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Steroid hormones and some evolutionary-relevant social interactions

Alicia Salvador

Abstract   The steroid hormones, testosterone and cortisol, have some common characteristics, but they are related to generally antagonic processes at both the physiological and psychological levels. In addition, they are the product of the activation of two axes, the hypothalamic–pituitary–gonadal (HPG) and hypothalamic–pituitary–adrenal (HPA), which are very sensitive to a wide range of stressors. Our review focuses on the role of testosterone and cortisol in some social situations, such as competition and others related to the challenge hypothesis, that are evolutionary-relevant and have a component of social stress. Research findings are presented on these points, especially emphasizing the relevance of how the individual interprets social stimuli and attributes of the other participant in the interaction, producing consequences in the response pattern to the social situation. This paper presents empirical support for the role of the interaction between the reproductive HPG and stress HPA axes in several social behaviors with important adaptive significance.

Keywords Testosterone · Cortisol · Competition · Social stress · Winning effect · Mating · Challenge hypothesis

Hormones and behavior: a reciprocal relationship

Traditionally, Behavioral Endocrinology, or Psychoendocrinology, has studied the way hormones influence behavior and psychological processes and the effects these processes

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have on hormonal secretion and functioning. A review carried out several years ago enabled us to follow the evolution of this scientific discipline over the last 150 years, and its progressive configuration as a scientific discipline since the pioneering experiments of Berthold. In the early twentieth century, the development of the discipline was closely related to Endocrinology, but in the middle of the century, important developments were associated with Neuroendocrinology and, finally, with Molecular Biology and Biochemistry, Genetics or Immunology, establishing new trends. However, this discipline's links with Psychology, particularly Comparative Psychology, have maintained it within a specific psychobiological field, characterized by a strong interest in the neurobiological mechanisms and adaptive value of behavior (Salvador and Serrano 2002).

In 1988, Svare published an analysis of research trends in this area, based on behavior patterns and species previously used by Beach in his classic paper "The Snark was a Boojum" (Beach 1950), and focusing on the journal *Hormones and Behavior*. Of 708 papers published between 1970 and 1986, more than half (54%) studied sexual behavior, and approximately 25% examined social communication and emotions. We extended this analysis to the next 12 years (1987–2000), employing the same criteria (Salvador et al. 2003). Of 462 papers analyzed, 44.32% studied sexual behavior, 28.85% emotional and aggressive behavior, and 26.83% social communication. On the other hand, despite the Beach's claim about the need to maintain the evolutionary framework in this discipline, with regard to species Svare (1988) concluded that rodents were still the most studied group (70%). In subsequent decades, a progressive decline in this number took place (up to 45.67% in our analyses), whereas studies employing other species, especially humans, were increasing. More recently, the benefits of a comparative approach and their

influence on many diverse fields in the coming years, including Neuroscience and Psychology, have been emphasized by Mehta and Gosling (2008).

Nevertheless, this scientific area has also developed closely with other disciplines such as Psychiatry, Neurology and Clinical Psychology. The other main journal in this area, *Psychoneuroendocrinology*, is a clear example of this approach. Employing the same criteria, we reviewed the period between 1993 and 1998. Of the 267 papers analyzed, 65.17% used humans, while 29.21% used rodents. In this case, stress (22.85%), mood disorders (17.6%), and aggression, sexual behavior and dimorphism (11.24%) were among the most widely-studied topics. Thus, although from somewhat different perspectives, both specialized journals published mostly studies on topics associated with adaptive and social behaviors and clearly integrated in an evolutionary approach. Furthermore, due to this greater dedication to sexual and stress topics for many years, steroid hormones stand out as the most studied hormones during long periods of time (Salvador and Serrano 2002).

Specific research questions can change throughout the decades, although many of these broad topics continue to be investigated. Furthermore, it is worth noting that the development of a scientific research area greatly depends on progress made in other close fields, as well as the availability of specific techniques that make it possible to answer old questions or propose new ones. Improvement in determination techniques in fluids like saliva has increased the possibilities for studying steroid hormones in relation to human behavior. This point has had an important effect on the number of studies on steroid hormones compared to other hormones whose measurement in saliva presents greater difficulties. Thus, a considerable amount of data about steroid hormones has been gathered using this non-invasive sampling technique. In addition, the widespread development and implementation of neuroimaging techniques has led to interesting possibilities for combining the study of endocrine and neural functioning in the human brain in vivo (see van Honk and Pruessner 2010).

Here I examine some evidence about the role of two important steroid hormones, testosterone (T) and cortisol (C), in some social behaviors whose adaptive value is noteworthy. We focused our review on T and C, regulated by the hypothalamic–pituitary–gonadal (HPG) and hypothalamic–pituitary–adrenal (HPA) axes, respectively, although it must be kept in mind that other hormones are also involved in such interactions. We have dedicated many years of research to these two hormones in relation to different behaviors and contexts, mainly agonistic/competitive behavior and social stress in mice and humans, adopting an apparently evolutionary perspective. These studies are based on the bidirectional relationship between hormones, and could be located within the framework of the Challenge Hypothesis (Wingfield et al. 1990). However, we have also defended (Salvador 2005; Salvador and Costa 2009) the need to study these behaviors taking into account other theoretical contributions, in order to better understand human complexity (e.g., Lazarus and Folkman 1984; Ursin and Eriksen 2004).

Steroid hormones and behavior

Both T and C, main exponents of androgens and glucocorticoids (GC), are steroid hormones that in very low concentrations can have strong effects on our organism at the morphological and physiological levels. They play an important role in the regulation of the metabolism, neural function and, ultimately, behavior, thinking and emotion.

T is the final product of the HPG axis. First, the hypothalamus delivers the gonadotropin-releasing hormone (GnRH), which reaches the anterior pituitary and causes the secretion of gonadotropins (luteinizing hormone, LH, and follicle-stimulating hormone, FSH). In turn, the released LH activates the gonads to synthesize estrogen and T. These hormones give feedback to both the pituitary and the hypothalamus in order to inhibit activity. In parallel, increasing levels of LH and FSH slow down the secretions from the pituitary and the hypothalamus. Likewise, as GnRH is secreted, the hypothalamus responds to increasing levels of the hormone by slowing down its secretion. T becomes effective (a) through activation of the androgen receptor; and (b) through aromatization to estradiol and activation of certain estrogen receptors. Free testosterone or its metabolite (DHT) is transported into the cytoplasm of target tissue cells, where it can bind to the androgen receptor. The testosterone-receptor-complex binds directly to specific nucleotide sequences of the chromosomal DNA, which triggers transcriptional activity of certain genes leading to the subsequent protein biosynthesis (Windisch et al. 2012).

On the other hand, the activation of the HPA axis begins with the hypothalamic release of the corticotropin releasing hormone (CRH) and arginine vasopressin (AVP) into the portal system. In the pituitary gland, both of these stimulate the production and secretion of the adrenocorticotropic hormone (ACTH), which acts at the adrenal gland on the common precursor of all steroid hormones, cholesterol, which is transformed into pregnenolone and, after a series of chemical reactions, into C, the main human glucocorticoid. At the molecular level, GC activity is mediated through cell-specific actions of the glucocorticoid receptor (GR) and mineralocorticoid receptor (MR), members of the nuclear receptor family (genomic action) (Suay and Salvador 2012).

Steroid-receptors, including all of those mentioned above, have an extensive representation in the brain, particularly in areas associated with emotional and cognitive processing,

such as the prefrontal cortex, amygdala, and hippocampus. These rich steroid-receptor neural structures have been shown to play an important role in social behavior. Moreover, for both hormones, T and C, a non-genomic action has also been reported. There are recent data about the moderating role of T and C on neural activity in the amygdala and the frontal cortex and their interconnections (Derntl et al. 2009; Mehta and Beer 2010; van Wingen et al. 2010). Endogenous stimuli like biological rhythms or the hormones themselves, as well as external stimuli (physical exercise or psychosocial stress, among others), activate both axes. The HPG axis interacts extensively with the HPA axis. T inhibits HPA functioning at the hypothalamic level by decreasing AVP functioning (Viau 2002), while cortisol has inhibitory effects on all three levels of the HPG axis (Johnson et al. 1992).

All of these basic effects and their underlying mechanisms are very important, and they ultimately have indirect and direct effects on behavior, emotion and thinking. Moreover, as we learn more about them, we know that they often have contrasting roles. We will see some of these aspects in the following epigraphs, but first a rapid mention of their effects on metabolism is appropriate. Concerning metabolism, T is important for anabolism, whereas C plays a catabolic function, with both being clearly relevant to the availability of energy and, ultimately to behavior and mental processes. This inverse role has been extensively taken into account in sports contexts, where the T/C ratio has been proposed as a good marker of adaptation to exercise. A large amount of research has been carried out since its proposal (Adlercreutz et al. 1986) as an early physiological indicator of important sports disorders related to stress, such as overtraining syndrome, overreaching or simply fatigue, although their use remains questionable (Kraemer and Ratamess 2005; Urhausen and Kindermann 2002). In this context, several studies in elite, physically-active and sedentary subjects reported the interest of this ratio in relation to response to physical stress (ergometry) and other types of stressors, such as mental tests like the Stroop task, and autonomic system measures (Moya et al. 2001a, b). The variations in T and C were clearly associated with other relevant responses to stress, such as cardiovascular measurements during physical effort (Salvador et al. 2001) or other simpler measures like lactic acid (Serrano et al. 2001). In addition, variations in the levels of these hormones usually appear related to mood changes, and even to some affective disorders such as depression (Suay et al. 1998).

Steroid hormones and some evolutionary-relevant social interactions

As mentioned above, the two hormones have shown mostly contrasting roles and relationships with specific behaviors.

T has mainly been associated with aggression, competitive behavior, courtship behavior or proactive response. Its role in social status hierarchies, promoting status-seeking and social dominance motives, has been claimed (Mazur and Booth 1998; Eisenegger et al. 2011). In contrast, C is related to fear, defensive behaviors, and distress response. In fact, C is usually called the "hormone of stress" (Suay and Salvador 2012). All of these behaviors and responses have a clear evolutionary significance and have been studied in mice and humans.

Research with mice

Social interactions are a main source of stress in mammals, with dominance/subordination relationships being an important result of these encounters. In social species, agonistic behavior displayed during social interactions plays a fundamental role in determining and/or maintaining the social status of an individual within a group. From an evolutionary perspective, social interactions are an important source of stress, with stressors of a social nature being the most common in the majority of mammals (Blanchard et al. 2001). Social stress is a chronic or recurrent factor in the majority of higher animal species, and its pattern of effects could be qualitatively different from that originated by other kinds of stressors, at both the behavioral and physiological levels.

During the fight and after its outcome, winning animals experience different responses in comparison with defeated animals (Henry et al. 1986). Furthermore, victory in successive interactions leads to a dominant position in the social hierarchy that includes certain behavioral patterns and physiological characteristics at central and peripheral levels, whereas defeat leads to a subordinate position with a different pattern.

Social defeat has probably been the most frequently-employed model to study social stress in rodents, due to its ecological and ethological validity (Miczek et al. 1991), and it is considered a good model of depression. On the contrary, behavioral and physiological changes experienced by the dominant animal have attracted less attention. More recently, however, there has been a strong interest in coping strategies and factors that could improve them, which would contribute to a better understanding of the characteristics of resilient individuals, possibly related to proactive coping (Koolhaas et al. 1999). It is worth noting that dominant animals are obviously submitted to social stress and potentially harmful effects, although different from what is experienced by subordinate animals.

Dominant and subordinate individuals present differences at several levels. For instance, at the physiological level they show differences in the weight and size of organs, cardiovascular parameters, temperature, immunological parameters and endocrine concentrations and/or

responses; at the neural level, differences have also been found in monoamines, monoacids, *c-fos* and receptors, among others. More apparent are the differences at the behavioral level, including non-social ones, such as motor activity and exploration or sensitivity to rewarding properties of psychoactive substances that could lead to a different susceptibility to consumption of various drugs of abuse. Especially striking are the differences in behavior displayed during social interactions. Since the pioneer studies of James Henry, it has been evident that dominant male mice were more active and responded to social interactions with a predominantly sympathetic adreno-medullary (SAM) pattern, whereas subordinate males were less active and predominantly responded with an HPA pattern (Henry and Stephens 1977).

The two main neuroendocrine axes activated in response to stress, SAM and HPA, have been related to "different and relatively independent dimensions of the hormonal activation in the coping to stress" (Weiner 1992). According to Koolhaas and Bohus (1989), who included aggressive/competitive behavior among the coping responses, there are two extreme coping strategies (active or proactive versus passive or reactive). The active strategy is characterized at the behavioral level by "fight or flight", and at the physiological level by high basal levels of T and noradrenalin and a high reactivity of SNS, represented by the reactivity of the plasma catecholamines and the BP. The passive strategy is characterized by scarce social activity and even immobility, and at the physiological level by a parasympathetic response, greater HPA response, and reduced levels of T. Years later, Koolhaas et al. (2007) maintained that coping styles are stable over time and across situations, can be identified in a range of species, and have a clear ecological validity. These formulations agree with the model proposed by Henry (1992), who also included the T within the neuroendocrine patterns of response [see also the neuroendocrine responses of hawks and doves to acute threat in Korte et al. (2005)]. Recently, Koolhaas et al. (2010) defended the existence of another independent dimension of individual variation in addition to the quality of the response to a challenging condition (coping style), the quantity of that response (stress reactivity).

Especially when social status is threatened, endogenous T levels are positively related to aggressive and dominant behaviors in a variety of animal species (Wingfield et al. 1990; Archer 2006). It is very interesting that dominant animals experience an increase in aggressive behavior; that is, victory in successive encounters facilitates aggressive behavior, which is very relevant in determining how offensive interactions increase and how patterns of dominance over other co-specifics develop. Several years ago, using Conditioned Place Preference (CPP), we were able to confirm that victory in successive encounters was rewarding for male OF1 mice (Martínez et al. 1995).

Based on this finding, we aimed to further the understanding of the influence of social interactions on T. Although the first references to rewarding effects of T were made many decades ago, systematic research was encouraged by the formulation of the addiction hypothesis by Kashkin and Kleber (1989) in relation to the abuse of T, the so-called Anabolic-Androgenic Steroids (AAS). In addition to the social problems stemming from this consumption, the rewarding properties of T also have a special importance in the context of aggression and coping styles, since they could account for the increased offensive behavior that appears when repeated agonistic behavior ends in victory. In social species, outcomes of social interactions influence the type of ongoing social interactions. Thus, individuals with a repeated experience of victory ("dominants") present certain neuroendocrine changes, in addition to typical behavioral patterns that include a reduced latency to attack and a greater occurrence and duration of offensive behavior. In contrast, animals that have been defeated in successive encounters display "subordination", with particular physiological and behavioral characteristics, including tendencies to avoid social contact.

During the last few years, the rewarding properties of T have been analyzed in several species, although publications on rewarding properties of T in mice are almost limited to our research group, employing CPP, a very common technique for analyzing the rewarding effects of drugs. First, we intended to confirm the reinforcing effects, employing the range of dosage utilized in male rats; thus, 0.8, 1 and 1.2 mg/kg or vehicle were subcutaneously administered 30 min before the conditioning in OF1 male mice, with T being associated with the less preferred compartment. In this study we found that T had rewarding effects, although dependent on the environmental cues employed as conditioned stimulus, since conditioning was only found when the association was with the black compartment, but not the white one (Arnedo et al. 2000). Curiously, similar findings were found when unconditioned stimulus of CPP was observed in a submissive male attacked by the experimental animal, who was always the winner; results showed that OF1 male mice preferred the compartment associated with victory, but only when it was black (Martínez et al. 1995). An important feature of our study was the behavioral variability observed, which suggests the potential role of individual differences in the rewarding capacity of T. This variability was also found in relation to the effects of the administration of propionate of T (PT) on agonistic behavior associated with basal levels of aggressiveness (Martinez-Sanchis et al. 1998, 2003). The aim of our second study (Arnedo et al. 2002) was, first, to verify rewarding properties of T after eliminating

conflictive environmental cues. For this purpose, we chose the experimental cage model employed by Cunningham (1995), in which both compartments are black. The second aim was to check the supposition that rewarding properties of T will be greater in more aggressive animals. To do so, prior to the CPP, experimental mice were pre-screened in an agonistic encounter and allocated to short and long attack latency (SAL and LAL) groups, depending on whether they attacked in the first 5 min from the beginning of the encounter or afterwards. Results supported the rewarding properties of T with both (1 and 2 mg/kg) doses employed, but they did not confirm the role of basal aggressiveness. Selection based on only one encounter may not be sufficient to detect basal aggressiveness or, since the test carried out for selection necessarily implied a victory (as the opponent was a non-aggressive animal), the potential rewarding effects of this experience could be more important than the basal level of aggressiveness.

The next experiment included the manipulation of agonistic experiences through exposure to social encounters with repeated victories or defeats. It aimed to test whether the repeated experience of victory produces greater sensitivity to rewarding effects of T, compared to the repeated experience of defeat. We hypothesized that the rewarding properties of T would be greater in dominant animals than in subordinates. After five consecutive days with daily 10-min encounters between pairs of animals matched by weight, they were separated into two groups, dominant and subordinate, depending on the exhibition of offensive (threats and attacks) or defensive (escape-avoidance and defense-submission) behaviors. All animals were submitted to a CPP procedure during the following days. Our results showed that dominant males spent more time in the compartment associated with T, whereas the subordinate males spent less time, always in comparison with the time registered in the preconditioning session. In dominants, 1.2 and 2 mg/kg of T produced significant increases, whereas in the subordinates only the highest doses produced marginally significant reductions. In sum, these results suggest that the experience derived from previous social interactions moderates the rewarding properties of T (Rodríguez-Alarcón and Salvador in preparation); in fact, following 5 days of aggressive confrontation, the mice consolidated patterns of responding (aggression vs. submission) that were already evident in the first agonistic session (Rodríguez-Alarcón et al. 2007). These results lead one to think that T could act by amplifying appetitive or aversive effects of social behaviors, contributing to discriminating between social interactions that could end in victory or in defeat (Johnson and Wood 2001). We speculate that, through experience, certain expectations are generated that will tend toward fight or avoidance of encounter; that is, the T response, when faced with the appropriate stimulus (co-specific), is integrated within the coping strategy adopted by the individual, active or passive. When there is a perspective of success, it is more likely that the strategy will be active, and contact and attack will be established with a T response (Salvador 2005). On the contrary, if the previous experience has been one of repeated defeat, the subject will avoid and not present offensive behavior, but instead show submissive signs, which will be accompanied by an absence of T response or perhaps an altered sensitivity to T that could become aversive. T response will be associated with expectations; thus it will be anticipatory and not the consequence of the outcome of the interaction. There are data about an anticipatory response of T in the mere presence of a co-specific, or even a stimulus associated with it. We will return to this point later.

Human research

In the past few years, the challenge hypothesis has had a great impact on Behavioral Endocrinology. It was originally proposed to explain the T-aggression associations in birds with a monogamous mating system (Wingfield et al. 1990). This hypothesis maintains that T levels rise during challenges in contexts that are relevant for reproductive physiology and behavior. This hypothesis takes into account aggressive, competitive, sexual, parental and social behaviors, suggesting T changes related to their functional meaning. More recently, the challenge hypothesis has been extended to research on humans, now also incorporating challenges facing human males, such as competitions and reactions to sexual stimuli (Archer 2006; van Anders and Watson 2006). Here I review some findings from studies carried out in men about competitive/agonistic behavior, courtship and affiliative behaviors, and also related to distress and negative emotions, and aggressive behavior.

Competition, implying that one or more individuals carry out some actions directed toward achieving a goal by confronting another individual or group motivated by the same goal, is a quite frequent situation in human communities or groups at different levels of "civilized" development. Competitive or agonistic behavior plays an important social role, not only to get primary reinforcements, but also to obtain other secondary resources, such as employment, promotion and admission to prestigious universities. Human competition is common, although the forms of interaction may vary from direct aggression and violent acts to the use of subtle strategies.

Previously, I argued that studying the effects of competitive situations on excretion levels of C and T might contribute to a better understanding of the effects of social stress and how people cope with it (Salvador 2005). From an evolutionary approach, the parallelism between the

agonistic behavior observed in other species and that displayed in human sports competition has been emphasized (Kemper 1990). Parallel to the behaviors shown by the mice during encounters, we studied the behaviors shown by judo fighters during a judo combat, and their relationship with T and C changes, in order to establish the similarities between the two situations (Salvador et al. 1999). It has been claimed participation in competitive sports is one way that aggressive behavior is ritualized among humans (Nelson 2000). Thus, the majority of the research on the "competition effect" was carried out in the sports context, although more recently a growing number of studies have been developed in the laboratory setting. On the whole, the results obtained do not reflect a clear, unanimous panorama, reporting T increases in winners, no statistically significant differences between winners and losers, and even T increases in losers, with very rare significant results in C levels. A lot of (moderating or mediating) interesting intervening variables have been proposed, including physical effort, relevance for status, motivation to win, mood, causal attribution, personality and trait characteristics, and coping styles (see Archer 2006; Salvador 2005; van Anders and Watson 2006).

Several studies from our laboratory indicate that the neuroendocrine response to competition depends more on subjective factors related to the appraisal of the situation than on the objective outcome obtained, as initially proposed by the biosocial status hypothesis (Mazur 1985; Mazur and Booth 1998) to explain the establishment of social status in primate groups. This hypothesis argues that, in competitive situations, victory would lead to increases in T, whereas defeat would produce decreases. Our findings suggest that when people are in a competitive situation, they assess it in such a way that it activates a psychobiological coping response. The extent (or intensity) of the coping response depends on several factors, for instance, perceived possibilities of controlling the outcome. The coping pattern displayed by the individual determines the T and C levels while facing competition (Salvador 2005; Salvador and Costa 2009). The importance of control is not the only relevant cognitive variable. Ongoing research invokes different cognitive processes, from the primary cognitive comparison of the immediate external event with some cognitive representation based on prior experiences to other much more complex processes, such as expectancies or response outcomes that can have a profound influence on the magnitude and direction of the stress response (Levine 2000). The situation the individual is faced with is evaluated based on the expectancies attached to it and the possible actions available to this particular individual. Consequently, to a large degree stress response depends on previous experience and how it is interpreted.

Our research on human competition started in an evolutionary context employing observational methods (Who

won or lost?), but empirical findings progressively showed that it was more essential to find out how the individual perceived, appraised, controlled and experienced the importance of competition and its outcome, in order to understand the neuroendocrine response. These and other cognitive processes are involved in triggering differentiated patterns of response. A proposal for integrating competition within a more general stress framework was formulated and defended, so that previous results on this topic can be better explained as a part of the coping response to competition (Salvador 2005). From this perspective, if the individual appraises the situation as important, controllable and depending on his or her effort, that is, if he/she interprets the competitive situation as a challenge, an active coping response pattern is more likely to develop. This pattern would be characterized by increases in T and sympathetic nervous system (SNS) activation, accompanied by positive mood changes, all of which would increase the probability of victory, although obviously it would not be guaranteed. On the other hand, if the individual assesses the situation as threatening or uncontrollable, he/she will probably present a passive coping response pattern characterized by insufficient T and SNS activation and increases in C, accompanied by negative affect changes. This appraisal and the associated responses will increase the probability of defeat. Additionally, the outcome finally obtained will be able to affect mood and satisfaction. Obviously, the appraisal in a specific situation is the result of the interactions among many dimensions and variables, some probably not at a conscious level. Moreover, the probability of success, or lack of it, associated with the response pattern will depend on the specific demands and processes involved in the specific competition in question. Finally, the emotions associated with the outcome obtained would depend on aspects such as the importance of the competition, motivation to win, status, etc. Post-competition complex cognitive evaluations may strongly moderate the psychobiological responses during the recovery period, as in the attribution processes (Salvador and Costa 2009). In sum, T increases after competition have typically been attributed to winning, i.e., the "winning" effect, yet there is strong evidence that being victorious is not in itself sufficient to provoke a T response. This effect seems to interact with the mechanisms of steroid hormone action to drive interspecific variations in behavior, as has been reported in mice (Fuxjager et al. 2011). Additionally, as mentioned above, it has been proposed that T responses are moderated by complex psychological processes (Salvador 2005; Salvador and Costa 2009), but other aspects must be taken in account in addition to those more associated with the protagonist subject.

Among other important contextual and situational aspects, in a competitive situation there is always an opponent whose characteristics clearly affect the

interaction. In animal behavior, there is evidence of the importance of some of them, such as size, aggressiveness, and previous experience. In humans, the complexity of potentially relevant characteristics of the opponent increases enormously. In a recent study, we investigated whether the opponent's psychological state affected hormonal changes in men competing face-to-face on a rigged computer task. Our results showed that, regardless of the outcome, the competition led to increases in heart rate and T levels. Both winners and losers were being challenged to compete for social status, and their responses did not differ, as stated in the challenge hypothesis. But more interestingly, we found that the T levels of the participants increased more when their opponents had high self-efficacy. Furthermore, the T levels of losers, but not winners, increased more when their opponent judged the competition to have low importance. Thus, the psychological state of the opponent makes a competition challenging, and subsequently triggers T responses (van der Meij et al. 2010a).

In line with the challenge hypothesis, other important and evolutionary-relevant social interactions are the behaviors related to mating, specifically the interaction with a person of the other sex. Previous studies have shown that situations relevant for human mating can affect the levels of many hormones. We have studied T and C changes related to young men's interaction with women in a neutral site. Informal contact with a woman lasting approximately 5 min resulted in an increase in salivary T among men, particularly in men with an aggressive dominant personality. In addition, higher salivary T levels were related to being sexual inactive for a month or more, and not being involved in a committed, romantic relationship (van der Meij et al. 2008). In another study employing the same type of social interaction, we focused on C 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 C levels of the participants declined according to the circadian rhythm. However, C levels in men declined less when they had contact with a woman. Furthermore, they increased when these young men perceived the woman with whom they had contact as attractive. Our findings provide indirect evidence for the role of the HPA axis in human courtship. During social contact with attractive women, moderate increases in C levels may reflect apprehension about an opportunity for courtship (van der Meij et al. 2010b).

Furthermore, although T is thought to play a key role in male–male competition and courtship in many vertebrates, its precise effects are unclear. In another study, we combined the two previous evolutionary-relevant social situations, and explored whether courtship behavior in humans is modulated by competition-induced changes in T. For this

purpose, 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' overall behavior. 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 elevated T during male–male competition is followed by increased affiliative behavior towards women (van der Meij et al. 2011).

In numerous species, social hierarchies are related to competitive behaviors, but also to dominance behaviors. The latter is associated with higher status across animal and human groups (Sapolsky 2005). As mentioned above, there are human studies indicating that T is linked to dominance under conditions of status threat or challenge, although other studies have found weak or null results. In order to find an explanation for the inconsistent findings, Mehta and Josephs (2010) proposed that T may interact with C to regulate dominance. According to these authors, only when C is low should higher T encourage higher status; when C is high, higher T may actually decrease dominance and, in turn, motivate lower status. In a subpopulation of delinquent adolescents, Popma et al. (2007) found a moderating effect of C on the relationship between T and some subtype of aggression, such as overt aggression.

Recently, the ratio of the basal levels of T and C has been proposed as a possible marker of proneness to social aggression (Terburg et al. 2009). These authors proposed a comprehensive neuro-evolutionary model, the Triple Imbalance Hypothesis (TIH), which could be adaptive among other species, but may have become socially maladaptive in modern humans. According to this model, reactive aggression is essentially subcortically motivated by an imbalance in the levels of C and T (Subcortical Imbalance Hypothesis). This imbalance also downregulates cortical–subcortical communication (Cortical-Sub-cortical Imbalance Hypothesis), hence diminishing control by cortical regions that regulate socially aggressive inclinations. In addition, the hypothesis suggests that reactive aggression is associated with left-sided frontal brain asymmetry (Cortical Imbalance Hypothesis), and this is especially observed when the individual is socially threatened or provoked (van Honk et al. 2010).

Related to this, previous research in our laboratory showed a clear response pattern in young men, employing combined measurements of neuroendocrine and mood responses together with changes in perceptual asymmetry on a consonant–vowel dichotic listening (DL) test. In a first

study, we observed that the induction of negative affect by means of the Velten Mood Induction Procedure, in comparison to neutral affect, in 44 healthy young men, provoked reductions in positive mood and increases in negative mood measured by PANAS, together with significant increases in C levels. Concerning DL, an increase in left ear items and a decrease in right ear items were reported for those subjects who obtained a right ear advantage (REA) in the neutral condition. These results confirmed C increases in response to negative affect, and an emotion processing linking negative affect to the right hemisphere (Gadea et al. 2005). In a second study with a similar procedure, we also aimed to evaluate cardiovascular responses following an anger mood induction laboratory task. We confirmed previous data that had shown an increase in heart rate and blood pressure as well as increased T and decreased C in response to anger and aggressive behavior. Based on the subjective perception and neuroendocrine and cardiovascular response of the subjects, we concluded that the self-referent statement anger-induction method by Engebretson et al. (1999) was able to generate the experience of anger affect in 30 healthy young men. Regarding DL, an enhanced REA was observed after anger, which indicates greater left hemisphere activity (Herrero et al. 2010). In sum, from these studies we can conclude that consequences of laboratory-induced mood on steroid hormones produced increases in T associated with anger, whereas C was related to negative affect. Concerning DL, there was a diminished REA for sadness and an increased REA for anger. These findings agree with previous positions indicating that the left frontal brain region is involved in the experience and expression of some emotions like anger (Harmon-Jones et al. 2006). The global results fit the approach-withdrawal motivational model of emotional processing, pointing to sadness as a right hemisphere emotion, while anger is processed bilaterally or even in the left hemisphere, depending on the subject's preferred mode of expression (Gadea et al. 2011).

Conclusions

Here I have reviewed evidence about the relationships between two important steroid hormones, T and C, and some evolutionary-relevant social behaviors, in mice and humans. I have presented empirical support for the role of the interaction of the HPG and HPA axes in several social behaviors with adaptive meaning in various contexts.

Within an evolutionary-based context that includes knowledge gained from very different species, particularly rodents, we now need improved techniques that would make it possible to study in humans some of the interrelationships found in animals. This effort would also imply

the incorporation of advances made in the study of cognitive and emotional components of social interaction. In our opinion, it is essential to consider different analysis levels that would contribute to a more complete understanding of social behavior.

Nowadays, knowledge is being integrated from different disciplines, which provides us with an opportunity to take advantage of an interdisciplinary approach (e.g., Social Neuroscience). Hence, in studying social interaction, we consider it necessary, while keeping the evolutionary background in mind, to incorporate conceptual, technical and methodological advances. Throughout the last few years, a clear progressive introduction of psychological concepts (even personality or behavioral syndromes) has occurred in animal research. Therefore, it is imperative for the research on human social interaction to take a similar path by addressing the higher complexity of the cognitive processes and social organization of our species. Advances in cognitive sciences could provide a strong impetus for our understanding of social behavior.

Finally, it is worth noting that it is necessary to delve into the underlying neurobiological mechanisms of this social behavior, taking into account the rewarding/punishing dimensions of social interactions and their outcomes. Furthermore, molecular and cellular techniques will facilitate the understanding of the intricate biochemical complexity of the underlying mechanisms of hormones. The increasing availability of neuroimaging techniques favors advances in knowledge about the involvement of neural structures and their interconnections. In summary, gaining understanding of human social interaction, its cognitive antecedents, its psychobiological response patterns, and its more basic neurobiological mechanisms will allow us to better comprehend the basis of individual differences.

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