen at −20 °C and shipped to the endocrinology laboratory at the University Medical Centre Utrecht, the Netherlands. Depending on the starting time of the session, the first saliva sample (T1) was approximately taken at 16.10 or 18.10 and the second saliva sample (T2) was taken at approximately 16.55 or 18.55. Second saliva samples were taken 10 min after completing the competition since psychological stimulation needs some time to affect T levels (Hellhammer et al., 1985). The saliva samples were tested using radio-immunoassays. Salivary T was determined with the double antibody T kit (DSL-4100) from Diagnostic Systems Laboratories Inc. (Webster, TX), according to the modifications of Granger et al. (1999). The detection limit was 4 pmol/L. The mean inter-assay coefficient of variation was 7.5% (±0.90) and the mean intra-assay coefficient was 5.3% (±1.30). Two outliers were removed, since one participant had an extremely low baseline T level of 28 pmol/L (differed 2.8 standard deviations below the mean, including this outlier did not influence the overall conclusions of the study) and another participant's T measurements differed by more than three standard deviations from the mean.

2.7. Statistical analysis

We first performed several independent *t*-tests to assess if there were any differences between the winning and the losing conditions for the socio-demographic variables and the psychological and physiological measures taken. We used a Pearson correlation and an independent *t*-test to investigate if baseline T was related to the opponent's psychological state. To investigate if the T change of opponents were related we performed a Pearson correlation. Spearman's Rho was performed to investigate if T levels were related to the sampling times.

To investigate if the competition and its outcome provoked any changes in positive and negative mood, we performed two repeated-measures ANOVAs with outcome (winner or loser) as a between-subjects factor and positive and negative mood as within-subject factors (before versus after the competition). To examine if the competition influenced heart rate we performed another repeated-measures ANOVA with outcome (winner or loser) as a between-subjects factor and phase (baseline, first competitive, middle competitive, last competitive and recuperation) as a within-subject factor. To investigate if the competition produced any difference in T levels we performed a repeated-measures ANOVA, with outcome (winner or loser) as a between-subjects factor and moment (first or second T measurement) as a within-subject factor. When a significant effect was found for any of these ANOVAs, post hoc planned comparisons were performed using the Bonferroni adjustments for the *p*-values. Where the assumption of sphericity was violated, we used the Greenhouse-Geisser adjustment.

To test for an interaction between the effects of the outcome of the competition and the opponent's psychological state on the change in T, we used regression analyses following Aiken and West (1991). Using forward stepwise regression, separate moderator regression analyses were performed for the participant's own and the opponent's self-efficacy, perceived importance of the competition and expectancy. The outcome of the competition was dummy-coded as 0 for losing and 1 for winning. Following Mehta et al. (2008), we entered T2 as dependent variable, in Step 1 we entered T1 as a covariate, in Step 2 we entered outcome and psychological state and in Step 3 we entered the interaction term psychological state × outcome. When Step 3 was significant, post hoc significance tests of the slopes were performed with dependent variable the unstandardized residuals scores from regressing T1 on T2. No violation of the normality assumption was found in the *T* values, so there was no need to transform them. A value of $p < 0.05$ (two-tailed) was considered statistically significant. Statistical tests were performed with SPSS version 15.0. When not otherwise specified values are mean ± SEM.

3. Results

3.1. Preliminary analysis

There were no differences between the winning and losing conditions for the following variables: age, height, weight, BMI, subjective socio-economic status, educational level, average weekly physical activity and alcohol use (*t*-tests, all $p \geq 0.10$). Before the competition there were no differences between the conditions for positive and negative mood or psychological state ($p \geq 0.14$). Baseline heart rate and T did not differ between winners and losers ($p \geq 0.67$). Baseline T was not correlated with the opponent's perceived importance of the competition ($r = -0.097$, $p = 0.388$), but was higher when their opponent reported a lower self-efficacy, $r = -0.295$, $p = 0.007$, and expected a defeat instead of a victory, $t(80) = -2.55$, $p = 0.013$. The T change (T2–T1) of opponents was not correlated ($r = 0.127$, $p = 0.434$). The time of saliva collection was not correlated with T1 ($r = 0.065$, $p = 0.562$), T2 ($r = 0.037$, $p = 0.742$) nor with the T change (T2–T1), $r = -0.053$, $p = 0.633$.

3.2. Psychological effects of the competition

3.2.1. Situational appraisal

Losers perceived the competition as more frustrating than winners, $t(71.68) = -7.68$, $p = 0.003$, and afterwards viewed it as less important than winners did, $t(82) = 2.70$, $p = 0.008$. No differences were found for perceived effort, perceived stress or perceived difficulty of the task (*t*-tests, all $p \geq 0.16$).

3.2.2. Mood

There was a significant interaction between moment of measuring positive mood and outcome of the competition, $F(1,82) = 24.64$, $p < 0.001$. Among winners, positive mood did not change, $F(1,82) = 1.41$, $p = 0.239$, whereas among losers, positive mood decreased $F(1,82) = 34.04$, $p < 0.001$. There was also a significant interaction between moment of measuring negative mood and outcome of the competition, $F(1,82) = 15.36$, $p < 0.001$. Among winners, negative mood decreased, $F(1,82) = 26.59$, $p < 0.001$, while among losers, negative mood did not change $F(1,82) = 0.15$, $p = 0.701$.

3.3. Physiological effects of the competition

3.3.1. Heart rate

There was a significant effect of phase on heart rate, $F(2.03,156.27) = 67.95$, $p < 0.001$, but no interaction between outcome and phase on heart rate, $F(2.03,156.26) = 0.60$, $p = 0.553$. Overall, heart rate was higher in the three competitive phases than at baseline levels (all $p < 0.001$), and during the recuperation phase it decreased to below baseline levels ($p = 0.006$). The mean heart rate was 76.5 bpm (±1.4) at baseline, in the first competitive phase 82.2 bpm (±1.5), in the middle competitive phase 82.5 bpm (±1.4), in the last competitive phase 79.3 bpm (±1.4) and in the recuperation phase 74.6 bpm (±1.3). Heart rate was highest in the middle phase of the competition, with an average increase of 8.2% (±0.8) over baseline levels.

3.3.2. Testosterone

There was a significant effect of moment of collecting the saliva sample on T, $F(1,80) = 14.74$, $p > 0.001$, but no interaction between the outcome of the competition and moment of collecting the saliva sample on T, $F(1,80) = 0.70$, $p = 0.406$. Overall, the T levels of the participants increased on average by 16.4% (±3.9) between the first and second measurement, from 266.4 pmol/L (±8.5) to 300.6 pmol/L (±10.5). For descriptive purposes we reported the *T* values for winners and losers separately (see Fig. 1). Losers increased their T

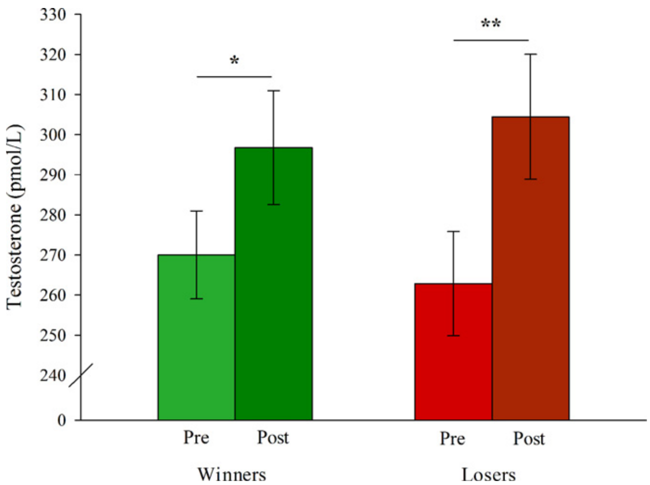

Fig. 1. Mean (±SEM) testosterone levels before (pre) and after (post) the competition separated for winners and losers. $^{*}p < 0.05$, $^{**}p \leq 0.001$.

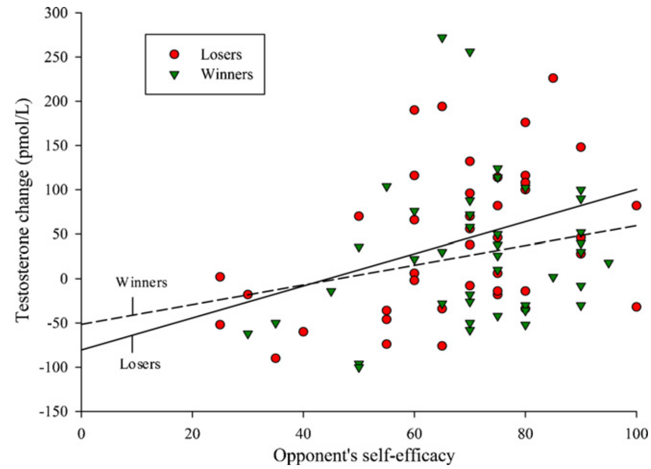

Fig. 2. The relationship between testosterone changes and the opponent's self-efficacy, plotted for winners and losers.

levels on average by 20.5% (±6.0) in response to the competition, $F(1,80) = 10.92$, $p = 0.001$, whereas winners increased their T levels by 12.2% (±4.9), $F(1,80) = 4.51$, $p = 0.037$.

3.4. Participant's own and opponent's psychological state as a moderator of a T response

3.4.1. Participant's own psychological state

Three different moderator regressions analysis were performed for each variable measuring the psychological state of the participants. T2 was used as dependent variable and in Step 1 baseline T was entered as a covariate. Entering Step 2, including outcome and participant's own psychological state as predictors (either: self-efficacy, importance, or expectancy), did not increase the amount of variance explained in T2 for any of the three regressions analysis ($p \geq 0.381$). Finally, entering Step 3, including the interaction term (outcome × psychological state) as predictor, did not increase the amount of variance explained in T2 for any of the three regressions analysis ($p \geq 0.606$).

3.4.2. Opponent's self-efficacy

After controlling for T1 in Step 1, entering Step 2 in the model, including outcome and the opponent's self-efficacy as predictors, increased the amount of variance explained in T2, $\Delta F(2,78) = 3.106$, $p = 0.050$, adjusted $R^2 = 36.0\%$, $\Delta R^2 = 4.9\%$. No main effect was found for outcome ($\beta = -0.091$, $p = 0.314$), but we did find a main effect of opponents reported self-efficacy, $\beta = 0.222$, $p = 0.020$. Fig. 2 shows that the T change was bigger when their opponent reported a higher self-efficacy. Entering the interaction term in Step 3 did not increase the amount of variance explained in T2, $\Delta F(1,77) = 0.87$, $p = 0.355$.

3.4.3. Opponent's perceived importance of the competition

After controlling for T1 in Step 1, entering Step 2, including outcome and opponent's perceived importance of the competition as predictors, did not increase the amount of variance explained $F(2,78) = 0.53$, $p = 0.592$. Entering the interaction term in Step 3 increased the amount of variance explained, $\Delta F(1,77) = 7.75$, $p = 0.007$, adjusted $R^2 = 37.3\%$, $\Delta R^2 = 6.0\%$. In this step there was a significant main effect of outcome ($\beta = -0.661$, $p = 0.005$) and perceived importance of the competition ($\beta = -0.358$, $p = 0.011$). However, these main effects were qualified by a significant 2-way interaction between opponent's perceived importance of the competition and outcome, $\beta = 0.672$, $p = 0.007$ (see Fig. 3 for absolute values). Using unstandardized residuals scores to test the slopes, revealed that, among losers, T increased more when the opponent thought the competition was of low importance, $\beta = -0.44$, $t(37) = -2.62$, $p = 0.011$, but among winners, how important the opponent the competition perceived did not affect T levels, $\beta = 0.17$, $t(37) = 1.23$, $p = 0.221$.

3.4.4. Opponent's expected result

After controlling for T1 in Step 1, entering Step 2, including outcome and the opponent's expectancy as predictors, did not increase the amount of variance explained, $\Delta F(2,78) = 1.78$, $p = 0.176$. Entering the interaction term in Step 3 did not increase the amount of variance explained, $\Delta F(1,77) = 0.39$, $p = 0.533$.

4. Discussion

Our study shows that the T responses during a competitive interaction between two men are moderated by the opponent's perceived self-efficacy, and is not influenced by one's own psychological state. We found that T levels increased when the opponent felt more capable and confident. This extends the evidence that the hormone T plays an important role in many human social behaviours (van Anders and Watson, 2006), indicating that the opponent's state is a crucial element in provoking a T response.

Our results complement some of the findings in the literature on non-human animals. In some species feedback of the oppo-

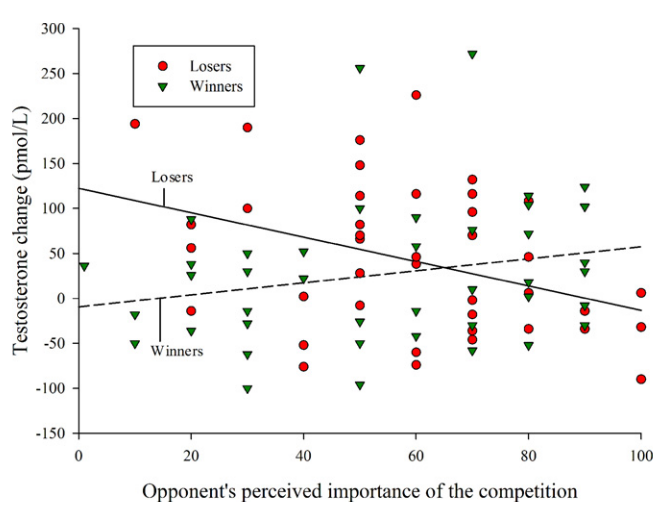

Fig. 3. The relationship between testosterone changes and the opponent's perceived importance of the competition, plotted for winners and losers.

nent is essential to provoke T changes during competition (Oliveira et al., 2005; Hirschenhauser et al., 2008). Here we have shown that in humans the influence of the opponent's feedback is also present, although it is in a different form. Humans most likely deduce information about their opponent's competitive ability from behavioural cues shown by that opponent. Opponents scoring high on self-efficacy probably exhibited non-verbal behaviour that implied their engagement and likewise made the competition challenging, which provoked an increase in T levels among competitors. During the competition, participants were seated at opposite sides of the same table and it was therefore relatively easy for them to deduce their opponent's psychological state by observing their reactions to the competition. Behaviours that provided information about the psychological state of the opponent have to have been non-verbal since participants were not allowed to talk during the competition. According to Bandura (1982), high self-efficacy causes behaviours such as persistence, assuredness and protesting, whereas low self-efficacy causes resignation, despondency and apathy. In our study, opponent's behaviours that could be an indicator of self-efficacy could have been: an active vs. depressed body-posture, apathy vs. attentiveness during the task and confidence vs. doubt during answering the items. To confirm this interpretation, research in the future should directly measure behaviour while linking it to T changes and the opponent's psychological state.

Our study did not find support for the biosocial theory of status since our results do not show a reciprocal relationship between T and winning, in contrast to some other studies (Gladue et al., 1989; Mazur et al., 1992). Ten minutes after the competition T had increased not only among winners but also among losers. This discrepancy can be explained in two ways. One possibility is that the observed T response did not reflect an actual change in social status. However, care was taken to make the competition sensitive to status alterations. For example, the non-physical competition used was especially designed to be as confrontational and competitive as possible, hence the close physical proximity of the participants, the monetary incentive and the observing experimenter. Furthermore, although the competition was non-physical, the heart rate of the participants increased substantially and the mood changes and subsequent perception were outcome-specific. Another explanation is perhaps more likely, since several authors have argued that perceived outcome is more relevant than real or objective outcome (Gladue et al., 1989; Gonzalez-Bono et al., 1999; Serrano et al., 2000). Although this study did not measure perceived outcome but real outcome, it could be that winning is not in itself enough to provoke a T increase, but it rather depends on the social context and on cognitive variables (Salvador, 2005). In support of this last notion, we found that only the opponent's, and not so much their own, perceived self-efficacy was an important cognitive factor that influenced the change in T.

The main findings of this study can also be interpreted from an evolutionary viewpoint. The competitive situation in this study was designed to provoke a challenge for social status, and according to the challenge hypothesis (Archer, 2006), T levels should then increase to meet this challenge. Although we did not measure competitiveness directly, our findings do suggest that a confident and capable-feeling opponent augments competitiveness and therefore increase the possible gains or losses in social status. An adaptive response to the increased value of the outcome is to increase competitiveness and consequently increase T levels even further.

The observed T rise may not only be explained by the challenge hypothesis, but also by reward processing since all participants received a monetary reward. Animal studies have shown that T has rewarding properties, for example, rats and mice prefer environments which are previously paired with T injections (Alexander et al., 1994; Arnedo et al., 2002, 2000). Therefore, it could be that those participants that increased their T levels learned that the competition was pleasant and worth repeating (Mehta and Josephs, 2006). Following this rationale, one might expect that the T increase would be greater in winners than in losers since they were informed that winners would receive double the money. However, our results did not show a stronger T response for winners than for losers. Therefore, it seems that reward processing is limited in explaining our findings.

Another important finding of this study was that, the T response provoked by the competition was moderated by an interaction between status, i.e. the outcome of the competition, and the opponent's perceived importance of the competition. The T levels of winners were not significantly affected by how important their opponent thought the competition was, but in losers T increased when their opponent did not perceive the competition to be important. This result seems to be at odds with the results mentioned earlier, but can actually be explained by the competitive nature of our competition. Losing to an opponent who is not motivated, in that he perceives the competition to be unimportant, probably provoked a larger loss of social status, since despite the low motivation of the opponent a loss could not be avoided. Behaviours that could have indicated a lack of motivation among winners are: emotional indifference upon winning an item and paying little attention to the task. It could be the case that this situation frustrated and challenged losers and as a reaction T increased to augment competitiveness and regain social status. In support of this explanation is the finding that losers judged the competition as more frustrating than winners, and that losers dropped significantly in their positive mood. In addition, there is evidence that the relationship between T and cognitive factors can be different for winners and losers. For example, Gonzalez-Bono et al. (1999) found that a T response was negatively related to external attribution in winners, but positively related in losers.

To our knowledge, this is the first study showing a moderating influence of the opponent's psychological state on T responses to competition. Our results fit with the view that when trying to identify the role of T in competition, one must control for a wide range of context-dependent factors. One such important factor is the interaction between T and the psychological state of the opponent.

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Chapter 4

Cortisol release in men during interactions with attractive women

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Contact with attractive women affects the release of cortisol in men

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ABSTRACT

Previous studies have shown that situations relevant for human mating can affect the levels of many hormones. This study focused on the hypothalamus–pituitary–adrenal axis by measuring salivary cortisol levels in 84 young men prior to and after a period of short social contact with a woman or man. Results showed that after contact with another man the cortisol levels of the participants declined according to the circadian release pattern of cortisol. However, cortisol levels in men declined less when they had contact with a woman. Furthermore, cortisol levels of men increased when they perceived the woman with whom they had contact as attractive. Our findings provide indirect evidence for the role of the hypothalamus–pituitary–adrenal axis in human courtship. During social contact with attractive women, moderate increases in cortisol levels may reflect apprehension over an opportunity for courtship.

Introduction

Hormones have been related to many aspects of human social behavior (van Anders and Watson, 2006). Many studies investigating the hormonal changes in men with respect to the function of sexual activity and mate acquisition have focused on the hypothalamus–pituitary–gonodal axis by measuring changes in salivary testosterone levels. For example, testosterone increases after men engage in sexual intercourse (Dabbs and Mohammed, 1992), after sexual activity resulting in an orgasm (Knussman et al., 1986) and even after watching erotic videos (Hellhammer et al., 1985; Stoléru et al., 1993). However, explicit sexual stimuli are not the only cues that provoke testosterone increases, as a non-physical social contact for 15 min or for just 5 min with novel women has been shown to provoke an increase in male testosterone levels (Roney et al., 2007; van der Meij et al., 2008). It is thought that in these contexts testosterone functions to promote behavior or cognitions that facilitate mate acquisition or mating directly (Roney et al., 2003). Besides testosterone other hormones have also been found to be related to the mating and sexual behavior of men. For example, sexual arousal causes an increase in vasopressin levels (Murphy et al., 1987), masturbation provokes the release of prolactin (Exton et al., 2001; Krüger et al., 2003) as well as epinephrine and norepinephrine (Krüger et al., 2003) and sexual intercourse stimulates the release of oxytocin (Carmichael et al., 1994). This study focused on the hypothalamus–pituitary–adrenal axis (HPA) by studying its end product; cortisol, and specifically investigated if this hormone changes in response to a brief social contact with a novel woman.

Originally it was thought that the release of cortisol was primarily caused by non-specific psychological or physiological stressors (Selye, 1956). Later studies have focused on the exact nature of these stressors and found that in situations where physical well-being is perceived to be threatened, e.g. jumping out of an airplane (Chatterton et al., 1997), can provoke an increase in the secretion of cortisol. In addition to physically threatening contexts it has also been proposed that cortisol responses are elicited when the psychological well-being is threatened (for a review see Dickerson and Kemeny, 2004). More specifically, the social self preservation theory predicts that cortisol increases when individuals are motivated to maintain their social status or acceptance. Evidence for this theory is provided by cortisol increases in situations when one's self-identity can be negatively judged by others (Seeman et al., 1995), and when the outcome of a negative situation is beyond control (e.g. Peters et al., 1998; Salvador et al., 2003). The secretion of cortisol in response to stress has an adaptive function as it diverts energy to exercising muscles, enhances cardiovascular tone, and suppresses unessential processes such as digestion, growth and reproduction (Sapolsky et al., 2000). However, exposure to physical or psychological stressors for a long period of time may cause chronically elevated cortisol levels that can have adverse effects on health as it worsens various disorders, such as myopathy, adult-onset diabetes, hypertension, amenorrhea and impotency (Munck et al., 1984; McEwen, 2008).

Many researchers view the release of cortisol as a coping mechanism to aversive psychological or physical conditions. However, there is also a substantial amount of research that suggests that cortisol may have other distinct functions. For example, in the non-

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human animal literature it has been shown that corticosterone (the non-human version of cortisol) facilitates pair bonding in male prairie wolves but not in females (DeVries et al., 1996). Other studies have consistently found that corticosterone increases after copulation in a wide range of species, including stallions, bulls, pigs (Borg et al., 1991; Rabb et al., 1989), rats (Retana-Marquez et al., 1998) and mice (Bronson and Desjardins, 1982). Nevertheless, in male rats, corticosterone levels may increase up to two fold after males are exposed to physical or non-physical contact with a receptive or non-receptive female (Bonilla-Jaime et al., 2006). In humans the effect of cortisol on male sexual functioning is less clear. For example, while some studies have found that cortisol decreases after watching erotic videos (Uckert et al., 2003), some have found that cortisol levels do not change after watching such videos (Rowland et al., 1987; Carani et al., 1990; Exton et al., 2000). Furthermore, chronically elevated cortisol levels such as those caused by Cushing's Syndrome tend to decrease sexual functioning (Starkman and Schteingart, 1981), whereas the administration of adrenocorticotropic hormone (which stimulates cortisol secretion) to patients with erectile dysfunction increases their sexual performance (Isidori et al., 1984).

Only one recent study assessed if men increase their cortisol levels in response to contact with women (Roney et al., 2007). In the first experiment of this study, men had to wait with a female confederate of the experimenter or had to wait alone. Their results showed that compared with waiting alone, cortisol increased after social contact with a woman. In their second experiment men interacted with a female experimenter who attempted to be flirtatious and signal interest or with a male experimenter who attempted a friendly conversation. This time they found that there was a non-significant cortisol increase after contact with a female experimenter and a significant decrease in cortisol after contact with a male experimenter. These findings suggest that it depends on the social context whether contact with women provokes an increase in male cortisol levels.

The present study tried to clarify the role of cortisol changes in men who are in a social environment where there is the potential for courtship. But when do men perceive a situation as potentially suitable to engage in courtship? In humans, due to our psychological complexity, the perception of such a situation is probably quite variable. In this study we considered that for most men the presence of an attractive woman may induce the perception that there is an opportunity for courtship. While some men might avoid attractive women since they might think they are 'out of their league', we predicted that the majority of men would respond with some apprehension and a concurrent hormonal response. To test this hypothesis, our study investigated the hormonal responses of men when they came into contact with a novel woman. An informal setting was staged in which male participants had to wait in a waiting room situation with either a female confederate or a male confederate. Salivary cortisol levels were measured before and after the contact period. We expected that as the female confederate was perceived as more attractive, participants would show a more pronounced change in cortisol after meeting this woman, whereas the perceived attractiveness of the male confederate would not affect cortisol levels.

Method

Participants

Eighty-four male students (mean age: 21.2 years ± 0.32) participated in this study in exchange for €10. The participants had a mean body mass index of 23.5 (±0.46) and were all Caucasian. Subjective socio-economic status (Adler et al., 2000) was measured on a scale from 1 (lowest) through 10 (highest) and the participants reported a mean subjective socio-economic status of 6.6 (±0.09). To recruit participants a male and female research assistant approached men in the cafeterias of the University of Valencia and held talks just before the start of several lectures.

All participants were first interviewed by a male or female collaborator and were asked to complete a questionnaire. We excluded individuals who were not heterosexual (open question: what is your sexual orientation?), who were enrolled in a psychology degree, and those who smoked more than 5 cigarettes a day or reported a serious medical or psychological problem or drug abuse. Participants were also excluded if they were using any medication directly related to cardiac, emotional or cognitive function, or one that was able to influence hormonal levels, such as glucocorticoids or β-blockers. One participant was excluded from analyses because after participating he indicated he was bisexual.

Up until 1 day before the experiment, the participants were asked to maintain their typical habits, including sleeping for as long as usual. Additionally, they were instructed to refrain from alcohol consumption and any heavy physical activity the day before the session. Furthermore, during the 2 h immediately prior to the session participants were asked to drink only water and avoid any stimulants, such as coffee, cola, caffeine, tea or chocolate. All participants received verbal information about the study and signed an informed consent form about the general procedure of the study and the measurements taken. Participants were not informed that they would have to wait for 5 min with another individual. This study was approved by the ethical committee of the Faculty of Psychology (University of Valencia).

Stimulus persons

Each participant came into contact with either a male or female confederate of the experimenter. In order to achieve this, twelve men and six women played the role of stimulus person. Confederates (mean age: 23.33 years ± 0.55) were chosen on the basis of being moderately attractive falling within an age matched range to the participants. After the contact period, each participant rated the attractiveness of the stimulus person they encountered on a scale from 1 (not attractive) to 7 (very much attractive). The male stimulus persons received an average attractiveness rating of 2.37 (±0.23) and the female stimulus persons received a 4.73 (±0.18). All stimulus persons received the instructions to engage in friendly conversation in a natural manner, were instructed to act as if they were participants in the same study, and were told to allow long pauses if the participants elected not to talk.

Procedure

Upon arrival at the laboratory the participants were greeted by the male experimenter and were briefed on the general procedure of the study. To avoid confounds, the experimenter did not engage socially and kept contact to a minimum. Participants filled in an informed consent form and their height and weight was measured.

As part of a larger study participants first performed a competitive computer task which randomly assigned half of the participants to a winner condition and the other half to a loser condition (for detailed information see: van der Meij et al., 2010). On this task, participants competed face-to-face on items similar to those used in intelligence tests. At the end of the task their computer screen announced if they had won or lost. Participants were told that winners would receive €10 and losers €5. However, the outcome of the task was manipulated by the experimenter and therefore at the end of the experiment each participant received €10. Subsequent to this study, for each previous condition half of the participants were then randomly assigned to have contact with a man and the other half to have contact with a woman.

Approximately 5 min after having heard the explanation of the study participants provided a saliva sample (C1) for the measurement of their cortisol level and worked on the computer task. Ten minutes after the completion of this task, the participants provided another saliva sample (C2). Participants were then brought into a room where they were instructed to work on a Sudoku. Within this room there was a confederate who appeared to be another participant completing a similar puzzle task. Upon entering the room the experimenter indicated he did not have the correct version of the puzzle for the participant. The participant and stimulus person were then asked to wait, so the experimenter could get the correct version. The experimenter then left and the participant and the stimulus person were left alone to wait together for 5 min.

After this, the experimenter returned with the correct version. The participants received the instruction to work on the Sudoku in a relaxed manner and were told that the only purpose of the puzzle was to keep them occupied until the next saliva sample. Then the stimulus person left the room with the experimenter. After working for 15 min on the Sudoku, the experimenter returned to collect the puzzle from the participant and asked the participant to provide a third saliva sample (C3).

Finally, participants were debriefed about the true nature of the experiment, and received €10. The whole procedure lasted one and a half hours and sessions were held from 16.00 h to 20.00 h to control for fluctuations in the circadian rhythm of cortisol (Weitzman et al., 1971).

Hormonal assays

Three saliva samples were collected by passive drool. Participants deposited 5 ml of saliva in plastic vials which took approximately 5 min to fill. The samples were frozen at −20 °C until the analyses were done. The samples were analyzed by a competitive solid phase radioimmunoassay (tube coated), using the commercial kit Coat-A-Count C (DPC, Siemens Medical Solutions Diagnostics). The within and inter assay variation coefficients were all below 8%. Two outliers were removed since these participants had cortisol values which differed by more than 3 standard deviations from the mean.

Statistical analysis

We first performed several independent *t*-tests to assess if there were any differences between conditions for the socio-demographic variables and baseline cortisol levels. To investigate if the task before the contact period produced a cortisol change we performed a repeated-measures ANOVA, with result of the task (winner or loser) as a between-subjects factor and moment (cortisol level before and after the task) as a within-subject factor. A Spearman correlation was used to investigate if starting time of the experiment affected the cortisol measurements and the perceived attractiveness of the stimulus persons.

To investigate if the contact period and the sex of the stimulus person provoked a change in salivary cortisol levels, we performed a repeated-measures ANCOVA with sex of the stimulus person (male or female) as a between-subjects factor and moment [cortisol level before (C2) and after contact (C3)] as a within-subject factor. We included age, the cortisol change from before to after the computer task and the result from this task (winner or loser) as covariates to control for their possible influence. When a significant effect was found, post hoc planned comparisons were performed using the Bonferroni adjustments for the *p*-values. We also investigated via an independent *t*-test if the percent change in cortisol levels was different between participants who had contact with a female or male stimulus person.

To test if the absolute cortisol change (C3–C2) and the cortisol percent change [(C3/C2)*100 − 100] were both related to the perceived attractiveness of the female or male stimulus persons we performed Pearson correlations. A value of $p<0.05$ (two-tailed) was considered statistically significant. Statistical tests were performed with SPSS version 15.0. When not otherwise specified values are Mean ± Sem.

Results

Preliminary analysis

There were no differences between conditions for the following variables: age, height, weight, BMI, subjective socio-economic status, educational level, average weekly physical activity, and alcohol use (*t*-tests, all $p \geq 0.24$). Cortisol levels before the contact period were no different between conditions, $t(79)=1.37$, $p=0.176$. The task previous to the contact period did not provoke a change in cortisol levels, $F(1,79)=0.27$, $p=0.606$, nor was there an interaction between moment of cortisol measurement and the result of this task, $F(1,79)=1.54$, $p=0.219$. Finally, there was no relation between the starting time of the experiment, nor with cortisol levels or the perceived attractiveness of the stimulus persons, all $p \geq 0.140$.

Cortisol and social contact

There was no effect of moment on cortisol levels, $F(1,76)=1.18$, $p=0.281$, but there was a significant interaction between the sex of the stimulus person and moment, $F(1,76)=10.80$, $p=0.002$ (see Fig. 1). Participants who had contact with a man decreased their cortisol levels more, $F(1,76)=56.71$, $p<0.001$, than participants who had contact with a woman, $F(1,76)=7.82$, $p=0.007$. These results remained significant when excluding the covariates: (i) result of the computer task and (ii) cortisol change from before to after the task. Among participants who had contact with a man absolute cortisol levels decreased on average with −2.19 nmol/L (±0.3), whereas among participants who had contact with a woman absolute cortisol levels decreased with only −0.86 nmol/L (±0.4). The cortisol levels among participants who had contact with a man decreased on average with −26.9% (±2.2), whereas among participants who had contact with a woman the relative cortisol change was no more than 0.1% (±7.9), $t(79)=-3.33$, $p=0.001$.

Cortisol change and the attractiveness of the stimulus person

The absolute cortisol change during contact with a male stimulus person was not related to the perceived attractiveness of the male stimulus persons, $r_{41}=0.198$, $p=0.215$ (see Fig. 2b). However,

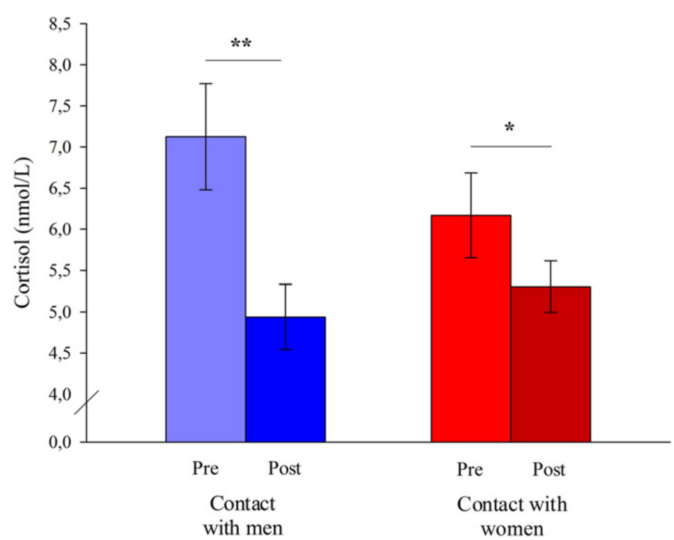

Fig. 1. Cortisol levels before (pre) and after (post) the contact period, separated for the sex of the stimulus person. Values are Mean ± Sem. *$p<0.05$, **$p \leq 0.001$.

results showed that that the absolute cortisol levels increased more as the participants perceived the females stimulus persons as more attractive, $r_{40} = 0.549$, $p < 0.001$ (see Fig. 2a). The cortisol percent change during contact with a male stimulus person was not related to the perceived attractiveness of the male stimulus persons, $r_{41} = 0.170$, $p = 0.289$ (see Fig. 3b). However, the cortisol percent change was higher as the participants perceived the female stimulus persons as more attractive, $r_{40} = 0.490$, $p = 0.001$ (see Fig. 3a).

Discussion

This study showed that male cortisol levels increased after exposure to a 5 min short social contact with a young attractive woman. This complements findings found in the non-human literature which have shown that corticosterone increases in males after a wide range of mating stimuli (Bonilla-Jaime et al., 2006). Among human males the relationship between cortisol and sexual stimuli is not so evident (Uckert et al., 2003; Carani et al., 1990; Isidori et al., 1984). Nevertheless, this study found that cortisol levels had increased after a potential situation for courtship by showing that during contact with women cortisol increased in men who perceived the women with whom they had contact as attractive.

This cortisol increase can be viewed through the perspective of the social self preservation theory which predicts that cortisol increases

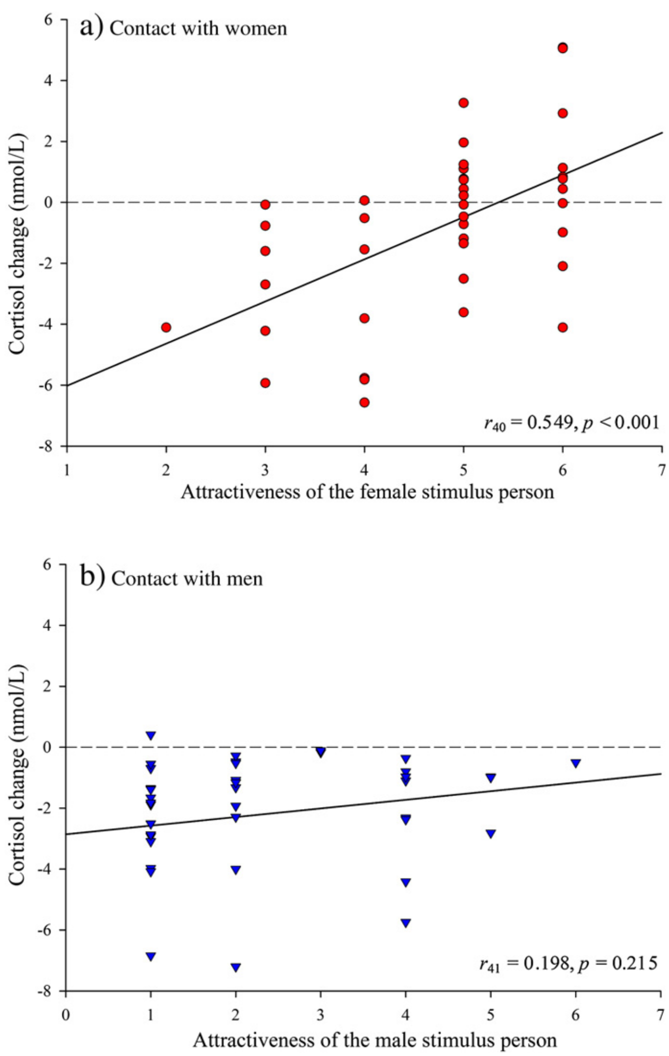

Fig. 2. The relationship between participant's absolute cortisol change and how attractive he perceived the stimulus person with whom he had contact. Separate figures are presented for contact with a female stimulus person (a) and a male stimulus person (b).

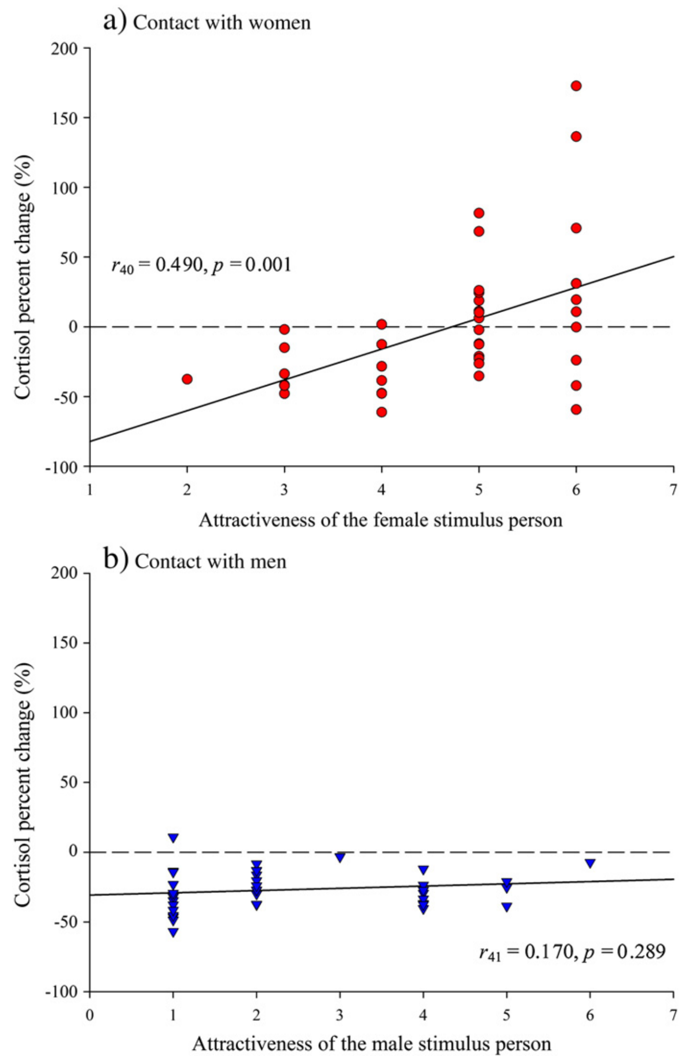

Fig. 3. The relationship between participant's cortisol percent change and how attractive he perceived the stimulus person with whom he had contact. Separate figures are presented for contact with a female stimulus person (a) and a male stimulus person (b).

when the psychological well-being is threatened (Dickerson and Kemeny, 2004). Men who perceived the female stimulus person as attractive may have viewed the contact period, consciously or unconsciously, as an opportunity for courtship. Being presented with such opportunity also entails the risk of being rejected, which could threaten psychological well-being. This threat is intensified when we consider that the contact period was (i) unpredictable: they suddenly had contact with an attractive woman without knowing for how long, and (ii) contained a social evaluative component: the attractive woman could decide that she is not interested. According to the social self preservation theory these are exactly the components which provoke a cortisol increase (Dickerson and Kemeny, 2004). Following this reasoning, increased HPA-axis activity during contact with attractive women could reflect the motivation to maintain the social status and acceptance and therefore avoid rejection by stimulating affiliative behavior. Studies in the future could measure the behavior and situation appraisal of men to assess how they actually perceive the contact period.

Without considering the attractiveness of the stimulus person we found that men maintained more stable cortisol levels when they had contact with a woman than with another man. Across conditions, absolute cortisol levels declined during the course of the experiment, which can be explained by the circadian release pattern of cortisol. The absence of an overall substantial cortisol increase after contact with a woman seems counterintuitive, but if cortisol is to play a role in human mating it will most likely be the modest changes in cortisol levels that facilitate male courtship, since large acute stress-like doses of cortisol actually suppress sexual functioning (for a review see Sapolsky et al. (2000)).

Unlike the present study, Roney et al. (2007) did find a modest increase in male cortisol levels after contact with novel women irrespective of the attractiveness of this woman. An explanation for this discrepant finding is that the stimulus in our study was weaker since our contact period was just 5 min in duration, where as Roney et al. (2007) used a contact period of 15 min. The results of their second experiment were more consistent with this study since they found a cortisol decrease after social contact with a male experimenter and no significant cortisol change after social contact with a female experimenter. These mixed results can be explained by taking in to account the attractiveness of the stimulus person, i.e. men only experience increases in cortisol levels when they perceive the woman with whom they have contact as attractive. To our knowledge, the study of Roney et al. (2007) did measure attractiveness but did not control for this variable when testing the cortisol responses of participants.

Our study provides evidence that interpersonal interaction can influence the secretion of cortisol. That this secretion in heterosexual men is affected by the perceived attractiveness of the woman with whom they are interacting, raises the possibility that elevated levels of this hormone may, in some yet undetermined way, affect the character of courtship interactions between men and women.

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Chapter 5

Testosterone and male behaviour during interactions with women

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Men with elevated testosterone levels show more affiliative behaviours during interactions with women

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Testosterone (T) is thought to play a key role in male–male competition and courtship in many vertebrates, but its precise effects are unclear. We explored whether courtship behaviour in humans is modulated and preceded by changes in T. Pairs of healthy male students first competed in a non-physical contest in which their T levels became elevated. Each participant then had a short, informal interaction with either an unfamiliar man or woman. The sex of the stimulus person did not affect the participants' behaviour overall. However, in interactions with women, those men who had experienced a greater T increase during the contest subsequently showed more interest in the woman, engaged in more self-presentation, smiled more and made more eye contact. No such effects were seen in interactions with other men. This is the first study to provide direct evidence that elevating T during male–male competition is followed by increased affiliative behaviour towards women.

Keywords: courtship; testosterone; affiliative behaviour; male–male competition; humans; sexual selection

1. INTRODUCTION

Humans, like other animals, communicate their interest to potential mates through courtship [1], which may then be followed by negotiation to determine whether this interest is mutual. In many species, sexual behaviour is regulated by sex hormones, in particular testosterone (T). For example, T initiates sexual development, controls sperm production and supports sexual function [2]. Moreover, T seems to play a key role in courtship. In several species of birds, it has been shown that a wide variety of courtship behaviours increase when castrated males are implanted with T crystals in specific brain areas [3]. Additionally, appetitive sexual behaviour (e.g. courtship) of male rats is inhibited by castration but restored after treatment with exogenous T [4]. The administration of T in both mice and rats stimulates the expression of various copulatory behaviours [5,6].

The function of T in these contexts can be explained by the challenge hypothesis [7]. This hypothesis states that T levels rise during challenges that are relevant for reproduction and thereby prepare the body for an adaptive response. The challenge hypothesis was first applied to birds, but more recently has been extended to humans, by focusing on challenges faced by men such as disputes over social status and reactions to mating stimuli [8]. It is thought that, during these challenges, T functions to promote behaviour that facilitates mate acquisition or mating directly [9]. In support of this, it has been shown that a non-physical social interaction of 15 min (or even as little as 5 min) with an unfamiliar woman can provoke an increase in male T levels [9–12].

If T promotes behaviours that stimulate mate attraction, which specific behaviours might be affected? As in other species, human male courtship may involve specific display behaviours. In support of this, it has been shown that in social interactions those men who responded with an increase in their T levels were perceived by their female interaction partners as trying to impress [9], displaying extrovert behaviour and self-disclosing [10]. However, it remains unclear whether the T increases caused these behaviours or *vice versa*, as they both occurred at the same time. Furthermore, it has been shown that during courtship men reveal more about themselves than women do and consequently speak longer with a woman when they are interested in dating her, particularly if she seems interested too [13]. Additionally, men may attempt to display their dominance status: those men who successfully make social contact with women in bars exhibit more dominant behaviours such as glances that are short and direct, make more space-maximization movements, change location more often, and make more non-reciprocated touches to surrounding men and fewer closed movements (e.g. outward limb movements that cross over the main body torso) [14]. Such male–male competitive interactions may be important for reproductive success if they influence patterns of female choice, as emphasized by research on other animals [15]. For example, females may prefer dominant males if they are better able to provide food and protection for their

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offspring [16]. Evidence from the biological literature suggests that male T levels can affect both competitive behaviour and courtship of females [17].

We hypothesized that courtship behaviours in men are preceded and modulated by T. While no study to date has shown a causal link between T and courtship in humans, clinical research has shown that T can affect male sexual function directly. For example, when administering T to hypogonadal men, the libido and sexual function of the men increase [18]. Furthermore, a pharmacologically induced gonadal steroid deficiency in healthy men causes reductions in sexual desire and intercourse, which are restored shortly after stopping this treatment, over roughly the same time period as it takes serum T levels to recover [19].

In the study reported here we investigated whether endogenous T is linked to male affiliative behaviours (i.e. behaviours that promote social bonding) used in courtship. We focused on three types of affiliative behaviours in men: (i) interest in another person, such as giving them attention and asking questions; (ii) self-presentation, such as talking and revealing details about oneself; and (iii) positive facial cues, such as smiling and making eye contact. We first attempted to induce a change in T levels by pitting male participants against each other in a non-physical pairwise contest, in which the outcome was rigged [20]. After the contest, these men had a short informal interaction with either an unfamiliar woman (experimental condition) or an unfamiliar man (control condition). Salivary T was measured before and after the contest, and the behaviour of the participants during the subsequent interaction was unobtrusively filmed and later analysed by trained observers. We expected that an increase in T occurring during male–male competition would stimulate more affiliative behaviours when men then interacted with a woman, whereas there would be no such effect during interactions with another man.

2. METHODS

(a) *Participants*

Eighty-four male students, aged 18–29 years (mean ± s.e.m.: 21.2 ± 0.32), participated in this study in exchange for €10. They were recruited by a male and a female research assistant, who approached men in the cafeterias of the University of Valencia and made announcements in the lecture halls. The participants had a mean body mass index (BMI) of 23.5 ± 0.46 and were all Caucasian. Average self-reported socio-economic status [21], on a scale from 1 (lowest) to 10 (highest), was 6.6 ± 0.09.

All participants were first interviewed by the research assistants and were asked to complete a questionnaire. We excluded individuals who were not heterosexual (open question: 'what is your sexual orientation?'), who were currently in a relationship, who were enrolled in a psychology degree, who smoked more than five cigarettes a day or who reported a serious medical or psychological problem or drug abuse. Participants were also excluded if they were using any medication directly related to cardiac, emotional or cognitive function, or medication that was able to influence hormone levels, such as glucocorticoids or β-blockers. One participant was excluded from analyses because after participating he indicated he was bisexual, while another was excluded because he indicated he was in a relationship.

Up until one day before the experiment, the participants were asked to maintain their typical habits, including sleeping for as long as usual. Additionally, they were instructed to refrain from alcohol consumption and any heavy physical activity the day before the session. During the 2 h immediately prior to the session, participants were asked to drink only water and avoid any stimulants, such as coffee, cola, caffeine, tea or chocolate. All participants received some basic verbal information about the study and signed an informed consent form outlining the general procedure and the measurements taken.

(b) *The competitive task*

Each participant competed face-to-face with another participant on a computer task [20]. This task comprised 27 items similar to those used in intelligence tests. The participants were informed that they would win an item if they were the first to enter the correct answer. During the task, the participants were seated roughly 1 m apart on opposite sides of the same table, each behind their own computer screen and facing their opponent. The experimenter remained clearly visible to the participants and observed the progress of the task. Unknown to them, the outcome of the task was actually manipulated by the experimenter for a different purpose, investigated in a separate paper [20]. One participant was randomly assigned to the winner condition (20 items won and 7 items lost) and the other to the loser condition (7 items won and 20 items lost). At the end of the task, each participant was shown his final score on his computer screen, together with a statement of whether he had lost or won. Half of the participants in each condition (winner and loser) were then randomly assigned to have contact with another man, and the other half with a woman.

(c) *Stimulus persons*

Twelve men and six women acted as the stimulus persons. These were confederates of the experimenter chosen on the basis of similar age (23.33 ± 0.55 years) to the participants, and were of representative height and weight for the Spanish student population. All stimulus persons were thoroughly instructed before participating, to reduce differences between them in spontaneous verbal or non-verbal behaviour. They were told to act as if they were participants in the same study, to engage in friendly conversation with the participant in a natural manner and to allow long pauses if the participants elected not to talk. After the interaction, participants who had met a stimulus woman were asked to rate her physical attractiveness on a scale from 1 (not attractive) to 7 (highly attractive); the average rating given was 4.73 ± 0.18.

(d) *Procedure*

On arrival at the laboratory, the participants were greeted by the male experimenter (L.v.d.M.) and were briefed on the general procedure of the study (without telling them about the planned interaction with the stimulus person). To avoid confounds, the experimenter did not engage socially and kept contact to a minimum. Participants filled in an informed consent form, and their height and weight were measured. Next, participants provided a saliva sample (T1) for the measurement of their baseline T level.

To provoke a change in T, each participant first competed against another participant on the computer task, which took approximately 18 min to complete. Ten minutes after the completion of this task, the participants provided a second

Table 1. Three indices of participants' behaviour during their social interaction with the stimulus person.

Indices	items	inter-observer reliability
interest in stimulus person	gave attention to stimulus person	0.93
	showed interest in stimulus person	0.93
	interacted confidently with stimulus person	0.95
	asked questions	0.76
	was talkative	0.96
self-presentation	talked about himself	0.90
	revealed details about himself	0.90
positive facial cues	was smiling	0.92
	made eye contact	0.92

saliva sample (T2). Each participant was then taken to a separate room where they were instructed to work on a Sudoku puzzle. Already in this room was a stimulus person, pretending to be another participant completing a similar puzzle. Upon entering the room, the experimenter indicated that he did not have the correct version of the puzzle for the participant. The participant was asked to wait for the experimenter to return with the correct version. The experimenter then left the room and the participant and the stimulus person were left alone together for 5 min [22], during which the behaviour of the participant was discreetly filmed from a partly hidden camera. This camera could be spotted by participants but their attention was drawn away from it by the presence of the stimulus person. When the 5 min had elapsed, the experimenter returned with the correct version and the stimulus person then left the room with the experimenter.

After a further 15 min, the experimenter collected the puzzle, participants were debriefed about the true nature of the experiment and received €10. The whole procedure lasted 1.5 h and sessions were held from 16.00 to 20.00 h to control for the circadian rhythm of T [23].

(e) *Behavioural measurements*

Four female observers (22.00 ± 1.29 years old) were trained to interpret and reliably rate the participants' behaviour from the video recordings, on the basis of the behavioural scale shown in table 1. We chose to use only female observers to minimize the variation between their ratings and because we were specifically interested in male courtship behaviour. These observers were aware of the stimulus person's sex but blind to the participants' increases in salivary T. The scale consisted of nine items and the general frequency of each item could be rated from 1 (not at all) to 7 (all the time).

Each observer rated the full set of videos on two separate occasions, with the second rating taking place one to three weeks after the first rating. To assess the repeatability of the ratings from a given observer, we calculated an intraclass correlation coefficient (ICC) for each item, based on the two separate ratings nested within each male subject. One item for one of the observers was removed from analyses as it had a repeatability score of ≤ 0.60. For each of the remaining items, the repeatability of the ratings ranged from 0.63 to 0.95 (0.82 ± 0.15) for the four observers.

We then averaged the observers' first and second ratings for each item, and used these average scores to assess the degree of agreement between the four observers. This was done by calculating an inter-observer ICC for each item (table 1) based on the four averages (one per observer) nested within each male subject.

Finally, for each item we took a grand average of that item's average scores from all four observers. We then created three composite indices on the basis of their theoretical relatedness, by averaging the final scores from each of the component items (table 1). These indices were: (i) interest in the stimulus person, ICC = 0.97; (ii) self-presentation, ICC = 0.98; (iii) positive facial cues, ICC = 0.75. The indices formed the dependent variables in our subsequent regression analyses (see below). Four participants were excluded from behavioural analysis as their interaction period was not correctly filmed owing to technical problems.

The three factors were correlated with each other (r between 0.506 and 0.799; all $p \leq 0.001$). Confirmatory factor analysis showed that a three-factor model had a better fit than a one-factor model ($\Delta\chi^2_3 = 171.76$, $p \leq 0.001$). The one-factor model did not provide an adequate fit to the data ($\chi^2_{27} = 226.40$, $p \leq 0.001$; comparative fit index, CFI = 0.87; standardized root mean square residual, SRMR = 0.072), whereas the three-factor model did provide an adequate fit ($\chi^2_{24} = 54.64$, $p \leq 0.001$; CFI = 0.98; SRMR = 0.037). Note that an adequate fit requires both CFI ≥ 0.95 and SRMR ≤ 0.08 [24].

(f) *Hormonal assays*

Both saliva samples (T1 and T2) were collected by passive drooling. Participants deposited 5 ml of saliva in plastic vials which took approximately 5 min to fill. The samples were frozen at -20° C and shipped to the endocrinology laboratory at the University Medical Center Utrecht, the Netherlands. Depending on the starting time of the session, the first saliva sample (T1) was taken at approximately 16.10 or 18.10 h and the second saliva sample (T2) was taken at approximately 16.55 or 18.55 h, respectively. The T2 samples were taken 10 min after completing the competitive task as psychological stimulation needs some time to affect T levels [25]. There was no effect of starting time of the session on T1, T2 or the change in T levels (T2−T1; t-tests, all $p \geq 0.57$). The saliva samples were analysed using radio-immunoassays. According to the modifications of Granger *et al.* [26], salivary T was determined with the double antibody T kit (DSL-4100) from Diagnostic Systems Laboratories Inc. (Webster, TX, USA). The detection limit was 4 pmol l^{-1}. The mean inter-assay coefficient of variation was 7.5 ± 0.90 per cent and the mean intra-assay coefficient was 5.3 ± 1.30 per cent. One participant drank water while giving the saliva sample and was therefore excluded from the analysis.

(**g**) ***Statistical analysis***

We first performed several independent *t*-tests to assess if there were any differences in the socio-demographic variables and baseline T levels between participants who interacted with a man or a woman. A multivariate analysis of variance (MANOVA) was then performed, including (i) interest in the stimulus person, (ii) self-presentation and (iii) positive facial cues as dependent variables, to investigate whether the behaviour of the participants was affected by the sex of the stimulus person (male or female), the outcome of the competition (winner or loser) and their interaction.

To test for an interaction between the sex of the stimulus person and the change in T during the competition on the behavioural indices, we used regression analyses following Aiken & West [27]. Using forward stepwise regression, three separate moderator regression analyses were performed with one of the behavioural indices as the dependent variable. The sex of the stimulus person was dummy-coded as 0 for a man and 1 for a woman. For calculating the change in T during the competition, we used the unstandardized residuals from regressing T1 on T2, because absolute changes in T levels are negatively correlated with baseline T and are sensitive to regression to the mean [28]. In step 1, the main effects of sex of the stimulus person and the change in T during the competition were entered. In step 2, the sex $\times$ change in T interaction was added and post hoc significance tests of the slopes were performed. For all behavioural indices, Bartlett's test [29] showed no violation of the assumption of homogeneity of error variance. For these final regression analyses, we excluded in total seven participants (one person who drank water during saliva sampling, one bisexual person, one person reporting to be in a relationship and four participants for whom we did not correctly film the contact period), leaving a final sample size of 77.

A value of $p < 0.05$ (two-tailed) was considered statistically significant. Statistical tests were performed with SPSS v. 16.0.

3. RESULTS

(**a**) ***Preliminary analysis***

As reported by van der Meij *et al.* [20], the change in salivary T between the first sample (before the contest) and the second sample (after the contest) did not differ between winners and losers ($F_{1,80} = 0.70$, $p = 0.406$). Overall, however, there was a significant increase in T of 16.4 per cent (± 3.9), from 266.4 (± 8.5) to 300.6 pmol l^{-1} (± 10.5; $F_{1,80} = 14.74$, $p < 0.001$). For the remainder of our analysis, we focus on the subsequent interaction with a stimulus person. There were no differences between participants who had contact with a man or a woman for the following variables: change in T, baseline T, sex drive, age, height, weight, BMI, subjective socio-economic status, educational level, average weekly physical activity, alcohol use (*t*-tests, all $p \geq 0.15$). Furthermore, the behaviour of participants as measured by the three behavioural indices was neither affected by the sex of the stimulus person (MANOVA: $F_{3,71} = 1.56$, $p = 0.208$) nor by the outcome of the competition ($F_{3,71} = 0.41$, $p = 0.745$), and there was no significant interaction effect between these variables ($F_{3,71} = 0.87$, $p = 0.459$). Behavioural ratings were equally variable for interactions with another man and with a woman (Levene's tests: interest in stimulus person, $F = 1.52$, $p = 0.221$; self-presentation, $F = 0.01$, $p = 0.931$; positive facial cues, $F = 3.79$, $p = 0.055$). The men's attractiveness ratings of the women were not correlated with the rated frequency of interest in the stimulus person ($r_{39} = 0.079$, $p = 0.634$), self-presentation ($r_{39} = 0.205$, $p = 0.212$) or positive facial cues ($r_{39} = 0.035$, $p = 0.831$).

(**b**) ***Testosterone and behaviour***

For the main analyses, we considered how the subjects' behaviour was affected by their change in T, the stimulus person's sex and the interaction between these two factors. The outcome of the competition did not moderate any of these effects (see electronic supplementary material, appendix A), so we do not discuss it further. In supplementary analyses, we also found that baseline T neither predicted affiliative behaviours nor interacted with any of the experimental conditions (see electronic supplementary material, appendix B). Our results did not change substantially when controlling for the psychological state of the opponent [20], except that for positive facial cues the interaction term dropped to non-significance (see electronic supplementary material, appendix C).

(i) *Interest in the stimulus person*

The model in step 1, including sex of the stimulus person and the change in T during the competition as predictor variables, did not explain a significant amount of variance in the index of interest in the stimulus person ($F_{2,74} = 0.40$, $p = 0.670$). However, entering the interaction term in step 2 significantly increased the amount of variance explained ($\Delta F_{1,73} = 5.13$, $p = 0.027$, adjusted $r^2 = 3.8\%$, $\Delta r^2 = 6.5\%$). In this step, there were no main effects of sex of the stimulus person ($p = 0.958$) nor the change in T ($p = 0.420$), but there was a significant two-way interaction between the change in T and sex ($\beta = 0.341$, $p = 0.027$). Significance tests of the slopes revealed that the change in T did not affect the display of interest in the male stimulus person ($t_{73} = -0.81$, $\beta = -0.12$, $p = 0.420$), but a greater change in T was associated with the display of more interest in the female stimulus person ($t_{73} = 2.31$, $\beta = 0.39$, $p = 0.024$; figure 1).

(ii) *Self-presentation*

The model in step 1, including sex of the stimulus person and the change in T during the competition as predictor variables, did not explain a significant amount of variance in the index of self-presentation ($F_{2,74} = 0.24$, $p = 0.789$). However, entering the interaction term in step 2 significantly increased the amount of variance explained ($\Delta F_{1,73} = 5.44$, $p = 0.022$, adjusted $r^2 = 3.7\%$, $\Delta r^2 = 6.9\%$). In this step, there were no main effects of sex of the stimulus person ($p = 0.820$) nor change in T ($p = 0.293$), but there was a significant two-way interaction between the change in T and sex ($\beta = 0.351$, $p = 0.022$). Significance tests of the slopes revealed that while the change in T did not affect self-presentation when interacting with a man ($t_{73} = -1.06$, $\beta = -0.16$, $p = 0.293$), a greater change in T was associated with more self-presentation when interacting with a woman ($t_{73} = 2.18$, $\beta = 0.372$, $p = 0.033$; figure 2).

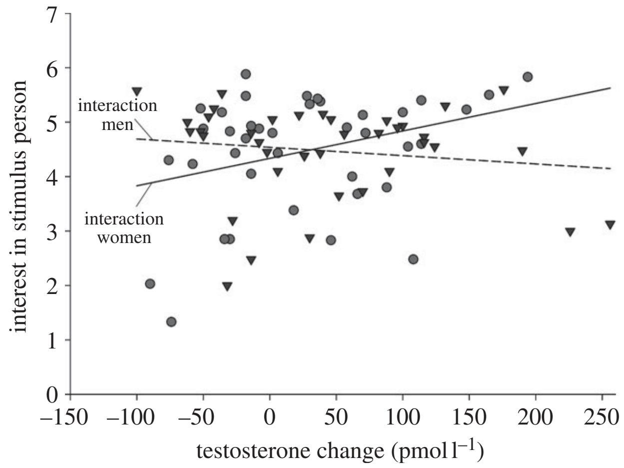

Figure 1. The relationship between the participant's change in testosterone and the extent to which he showed interest in a stimulus man (triangles) or woman (circles). Separate regression lines are plotted for each sex of the stimulus person.

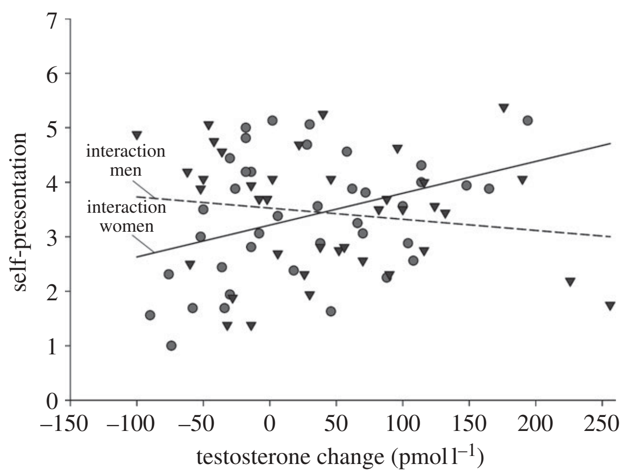

Figure 2. The relationship between a participant's change in testosterone and the extent to which he self-presented when interacting with a man (triangles) or woman (circles). Separate regression lines are plotted for each sex of the stimulus person.

(iii) *Positive facial cues*
The model in step 1, including sex of the stimulus person and the change in T during the competition as predictor variables, explained a significant amount of variance in positive facial cues ($F_{2,74} = 3.41$, $p = 0.038$). In this step, the sex of the stimulus person did not affect the expression of positive facial cues ($p = 0.126$), but the change in T did ($\beta = 0.253$, $p = 0.027$). However, entering the interaction term in step 2 marginally increased the amount of variance explained ($\Delta F_{1,73} = 3.34$, $p = 0.072$, adjusted $r^2 = 8.9\%$, $\Delta r^2 = 4.0\%$). In this step, there were no main effects of sex of the stimulus person ($p = 0.124$) nor change in T ($p = 0.616$), but there was a marginally non-significant two-way interaction between the change in T and sex ($\beta = 0.268$, $p = 0.072$). Significance tests of the slopes revealed that while the change in T did not affect the display of positive facial cues when interacting with a man ($t_{73} = 0.50$, $\beta = 0.074$, $p = 0.616$), a greater change in T was associated with more positive

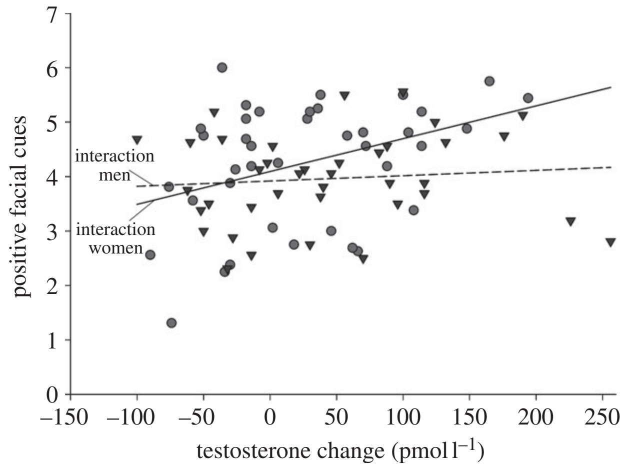

Figure 3. The relationship between a participant's change in testosterone and his expression of positive facial cues when interacting with a man (triangles) or woman (circles). Separate regression lines are plotted for each sex of the stimulus person.

facial cues when interacting with a woman ($t_{73} = 2.89$, $\beta = 0.480$, $p = 0.005$; figure 3).

(iv) *Overall affiliative behaviour*
To check that our results were not driven by the particular grouping of the items into our three composite indices, we ran a similar analysis with all nine items grouped into a single variable: overall affiliative behaviour (electronic supplementary material, appendix D). This confirmed the previously reported effects: change in T did not affect overall affiliative behaviour when interacting with a man ($t_{73} = -0.639$, $\beta = -0.096$, $p = 0.525$), whereas a greater change in T was associated with more affiliative behaviour when interacting with a woman ($t_{73} = 2.617$, $\beta = 0.443$, $p = 0.011$).

4. DISCUSSION
This is the first study to show that men experiencing elevated T levels during intrasexual competition subsequently show more affiliative behaviour during interactions with women. Those men with greater rises in T levels subsequently showed more interest in a woman, engaged in more self-presentation, smiled more and made more eye contact with her, but did not show a similar increase in these behaviours when interacting with a man. Although the behavioural ratings could have been affected by knowledge of the stimulus person's sex, this cannot account for the reported effect of the change in T on participants' behaviour as the raters were completely blind to this change. Our findings complement previous studies showing that contact with an unfamiliar woman may provoke an increase in T levels [9–12].

In addition, we report the novel finding that an endogenous T increase prior to social contact has an effect on subsequent behaviours, while previous work has shown the simultaneous occurrence of a T increase and an increase in display behaviours [9,10]. Taken together, the evidence suggests that during encounters with the opposite sex, T may function to promote the display of affiliative behaviours that increase a man's mating prospects. Although we did not specifically measure romantic or sexual interest, our findings suggest that the release of T in men during social contact with women is linked to the initiation of courtship behaviours.

The detection of these behavioural changes in men very soon after the competitive interaction suggests that T may have dynamically regulated their behaviour through non-genomic mechanisms [30]. Genomic mechanisms involve the activation of intracellular androgen receptors that modulate nuclear transcription after translocation of steroid–receptor complexes into the nucleus, typically taking days or hours to exert an influence [30]. By contrast, the non-genomic route can affect an organism rapidly through T binding to extracellular androgen receptors that can raise the intracellular calcium concentration, change membrane fluidity and activate second messenger pathways [31]. Through these changes, the activity of the central nervous system is modulated, thereby leading to a change in behaviour. The main findings of our study are consistent with the fast non-genomic actions of androgens, suggesting that transient changes in T levels can promote certain forms of social behaviour.

Our findings are also in line with the non-human animal literature, which shows that in a variety of species T causes more appetitive and consumptive sexual behaviours [3,4]. Interestingly, our study suggests that courtship in humans involves subtle verbal and non-verbal cues that are perhaps not specific to courtship. There was no overall difference in the frequency of affiliative behaviours between those men who interacted with a woman and those who interacted with another man. This was probably owing to the short contact period (5 min), as in the first few minutes of contact it may be quite normal to establish a rapport by smiling, making eye contact, speaking about one's experiences and showing interest in the other person. What our findings suggest is that when men meet an unfamiliar woman, a first step to show their romantic interest might be to display various forms of general affiliative behaviour.

Our findings are also consistent with the challenge hypothesis [8]. Those men who experienced a greater rise in T during the competitive task may have perceived that they were challenged [20] as, according to the challenge hypothesis, T should increase in contexts such as disputes over social status [8]. After this challenge, their elevated T levels not only prepared them for competing with other men but may also have had a generalized preparatory effect on mate acquisition by stimulating affiliative behaviours directed specifically towards women. However, the effect of intrasexual competition on our main results should be treated with caution as we cannot rule out that men with increased T levels owing to other circumstances also show more affiliative behaviours towards women. Despite this possibility, it seems plausible that intrasexual competition is associated with T and mating effort in humans, just as it has been shown in many non-human species that male–male competition is closely linked to mate acquisition [32]. Dominant males may have access to more or better females because they compete directly for those females (female-defence polygyny), or because they compete for resources to which females are attracted (resource-defence polygyny) [15]. This is one probable reason why high- and middle-ranking males typically have a lifetime reproductive advantage over the lowest-ranking males [16].

Instead of a direct, stimulatory effect of T on courtship behaviour, an alternative possibility is that those men whose T levels responded most to the competitive situation were also more focused on mating. In other words, those men who are more physiologically sensitive to challenges to their social status might be the same men who frequently engage in courtship. Following this reasoning, their high responsiveness to challenges relevant for reproductive success might have also have induced them to display more specific affiliative behaviours directed at women. To unravel these interesting possibilities, follow-up studies could pharmacologically administer T to men prior to social contact with a woman, to clarify its stimulating effects on affiliative and courtship behaviours.

This study was approved by the ethical committee of the Faculty of Psychology (University of Valencia) and conforms to the Declaration of Helsinki.

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Chapter 6

The relationship between 2D:4D and dominance

This chapter has been published: van der Meij, L., Almela, M., Buunk, A.P., Dubbs, S., and Salvador, A. (accepted pendings revisions). 2D:4D in men is related to aggressive dominance but not to sociable dominance. Aggressive Behavior.

1. Introduction

Exposure to testosterone (T) in utero proliferates the development of male structures and causes masculinization of the central nervous system (Morris et al., 2004). It has been found that a marker of prenatal exposure to T is the ratio between the length of the second and fourth digit (2D:4D), showing that high exposure to prenatal T is related to lower ratios and that low exposure is related to higher ratios. Indeed, since men experience more exposure to prenatal T than women, men tend to have lower 2D:4D than women (Manning et al., 2000), Furthermore, it has been shown that higher fetal T exposure is related to a lower 2D:4D in two year old children (Lutchmaya et al., 2004), that lesbians have more masculine, i.e. lower ratios (for a meta-analysis see Grimbos et al., 2010), and that sexual dimorphism in 2D:4D is also prevalent in non-human primates (Roney et al., 2004). It has been suggested that the Hox genes are responsible for this relationship between fetal T and 2D:4D (Manning and Wood, 1998) since these genes differentiate digit length as well as stimulate the development of the genitalia (Kondo et al., 1997).

Due to the organizing effect of T on the central nervous system and its influence on digit length development, 2D:4D has been found to be related to several personality traits typically associated with masculinity. For example, a masculine (low) 2D:4D is related to shorter length of intimate relationships in women (Scarbrough and Johnston, 2005), greater courtship display by men (Roney and Maestripieri, 2004), higher sensation seeking in men (Fink et al., 2006), lower agreeableness in men (Luxen and Buunk, 2005) and more openness to experience in both sexes (Lippa, 2006). However, other studies have found counterintuitive relationships between 2D:4D and masculine traits. For example, a masculine 2D:4D is related to more depression in boys (Vermeersch et al., 2008) and to worse spatial navigation among women (longer platform-finding latency) (Csathó et al., 2001). Furthermore, a recent study found no relation between 2D:4D and dominance as a personality trait in either sex (Vermeersch et al., 2008). Similarly, another study showed no relationship between 2D:4D and social or physical dominance among men (Putz et al., 2004). These findings suggest that the relationship between 2D:4D and personality is a complex topic (Putz et al., 2004).

A possible cause for these inconsistent results are variations in methodology employed (Putz et al., 2004). For example, there are many possible ways of defining a dominant personality (Mazur and Booth, 1998). A dominant personality can at least be separated into two different personality types: sociable dominance and aggressive dominance (Kalma et al., 1993). Observational as well as self-report data has shown that the two types of dominance are associated with the use of power strategies to influence others (Kalma et al., 1993). Indeed, there is evidence that people who score high on sociable and aggressive dominance succeed best at getting their preferences represented in a group (Kalma et al. 1993). However, there are differences between both types of dominance regarding the tactics individuals use to influence others. Aggressively dominant men tend to use a mix between “stating what one wants” and Machiavellian tactics, whereas sociably dominant men expect to be the center of social activity and tend to use reasoning strategies to influence people. Moreover, individuals high in sociable dominance are characterized by a positive attitude towards other people, a central position in groups, a strong need to dominate others in a reasonable way, a solid self-esteem, and an independent and active attitude. In contrast, individuals high in aggressive dominance have a negative attitude toward others, and a strong motivation to realize their own, rather material aims, even at the expense of personal relationships (Kalma et al., 1993).

This study examined if 2D:4D is related to a dominant personality. However, our study is novel in that we differentiated a dominant personality into two separate types of dominance: aggressive and sociable dominance. We investigated in a sample of healthy men if the exposure to more prenatal T (operationalised as low 2D:4D) makes it more probable that they develop a more aggressive and sociable dominant personality later in life.

2. Methods

2.1 Participants

Eighty-four male students from the University of Valencia in Spain, aged 18-29 years (21.2, SEM ± .32), participated in this study in exchange for €10. The participants had a mean body mass index of 23.5 (± .46) and were all Caucasian. Subjective socio-economic status (Adler et al., 2000) was measured on a scale from 1 (lowest) through 10 (highest) and the participants reported a mean subjective socio-economic status of 6.6 (± .09). All potential participants were first interviewed and were asked to complete a questionnaire. Individuals who reported a serious medical or psychological problem or drug abuse were not allowed to participate.

2.2 Sociable and aggressive dominance

Participants completed two questionnaires measuring sociable and aggressive dominance, consisting of ten items for the sociable dominance scale and ten items for the aggressive dominance scale (Kalma et al., 1993). See Table 1 for all the items. Both scales are reliable and have been validated using observational data of social interactions (for more details see Kalma et al., 1993). For every item in the two questionnaires, the participants rated to what extent they agreed with the statements on a scale from 1 (strongly disagree) to 6 (strongly agree). Two participants failed to return these questionnaires.

We performed a principal component factor analysis with varimax rotation and chose a rotated two factor solution based on the scree plot. These factors were *sociable dominance*, which explained 22.78% of the total variance and *aggressive dominance* which explained an additional 15.47% of total variance. Scale scores were calculated by averaging those items that had a factor loading of 0.40 or greater on only one of the factors (see Table 1). Four items were removed because two items had factor loadings of less than 0.40 and another two items loaded on both factors more than 0.40. The final score for *sociable dominance* consisted of 9 items with factor loadings ranging from 0.54 to 0.74 (Cronbach's Alpha of 0.85) and *aggressive dominance* consisted of 7 items with factor loadings ranging from 0.49 to 0.73 (Cronbach's Alpha 0.72). The two factors were not significantly correlated (r_{82} = 0.13, p = 0.256).

Table 1: Factor loadings of each item onto the rotated two factors: sociable dominance (SD) and aggressive dominance (AD).

Scale	Item	Sociable dominance	Aggressive dominance
SD	I have no problems talking in front of a group	0.74	0.06
SD	At school I found it easy to talk in front of the class	0.73	0.06
SD	No doubt I'll make a good leader	0.62	0.11
SD	I like taking responsibility	0.54	-0.18
SD	I certainly have self-confidence	0.65	0.03
SD	For me it is not hard to start a conversation in a group	0.70	0.06
SD	I am not shy with strangers	0.68	0.29
SD	People turn to me for decisions	0.64	0.01
SD	I generally put people into contact with each other	0.63	>0.01
AD	When a person is annoying, I put him in his place	0.08	0.49
AD	If I need something I borrow it from a friend without his approval.	0.05	0.49
AD	I find it important to get my way, even if this causes a row	-0.02	0.69
AD	I find it important to get my way	0.06	0.73
AD	I like it when other persons serve me	0.15	0.60
AD	I quickly feel aggressive with people	-0.11	0.50
AD	I think that achieving my goals is more important than respecting others	-0.14	0.67
-	I can look everybody in the eye, and lie with a straight face	0.48	0.41
-	I can lie without anybody noticing it	0.53	0.41
-	I'd rather be disliked (for being unkind) and that people look down on me (for not achieving my aims)	-0.13	0.08
-	I make smart, sarcastic remarks if people deserve it	0.20	0.28

- = Item removed from final scale scores

2.3 Measurement of 2D:4D

Both hands of the participants were scanned with a Canon Scan 8600F and images were saved as a JPG file with a resolution of 96 dpi, 24 bit color depth and a size of 3508×2552 pixels. Before measuring finger length, the color of the image was adjusted with the level tool of Adobe Photoshop to make the greaves more clearly visible in the image. The second and fourth digit finger lengths were measured independently by two observers with the measurement tool of Adobe Photoshop by zooming in on the ventral proximal creases at the base of the digit. When the difference between the measurements of both observers was greater than three standard deviations the measurement of that particular finger was repeated. Intraclass-coefficients (ICC) for average measurements were used to calculate inter-observer-reliability. For all finger measurements the inter-observer reliability ranged from 0.979 to 0.992 (Mean = 0.986, SEM = ± 0.003). To calculate the 2D:4D for each hand the length of the index finger was divided by the length of the ring finger. The 2D:4D of both hands were averaged to obtain an average 2D:4D. Both hands from two participants and another participant' left hand were not correctly scanned and could therefore not be measured.

3. Results

We calculated Pearson correlations to investigate if aggressive and sociable dominance were related to the average 2D:4D and the 2D:4D of the right and left hand. Results showed that an average lower 2D:4D was related to a higher aggressive dominance personality (r_{79} = -0.23, p = 0.046) but was not related to sociable dominance, r_{79} = -0.09, p = 0.446 (see Figure 1). Results were similar when controlling for social economic status and age (aggressive dominance: p^r (75) = -0.23, p = 0.047, sociable dominance, p^r (75) = -0.09, p = 0.416).

Looking at each hand separately, we found that the right hand 2D:4D was significantly negatively correlated to an aggressive dominant personality (r_{80} = -0.23, p = 0.038), whereas this relationship was only marginally significant for the left hand 2D:4D (r_{79} = -0.19, p = 0.092). There were no significant relationships between sociable dominance and the 2D:4D of both hands (all $p \geq 0.206$). Furthermore, the dominance scales were not related to fluctuating asymmetry as measured by the difference between the right and left hand 2D:4D (all $p \geq 0.115$).

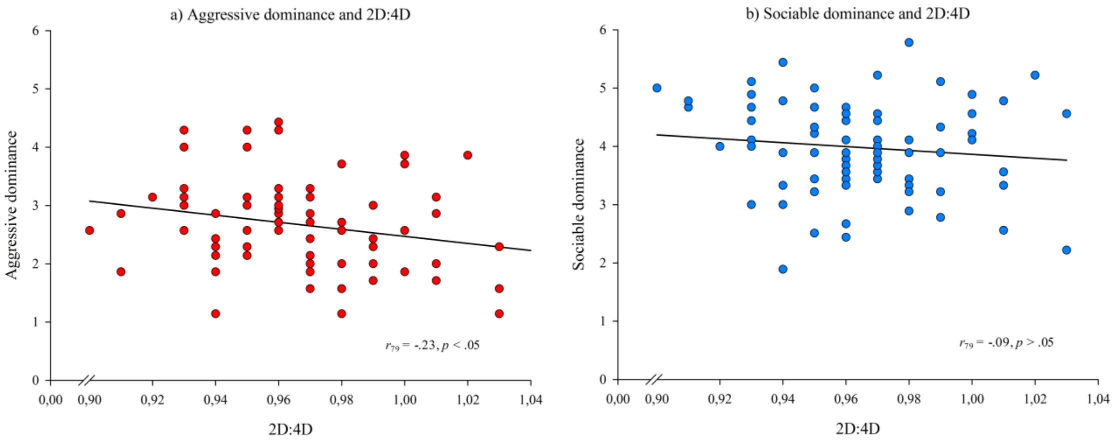

Figure 1. The relationship between participant' average 2D:4D and their scores on the aggressive dominance (a) and sociable dominance (b) questionnaire.

4. Discussion

This study showed that masculine (low) 2D:4D is related to a higher aggressive dominant personality while we did not find a relationship between sociable dominance and 2D:4D. These results suggest that among men the exposure to prenatal T is positively associated with a more aggressive dominant personality later in life. This complements findings that link aggressiveness with high levels of prenatal T, since it has been shown that girls with an opposite sex twin (i.e. high prenatal T levels) are more prone to aggressive behavior than girls with a same sex twin (i.e. low prenatal T levels) (Cohen-Bendahan et al., 2005). Furthermore, it has been shown that masculine 2D:4D ratios are related to higher trait aggressiveness (Bailey and Hurd, 2005). Our findings also complement findings that show that a masculine 2D:4D is related to the expression of dominant behaviors in other primates. Indeed, it has been shown that among rhesus macaques (*Macaca mulatta*) a masculine (low) 2D:4D is related to higher female rank (Nelson et al., 2010). Of interest is that we found a stronger relationship between 2D:4D and aggressive dominance for the right hand than for the left hand. This complements findings by Williams and Pepitone (2000) since they found a greater sex difference in 2D:4D for the right hand than for the left hand. These last results combined with the results from this study suggest that right hand 2D:4D is more sensitive to fetal androgens than the left hand.

However, our findings contradict other findings in the literature and it seems that mixed findings are rather the rule than the exception (Putz et al., 2004). For example, our findings differ from the results shown by Vermeersch et al. (2008), since they did not find a relationship between a dominant personality and 2D:4D. It appears that in their study they measured one broad form of dominance, whereas we divided dominance into two separate components; a more friendly kind of dominance (sociable dominance) and a more anti-social kind of dominance (aggressive dominance). The questions used by Vermeersch et al. (2008) seem to tap a combination of both types of dominance that may have obscured the relationship between aggressive dominance and 2D:4D. Our results partially confirm results found by Putz et al. (2004) as they also did not find any relationship between 2D:4D and social dominance, which seems similar to sociable dominance as assessed in the present study. Furthermore, they also did not find a relationship between physical dominance and 2D:4D. Physical dominance, as proposed by Putz et al. (2004), measures physical aggressive tactics to achieve dominance, which is different from the aggressive dominance scale we used since we measured non-physical tactics to achieve dominance.

Apart from a different methodology in measuring dominance, there may also be another explanation for these divergent results. According to Putz et al. (2004), it may be that the development of some traits and finger digit differentiation do not occur around the same time. Consequently, fetal hormonal levels that influence the development of these traits will be unrelated to the hormonal levels around finger digit differentiation. This difference in development timing might be the reason why we found that 2D:4D is related to aggressive dominance and not to sociable dominance. It could be that a predisposition to form an anti-social dominant personality later in life is developed around the same time as finger digit length differentiation, whereas development timing is not the same for social dominance and 2D:4D.

This study adds more evidence to the idea that exposure to T in a developing fetus can have an impact on its personality later in life. We showed that men with a low 2D:4D are more likely to develop an aggressive dominant personality as these men most likely have a more masculinized central nervous system.

Chapter 7

Discussion of the main findings

The saying goes that women are governed by hormones, but this dissertation shows that the same can be said for men. The studies reported in the previous chapters of this dissertation have shown that among men the release of testosterone and cortisol are important in situations relevant for human mating. What now follows is a short description and conclusion of these empirical chapters and a global reflection of their implications.

1. Summary of main findings

1.1 Chapter 2

Following the challenge hypothesis, this study investigated the effects of the presence of a woman on the testosterone levels of young men. An informal contact with a woman of approximately five minutes resulted in an increase in salivary testosterone among men. These effects occurred particularly in men with an aggressively dominant personality. In addition, higher baseline salivary testosterone levels were related to a more aggressively dominant personality, being sexual inactive for a month or more, and not being involved in a committed, romantic relationship. The most important findings of this study are that the short presence of a woman induces specific hormonal reactions in men, and that these effects are stronger for aggressively dominant men.

1.2 Chapter 3

An increase in testosterone levels after competition have typically been attributed to winning, yet there is also evidence that being victorious is not in itself sufficient to provoke a testosterone response. Instead, it has been proposed that testosterone responses are moderated by competitors' appraisal of the situation (Salvador, 2005; Salvador and Costa, 2009). Here, I investigated whether the opponent's psychological state affected hormonal changes in men competing face to face on a rigged computer task. The results showed that, irrespective of the outcome, the competition led to increases in heart rate and testosterone levels. I found that the testosterone levels of the participants increased more when their opponents had high self-efficacy and that testosterone levels were not influenced by participants' own psychological state. Furthermore, the testosterone levels of losers, but not winners, increased more when their opponent judged the competition to have low importance. The findings from this study are consistent with the challenge hypothesis. Both winners and losers were challenged to compete for social status; therefore their testosterone responses did not differ. In addition, the psychological state of the opponent makes a competition challenging and subsequently triggers testosterone responses.

1.3 Chapter 4

Previous studies have shown that situations relevant for human mating can affect the levels of many hormones. This study focused on the hypothalamus-pituitary-adrenal axis by measuring salivary cortisol levels in young men prior to and after a period of short social contact with a woman or man. Results showed that after contact with another man the cortisol levels of the participants declined according to the circadian release pattern of cortisol. However, cortisol levels in men declined less when they had contact with a woman. Furthermore, cortisol levels of men increased when they perceived the woman with whom they had contact as attractive. These findings provide indirect evidence for the role of the hypothalamus-pituitary-adrenal axis in human courtship. During social contact with attractive women, moderate increases in cortisol levels may reflect apprehension over an opportunity for courtship.

1.4 Chapter 5

Among several species it has been shown that testosterone fosters courtship behaviours in males. This study explored whether courtship behaviour in humans is also modulated and preceded by testosterone. To this end, we calculated the testosterone change during the competition of Chapter 3. After the competition, each participant had a short, informal interaction with either a male or a female stimulus person. The sex of the stimulus person did not affect the participants' behaviour. However, during interactions with women, those men who had experienced a greater increase in testosterone levels prior to interaction showed more interest in the woman, engaged in more self-presentation, smiled more and made more eye contact. No such effects were seen in interactions with other men. This is the first study to provide direct evidence that elevated testosterone during male-male competition is followed by increased affiliative behaviour with women.

1.5 Chapter 6

It has been shown that a smaller ratio between the length of the second and fourth digit (2D:4D) is an indicator of the exposure to prenatal testosterone. This study measured the 2D:4D of men and assessed dominance as a personality trait to investigate indirectly if the exposure to prenatal testosterone is related to a dominant personality later in life. Results showed that men had a more aggressively dominant personality when having a more masculine (lower) 2D:4D, while there was no relationship between sociable dominance and 2D:4D. Findings from this study indicate that it is important to distinguish different forms of dominance since other studies failed to find relationships between dominance and 2D:4D.

2. Some caution

The findings presented in this dissertation have to be treated with some caution. Any hormone, and therefore also testosterone and cortisol, form part of an intricate balance between a wide range of complex bodily processes. An increase or decrease in hormonal levels can lead to activation or deactivation of a wide range of other processes and, therefore, one specific hormone is never the only substance involved. A similar reasoning can also be applied on human mating behaviour. Human behaviour is a complex product of previous social experiences, personality, and social contexts. The studies described in this dissertation have tried to control for these confounding effects as much as possible. This was done by, for example, standardising the experiment as much as possible and by selecting healthy participants of a similar age range. However, results reported in this dissertation should be treated with caution, as no control is perfect, and frequently it is possible to think of an alternative explanation.

Some might see this as a limitation of the research linking human social behaviour to hormonal levels, but I believe that not always finding clear-cut explanations make social hormones so stimulating and fascinating to study. Furthermore, as the chapters in this dissertation have shown, fluctuations in hormonal levels can explain an important part of the variation in human social behaviour.

3. Conclusions

The results from the studies presented in this dissertation underscore the idea that testosterone and cortisol are important to consider when studying social interactions. The first chapter has provided some physiological mechanisms as how the secretion of these different hormones may affect male psychology and behaviour. The next chapters assumed the existence of these hypothetical mechanisms and measured the hormonal levels of men in situations relevant for human mating, such as competitive interactions with other men and social contact with women. In my opinion, the findings shown by these studies have added new evidence to the existing literature of hormones and behaviour. The main findings of this dissertation are highlighted below:

- Aggressively dominant men react with a stronger increase in testosterone levels when they meet an unfamiliar woman.
- Male testosterone levels increase more when competing with a confident opponent.
- Cortisol levels of men increase during contact with attractive women
- Male affiliative behaviours towards women are stimulated by elevated testosterone levels.
- Men having a more masculine (lower) 2D:4D have a more aggressive dominant personality.

3.1 The implications of testosterone

The findings shown in this dissertation provide support for the challenge hypothesis. The empirical chapters in this dissertation show that testosterone is relevant in domains such as intra-sexual competition (chapter 3) and during contact with an unfamiliar potential mate (chapter 2 and 5). I think that in situations relevant for human mating an increase in testosterone levels can be viewed as an adaptive response, aimed to improve performance in that particular situation. The best support for this reasoning can be read in chapter 5, where I have shown that the secretion of testosterone can influence the display of various forms of affiliative behaviours directed at women. Interestingly, these affiliative behaviours are perhaps not the most obvious behaviours to be influenced, since testosterone is usually associated with dominating and aggressive behaviours (e.g. Archer et al., 2005). The finding that testosterone can also enhance positive social behaviours, suggests that the interpretation of its release depends highly on the specific social context studied. I argue that the release of testosterone focuses men on mating effort by preparing their body to engage in mate acquisition, but what these preparations specifically entail, depends on the situational demands.

3.2 The implications of cortisol

Chapter 4 has shown that the release of cortisol also strongly depends on the specific social context. But the interpretation of its release is somewhat less straightforward when studying male mating behaviour. On average, cortisol levels did not increase after contact with a woman. However, cortisol levels did increase among those men who perceived their female interaction partner as attractive. It might be that cortisol relies on a different psychological mechanism than testosterone and is even more context specific in its release. It could be that cortisol levels only increase in situations requiring a substantial amount of energy and effort, e.g. contact with an attractive woman, whereas this increase in cortisol levels is absent in social situations requiring less or no effort, e.g. contact with an unattractive women.

4. The future

After reading this dissertation and observing the different relationships between hormones and male psychology, one could ask the following question: so what causes what? Do changes in hormonal levels affect male psychology and behaviour, or does male psychology and behaviour also affect the release of hormones? The studies reported in this dissertation cannot answer this question because most findings in the different empirical chapters are associations; a change in hormonal levels is accompanied by a change in behaviour and vice versa. In my opinion, the best way to answer this question is to administer pharmacologically testosterone and cortisol, or administer agents that block, emulate, or stimulate the release of these hormones. Including such manipulations in similar experimental designs as used in this dissertation can untangle this interesting question. For example, are men who have pharmalogically induced high testosterone levels more social towards women as compared to men who received a placebo? Only such experimental designs may establish causality and I would like to do such studies in the future. Although this question remains to be answered, it is my hope that the studies presented in this dissertation have provided new insights in the intricate relationship between hormones and male psychology and behaviour.

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Nederlandse samenvatting

Men zegt dat vrouwen worden beheerst door hormonen, maar dit proefschrift toont aan dat hetzelfde gezegd kan worden voor mannen. De studies die beschreven staan in dit proefschrift tonen aan dat voor mannen testosteron en cortisol belangrijke hormonen zijn in sociale situaties die relevant zijn voor de paarvorming in mensen. Wat nu volgt zijn korte samenvattingen van de uitgevoerde studies en hun globale implicaties.

Studie 1

In lijn met de "challenge hypothesis " onderzocht deze studie de effecten van de aanwezigheid van een vrouw op de testosteronspiegel van jonge mannen. Een informeel contact met een vrouw van ongeveer vijf minuten resulteerde in een toename van de testosteronspiegel van mannen. Deze effecten traden vooral op bij mannen met een agressief dominante persoonlijkheid. Daarnaast was een hogere baseline testosteronspiegel gerelateerd aan een meer agressieve dominante persoonlijkheid, seksueel inactiviteit van een maand of meer en de afwezigheid van een vaste relatie. De belangrijkste bevindingen van deze studie zijn dat de korte aanwezigheid van een vrouw een hormonale reactie bij mannen induceert, en dat deze effecten sterker zijn voor mannen met een agressief dominante persoonlijkheid.

Studie 2

Een stijging in de testosteronspiegel na een competitie wordt doorgaans toegeschreven alleen aan winnaars, maar er is ook bewijs dat een overwinning op zichzelf niet voldoende is om een verandering in de testosteronspiegel te produceren. In plaats daarvan is voorgesteld dat een verandering in de testosteronspiegel wordt gemodereerd door de beleving van de situatie. In deze studie onderzocht ik of tijdens een competitie de psychologische toestand van deelnemers en hun tegenstanders een verandering in de testosteronspiegel modereert. Om dit te onderzoeken streden deelnemers face-to-face tegen elkaar op een computertaak. De resultaten lieten zien dat, ongeacht de uitkomst, de competitie leidde tot een toename in de testosteronspiegel en de hartslag. Ook vond ik dat de testosteronspiegel van de deelnemers vooral toenam wanneer hun tegenstanders een hoge self-efficacy rapporteerden. De testosteronspiegel werd niet beïnvloed door de deelnemers eigen psychologische toestand. Bovendien steeg de testosteronspiegel van de verliezers, en niet van winnaars, wanneer hun tegenstander aangaf de competitie niet belangrijk te vinden. De bevindingen van deze studie zijn in overeenstemming met de "challenge hypothesis". De veranderingen in testosteronspiegels waren niet verschillend voor winnaars en verliezers omdat beiden werden uitgedaagd om te strijden voor sociale status. Deze studie laat zien dat de psychologische toestand van de tegenstander een competitie uitdagend maakt en dat dit vervolgens een verandering in de testosteronspiegel veroorzaakt.

Studie 3

Eerdere studies hebben aangetoond dat de concentraties van verschillende hormonen worden beïnvloed door situaties die relevant zijn voor de menselijke paarvorming. Deze studie richtte zich op de hypothalamus-hypofyse-bijnier-as door het meten van cortisol in jonge mannen, na en voor een periode van sociaal contact met een vrouw of man. De resultaten lieten zien dat na contact met een andere man de cortisolspiegel van de deelnemers daalde, wat in overeenstemming is met het circadiane ritme van cortisol. De cortisolspiegel daalde echter minder bij mannen als zij contact hadden met een vrouw. Daar komt nog bij dat de cortisolspiegel van mannen toenam wanneer zij de vrouw met wie ze contact hadden aantrekkelijk vonden. Deze bevindingen leveren indirect bewijs voor de rol van de hypothalamus-hypofyse-bijnier as in de menselijke paarvorming. Een matige stijging in de cortisolspiegel tijdens sociaal contact met een aantrekkelijke vrouw kan aangeven dat mannen de sociale situatie beschouwen als een kans voor hofmakerij.

Studie 4

Onder verschillende diersoorten is aangetoond dat testosteron de paarvorming stimuleert. Deze studie onderzocht of hofmakerij in mensen ook gemoduleerd wordt en voorafgegaan wordt door testosteron. Om dit te onderzoeken hebben we de testosteron verandering gemeten tijdens een competitie. Na deze competitie had iedere deelnemer een korte informele interactie met ofwel een mannelijke ofwel een vrouwelijke stimulus persoon. Het geslacht van de stimulus persoon had geen invloed op het gedrag van de deelnemers. Tijdens de interacties met vrouwen, toonden die mannen die een eerdere verhoging in hun testosteronspiegel hadden, meer interesse, presenteerden ze zichzelf meer, glimlachten meer en maakten meer oogcontact. Dergelijke effecten werden niet gezien in interacties met andere mannen. Dit is de eerste studie dat met direct bewijs laat zien dat een verhoogde testosteronspiegel veroorzaakt door intra seksuele competitie wordt gevolgd door meer mannelijk affiliatief gedrag gericht op vrouwen.

Studie 5

Deze studie heeft indirect onderzocht of de blootstelling aan prenatale testosteron is gerelateerd aan een dominante persoonlijkheid later in het leven. Het is aangetoond dat een kleinere verhouding tussen de lengte van de tweede en vierde vinger (2D: 4D) een indicator is van de blootstelling aan prenataal testosteron en daarom heeft deze studie de 2D: 4D van mannen gemeten. Dominantie als een persoonlijkheidskenmerk werd gemeten aan de hand van een vragenlijst. De resultaten lieten zien dat mannen met een meer agressief dominante persoonlijkheid een meer mannelijke (lagere) 2D: 4D hadden, terwijl er geen relatie was tussen sociale dominantie en 2D: 4D. De bevindingen uit deze studie geven aan dat het belangrijk is om onderscheid te maken tussen verschillende vormen van dominantie, omdat eerdere studies geen relatie tussen dominantie en 2D:4D vonden.

De implicaties van testosteron

De resultaten van de studies beschreven in dit proefschrift geven ondersteuning voor de "challenge hypothesis". Deze hypothese verondersteld dat de testosteronspiegel stijgt in situaties die relevant zijn voor de paarvorming en tijdens intraseksuele competitie. Dit proefschrift heeft laten zien dat testosteron relevant is in domeinen zoals intra-seksuele competitie en sociaal contact met een onbekende potentiële partner. Ik denk dat in situaties die relevant zijn voor de menselijke paarvorming een verhoging in de testosteronspiegel kan worden gezien als een adaptieve respons, gericht om de prestaties in die specifieke situatie te verbeteren. De beste ondersteuning voor deze redenering komt uit de studie waar ik heb laten zien dat een verhoogde testosteronspiegel verschillende vormen van affiliatief gedrag gericht naar vrouwen kan stimuleren. Het interessante is dat affiliatief gedrag niet het meest voor de hand liggende gedrag is dat wordt beïnvloed door testosteron, omdat testosteron vaak wordt geassocieerd met dominant en agressief gedrag. De bevinding dat testosteron ook positieve sociale gedragingen kan stimuleren, suggereert dat de interpretatie van testosteron sterk afhankelijk is van de specifieke sociale context. Ik denk dat een stijging in de testosteronspiegel van mannen hun lichaam voorbereid op paarvorming en intra-seksuele competitie, maar wat deze voorbereidingen specifiek inhouden hangt af van de eisen van de situatie.

De implicaties van cortisol

Uit dit proefschrift blijkt ook dat de afgifte van cortisol sterk afhankelijk is van de specifieke sociale context. De interpretatie van cortisol is echter minder duidelijk wanneer men dit hormoon bestudeert in relatie tot de menselijk paarvorming. Het bleek dat gemiddeld gezien de cortisolspiegel niet steeg na contact met een vrouw, maar wat wel bleek is dat de cortisolspiegel steeg bij die mannen die hun vrouwelijke interactiepartner als aantrekkelijk beschouwden. Het kan zijn dat een verandering in de cortisolspiegel wordt gedreven door een ander psychologisch mechanisme dan testosteron en meer context specifiek is. Het kan zijn dat de cortisolspiegel alleen stijgt in situaties waarbij een aanzienlijke hoeveelheid energie en inspanning nodig is, zoals tijdens contact met een aantrekkelijke vrouw. Deze verhoging van de cortisolspiegel is dan afwezig in sociale situaties waarin minder of geen inspanning nodig is, bijvoorbeeld tijdens contact met minder aantrekkelijke vrouwen.

Conclusies

De studies opgenomen in dit proefschrift laten zien dat testosteron en cortisol belangrijke hormonen zijn om te bestuderen in onderzoek naar sociale interacties. Naar mijn mening heeft dit proefschrift een aantal nieuwe bevindingen toegevoegd aan de bestaande literatuur over hormonen en gedrag. De belangrijkste bevindingen van dit proefschrift zijn:

- Agressief dominante mannen reageren met een sterkere stijging in hun testosteronspiegel wanneer zij sociaal contact hebben met een onbekende vrouw.
- Tijdens een competitie stijgt de testosteronspiegel in mannen vooral wanneer hun tegenstander zelfverzekerder is.
- De cortisolspiegel van mannen stijgt tijdens contact met een aantrekkelijke vrouw
- Een verhoogde testosteronspiegel door intra-seksuele competitie stimuleert affiliatief gedrag van mannen gericht naar vrouwen.
- Mannen met een meer mannelijke (lagere) 2D: 4D hebben een meer agressieve dominante persoonlijkheid.

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