Social Modulation of Androgens in Vertebrates: 
Mechanisms and Function

RUI F. OLIVEIRA
INSTITUTO SUPERIOR DE PSEICIOLOGIA APLICADA 
1149-041 LISBON, PORTUGAL

I. INTRODUCTION

The approaches of the social and the biological sciences to the study of behavior have been seen as almost mutually exclusive. The nature versus nurture debate has been almost permanently present in the history of the behavioral sciences. As examples one can mention the Cartesian dualism in the neurosciences, the Lorenz versus Lehrman debate on innate behaviors and on the nature of instinct in classic ethology in the 1950s (Lehrman, 1953, 1976; Lorenz, 1939, 1965), or the antagonistic views of social constructivism versus genetic (biological) determinism in psychology (e.g., Lewontin et al., 1994). However, more recently, a growing body of literature has documented social influences on genetic constitution and gene expression, functioning of the endocrine and nervous systems, and immune activity (Cacioppo et al., 2000). Thus, the effects of social factors on the expression of behavior may involve underlying biological processes. Therefore, the classic dichotomy of nature versus nurture should be abandoned and it should be recognized that for most behavioral traits there is a nonadditive contribution of both biological and social factors, and that the latter are expressed through biological mechanisms. This conciliatory view has emerged in psychology and has been labeled social neuroscience (Cacioppo and Berntson, 2002). The central topic of this review, the social modulation of androgens, its mechanisms and function, can be seen as another contribution toward expanding this new view of nature and nurture, as being complementary rather than mutually exclusive, to the field of behavioral endocrinology.

The responsiveness of the endocrine system to social stimuli has been well established in behavioral endocrinology for many years (e.g., Cannon, 1929; Selye, 1976). However, most studies have concentrated on the response of the hypothalamus-pituitary-adrenocortical (HPA) axis.
to stressors, and glucocorticoids came to be known as stress hormones (Sapolsky, 2002). On the other hand, less research has been carried out on the response of the reproductive axis (i.e., hypothalamus-pituitary-gonadal axis, HPG) to the social environment, and on its behavioral significance. Sex steroids, as the name implies, have been classically viewed as hormones directly involved in reproduction, and other potential roles for these hormones have only started to be hypothesized. Gonadal steroids, being secreted by cell populations intimately associated with gamete-producing cells, are especially well suited as coordinating agents between gonadal maturation and the expression of displaying traits (Oliveira and Almada, 1999). Displaying traits, both behavioral and morphological, have associated costs that are compensated for only when the individual is effectively capable of mating. In other words, it would make no sense from an evolutionary perspective for an individual to express reproductively behaviors and secondary sex characters if its gonads are not ready for gamete release and if there is no partner available. Thus, androgen responsiveness to the social environment can be expected in adult males in a breeding context, as a way to coordinate an integrative response of the organism to the environmental conditions (Wingfield et al., 1990, 1999, 2000). More specifically, the social modulation of androgens can be viewed as a mechanism for adjusting androgen-dependent behaviors to the current social environment of the individual. According to this hypothesis, the social interactions in which an individual participates influence its androgen levels, which in turn will modulate perceptive, motivational, and cognitive mechanisms as well as somatic releasers, which in turn may affect its subsequent behavior in social interactions (Fig. 1).

In the current review, the mechanisms of androgen action on behavior are discussed first. The evidence for social modulation of androgen levels are then presented. Finally, androgen responsiveness to the social environment is discussed using an integrative approach, that is, by exploring both its proximate (i.e., physiological/developmental) and ultimate (i.e., functional/evolutionary) causes. The article ends with a discussion on the social modulation of androgens and its behavioral consequences in humans.

II. ANDROGENS AS CAUSAL AGENTS OF BEHAVIOR

A. HISTORICAL BACKGROUND

In the words of one of its founders “behavioral endocrinology has a short history but a long past” (Beach, 1974). With these words Frank Beach meant that although the discipline was formally founded in 1948 with the
Fig. 1. Model for the interplay between androgens and social behavior. Androgens can affect the expression of an individual’s behavior either by acting on the neural mechanisms underlying behavior (i.e., perception, motivation, and cognition) or by changing social releasers at the periphery of the organism. The social interactions in which an individual participates may feedback on its androgen levels, which in turn will affect its behavior in subsequent social interactions (grey area, nervous system).

Publication of its first textbook (Beach, 1948), knowledge about the effects of hormones on behavior was present even in ancient societies. A vivid view of ancient endocrinology is provided by Sapolsky (1997) in his essay “The Trouble with Testosterone,” where he describes the probable scenario of the discovery of the effects of testosterone (T) on behavior as follows: A dozen millennia years ago or so, an adventurous soul managed to top off a surly bull’s testicles and thus invented behavioral endocrinology. It is unclear from historical records whether this individual received either a grant or tenure as a result of this experiment, but it certainly generated an influential finding—something or other comes out of the testes that helps to make males such aggressive pains in the ass. That something or other is testosterone.

In fact, since mammals have their testes located in a scrotum outside the body cavity, which facilitates their removal, it is not hard to imagine that during the process of animal domestication or neolithic farmer ancestors accidentally discovered the benefits of castration. Thus, the link between something produced by the testes and behavior may have been implicitly established for some millennia (Freeman et al., 2001). The castration of boys before puberty to serve as eunuchs (i.e., harem attendants) started before 700 B.C. in Asian courts. The recruitment of these loyal servants, who would not be tempted to challenge the paternity of their lords, to guard and serve in harems became a common practice in the courts of Egypt, Byzantium, and China (Scholz, 2001). In China they were used as
guards of the Emperor's inner court and their numbers reached a peak of 70,000 at the end of the Ming Dynasty, when they gained immense political power (Tsoa, 1996). Human castration has also been used as a form of punishment in some societies (e.g., from the Sui Dynasty in China to some current Western societies in the case of sexual offenders), and as an act of rejection of sexual identity in some religious traditions (e.g., ancient paganism, Christianity, and Buddhism; Scholtz, 2001). In the sixteenth century, the effects of castration on the maintenance of a higher pitched voice in boys were used to produce male sopranos to sing in church, where women were not allowed to sing. These sopranos were known as castrati and became very popular in the seventeenth and eighteenth centuries, singing in church choirs (e.g., the Sistine Chapel in the Vatican) and as male leaders in opera, mainly in Italy. This practice was banned in the late nineteenth century, when females or castrati were started to take their roles in operas (Jenkins, 2000). The Sistine Chapel stopped using castrati in 1903; the last of the castrati, Alessandro Mareschi, was recent enough to have made gramophone recordings and died in 1924 (Jenkins, 2000). In all these cases the knowledge of the link between prepubertal castration and physical and behavioral changes was implicit; castration was known to prevent the emergence of male sexual characters such as the development of muscle mass, the growth of the penis, the masculine pattern of fat accumulation, deepening of the voice, and a lack of interest in sexual behaviors.

Explicit knowledge of the effects of androgens on behavior was clearly present in written form in classical antiquity. In his Historia Animalium (ca. 350 B.C.), Aristotle describes the effects of castration in birds and in men, and subsequently a humoral basis of biological functioning was established in the Western world with the theory of the four humors to explain the equilibrium between health and disease (Freeman et al., 2001). Only in the eighteenth century did the dawn of the experimental approach to behavioral endocrinology start to emerge with the first attempts at testicular transplants. John Hunter (1728–1793) was the first to transfer the testis of a cock into the peritoneal cavity of a hen, but he was more interested in the surgical technique of tissue transplantation than in its effects (Schulteis et al., 2000). Thus, it was not until 1849 that the first experiment in behavioral endocrinology was performed. Arnold Berthold (1801–1863) reimplanted or transplanted testes in castrated cockerels and showed that, by returning the testis to the abdominal cavity, the expression of male behaviors such as mounting, fighting, and crowing, was restored. While castrated cockerels did not develop either male behavior or male secondary sex characters, such as the development of a comb. Since the implanted testis lacked neural connectivity to the animal, Berthold
concluded that the testes must secrete a substance into the bloodstream that affects the expression of these behavioral and morphological traits (Freeman et al., 2001; Nelson, 2000). Berthold's study is now credited as a landmark in endocrinology since it established the concept of hormone, that is, the "secretory blood-borne product" in his own words (Nelson, 2000). The term hormone was later introduced into the scientific vocabulary by Ernest Starling in 1905 (Freeman et al., 2001).

Meanwhile, testis-borne hormones started to be seen as causal agents of intellectual and sexual performance, which led to their use in physical and sexual rejuvenation. The first proponent of the rejuvenation hypothesis was Brown-Séquard (1817–1894) who, at the age of 72 years, experimented on himself with an injection of animal testicular extract (Schultheiss et al., 1997). Subsequently Steinach (1861–1944) proposed vasectomy as a way to increase male hormone production, on the ground that blocking of the secretory output would increase the endogenous levels. This rejuvenation treatment became very popular and notable figures such as Freud (1856–1939) and Yeats (1865–1939) underwent the "Steinach operation" (Freeman et al., 2001; Schultheiss et al., 1997; Wyrdham, 2003).

E. ANDROGENS FROM DETERMINISTIC FACTORS TO NEUROMODULATORS

Following Berthold's study the ablation and replacement experiment became the classic paradigm in behavioral endocrinology, to establish a link between a given hormone and a given behavior. First, a tissue suspected of being the source of a particular hormone was removed and a decrease in the expression of a hormone-dependent behavior was predicted. If so, exogenous administration of the suspected active hormone should restore the expression of the affected behavior. Using this approach, androgens have been implicated in the expression of agonistic and sexual behaviors in a number of vertebrate species (for reviews, see Ball and Balhazart, 2002; Baum, 2002; Nelson, 2000).

Berthold's study can also be used as an example to introduce a classic dichotomy in behavioral endocrinology the division of influences of androgens on behavior into activational versus organizational effects. In fact, Berthold manipulated (e.g., castrated) the individuals at a young age and looked for effects of the treatment several months later in adult animals. Therefore, his experiment is an example of how a manipulation at an early stage of the life of the individual might have a permanent effect on its adult behavior, that is, an organizational effect (Arnold and Breedlove, 1985). On the other hand, in adulthood hormones may affect behavior in a transient way, by activating proximate mechanisms underlying behavior, that is, by having an activational effect on behavior (Arnold and
Breedlove, 1985). This dichotomy was formally introduced by Phoenix and associates while studying the sexual behavior of female guinea pigs (Phoenix et al., 1959).

Studies in which the behavioral effects of castration were reversed by androgen replacement, either at the organizational level or at the activational level, led to the view of hormones as deterministic causal agents of behavior, acting as “pushbuttons” on the display of particular behaviors. This view was challenged by experiments in which androgen replacement therapy was not on its own sufficient to activate a behavior, but would be effective in the presence of the right stimuli (e.g., Albert et al., 1993). These results suggest that androgens are necessary for the persistence of the behavior but are not sufficient to activate the expression of the behavior. Another type of evidence that supports this view comes from electrophysiological studies of the stria terminalis, a key component in the neural circuits of aggressive behavior in mammals, which connects the amygdala and the hypothalamus. In castrated Wistar rats T microinjections into the stria terminalis increase its neural activity by reducing the refractory period of action potentials (Kessl and Drewett, 1979). However, the administration of T to the stria terminalis in the absence of preexisting neural activity has no effect. These results support the idea that T per se does not promote aggression but that it may exaggerate a preexisting pattern of aggression.

The accumulation of these kinds of data shifted the conceptual paradigm of behavioral endocrinology from hormones as deterministic agents of behavior toward a more probabilistic view, according to which androgens started to be seen as facilitators of behavior. That is, the hormones would not activate per se the expression of the behavior but would increase the probability of its expression, by acting as modulators of the neural pathways underlying that behavioral pattern (Simons, 2002). Many studies have implicated androgens in the modulation of different neurotransmitter pathways, for example, in the serotonergic and vasopressinergic systems involved in the control of social behaviors in mammals (e.g., Simons, 2002).

C. MECHANISMS OF ANDROGEN ACTION ON BEHAVIOR

The above-mentioned neurochemical pathways modulated by androgens can be part of one of three major functional compartments of the nervous system: sensory systems (i.e., information input systems), central processors (i.e., the central nervous system) and effectors (i.e., output systems) (Nelson, 2000; Fig. 2). Androgens can also affect behavior by acting peripherally on somatic structures (Hinde, 1970) that have a role as sign
stimuli or releasers (in the sense of Tinbergen, 1951), thus evoking a behavioral response in conspecifics (Fig. 2; see Table I for examples).

1. Central Actions of Androgens: Motivational Systems

The localization of sex steroid receptors, both androgen receptors (ARs) and estrogen receptors (ERs), in the brain was a first indication that the brain is a major target of androgen action related to behavioral expression. Furthermore, identification of the specific brain areas that express AR and/or ER led to detection of neuronal circuits involved in the control of behavior that could be influenced by gonadal steroids. It should be noted here that some of the behavioral effects of androgens are mediated by estradiol (E2) after it is formed by the aromatization of T (e.g., Balthazart et al., 1995). In fact, in most cases T acts as a prohormone that needs to be metabolized either into another biologically active androgen (e.g., 5\(^\alpha\)-dihydrotestosterone [DHT] in mammals or 11\(^\beta\)-ketotestosterone [KT] in fish), or into E2 (through aromatization) to exert its effects using either AR or ER, respectively. In terms of the neural localization of these circuits, after the earlier maps of brain AR and ER were compiled, it became clear that the preoptic area/anterior hypothalamic region and a few other limbic areas were the main targets of androgens in the vertebrate brain (Ball and Balthazart, 2002; Schulkin, 2002), which suggested that motivational systems were one of the main target circuits. By acting on neural systems
<table>
<thead>
<tr>
<th>Mode of action</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Sensory systems</td>
<td>1. Testosterone-treated juvenile cichlid fish show an increased electro-olfactogram response to female sex pheromone and increased sexual behavior toward females</td>
</tr>
<tr>
<td></td>
<td>2. Male angelfish (<em>Pterophyllum scalare</em>) treated with dihydrotestosterone shift the frequency response of their olfactory electroreceptors, increasing their mate electrolocation efficiency</td>
</tr>
<tr>
<td></td>
<td>3. Androgens increase penile sensitivity in rats, promoting ejaculation</td>
</tr>
<tr>
<td>B. Effectors</td>
<td>1. Testosterone increases sympathetic muscle mass and the density of acetylcholine receptors in sympathetic muscles of male zebra finches (<em>Taeniopygia guttata</em>) and inhibits the activity of cholinesterase in the neuromuscular junctions of the penis</td>
</tr>
<tr>
<td></td>
<td>2. Androgen treatment induces the differentiation of the laryngeal masseter muscles, muscle fibers, and cartilage of the male African frog (<em>Xenopus laevis</em>) vocal system used to produce male calls</td>
</tr>
<tr>
<td></td>
<td>3. Castration reduces and testosterone replacement therapy restores the sex pheromone content in the abdominal glands of red-bellied newts (<em>Cynops pyrrohogaster</em>) males</td>
</tr>
<tr>
<td></td>
<td>4. Castration reduces and testosterone restores pheromone production and scent marking in meadow voles (<em>Microtus pennsylvanicus</em>), tree shrews (<em>Tupaia belangeri</em>), and Winter rats</td>
</tr>
<tr>
<td>C. Somatic releases</td>
<td>1. Nuptial coloration is suppressed in castrated males and promoted by androgen treatment in African cichlids and sticklebacks (<em>Gymnocorymbus aequetus</em>)</td>
</tr>
<tr>
<td></td>
<td>2. Testosterone induces the development of the sword in male swordtails (<em>Xiphophorus helleri</em>) caudal fin, which is used by females in mate choice</td>
</tr>
<tr>
<td></td>
<td>3. Castration suppresses and testosterone induces the plumage ornamental coloration in charadriiform birds</td>
</tr>
</tbody>
</table>

Cardwell *et al.* (1995)  
Simeros and Tricas (2000)  
Bosch and Levinson (1955); Larsen *et al.* (1973)  
Blech *et al.* (1984); Lai et al. (1980)  
Kelley (2002)  
Yamamoto *et al.* (1996)  
Ferkin and Johnston (1995); Gawlowsky *et al.* (1976); Habe and Ichikawa (1998); Manso *et al.* (2002)  
Fernald (1976); Ikeda (1933); Levy and Aronson (1955); Rome *et al.* (1977); Wagler-Leong and Reitz (1974)  
Baldwin and Goldin (1939); Rosenthal and Evans (1998)  
Kimball and Ligon (1999)
underlying motivation, androgens may affect both appetitive (e.g., courtship) and consummatory (e.g., copulation) aspects of behavior (Ball and Balthazart, 2002). As an example of an androgen effect on a motivational system underlying appetitive behaviors, one can mention the effects of T on territorial aggression and rank-marking behavior in rats and hamsters (Mesocricetus auratus), by preventing apoptosis of arginine vasopressin (AVP) neurons and by activating these neurons in the medial preoptic area, the anterior hypothalamus, and the medial amygdala (De Vries, 1995; Ferris et al., 1997). On the other hand, the induction of copulatory behavior in male birds by implants of T placed in the preoptic area is a classic example of an androgen effect on a motivational system underlying consummatory behaviors (Barfield, 1969, 1971; Hutchison, 1971; for a detailed review see Ball and Balthazart, 2002).

However, central actions of androgens are not restricted only to motivational systems, since they can also affect central neural circuits underlying perception and cognition (for reviews on these topics, see Becker (2002) and Dohanich (2002), respectively).

2. Central Actions of Androgens: Cognitive Performance

The effects of androgens on cognitive function and os perception have been investigated using two complementary approaches: (1) documenting the occurrence of AR and ER in brain areas known to be involved in these processes, and (2) testing hormone-treated subjects in perceptual and cognitive tasks. The presence of AR in the hippocampus of mammals and birds (Kerr et al., 1995; Saldanha et al., 1999), a brain area known to be involved in relational memory processes, namely in spatial memory (Eichenbaum et al., 1992; Squire, 1992), and in cortical pyramidal cells in rats, monkeys, and humans (Kerr et al., 1995; Pomerantz and Scholl, 1987; Tohgi et al., 1995) supports the potential role of androgens as modulators of cognitive mechanisms in birds and mammals. ARs have also been found in the telo-real lateral telenephphalic pallium (Gudin and Callard, 1997) and in the reptilian medial cortex (Rosen et al., 2002), which are neural mechanisms homologous to the mammalian/avian hippocampus that are selectively involved in spatial cognition both in fish and in reptiles (Salas et al., 2003). Also, cognitive performance can be influenced by androgens. Castration of male rodents and birds reduces, and systemic androgen replacement restores, their performance in a number of cognitive tasks. T facilitates conspecific song discrimination in zebra finches, Taeniopygia guttata (Cynx and Nottebohm, 1992), and in the case of rodents, castration reduces and androgen replacement restores their performance in the following tasks: object recognition, radial arm maze, T-maze, inhibitory avoidance, and social memory (Cecarelli et al., 2001; Frye and Seliga,
2001; Harrel et al., 1990; Havens and Rose, 1992; Kritzer et al., 2001; Sawyer et al., 1984; Vazquez-Pereyra et al., 1995). Furthermore, DHT intrahippocampal implants enhance cognitive performance of male rats (Frye et al., 2004), probably because of neuroprotective actions of androgens in the hippocampus (Frye and Reed, 1998; Mizoguchi et al., 1992).

3. Central Actions of Androgens: Perception and Action

Apart from affecting brain areas directly involved in motivational states (e.g., hypothalamus and limbic system) or cognitive processes (e.g., hippocampus), androgens can also modulate the functioning of brain areas involved in the processing of sensorimotor information.

The fact that there are often sex differences in perceptual thresholds suggests a potential role for sex steroids in the processing of sensory information (Becker, 2002). For example, when exposed to an electric shock, female rats have shorter latencies in an escape response and lower shock thresholds (Beaty, 1979). Such differences are found even when noxious reactivity is similar for both sexes, which indicates that the sex difference is located in the brain mechanisms mediating pain perception and not at the level of peripheral sensitivity (Ryan and Maier, 1988). This conclusion is further supported by the fact that shock sensitivity can be manipulated by organizational androgen treatments (Beaty, 1979).

Motor circuits in the brain can also be sexually dimorphic. The vocal pattern generator in Xenopus is more active in males than in females (Wetzel et al., 1985) and males have a larger number of larval age motorneurons and os vocal interneurons (Kelley and Dennison, 1990; Kelley et al., 1988). These sex differences suggest that androgens may have organizational effects on the development of the vocal circuitry in amphibians. Androgens can also prevent the apoptosis of motoneurons in the spinal nucleus of the bulbocavernosus system that regulates penile erection in mammals (Breedlov and Arnold, 1981, 1985). Finally, the presence of ARs has been documented in the descending pathways of the song-control system in songbirds (Scharbji et al., 1989; for a review, see Schlinger and Brenowitz, 2002).

4. Peripheral Actions of Androgens

There is a growing body of evidence for the peripheral actions of androgens both on sensory systems and on effector pathways. ARs have been identified in several effector pathways, involved in a wide range of behaviors in different vertebrate taxa, ranging from electrolytes that produce an electric organ discharge which is used as a social signal in weakly electric fish (Dunlap and Zakon, 1998), to the perineal muscles (i.e., bulbocavernosus and levator ani) that innervate the penis in mammals and thus are
involved in copulatory behavior (Fishman et al., 1990). In the same vein, there is compelling evidence that sensory systems are the target of sex steroids including androgens. For example, ARs (and ERs) have been identified in a number of ocular structures of mammals including humans (Wicham et al., 2000), and 5α-reductase and aromatase activity have been detected in the retina of humans and teleosts respectively (Callard et al., 1993; Rocha et al., 2000), suggesting that androgens might interfere in the peripheral processing of visual stimuli in vertebrates. ARs have also been found in the auditory system of a vocal lizard (Gekko gecko), namely in the cochlear nuclei and in the torus semicircularis (Tang et al., 2001), again suggesting a role for androgens in the peripheral processing of sensory (acoustic) stimuli. Apart from the localization of AR in sensory systems there are several experimental studies that demonstrate a peripheral effect of androgens on behavior. In Table I a few examples have been selected from the literature to illustrate these effects, trying to cover different behavioral modalities (i.e., acoustic, visual, chemical) in different vertebrate taxa.

III. BEHAVIORAL FEEDBACK ON ENDOCRINE FUNCTION

A. HISTORICAL BACKGROUND

Contrary to the long history of implicit knowledge about the effects of androgens on behavior, the idea that hormones can be affected by behavior is a relatively recent concept. Apart from seasonal variations relating to reproductive function, levels of sex steroids were thought to be relatively stable over time. The first indications suggesting that social stimuli could influence sex steroid secretion came from a series of studies during the 1950s on the effects of the social environment on female reproductive cycles in mammals. First, Van der Lee and Boot (1955) showed that female mice (Mus musculus) housed together in the absence of conspecific males extended the length of their cycles by increasing the diestrous stage. This condition, considered similar to pseudopregnancy, came to be known as the Lee–Boot effect. Another effect of the social environment on the female reproductive cycle was described shortly afterward by Whitten (1956). This consisted in estrus induction by the presence of a familiar male and estrus synchronization among females within the same colony (the Whitten effect). Finally, Bruce (1959) found that exposure of pregnant females to an unfamiliar male would induce pregnancy failure, that was subsequently followed by mating with the “alien male” within 3–6 days (the Bruce effect). All these effects are mediated by chemical signals.
emitted by conspecifics. By this time, social influences on male sexual behavior had also started to be described. The most famous effect was the rearousal of male rats after mating, induced by the presence of a novel female (Wilson et al., 1963), which was termed the “Coolidge effect” by Frank Beach (Bernant, 1976) in an allusion to the following story involving the former U.S. President Calvin Coolidge and the First Lady:

One day the President and Mrs. Coolidge were visiting a government farm. Soon after their arrival they were taken off on separate tours. When Mrs. Coolidge passed the chicken pens she paused to ask the man in charge if the rooster copulates more than once each day. “Duzens of times,” was the reply. “Please tell that to the President.” Mrs. Coolidge requested. When the President passed the pens and was told about the roosters, he asked, “Same hun every time?” “Oh no, Mr. President, a different one each time.” The President nodded slowly, then said, “Tell that to Mrs. Coolidge.” (Bernant, 1976, pp. 76-77)

The Coolidge effect may be explained by transient variations in androgen levels. When male mice are first exposed to a female they show a rapid increase in luteinizing hormone (LH) levels, while successive presentations of the same female progressively elicit smaller increases, suggesting an habituation effect. However, the presentation of a new female to these unresponsive males induces an acute burst of LH secretion (Coquelin and Bronson, 1979). These LH variations may mediate variations in androgen responsiveness to the presence of the female, which in turn may influence the activity of the mesolimbic dopaminergic system, involved in the initiation and maintenance of sexual behavior. In agreement with this hypothesis, an increase in dopamine transmission in the nucleus accumbens in satiated males, when exposed to a novel female, that peaks during copulation with the new female, has been demonstrated (Fiorino et al., 1997).

In the early 1940s the suggestion that agonistic interactions and social dominance could affect sex hormone secretion was proposed for male mice (Ginsburg and Allee, 1942). Later on, contradictory results were collected with some studies suggesting an effect of social challenges on the reproductive axis (e.g., Bronson and Eleftheriou, 1964; Bronson and Marsden, 1973; Bronson et al., 1973) whereas others found no effect (e.g., Vale et al., 1970, 1971). It was only with the development of immunoassays (e.g., radiomunoassays) that a more precise and sensitive method became available to measure rapid changes in circulating levels of hormones in response to social interactions. With this technique a new experimental paradigm in behavioral endocrinology emerged: to manipulate the social environment or to expose the subject to a behavioral/social stimulus while measuring pre- and postexposure levels of the hormone in the plasma to assess its responsiveness. Using this new approach, Bernstein and associates conducted a series of studies, using rhesus monkeys, that showed that
both male–male fighting behavior (e.g., Rose et al., 1971) and access to females (e.g., Rose et al., 1972) influence T levels in males (for a review see Bernstein et al., 1983). Data of this type led Leshner (1983, p. 397) to propose that "hormonal responses to competition ... not only provide a mechanism for physiological adaptation to the stresses imposed by that experience but also feed back and affect ongoing and future agonistic response to patterns." This hypothesis, describing the feedback effect of hormones on behavior, was termed by Leshner the "behavioral feedback hypothesis" (Leshner, 1979), and was the first formal conceptualization of the interplay between hormones and behavior. However, two studies published during the 1970s (Maruniak et al., 1977; Nock and Leshner, 1976), both using mice, raised some difficulties for this hypothesis. To test whether hormonal responses to competition were behaviorally effective they manipulated the postexperience endocrine levels by castrating the subjects and subsequently replacing the target hormone with the dose expected to be induced by the behavioral interaction. In both studies, there was no effect of preventing the behaviorally induced changes in androgen levels on either ongoing or future agonistic behavior.

Meanwhile data on a wider variety of vertebrate taxa and in field conditions started to be collected (e.g., Harding and Follett, 1979; Wingfield, 1984b, 1985) and evidence accumulated suggesting that both exposure to and interaction with potential mates, and male–male competition, influence circulating levels of androgens (Harding, 1981: Oliveira et al., 2002; Wingfield, 1999, 2000, 2001).

In male–male contests a general pattern has been described for the variation of circulating T concentrations. At an early stage of the encounter there is a short-term increase in T levels in both participants, which might contribute to the escalation of the fight (Huntingford and Turner, 1986). After the fight is over and the status of each animal has been established, winners keep T levels high while losers experience a sharp decrease in circulating T (Harding, 1981). These endocrine changes tend to last for longer periods in subordinates than in dominants (Harrington, 1981), and in subordinates they can be reversed by manipulating their social status (e.g., mice: Machida et al., 1978; rats: Schuurman, 1980) or by giving them access to females (e.g., rhesus monkeys: Rose et al., 1975).

B. SOCIAL INTERACTIONS AFFECT ANDROGEN LEVELS IN MALES: THE CHALLENGE HYPOTHESIS

As shown above, androgens can be viewed as causal agents of appetitive and consummatory aspects of sexual and aggressive behavior while, on the other hand, the endocrine system is responsive to social stimuli and to
social interactions in which the animal is involved. Several studies have shown rapid effects of social interactions on transient changes in androgen levels in a wide variety of vertebrate taxa, ranging from fish to primates including humans. This set of results led to the proposal of the “challenge hypothesis” by Wingfield and associates (Wingfield et al., 1987, 1990), according to which the social interactions in which the subject is involved would determine its androgen levels. The challenge hypothesis postulates the existence of three levels of circulating androgens: (1) a constitutive level (level A) inherent in the baseline activity of secretory (Leydig) cells; (2) a breeding level (level B), which is sufficient for successful reproduction; that is, for spermatogenesis, for the full expression of secondary sex characters and for the complete expression of male reproductive behaviors; and (3) a physiological maximum (level C) that can be reached by social stimulation provided by male–male aggression or by interactions with receptive females (Wingfield et al., 1990, 1997, 2000; Fig. 3). From the measure of these three levels a level of androgen responsiveness can be expressed as the ratio \((C - A)/(B - A)\), which allows androgen responsiveness to social challenges to be compared, independent of individual variation in nonbreeding baseline levels. The use of this ratio also overcomes the potential problem of variation in responsiveness levels that would be present if absolute androgen levels were used. Finally, this ratio may be used not only at the intraspecific level, but also for comparisons of androgen responsiveness between different species.

The challenge hypothesis has the added value of providing a conceptual framework for the study of the interplay between social factors and endocrine responses, by generating a number of testable predictions.

![Diagram](https://via.placeholder.com/150)

**Fig. 3.** The three levels of endocrine states postulated by the “challenge hypothesis”: level A indicates constitutive levels at homeostasis; level B represents the increase to a breeding baseline needed for successful reproduction; level C represents a further increase up to a physiological maximum induced by male–male competition or by interactions with receptive females.
1. First Prediction: Androgen Responsiveness and Mating System

Androgen patterns during the breeding season are predicted to vary between species as a function of the number of social interactions to which individuals are exposed. In monogamous species with high levels of paternal care androgen levels should increase above the breeding baseline only when males are challenged by other males or by mating. At other times androgens should remain at the breeding baseline so that they do not interfere with paternal care. Conversely, androgen levels in polygynous males should be near the physiological maximum throughout the breeding season because of high levels of male-male competition in this type of breeding system (Fig. 4). Wingfield et al. (1990) reviewed the available literature on T and aggression in free-living birds and the results support these predictions; male androgen responsiveness was higher in monogamous and polyandrous species, which have monogamous males, than in polygynous species (Wingfield et al., 1990). Later on the number of species included in the analyses was expanded from the initial 20 covered by Wingfield et al. (1990) to 60, and the prediction was reevaluated, reaching the same conclusions (Wingfield et al., 2000). However, the observed relationship between androgen responsiveness and mating system could have been confounded by phylogenetic bias in the database (Harvey and Pagel, 1991), prompting a third analysis of this prediction, expanding further the number of avian species included in the analysis to 84 and using:

![Diagram](image)

**Fig. 4.** The effect of the mating system on androgen responsiveness to social challenges. (A) During the breeding season males of polygynous species (Ma) are expected to have androgen levels closer to the physiological maximum than males from monogamous species (Mm) thus, the androgen responsiveness (Δ) to social challenges is predicted to be lower in polygynous males than in monogamous males (Δm ≫ Δp). Androgen levels: A, constitutive baseline; B, breeding baseline; C, physiological maximum. (B) Predicted relationship between androgen responsiveness and mating system based on (A).
comparative methods to control for phylogenetic bias (Hirschenhauser et al., 2003). In general, the same results appear to hold after controlling for phylogenetic relationships among the studied species (Hirschenhauser et al., 2003; see further details in Section VII.B). This prediction of the challenge hypothesis has also been tested in teleosts (Oliveira et al., 2001f, 2002). Using a literature survey, the constitutive baseline, breeding baseline, and physiological maximum androgen levels of male teleosts were compiled for 59 species with different mating systems, and then androgen responsiveness rates were computed for each species (Oliveira et al., 2002). A preliminary analysis of these data, in which the effects of mating system were tested separately from the effects of parenting type (i.e., the male contribution to parental care), revealed an effect of parenting but failed to detect significant differences in male androgen responsiveness among species with different mating systems (Oliveira et al., 2002). However, this result should be taken with caution since no control for potential phylogenetic bias was included. One way to overcome this potential flaw is to restrict the analysis to teleost families for which data are available for more than one species and variation in mating system also occurs. Contrary to the above-described study, a pairwise comparison of male androgen responsiveness between closely related teleost species with different mating systems suggests an effect of the mating system (Oliveira et al., 2002f, Fig. 5).

Since using published data increases the probability of potential errors due both to variations in assays between different laboratories and to different blood sampling protocols based on which the A, B, and C circulating androgen levels are calculated, it was decided to experimentally test this prediction of the challenge hypothesis in a group of closely related species with different mating systems, using a standard experimental protocol. The family Cichlidae is a taxon in which a great variety of breeding systems is present (Fryer and Iles, 1972; Barlow, 1991), making it an ideal group for such a comparative study. Two extreme breeding patterns are present in cichlids: (1) monogamous substrate-brooding species, lacking sexual dimorphism, with a prolonged pair bond, and with parental care provided by both members of the pair (most neotropical species; Barlow, 1991); (2) polygamous mouthbrooding species, with strong sexual dimorphism and/or dichromatism, with short courtship episodes and no pair bond (most African species from the Great Lakes; Barlow, 1991; Fryer and Iles, 1972). Mouthbrooding among African cichlids is mainly maternal (or biparental), with paternal mouthbrooding occurring in only two cases (Sarotherodon melanocephalus and S. occidentalis) (Trewavas, 1983). Thus, closely related cichlid species that differed in their prevalent mating system were selected to conduct a simulated territorial intrusion experiment to
assess the responsiveness of the breeding males of each species to behavioral interactions (Hirschenhauser et al., 2004). Two pairs of species of haplochromine cichlids were selected.

1. Neolamprologus pulcher versus Lamprologus callipterus. Neolamprologus pulcher is a monogamous species forming territorial pairs with helpers of both sexes, while *L. callipterus* is polygynous with small parasitic (sneaker) males; both species are biparental substrate brooders (Balshine et al., 2001; Sato, 1994; Taborsky, 1994; Taborsky and Limberger, 1981)

2. *Tropheus moorii* versus *Pseudosimochromis curvimontes*. Both species are polygynous maternal mouthbrooders but in *T. moorii* temporary pair formation occurs, while *P. curvimontes* breeds in high-density leks (Kuwamura, 1987; Nishida and Yanagisawa, 1991; Wickler, 1969).

A fifth species, the Mozambique tilapia (*Oreochromis mossambicus*), was also included in this study, although a pair for it was lacking, since it represents an extreme situation for this prediction: a lekking species with exclusive female mouthbrooding (Trewavas, 1983). For each species we
assessed the constitutive nonbreeding androgen level (A), the male’s androgen response to the presence of and interaction with an ovulating female (level B), and the male’s response to an additional challenge by a conspecific intruder male (level C). Androgens [i.e., 11-ketotestosterone (KT) and T] were measured using a noninvasive method (i.e., fish-holding water; for details of this method see Hirschenhauser et al., 2002b, 2004). In all species sampled the KT circulating levels were highly responsive to territorial intrusions, while the KT responses to interactions with ovulating females were observed only in maternal mouthbrooders and not in biparental species (e.g., Lamprologus). At the interspecific level, the results not only confirmed expectations of higher androgen responsiveness among males from monogamous species, but the response was more pronounced in species with more intense pair bonding (i.e., Tropheus moorii; Fig. 6).

Thus, this study confirms the predictions of the challenge hypothesis in cichlid fish at both an intra- and an interspecific level (Hirschenhauser et al., 2004).

However, the question remained whether the variation in androgen responsiveness to social stimuli in relation to the mating system is a result of varying breeding baseline levels (B), or a consequence of different maximum physiological levels (C). To disentangle these two possibilities the mean and standard error of levels B and C for 10 species with different mating systems were compared (Fig. 7). The results suggest that variation in androgen responsiveness is related mostly to lower breeding

![Diagram](image-url)

Fig. 6. Androgen responsiveness in cichlid species with various mating systems. Lines link closely related species. Data points are means of all sampled individuals within each species. Adapted from Hirschenhauser et al. (2004).
baseline levels among monogamous and polyandrous male teleosts, rather than to a difference in maximum physiological levels among fish with different mating strategies (Oliveira et al., 2001) as was originally proposed by Wingfield et al. (1990).

In summary, the first prediction of the challenge hypothesis, that androgen responsiveness should be higher in monogamous than in polygynous species due to different regimes of intrasexual selection (i.e., male–male competition), has been confirmed both in teleost and in avian species.

On the other hand, androgens may also play a role in shaping mating systems by facilitating social behaviors that promote polygyny. This could be due either to effects on motivational systems that promote sexual appetitive behaviors and a subsequent shift from monogamous to polygynous behaviors, or to an increase in territory size that might then include several females, thus promoting a transition from pair breeding to holding an harem (Beletsky et al., 1995; Ketterson and Nolan 1992; Wingfield et al., 1990). Experimental elevation of T levels of monogamous males resulted in a behavioral shift of these males toward polygyny (e.g., white-crowned sparrow (Zonotrichia leucophrys) and song sparrow (Melospiza melodia); Wingfield, 1984c; European starlings (Sturnus vulgaris): De Riedt et al., 2000; see Beletsky et al., 1995, for a review). However, this effect is not universal (see Ketterson et al., 1996, and Oliveira et al., 2001, for a discussion of this topic in birds and fish, respectively). For example, in the St. Peter’s fish (Sarotherodon galilaeus; Cichlidae), a species that shows
great flexibility in its mating system with facultative monogamous/polygynous males that may or may not contribute to parental care of the offspring (Bashine-Earn, 1996; Fishelson and Hilzerman, 2002), we tested whether males that were more attached to their partners (i.e., with more intense pair bonds) would have lower androgen levels. Paired males were offered access to a novel female out of sight from their female partner and the time spent with each female was measured (Fig. 8). At the end of the behavioral test the male-holding water was collected to assay 11-KT levels. A significant negative correlation between KT levels and partner preference occurred, suggesting that the more polygynous males had higher androgen levels (Oliveira et al., 2001f). In a second experiment, the effects of exogenous administration of T were assessed by giving male St. Peter’s fish intraperitoneal silastic implants of either T or vehicle only. Since in the first experiment a relationship between higher KT levels and a higher propensity to become polygynous had been found, it was predicted that T-treated males would have a lower partner preference than controls. Contrary to expectations, T treatment did not affect partner preference significantly (Oliveira et al., 2001f). The results from these two experiments taken together suggest that the association between partner preference and androgen levels in St. Peter’s fish is not due to a causal effect of androgens on partner preference but, since the androgen levels were measured at the end of the experiment, it is more parsimonious to consider that they probably reflect variation in partner preference behavior observed among
males. This interpretation is supported by data collected in semi-
natural conditions in Lake Kinneret, Israel, where KT levels of polygynous
males did not differ from those of monogamous males (Ros et al., 2003).
This result, together with the fact that T treatment had no effect on
male mating strategy, apparently contradicts the effects of androgens on
mating systems in wild male birds referred to earlier (e.g., Beleksky et al.,
1995). One possible explanation for this difference may be the fact that St.
Peter's fish males are sequentially polygynous, that is, they do not establish
harem but desert females after spawning to court other receptive females.
In some other species, by contrast, T treatment increases home range/
territory size and as a consequence the number of females present in the
territory is larger, thus, promoting simultaneous polygyny (Beleksky et al.,
1995).

2. Second Prediction: Androgen Levels and Social Stability

Androgen levels should be higher during periods of social instability
when social interactions are more frequent and more intense. This predic-
tion is supported by the fact that T levels are higher during the period of
territory establishment than when territories are already established in
both bird and fish species [see Oliveira et al. (2002) and Wingfield et al.,
(1999, 2000) for reviews on birds and teleosts, respectively]. For example,
the effects of experimental territorial intrusions on androgen levels
have been tested in a natural population of the stoplight parrotfish (Spar-
isoma viride), where it was found that peaks of androgens could be induced
in established territorial males by experimental intrusions of other
males (Cardwell and Liley, 1991). Also, in the above-mentioned compara-
tive study on simulated territorial intrusions in cichlid fish, for the five
species studied the resident always responded to the presence of the
intruder male with a significant increase in KT level (Hirschenhauser
et al., 2004). Furthermore, in dyadic interactions of the swordtail fish
(Xiphophorus helleri) there was an association between some aspects of
aggressive behavior and high levels of androgens (Hannes, 1986), whereas
when androgen levels of dominant and of subordinate males from
a socially stable community tank were compared no relationship between
dominance and androgens was found (Hannes, 1984). Taken together,
these two latter results are consistent with the suggestion that a causal
relationship between androgens and the expression of aggression is present
only in periods of social challenge. In conclusion, the available data sup-
port the prediction that the association between androgen levels and
social status should emerge only during periods of social instability and
that in stable social groups androgen levels become dissociated from social
status.
3. Third Prediction: Androgens, Territoriality, and Social Status

Territorial and/or dominant males are expected to show higher androgen levels than nonterritorial and/or subordinate males. This is because territorial males must defend their territories from intruders and dominant males must actively keep their status, thus having to engage in a higher proportion of aggressive interactions than either nonterritorial males or subordinates [see Wingfield et al. (1999, 2000) and Oliveira et al. (2002) for reviews on birds and teleosts, respectively].

The causal relationship between androgen levels and territoriality/dominance may be viewed in two ways: (1) androgen levels are predictors of social status; or (2) social status is itself the cause, and not the consequence, of higher androgen levels. To disentangle these two hypotheses, Oliveira et al. (1996) computed correlations between androgen levels and a social dominance index before and after group formation in the cichlid fish O. mossambicus. The rationale behind this experiment was that if androgen levels are the determining factors of social status acquisition, then androgen levels before group formation would be expected to be good predictors of the social status achieved by the individuals after group formation. Conversely, if androgen levels were a response to the acquired social status, it would be predicted that only after group formation would the correlation between androgen levels and social status be present. The latter hypothesis was the one supported by the data, which showed a lack of correlation between androgen levels prior to group formation and the social status achieved, but strong correlations between androgen levels measured after group formation and the acquired social status (Oliveira et al., 1996). However, it should be noted that these two hypotheses are by no means mutually exclusive. For example, a marginal advantage in terms of T levels might help an animal to become dominant, whereas its T levels would increase further. Therefore, preceding and succeeding hormone levels might be linked in a positive feedback loop (see Oliveira and Almada, 1998b).

Thus, the associations found between androgen levels and social status in male teleosts may potentially be explained by the challenge hypothesis, reflecting a more challenging social environment for territorial/dominant males than for nonterritorial/subordinate ones. A paradoxical confirmation of this prediction comes from a study with another cichlid, Neolamprologus pulcher, with male helpers at the nest (Limberger, 1983; Taborsky, 1984; Taborsky and Limberger, 1981). In this species male helpers are subordinate to breeding males, but they also participate actively in the defense of the family's breeding territory, and thus are exposed to high rates of territorial challenges. Notably, there is no difference between
breeding and helper males in androgen levels (Oliveira et al., 2003), which suggests that the differences observed between territorial and nonterritorial males of other species are due to the differential rates of social challenges to which they are exposed and not to differences in social status per se.

4. Fourth Prediction: Androgen Levels and Breeding Density

Androgen levels of males breeding at different densities are predicted to be different because of a differential probability in territory intrusions. This prediction should be taken with caution since in a population with increased density, physiological and/or behavioral mechanisms may be present to avoid aggression. Nevertheless, positive correlations have been found between density of breeding territories in different populations and androgen levels both in fish and in birds (e.g., Ball and Wingfield, 1987; Beletsky et al., 1990, 1992; Pankhurst and Barnett, 1993). Moreover, in the peacock blenny (Salarias pavo), a species with alternative reproductive tactics, sexual variations in sneaker (i.e., potential intruder) density within the same population are also directly associated with variations in androgen levels (Oliveira et al., 2001a).

5. Fifth Prediction: Androgens and Mating Success

Males with higher reproductive (or mating) success should also have higher levels of androgens, since they should hold the best territories, being more challenged by other breeding males and visited by a larger number of females. This prediction has been tested in the satin bower bird (Pilionorhynchus violaceus) (Borgia and Wingfield, 1991) and in red-winged blackbirds (Beletsky et al., 1989). In both species the levels of T during the mate-guarding phase were well correlated with reproductive success. Moreover, T levels of male black ground (Teucrius tetrix), which breed in leks, are positively correlated with mating success, providing further support for this prediction (Alatalo et al., 1990). In addition, T treatment of male dark-eyed juncos (Junco hyemalis) in the wild increased their attractiveness toward their mates (Unnstrom et al., 1997), their mate-guarding behavior during the fertile period of their mates (Chadler et al., 1997), and the frequency of extrapair copulations (Rauf et al., 1997). All these effects potentially contribute to increased reproductive success. However, androgens may also have deleterious effects on male reproductive success because of their interference with parental care (see Section VII A, below).

This prediction may not hold in species with alternative mating tactics, in which males with lower competitive ability use sneaker fertilizations using a variety of tactics. Male alternative reproductive tactics are especially
C. Levels of Analysis and the Social Modulation of Androgens: The Tinbergen Legacy

Tinbergen (1963) pointed out that there are four fundamental levels of analysis in biology. Thus, when asking questions about behavior four different kinds of questions can be posed. What is the underlying mechanism for that behavior? How did the behavior develop during the ontogeny of the animal? What is the function of the behavior, that is, how does it contribute to the animal's fitness? And finally, how has the behavior evolved and changed during phylogeny? The answers to these questions are complementary and not mutually exclusive, and necessitate the behavioral pattern being studied at each of the levels of mechanisms, development, function, and evolution. The first two are considered as proximate levels of analysis, because they ask how mechanisms operate within an animal in order to produce the observed behavior, that is, the proximate causes of behavior (Alcock, 1993). In the same way, the other two are considered as ultimate levels of analysis, since they deal with the question of why the animal has evolved over phylogenetic time the mechanisms that produce the observed behavior (Alcock, 1993). The analysis of any behavior is complete only if both proximate and ultimate explanations are achieved using an integrative approach. Therefore, in the following sections, Tinbergen’s “four why’s” will be applied to the study of the social modulation of androgens and behavior.

IV. Proximate Mechanisms for the Social Modulation of Androgens

The question of the mechanisms by which the social environment feeds back onto the endocrine system, in order to modulate androgen levels, can be approached at two different levels: (1) what are the neuroendocrine mechanisms involved in the transduction of the relevant social stimuli into an endocrine response (i.e., androgen response)? And (2) what are the psychological (perceptual/cognitive) mechanisms that trigger a response from the neuroendocrine system? These two different levels of analysis are not mutually exclusive but complementary (Fig. 9).
A. Neuroendocrine Mechanisms

Since peripheral production of androgens is under the control of the hypothalamus–pituitary–gonadal (HPG) axis, the most parsimonious explanation for the social modulation of androgens would be social regulation of the activity of the HPG (Fig. 9). In the African cichlid fish *Haplochromis burtoni*, juveniles raised in the presence of adult territorial males show suppressed gonadal maturation together with smaller gonadotropin-releasing hormone (GnRH) neurons in the preoptic area (Davis and Fernald, 1990). Since this neuronal population projects to the pituitary, through which it regulates the activity of the HPG axis, these results indicate that the social environment during rearing can modulate sexual maturity by acting on the reproductive axis. In adults two male types occur: (1) territorial males, which express the full set of male displaying traits including nuptial coloration, defend a breeding territory, court females, and have mature testes; and (2) nonterritorial males, which lack the expression of male displaying traits, both morphological and behavioral, and have low gonadosomatic values (Fernald, 1977, 1984). A difference between the two male types also occurs at the level of forebrain neurochemistry: territorial males have larger GnRH neurons in the preoptic area than do nonterritorials (Francis et al., 1993). Since soma size is regarded as an
indicator of cellular activity, this result indicates that territorial males have a more active reproductive axis than subordinates. However, a causal relationship is not clear: the social status of territorial males may be due to a more active HPG that translates into higher androgen levels than would have granted them their dominance; or conversely, perhaps it is their social status that activates the HPG, resulting in higher androgen levels. To disentangle these two alternative explanations an experiment was performed in which the social status of adult males was manipulated in two opposite directions: (1) from territorial to nonterritorial (T → NT), by moving territorial males into groups with larger territorial males that would dominate them; and (2) from nonterritorial to territorial (NT → T), by placing NT males into groups consisting of smaller males that they could dominate (Francis et al., 1993). The T → NT males had larger GnRH neurons in the preoptic area than did nonterritorials, but no differences were found in the size of other GnRH neuron populations, either in the terminal nerve of the telencephalon or in the midbrain. This suggests that changes in social status selectively modulate the activity of the HPG by regulating the activity of preoptic area GnRH neurons in adult individuals (Francis et al., 1993). More recently, it has been found that changes in the size of GnRH neurons are accompanied by changes in GnRH gene expression (White et al., 2002). Thus, in the NT → T individuals the change in social status was found to activate GnRH expression only in the preoptic area.

These studies give support to the hypothesis that the social modulation of sex steroids including androgens is mediated by the HPG, through the regulation of the activity of GnRH neurons. Therefore, the sensory systems processing the stimuli from the social environment to which androgens are responding must connect with the GnRH neurons in the preoptic area (Wilczynski et al., 1995). In frogs conspecific advertisement calls have been shown to influence androgen levels. Circulating concentrations of DHT are higher in males exposed to a conspecific chorus than in males exposed to manipulated (i.e., recording of the same chorus in which frequencies had been shifted to higher values) versions of the chorus (Chu and Wilczynski, 2001). Thus, auditory pathways in this group are good candidates to act as signal transduction mechanisms of relevant social stimuli for the HPG. In fact, both the preoptic area and the ventral hypothalamus receive projections from thalamic and midbrain auditory nuclei (Allison and Wilczynski, 1991; Wilczynski et al., 1995). It is expected that in other taxa, using different sensory modalities, similar circuits will link the relevant sensory system to the areas controlling HPG function and hence androgen responsiveness to social stimuli (e.g., for examples on birds see Ball and Balthazart, 2002).
In both mammals and birds expression of immediate-early genes (e.g., c-fos) has been used as a marker of neuronal activation by social stimuli. Since these genes are rapidly transcribed in response to a change in stimulus conditions, they allow the study of the selective activation of different brain regions in response to specific social stimulation. For example, it has been shown both in birds and in mammals that both appetitive and consummatory aspects of sexual behavior induce the expression of these immediate early genes (for a review see Ball and Balthazart, 2001). In the Japanese quail (Coturnix japonica) the exposure of males to receptive females induces c-fos expression in the preoptic region of the hypothalamus and copulation activates c-fos in the ventromedial hypothalamus (Meddle et al., 1997). Also, in rodents, copulation induces c-fos expression in hypothalamic and limbic areas such as the medial amygdala, the bed nucleus of the stria terminalis, the central tegmental field, and the medial preoptic area (e.g., Baum and Everitt, 1992; Coolsen et al., 1996; Robertson et al., 1991). However, it is not always clear whether the observed activation is related to perception of the stimuli or to activation of motor systems in response to it (Pfaus and Heeb, 1997). Nevertheless, this approach is a useful tool to unravel the circuits underlying the transcription of social stimuli into a neuroendocrine response. In songbirds another immediate-early gene named zenk has been found to respond to social context in brain areas involving song perception and production, in both canaries (Serinus canaria) and zebra finches (Mello et al., 1992). zenk induction in the auditory forebrain is more pronounced when listening to a conspecific song than to heterospecific songs, and no response is observed after exposure to simple tones (Mello et al., 1992). Moreover, zenk induction decreases with repeated presentations of the same conspecific song while a different conspecific song leads to a still higher induction level, suggesting habituation to the stimulus (Mello et al., 1995). zenk is also induced in several brain structures involved in song perception and production by territorial challenges (i.e., conspecific song playbacks) in breeding male song sparrows in the field (Jarvis et al., 1997). Finally, and most interestingly, in the European starling (Sturnus vulgaris) a socially relevant variation in conspecific song induced significant differences in zenk activation (Gentner and Hulse, 2001). Concordantly, zenk induction in a subregion of the auditory telencephalon (i.e., caudal and medial neornistrum) of females was much higher in females exposed to longer songs than in females exposed to shorter ones (Gentner et al., 2001). Thus, this brain area could potentially play a major role in female mate choice in songbirds.
In summary, the studies with immediate-early genes in birds and mammals suggest that no induction is observed in peripheral systems that would involve a generalized response to the stimulus. Rather, activation is restricted to sensory integration areas in the telencephalon, as well as to limbic areas underlying motivational systems (e.g., amygdala, hypothalamus, preoptic area) and to premotor systems in the mesencephalic central gray (Ball and Balthazart, 2001).

B. PSYCHOLOGICAL MECHANISMS

Independently of the neuroendocrine mechanisms that translate a social stimulus into an endocrine signal, another important question to be addressed in relation to social influences on endocrine function concerns the key element in the social interaction that triggers the endocrine response. In other words, what are the psychological (perceptio/cognition) mechanisms that translate a social stimulus into a signal for the HPO to respond?

One of the central axioms of modern social cognition theory is the fact that what influences behavior is not the objective structure of the situation but the subject’s perception of the situation (Smith and Mackie, 1995). This principle has been extended to physiological responses to behavioral contexts. Mason and Brady (1995), by showing a corticosteroid response to a conditioned anxiety paradigm, were the first to propose that the physiological effects of stressors were due mainly to their psychological action and not to their physical characteristics. Later on, Mason (1989a,b) proposed that situations of uncertainty, unpredictability, or novelty were the most important psychological stressors, associated with an increased stress response.

One of the first reports suggesting that the subject’s perception of the social situation could influence its androgen levels appeared as an anonymous communication to the journal Nature (Anonymous, 1970). The author, who had been living in isolation on a remote island for professional reasons, noticed a decrease in his beard growth. Interestingly, he also noticed an increase in beard growth in anticipation of his visits to the mainland, where he met with his fiancée. He concludes that the stimulus for his increased beard growth when visiting the mainland was related to the expectation of sexual activity, which in turn would stimulate androgen production, promoting beard growth. Thus, the mere anticipation of sexual activity would have increased androgen levels in this subject. Although this is not robust evidence that a subject’s perception of the situation can activate an androgen response to that situation (e.g., the anonymous author could have shaved more closely when preparing himself to meet his fiancée), subsequent studies do support this hypothesis. There is an association
between sexual activity and androgen levels in human males (Brown et al., 1970; Fox et al., 1972), with circulatory T levels increasing during and after copulation when compared with resting conditions. However, no androgen response to maculation was detected (Fox et al., 1972), which suggests that a stimulus from the female partner is needed to activate the response that hence is not a mere consequence of the ejaculation or of penile stimulation. It has been shown that brief social encounters with potential mating partners are enough to produce significant increases in salivary T levels in human males (Roney et al., 2000). In another study on the long-term relationship between T and social behaviors in men, it was found that prospective fathers (i.e., those who reported a wish to have children with the current partner) have a higher association between T peaks and sexual activity than do unpaired males or those who did not wish to have children with their current partner (Hirschenhauer et al., 2002a). Furthermore, only prospective fathers also displayed 28-day cycles of T, suggesting that men have the facultative potential to adjust their androgen responsiveness to their partner’s menstrual cycle (Hirschenhauer et al., 2002a).

The perception of the situation seems to modulate androgen responsiveness not only in sexual but also in competitive contexts. In humans, sports contests can be seen as ritualized competition between participants, and thus offer an opportunity to study short-term endocrine responses to social challenges. As a general rule it was found that T levels increase in anticipation of the confrontation and that after the interaction they remain high in winners and drop in losers (e.g., Booth et al., 1989; Mazur and Booth, 1998). However, this transient response of T to competition was not present when a change in mood was not detected (i.e., when the subjects did not perceive a victory or a defeat, independently of the outcome of the interaction; Mazur and Lamb, 1980; McCall et al., 1992). It should be added that this endocrine response is present in both physical (e.g., judo, tennis, hockey) and nonphysical contexts (e.g., chess, Mazur et al., 1992), and that even individuals who do not participate directly in the contest but who identify themselves with one of the teams (i.e., fans) show the same androgen response and associated change in mood (Bernard et al., 1998). Together these results suggest that, at least in humans, social modulation of androgen levels is mediated by the individual’s perception of the social challenge they are facing and of its outcome.

In fish there is anecdotal evidence that an individual’s perception of its status also activates its androgen response. In the Mozambique tilapia it was previously demonstrated that androgen levels were not good predictors of social status before a group formation experiment, whereas androgen levels at the end of the experiment were highly correlated with the
social status of each individual. This suggests that androgens are being modulated by the social interactions experienced by the individuals (Oliveira et al. 1996). Moreover, a significant positive correlation was found between the ratio of KT to T and social dominance expressed as the number of victories over the total number of victories plus defeats (Oliveira and Canario, 2001). Since T is a precursor of KT this result suggests that a rise in social status also promotes the conversion of T into KT, whereas a consequence of subordination would be the blockage of KT production, possibly through the inhibition of 11β-hydroxylase (Oliveira and Canario, 2001). Further support for this hypothesis comes from a study in the Siamese fighting fish (Betta splendens), where it was found that subordinate individuals have lower expression of male sex characters, reduced behavioral displays and the activity of 11β-hydroxylase is blocked (Leitão, 1987). Most relevant to our discussion here is the fact that in our experiment all the individuals that were successful in establishing a territory had high KT-to-T ratios, while nonterritorial displayed low ratios. Interestingly, one individual that, despite having a high dominance index (it won ~70% of the interactions in which it was involved), failed to establish a territory and had a low KT-to-T ratio that was within the range of subordinate individuals (Fig. 10; Oliveira and Canario, 2001). This suggests that it is the individual's perception of its status, rather than an objective measure of its dominance behavior, that triggers KT production.

Fig. 10. Effect of holding a territory (T) on the relationship between metabolization of testosterone into 11-ketotestosterone (measured as the ratio of 11-ketotestosterone to testosterone), and social dominance (measured as the number of victories over the number of victories plus defeats). The arrow indicates an individual that, despite having a high dominance index, was not successful in establishing a territory. Data compiled from Oliveira et al. (1996).
To investigate this idea experimentally, the effect of mirror-elicited aggression on androgen levels was tested in the Mozambique tilapia (L. A. Carneiro and R. F. Oliveira, unpublished data). The mirror image stimulation test (MIS) is widely used to assess fish aggressiveness, because fish do not recognize their own image and so see the image as an intruder and attack it (Rowland, 1999). In Oreochromis mossambicus an increase in androgen levels in response to territorial intrusion by a live intruder has been shown (Frischenhauer et al., 2004). With the MIS test we created a situation in which the perception of the outcome of the interaction (winning versus losing) is not available to the individual, since whatever the behavior expressed by the subject the "intruder" will reply with exactly the same behavior and so there will be no winner or loser. Therefore, if activation of the endocrine response to the social interaction is triggered by the behavioral (motor) output during the interaction (e.g., number of displays or time spent displaying) a variation in androgen levels is predicted. On the other hand, if the androgen response depends on behavioral feedback received from the opponent (i.e., perception of the situation) then an androgen variation is not predicted. In our experiment we found a strong behavioral response in fish toward their own mirror image but no androgen response (L. A. Carneiro and R. F. Oliveira, unpublished data), which suggests that if the endocrine system is to respond to a competitive interaction, that interaction must have a clear outcome. This result is also interesting because it shows that it is the dynamic component of the social interaction that may affect hormone levels, and not static social stimuli from the opponent. However, this result should not be taken as universal since, in songbirds for example, a simulated territorial intrusion using a loop-playback and a decoy is efficient in eliciting both a behavioral and an endocrine response (e.g., Wingfield, 1985). This suggests that activation of the motor circuit per se, that is, the proprioceptive stimuli from the subject's behavioral performance or some sensory stimuli resulting from its own behavior, is activating the response. In birds the effect of behavioral self-feedback on endocrine responses has been demonstrated in female ring doves, in which female cooing autoinduces gonadal maturation of the female (Cheng, 1986, 1992).

V. Ontogeny of the Social Modulation of Androgens

Although the challenge hypothesis was initially proposed to explain social influences on androgen levels in adult males, some studies on the endocrine response to social challenges have been performed in young animals, which in some species also perform significant amounts of
aggressive behavior. Aggression displayed by young animals may occur between siblings (e.g., bird chicks hatching from the same clutch; Drummond, 2001) or toward unfamiliar conspecifics in the context of nonsexual territorial defense (e.g., Groothuis, 1989).

Contrary to the predictions of the challenge hypothesis, T does not increase in response to sibling competition (Nuñez de la Mora et al., 1996; Ramos-Fernandez et al., 2000; Tarlow et al., 2001). T levels were undetectable even after brood starvation in blue-footed booby (Sula nebouxi) chicks in order to increase sibling competition (Nuñez de la Mora et al., 1996). Also, in another study with the same species, within-clutch T variation was not associated with chick status (i.e., dominant versus subordinate), and when unrelated chicks were paired no increase in T was detected although there was an increase in aggressiveness (Ramos-Fernandez et al., 2000). Finally, in the Galápagos Nazca booby (Sula granti) no correlation was found between T levels and chick status (i.e., dominant versus subordinate versus singleton). However, in this study one reversal in the dominance relationship was observed in a pair of chicks, and in this case the previously subordinate chick that was becoming dominant had a significantly higher T titler (Tarlow et al., 2001). This suggests that androgen responsiveness in young animals may be restricted to specific periods of time when behavioral persistence is needed. This would be a similar mechanism to that described for adult males of year-round terrestrial birds in the tropics (Wienski et al., 1999a), and would be consistent with the hypothesis that androgens are elevated when the offspring are successfully cared for by one parent (Wingfield et al., 2001). Alternatively, sibling competition may not be regulated by androgens, at least in an activational fashion, if the development of the older sibling (Mock and Parker, 1997) is sufficient to facilitate siblicide without increased androgen-dependent aggression. Interestingly, androgens present in the eggs are known to influence the social rank of juvenile birds, suggesting a maternal effect on the development of aggressive behavior in their offspring (e.g., canary, Serinus canaria; Schwabl, 1991). Among birds, yolk T either increases with laying sequence and so mitigates the effect of hatching asynchrony in younger chicks (red-winged blackbird (Agelaius phoeniceus); Lipa et al., 1999; American kestrel (Falco sparverius); Sockman and Schwabl, 2000; lesser black-backed gull (Larus fuscus); Royle et al., 2000; common tern (Sterna hirundo); French et al., 2001; black-headed gull (Larus ridibundus); Eisig et al., 2001), or conversely it decreases with laying order, thus facilitating brood reduction when food conditions are poor (cattle egret (Bubulcus ibis); Schwabl et al., 1997; zebra finch: Gil et al., 1999). Moreover, between-clutch variation in yolk androgen content is associated with higher T deposition at higher breeding densities (canary: Schwabl, 1996; house sparrow (Passer
domestius): Schwalb (1997) and Mazuc et al. (2003); American coot (Fulica americana); Reed and Vleck, 2001; black-headed gull: Groothuis and Schwalb, 2002; European starling: Pilz and Smith, 2004), which may be a result of increased maternal T during the prelaying and laying period due to social interactions [e.g., tree swallow (Tachycineta bicolor); Whittingham and Schwalb, 2002; house sparrow: Mazuc et al., 2003]. Functionally this may be interpreted as a mechanism to prepare the offspring for higher levels of competition in adulthood, should they breed in their natal colonies. These data taken together suggest that the influence of maternal androgens on chick competitive behavior reflects organizational effects rather than activational effects of T on sibling competition (see also Ros et al., 2001).

In contrast to the described lack of association between androgens and sibling competition, territorial defense by young animals has been associated with androgens. In the black-headed gull, chicks display very intense aggressive behavior toward unfamiliar conspecifics that is associated with T (Groothuis and Meeuwissen, 1992). Since androgen-dependent aggression has a number of associated costs for juvenile birds, such as growth reduction, decrease in begging behavior, and changes in plumage coloration (Groothuis and Meeuwissen, 1992; Ros, 1999), it is to be expected that androgen levels are under strict influence of social context so that unnecessary increases of circulating androgens are avoided. As predicted, gull chicks respond to short-term social challenges with a transient increase in T levels (Ros et al., 2002). Moreover, the association between androgen levels and breeding density described above, both for adults and for eggs, is also found in black-headed gull chicks: chicks raised in isolated families have lower T levels than ones raised in families kept together in large groups (Ros et al., 2002).

VI. ADAPTIVE SIGNIFICANCE OF SOCIAL MODULATION OF ANDROGENS

As discussed above, social modulation of androgens allows individuals to adjust their agonistic behavior to a variable social environment according to their relative competitive ability. This flexibility has advantages over a fixed androgen level, due to the high costs associated with keeping high androgen levels (see Section VII.A, below). In social species this must be of the utmost importance since one of the key environmental factors to which individuals must respond is the social context. Animals interact with each other frequently and these interactions modulate subsequent interactions among them and with other group members (e.g., in dominance hierarchies, on territories). Thus, animals must fine-tune the expression of their
social behavior to the social environment in which they live, and androgens may be seen as endocrine mediators of the modulation of social behaviors by social context (Oliveira, 2004). This role of androgens can be played both at the activational level, by modulating the expression of behavior in the short term in response to social context, and at the organizational level, by influencing life-history stage decision-making processes (e.g., when and how to reproduce, depending on the social environment). For example, at the activational level this mechanism would allow subordinate individuals to downregulate the expression of their aggressive behavior, thus avoiding the costs associated with agonistic interactions that they have low probabilities of winning (Oliveira, 2005). Similarly, at the organizational level, individuals of lower competitive ability may adopt alternative condition-dependent tactics, such as breeding as parasitic males (Taborsky, 1994, 2001) or even a change of sex (Grober, 1998; Grober and Bass, 2002), and these transitions may be mediated by androgens (e.g., Oliveira et al., 2001b,d).

A. Short-Term (Activational) Effects: Androgens and Social Context

Animals from social species live in social networks, raising the possibility that dyadic social interactions can be both observed by and influenced by the presence of conspecifics (McGregor, 1993). This scenario potentially makes more complex the interplay between hormones (androgens) and behavior in all the individuals involved (i.e., the interacting pair plus other conspecifics exposed to the interaction). For example, the presence of a bystander may affect androgen levels in both the interacting individuals and the bystander, which could then affect the bystander’s subsequent social behavior (Oliveira, 2005). Thus, a number of phenomena that have been described in social ethology (e.g., territoriality, bystander effects, audience effects, winner-loser effects, dear enemy effects) may be physiologically mediated by transient changes in androgen levels.

1. Territoriality Effects

Territoriality is widespread in vertebrates and its function seems to be in most cases an attempt to monopolize resources, especially food and access to mates (Huntingford and Turner, 1986). In territorial species there is a site-dependent advantage in social conflicts, such that prior residence in an area gives an individual a higher probability of aggressively dominating a conspecific. Individuals attack more readily and with greater intensity when defending their own territory than when they fight away from their home site (e.g., Bradlock, 1949; Gosler and Beaugrand, 2004; Henderson
and Chizaz, 1977; Tinbergen, 1953; Zayan, 1975). Even when the territory owner is smaller than the intruder a size-advantage effect may still be observable in its fighting behavior (Beauprand et al., 1986). Transient changes in androgen levels may mediate this prior-residence increase in competitive ability. In fact, the establishment of a territory is associated with increased androgen levels and territorial intrusions induce a rise in androgen level in territory owners (e.g., Cardwell and Lilley, 1991; Hirschenhauser et al., 2004; Oliveira et al., 1996; Wingfield, 1985). As already mentioned (see Section IV.A), territory status reversal in an African cichlid fish is accompanied by a change in GnRH gene expression and activity in the preoptic area, which may lead to changes in constitutive androgen levels (Francis et al., 1993, White et al., 2002). However, these changes were detected on a time scale not compatible with short-term fluctuations in androgen levels. Endocrine data also became available on the effects of prior-residency reversal situations in human subjects. In humans, sports contests can be seen as a form of ritualized aggression. A home-advantage effect, equivalent to prior residency in animal contests, is well established in team games such as football, ice hockey, rugby, soccer, and basketball (Courneya and Carron, 1992; Neave and Wolfson, 2003; Nevill and Holder, 1999), and there is evidence of increased arousal and aggression at home venues (Kerr and Vanschaik, 1995; McGuire et al., 1992). Concomitantly, salivary T levels in soccer players were higher before home games than before away games (Neave and Wolfson, 2003).

2. Dear Enemy Effects

Territorial males react less aggressively toward familiar intruders than to intrusions by strangers, a phenomenon called the “dear enemy effect” (Temeles, 1994; Ydenberg et al., 1988). At a functional level this process allows the resident to adjust its territorial behavior according to the threat posed by the intruder, thus reducing the costs of territorial defence (Temeles, 1994; Leiser and Itzkowitz, 1999; Whiting, 1999). At a proximate level this differential response to familiar versus unfamiliar intruders requires an ability of the resident individual to discriminate between the two intruder types, together with habituation to neighbors. Habituation to conspecific neighbors has been documented in several species, using different sensory modalities such as visual habituation in Siamese fighting fish (Bronstein, 1994) and auditory habituation to neighbor’s calls in frogs (Owen and Perrill, 1998). Since androgens are proposed to play a role as mediators of the dear enemy effect, it is predicted that the resident’s androgen responsiveness to an intrusion should be higher toward a stranger than toward a familiar intruder. We have run a pilot study to test this hypothesis in the Mozambique tilapia, in which intrusions were promoted
using either territorial neighbors, which were separated from the focal male by a transparent partition, or unfamiliar intruders (kept in separate tanks). For four consecutive days the residents were faced with two intruders per day, one in the morning and the other in the afternoon. The order of presentation of the two intruder types was randomized. Resident tilapia males exhibited lower latencies to attack stranger intruders than neighbors, and the latency to attack the familiar intruder increased with the day of the experiment, suggesting a habituation process. Moreover, the androgen response to the intrusions showed an effect of intruder type, with strangers eliciting higher KT levels than neighbors; there was also a reduction in the response from the first to the fourth day, indicating habituation of the endocrine response (R. F. Aires, A. F. H. Ros, and R. F. Oliveira, unpublished data; Aires, 2003). Similarly, in humans it has been shown that in adult males from a rural Caribbea village competing at dominoes, T response was higher when playing against strangers from another village than when playing with familiar men from their own village (Wagner et al., 2002). Taken together, these results suggest a mediating role for androgens in the dear enemy effect.

3. Winner-Loser Effects

Experiential factors may affect the outcome of social interactions. It is known that, in animal contests, individuals that have won in an interaction increased their probability of winning in a subsequent interaction and vice versa for losers. This effect of prior experience may last from minutes up to hours or even days and has been described for a variety of vertebrate taxa (e.g., fish: Beacham and Newman, 1987; Beaurgrand and Zayan, 1985; Beaurgrand et al., 1991, 1996; Francis, 1983; Frey and Miller, 1977; reptiles: Schuett, 1997; birds: Drummond and Osorio, 1992; mammals: Ginsburg and Allee, 1942). The winner effect is usually of shorter duration than the loser effect (Chase et al., 1994) and more recent experiences weigh more than former ones in this prior-experience effect (Hsu and Wolf, 1999).

It is hypothesized that winner/loser effects may be mediated by short-term changes in androgens. Ginsburg and Allee (1942) were the first to suggest a potential role for androgens as mediators of experiential effects on social behavior in mice. Data on mammals support a role for T in the loser effect, but not in the winner effect. In mice, seminal vesicle weight, a bioassay for androgen levels, was inversely correlated with the number of defeats (Bronson and Eleutheriou, 1964), and although levels of circulating gonadotropins decreased in both winners and losers after an agonistic interaction, the decrease was more marked and lasted longer in losers, suggesting lowered T secretion (Bronson et al., 1973). Rats that were defeated in a social interaction behaved less aggressively and showed
lowered levels of T, while no behavioral or endocrine effect was detected in winners (Schuurman, 1980). In theus monkeys (Macaca mulatta), defeat induced a long-term reduction in T levels, and transitory but significant elevations of androgens levels were reported after winning (Bernstein et al., 1974, 1985; Rose et al., 1972). In male golden hamsters (Mesocricetus auratus), repeated defeats significantly suppress T levels, and influence subsequent submissive behavior (Huhman et al., 1991).

Two studies on male mice have addressed the behavioral significance of androgen responses to social competition in rodents. In both studies the normal androgen response to competition was prevented by castration and subsequent T administration, either by an injection regimen (Nock and Leshner, 1976) or by using Silastic implants (Maruniak et al., 1977). The agonistic behavior displayed by winners and losers over a series of winning and losing experiences was then recorded. No effects of the treatment were found on the subsequent aggressive behavior, suggesting that winner/loser effects were not being influenced by transient fluctuations in circulating androgens induced by the dominance/subordinance experience. Moreover, the profound behavioral changes observed in chronically defeated male rodents (i.e., conditioned defeat), which subsequently fail to defend their territories even against smaller nonaggressive intruders, have not been attributed to changes in T levels but to the hypothalamus–pituitary–adrenal (HPA) axis (Huhman et al., 1990, 1991, 1992, 2003; Leshner, 1983).

We tested the hypothesis that androgens could mediate winner/loser effects in fish using male Mozambique tilapia (A. Silva and R. F. Oliveira, unpublished data). After staging a first fight between two males, 2 h later the winner and the loser fought two independent individuals that had not been involved in recent social interactions. As predicted, winners of the first encounter won the majority of the interactions with the naïve fish and vice versa for losers. However, if winners were treated with an antiandrogen (cyproterone acetate) between the two interactions, the winner effect was no longer detectable in the second fight, suggesting an involvement of androgens in the winner effect. Contrary to predictions, the loser effect was not reduced in the second interaction by treating losers with exogenous androgens (i.e., ET), which suggests that, although a drop in androgens is observed in losers, it is not the underlying mechanism for the loser effect. This result is in agreement with the previously mentioned results for conditioned defeat in male rodents and suggests that other neuroendocrine mechanisms must be involved in the loser effect, namely the HPA axis and/or the serotonergic system.

Evidence from studies using different teleost species seems to support the involvement of the serotonergic system in the loser effect. First,
defeat increases brain levels of serotonin and subordinates have chronically elevated brain levels of serotonin (Winberg and Lepage, 1998; Winberg and Nilsson, 1993a,b; Winberg et al., 1997). Second, serotonin inhibits behavioral responsiveness in general and aggressive behavior in particular (Adams et al., 1996; Edwards and Kravitz, 1997; Winberg and Nilsson, 1993a,b). Thus, losers display a marked behavioral inhibition, with increased attack latencies in subsequent interactions, which prevents them from winning these interactions and reinforces their subordinate role.

The evidence presented above suggests that the role of androgens in experimental effects on social interactions is not universal among vertebrates and that different neuroendocrine mechanisms may be involved, as well as cognitive processing of social information (e.g., Oliveira et al., 1998).

4. Bystander Effects

The bystander effect consists of a priming effect on the aggressive motivation of spectators of agonistic interactions (Bromstein, 1989; Hogan and Bols, 1983). This priming response seems to be adaptive since it prepares the bystanders for forthcoming interactions in a context of social instability (i.e., where agonistic interactions are already present in the social environment). It was shown that bystanders increase their probability of winning their next social interaction (Clotfelter and Paolino, 2003).

The priming of agonistic motivation in bystanders is another social phenomenon that might be mediated by androgens.

To test this hypothesis we have conducted an experiment on Mozambique tilapia, in which a bystander male was able to observe two conspecific neighbors through a one-way glass. The neighboring males were separated by an opaque partition. In the experimental treatment, the opaque partition was removed and the bystander could observe an agonistic interaction between its neighbors, but in which it was prevented from participating. In the control treatment, the bystander could see its two neighbors resting or performing maintenance activities, each in its own compartment. Both KT and T increased in the observer in the experimental treatment while no significant variations in androgen levels were found in the control treatment (Oliveira et al., 2001c). As already discussed (see Section IV.B), sports fans also experience variations on their androgen levels depending on the outcome of the game they have attended, with supporters of the winning team experiencing an increase in circulating T whereas a reverse effect is observed in fans of the losing team (Bernhardt et al., 1998). These results suggest a mediating role for androgens in the priming of bystanders.
B. LONG-TERM (ORGANIZATIONAL) EFFECTS: ANDROGENS AND LIFE HISTORIES

1. Life History Trade-Offs and Phenotypic Plasticity

Trade-offs are fitness costs that result from the linkage between a beneficial change in one trait and a detrimental change in another (Stearns, 1989). Life histories are shaped by such evolutionary trade-offs, in the form of current versus future reproduction, or the investment in offspring quality versus quantity. Negative genetic correlations and life-history trade-offs can be better understood if their proximate mechanisms are known (Sinervo and Svensson, 1998). Hormones are good candidates to play a major role as physiological mediators of life-history trade-offs, since they may have opposite effects on two or more traits (Ketterson and Nolan, 1992; Sinervo and Svensson, 1998). Phenotypic plasticity is a life-history trait that might have evolved to allow animals to shift resources from one life-history stage to another, for example, from reproduction into growth or vice versa, in a condition- or frequency-dependent fashion (West-Eberhard, 1989). Those shifts between life-history stages may also be controlled by endocrine mechanisms, and it is expected that in some cases the life-history trade-offs and the associated phenotypic plasticity have the same underlying physiological mechanism (Sinervo and Svensson, 1998). Since androgens are both involved in the animal’s investment in current reproduction and have multiple effects on different phenotypic traits, they are excellent candidates to orchestrate transitions between life history stages.

In the Mozambique tilapia, the acquisition of dominant status is associated with an increase in androgen levels, which in turn mediate the expression of male display traits, both morphological (i.e., secondary sex characters) and behavioral (e.g., courtship behavior, nest building, nuptial coloration) (Oliveira et al., 1996). Subordinate males have lower androgen levels and display pseudo-female behavior so that they are not ejected from breeding colonies (leks) and obtain access to parasitic fertilizations when spawns occur (Oliveira and Almada, 1998a). With time, an androgenization of dominant males occurs (i.e., they present exaggerated male displaying traits), which may reinforce their dominance status (Oliveira and Almada, 1998b). Thus, male investment in current reproduction seems to be mediated by androgens that are responding to social status. It should be noted that these two male types are interchangeable, and that individuals may switch between being territorial dominant males and nonterritorial subordinates several times during their life time in response to the social environment (Oliveira and Almada, 1996). Thus, phenotypic plasticity in this species seems to be driven by social stimuli and also to be mediated by androgens.
Socially modulated androgens can also impose constraints in life-history pathways. An example of such an organizational constraint on life-history pathways comes from Mongolian gerbils (*Meriones unguiculatus*). In this species, male fetuses vary in their intrauterine positions, and this variation is reflected in adult T levels: males gestated between two females (2F males) have lower T levels when adults than their brothers that were gestated between two males (2M males) (Clark et al., 1992b). As might be expected, the development of male sex characters and of sexual behavior is also affected by intrauterine position: 2F males have reduced bulbocavernous muscle mass and alterations in their copulatory and scent-marking behavior, achieving a lower reproductive success than their 2M siblings (Clark et al., 1990, 1992a). On the other hand, 2F males express more paternal behavior than the 2M males (Clark et al., 1996). This, it has been suggested that 2F males that fail to reproduce and that are highly parental, trade direct reproduction by helping at the nest, thus increasing their inclusive fitness (Clark and Galet, 2000). This trade-off between direct reproduction and obligatory alloparenting is mediated by androgen levels modulated by the early (i.e., prenatal) social environment.

2. Sex Change

An extreme example of a life-history transition is sex change. Sequential hermaphroditism is present in a number of teleost families, with protogynous sex change [female → male; e.g., wrasses (*Labridae*) and parrotfishes (*Scaridae*)] being more common than protandry [male → female; e.g., anemone-fish (*Pomacentridae*)] (Warner, 1984). In most cases sex change is functionally explained by the "size advantage model," according to which if reproductive success varies with body size between the sexes, then an individual that changes sex at the right size (age) will have a higher lifetime reproductive success than one that remains exclusively male or female for its lifetime (Warner, 1975; but see St. Mary, 1997). At a proximate level of analysis, sex change has been shown to be induced by social factors, for example, either inhibition by the presence of males or social stimulation by other females (Shapiro, 1979). In protogynous species the critical cue to trigger sex change seems to be the perceived status of the fish, as indicated by the ratio of attacks given and received from other group members (Grober, 1996; Reavis and Grober, 1999; Shapiro, 1981). Removal of the male induces a behavioral change in the largest female that dramatically increases her aggressive behavior. This initial behavioral change is completely independent of gonadal steroids since it can be induced in ovariectomized females (Godwin et al., 1996): it is probably needed to inhibit sex change in the other females. Subsequently, however, a cascade of changes in neuroendocrine and morphological traits occurs in
the dominant female becomes male: the change in status is presumably transcribed into a neuroendocrine signal by sensory pathways that project to the hypothalamus affecting GnRH activity, which in turn will affect the gonad anatomy and physiology, the levels of circulating sex steroids, and body coloration (Groher, 1998). A rapid decrease in the activity of brain aromatase (an enzyme that converts androgens into estrogens) was observed at the initial stages of sex change in the sex-changing goby Lythrypnus dalli (Black et al., 2003). This suggests that a change in brain steroidsogenesis occurs early in the process and that this modifies the estrogen-to-androgen ratio toward androgens, since a lesser amount of androgens is being metabolized into estrogen. This androgen-biased neural environment would then trigger the cascade of changes described above. Thus, social modulation of brain androgen levels may mediate another life-history transition.

3. Alternative Reproductive Tactics

Within the vertebrates, the highest incidence of species with male alternative reproductive tactics occurs in teleost fishes (Taborsky, 1994, 2001). Usually two male types are present: bourgeois males, which actively compete among themselves, investing in the acquisition of mates (e.g., by defending breeding territories); and parasitic males, which exploit the investment of bourgeois males to get access to females and fertilize eggs (e.g., sneakers, satellites; Taborsky, 1994, 2001).

Moore (1991) proposed the “relative plasticity hypothesis” as a conceptual framework for the functional basis of alternative reproductive tactics. The rationale behind this hypothesis is that the effects of hormones in the differentiation of alternative reproductive tactics are equivalent to their effects in primary sex differentiation (Moore, 1991; Moore et al., 1998). Thus, by making a distinction between fixed alternative phenotypes (in which individuals adopt one of the tactics for their entire life) and flexible alternative phenotypes (in which individuals may switch tactics during their lifetime) this hypothesis predicts an organizational role of hormones in the former case and an activational role in the latter (Moore, 1991). Therefore, hormone profiles should differ in plastic adult males but not in fixed ones. In all the fish species with alternative reproductive tactics for which data are available (i.e., Salmonidae: Atlantic salmon, Salmo salar; Centrarchidae: bluegill sunfish, Lepomis macrochirus; Scardidae: stoplight parrotfish, Sparisoma viride; Labridae: saddleback wrasse, Thalassoma saida; corkwing wrasse, Symphodus melops; Batrachodidae: plainfin midshipman Porichthys notatus; Cichlidae: Mozambique tilapia; Blenniidae: rock-pool blenny, Parablennius sanguinolentus paricorne; peacock blenny), bourgeois males have significantly higher KT levels
than parasitic males, whereas no clear pattern has been found for T (Brantley et al., 1995a; Oliveira et al., 1996, 2001b,c; Uglen et al., 2002). These results suggest either that KT plays a major role in the expression of the male bourgeois tactic, or that KT levels are highly responsive to the expression of the tactic itself (i.e., they are a consequence and not a cause of the expression of alternative mating tactics). However, the prediction concerning relative plasticity is not confirmed by this data set, since differences in KT levels between male types are present in all species irrespective of whether their tactics are fixed or flexible.

VII. EVOLUTION OF THE SOCIAL MODULATION OF ANDROGENS

The evolution of a phenotypic trait requires that the observed phenotypic variation in that trait be partially dependent on genetic variability. Therefore, an implicit assumption for the evolution of a mechanism of social modulation of androgens, as a way of adjusting behavior to social context, is that androgen levels have some heritability. A study performed on human families revealed significant parent–offspring and sibling correlations in circulating T levels and estimated a heritability of approximately 70% (Hong et al., 2001). It should be pointed out, however, that in the same study significant spousal correlations in T levels were also found, suggesting that familial resemblance in androgens should be viewed as a result of both genetic resemblance and common familial environments (Hong et al., 2001). If one considers only the production rate of androgens the heritability estimate decreases to 40%, with more than 50% of variation in androgen production being explained by environmental variables (Meikle et al., 1988).

In nonhuman animals there is evidence for a genetic influence on both circulating androgen levels and androgen production patterns. In a well-known study on canid domestication, that on the effect of genetic selection for tameness in silver foxes (Vulpes vulpes), animals have been successfully selected for reduced aggression and fear toward humans (Bel/æv, 1979; Trut, 1999). During the breeding season males in the selected line were found to show both lower plasma concentrations and testicular production of T than their wild counterparts (Osadchuk, 2001). Moreover, selected males showed a more pronounced androgen response to exposure to a receptive female (Osadchuk, 2001). This is in accordance with the first prediction of the challenge hypothesis (see Section II.B., since selected males have lower breeding baseline levels of T and thus a potentially higher androgen responsiveness to social stimuli. In summary, variation in androgen plasma levels and gonadal production seems
to be in part due to underlying genetic variability, and so is open to selection.

For a phenotypic trait to be selected, the benefits it confers must outweigh the costs associated with its expression. Therefore, a cost–benefit analysis should be carried out to try to uncover all the beneficial and detrimental effects associated with the expression of the trait, and weigh the former against the latter.

A. **Cost–Benefit Analysis of Androgen Responsiveness to the Social Environment**

Despite the benefits of high androgen levels for the fitness of the individual, androgen levels are not fixed phenotypic traits selected for an optimal value. On the contrary, they represent a physiological state that is tightly regulated by environmental stimuli and by the internal state of the animal. This suggests that there should be costs of keeping high levels of androgens and that social modulation of circulating levels of androgens is a way to minimize these costs (Wingfield *et al.*, 2001). From an adaptationist point of view, androgen-dependent mechanisms can be selected only when the associated benefits outweigh the associated costs (Fig. 11).

**FIG. 11.** The selection of androgen-dependent mechanisms depends on the relationship between potential associated benefits and potential associated costs. For the mechanism to be adaptive, the former must outweigh the latter.
1. Potential Benefits of High Androgen Levels

In the preceding sections the potential fitness benefits of high androgen levels have already been discussed, such as an association of T with mating success (see Section III.B) and the effects of androgens on reproduction (i.e., spermatogenesis, expression of male traits, etc.). For example, in the Mozambique tilapia, a lek breeding cichlid fish, female mate choice is based mainly on the size of the spawning pit dug by territorial males (Nelson, 1995), a characteristic that is positively associated with male androgen levels (Oliveira and Almada, 1998b; Oliveira et al., 1996). At periods of social challenge, increased androgen levels may also be beneficial by acting on motivational systems underlying aggressive behavior so that competitive behavior is adjusted to the social environment (see Section II.C) and by acting on other mechanisms that enhance the success of the individual in competitive interactions such as social attention, social learning, memory, and risk taking (Andrew, 1991; Cyx and Nottebohm, 1992).

Observing social interactions among conspecifics (eavesdropping) is a way of collecting information on the relative competitive ability of neighbors without paying the costs associated with fighting behavior, which would be an alternative way of collecting such information (McGregor, 1993). Thus, selective attention toward social interactions should benefit in territorial species. In the Siamese fighting fish it has been shown that, when given a choice, territorial males spent more time observing social interactions between pairs of conspecifics than observing pairs of conspecifics that were prevented from interacting (Oliveira et al., 1998). Moreover, territorial males of this species eavesdrop on agonistic interactions among conspecific neighbors, gathering information on relative fighting ability that they use in subsequent interactions with the previously observed individuals (Oliveira et al., 1998). The effect of androgens on selective attention to social interactions has been tested in the Siamese fighting fish, when it was found that androgen-treated males significantly increase the time spent observing conspecific interactions when compared with control males (R. F. Oliveira and L. A. Carneiro, unpublished data). This result suggests that androgens may promote selective attention to relevant social stimuli in the environment.

Increased risk-taking behavior in a competitive situation may also confer an advantage to the individual. An experiment gives some support to this idea. Male mice were preexposed to the odor of an estrous female and subsequently exposed to the odors of predators. Mice in a situation of increased perception of predation risk, that is, mice that were exposed only to the predator’s odor, showed increased corticosterone and decreased
circulating levels of T (Kavaliers et al. 2001). Preexposure to female odor attenuated this response to the odor of the predator, which might reflect a greater tendency for risk-taking behaviors modulated by hormones (Kavaliers et al. 2001).

2. Potential Costs of High Androgen Levels

A number of potential costs associated with high levels of androgens have been identified (Fig. 11), namely, increased energy consumption, interference with immunocompetence, increased risk of predation, higher incidence of injuries from agonistic interactions, trade-off with parental care, and carcinogenic effects (for reviews see Wingfield et al., 1999, 2001). Some of these costs are discussed here.

The evidence on metabolic costs of high androgen levels is contradictory (Table II). The discrepancy in the results may be due to variations in the methods used in the different studies, such as the measures used, the duration of the experiment, and the season when it was performed. Nevertheless, there is evidence for a negative effect of androgens on metabolic rates in species from different taxa (teleosts, reptiles, and birds). Moreover, in the two bird species with discrepant results, explanations are available. In the dark-eyed junco the measure used was daily energy expenditure using doubly labeled water, which incorporates not only resting metabolism but also thermoregulatory and activity costs (Lynn et al., 2000). Furthermore, despite the absence of an effect of T on daily energy expenditure, androgen-treated birds increased their activity and reduced resting and self-maintenance behaviors. Thus, T may be reallocating the relative contributions of the different components of daily energy expenditure. This interpretation is in accordance with the fact that in the white-crowned sparrow T may also increase activity, and thus the observed reduction in the resting metabolic rate in T-treated individuals in this species can be interpreted as a way in which males compensate for increased activity metabolism (Wilkens et al., 1999b). In summary, androgens seem to affect metabolic activity in a nonlinear fashion and there seems to be both direct and indirect metabolic costs of high androgen levels.

Another potential cost of high androgen levels is interference with immune function. Although initial studies suggested a negative effect of T on humoral immune function in mammals (Grossman, 1985, 1990), the currently available data are equivocal (see Table II for examples) and several hypotheses concerning the relationship between androgens and immunocompetence have been advanced (Braude et al., 1999; Folstad and Karter, 1992; Hillgarth et al., 1997; Wedekind and Folstad, 1994). The "immunocompetence handicap hypothesis" (Folstad and Karter, 1992) predicts a trade-off between androgens and immunocompetence,
<table>
<thead>
<tr>
<th>Type of cost</th>
<th>Examples</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Increased energy expenditure</td>
<td>1. Increased resting metabolic rate and metabolic scope in ciclid fish</td>
<td>Ron et al. (2004a)</td>
</tr>
<tr>
<td></td>
<td>(O. mossambica) treated with 11-ketotestosterone</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2. Androgen treatment induced higher maximal metabolic rate but had no effect on basal metabolic rate in the lizard Sceloporus jarrovi</td>
<td>Marker et al. (1995)</td>
</tr>
<tr>
<td></td>
<td>3. Testosterone treatment increased the basal metabolic rate in house sparrows (Passer domesticus)</td>
<td>Buchanan et al. (2001)</td>
</tr>
<tr>
<td></td>
<td>4. Testosterone implantation decreased resting metabolic rate in both intact and castrated white-crowned sparrows (Zonotrichia leucophrys)</td>
<td>Wikelski et al. (1999b)</td>
</tr>
<tr>
<td></td>
<td>5. Testosterone treatment had no effect either on basal metabolic rate or in daily energy expenditure in dark-eyed junco (Junco hyemalis)</td>
<td>Deviche (1992); Lynn et al. (2000)</td>
</tr>
<tr>
<td></td>
<td>6. Testosterone implants decrease fat stores in song sparrows (Melospiza melodia)</td>
<td>Wingfield (1984c)</td>
</tr>
<tr>
<td>B. Interference with immune function</td>
<td>1. Testosterone treatment has a negative effect both on leucocyte numbers and on antibody production in salmonid fish</td>
<td>Slater and Schreck (1993, 1997); Slater et al. (1995)</td>
</tr>
<tr>
<td></td>
<td>2. Lymphocyte tiers and antibody response to SRBCs are lower in satellite males than in bourgeois males, and negatively correlated with levels of 11-ketotestosterone in the rock-pool blenny (Parabramias parvicornis)</td>
<td>A. F. H. Rus, N. Bouton, R. S. Sansom, and R. F. O'Brien (unpublished data)</td>
</tr>
<tr>
<td></td>
<td>3. No relationship was found between androgen divergent alternative reproductive male morphs and leucocyte count in the cokwing sease (Symphodus macrocephalus)</td>
<td>Vglum et al. (2001)</td>
</tr>
<tr>
<td></td>
<td>4. Testosterone treatment enhanced the antibody response to immunization with SRBC in chicks of the black-headed gull (Larus ridibundus)</td>
<td>Ron et al. (1997)</td>
</tr>
<tr>
<td></td>
<td>5. Higher testosterone levels in a selected line of domestic fowl (Gallus domesticus) selected for antibody responsiveness to sheep red blood cells</td>
<td>Verhulst et al. (1999)</td>
</tr>
</tbody>
</table>
6. No relationship between plasma testosterone levels and immunocompetence* in free-living male red-winged blackbirds (Agelaius phoeniceus).

7. Testosterone treatment is immunosuppressive, but in free-ranging males testosterone levels are positively correlated with immunocompetence* in superb fairy-wrens (Malurus cyaneus).

8. Viremia decreases early and increases late in the course of infection of testosterone-treated male greenfinches (Carduelis chloris) infected with Sindbis virus, and for total viremia or antibody response there was no difference between treated and control males.

C. Paternal care trade-off

1. Androgen levels are lower during the brooding phase than during the nestling phase in some male tanagers (e.g., Chorosia, Chloris reguloides; geese, Chloephaga rubecollis).

2. 11-Dehydrotestosterone levels are lower in parental male mockingbirds (Mimus polyglottos) guarding embryos than in males guarding eggs.

3. Mouth-brooding eggs in the paternal mouthbrooder cichlid Sarotherodon melanorhabdus induces a reduction in circulating levels of testosterone.

4. Androgen levels are lower during the brooding phase than during the nestling phase in male birds; e.g., song sparrow, Melospiza melodia, white-crowned sparrow, Zonotrichia leucophrys palustris, Z. leucophrys.

5. Birth of offspring is associated with a decrease in testosterone levels in male mammals displaying paternal behaviors; e.g., Mongolian gerbils, Meriones unguiculatus; Damaraland hamsters, Phodopus campbelli; common marmosets, Callithrix jacchus; cotton-top tamarins, Saguinus oedipus; humans, Homo sapiens.

Hanselquint et al. (1999)

Peters (2000)

Lindstrøm et al. (2001)

Kinsel et al. (1989); Pankhurst and Barnett (1995); Sikkil (1993)

Knapp et al. (1999)

Specker and Kishida (2000)

Wingfield (1984a, 1984b); Wingfield and Farner (1973a, b)

Brown et al. (1995); Nunes et al. (2001); Roberts and Wayne-Edwards (1999); Storey et al. (2000); Ziegler et al. (1996)

---

*Immunocompetence was measured as secondary antibody production to a nonpathogenic antigen (e.g., sheep red blood cells; keyhole limpet hemocyanin).

**Viremia, blood virus concentration.
and is an extension of the handicap principle proposed by Zahavi (1975) to explain the evolution of costly secondary sex characters. The rationale of this hypothesis is that one cost of honest androgen-dependent signals is that androgens have an immunosuppressive effect. However, this hypothesis is flawed in a Popperian sense as it cannot be disproved, since both positive and negative correlations, and even the lack of a relationship between T levels and arbitrary indices of immunity, all find support from it (Braude et al., 1999). Positive correlations between androgen levels and immunocompetence measures are interpreted as males having high-quality immune function that can resist the immunosuppressive effect of T. Negative correlations are interpreted as indicating that males are of such high quality that they can still display and court females despite being immunosuppressed and exposed to higher parasite loads. Finally, if no correlation is found it is argued that high-quality males reliably signal their resistance to parasites since they manage to resist infection even with high T levels (Braude et al., 1999).

Subsequently Wedekind and Folstad (1994) have proposed that androgen immunosuppression would allow the individual to reallocate resources from the immune system to sexual display characters, both morphological (e.g., horns) and behavioral (e.g., courtship song). This explanation supports the assumption of the immunocompetence handicap hypothesis that there is a trade-off between androgens and immunity. The weakness of this hypothesis is that the risk of infection due to immunosuppression most probably outweighs the metabolic resources saved by it (Hillgarth and Wingfield, 1997).

An alternative explanation for the association between T, leukocyte titers, and male display traits has been advanced by Braude et al. (1999) and is termed the “immunoregulation hypothesis.” According to this hypothesis, androgens may have a similar effect to corticosteroids in promoting a redistribution of leukocytes to different compartments of the immune system, and this may suggest an immunosuppressive effect if only one measure of immune function is taken at a time (Braude et al., 1999). Thus, the main distinction between this hypothesis and that of Wedekind and Folstad is that the immunocompetence handicap hypothesis implies a reduction of immune function associated with T while the immunoregulation hypothesis merely involves a reversible relocation of immune cells to tissues where they are temporarily needed. Moreover, it has also been shown that T may have both positive and negative effects on immune function and that the direction of the effect may depend on when it is measured (Lindstrom et al., 2001; Marsh, 1992; Olens and Kovacs, 1996).

Finally, suppression of parental care has also been proposed as a potential cost of high T levels in species in which males provide parental care
(Wingfield et al., 1990). If androgen levels increase due to social challenges, males will invest less time in paternal activities, and thus a trade-off will occur between social interactions and paternal care mediated by androgens (Wingfield et al., 1990). The reduction in time available for paternal care may emerge for two reasons: (1) because T results in more time spent on other behaviors (e.g., territorial defense), or (2) because T directly suppresses parental care. Thus, a decrease in androgen levels during parenting has been interpreted as a way of avoiding tifanticide, reducing male distraction by courtship toward other females, and facilitating affiliative behaviors toward the young (Clark and Galef, 1999, 2000; Gubernick et al., 1994).

Several studies on the temporal variation of androgen levels in fish, bird, and mammal species with male parental care show that during the breeding season male androgen levels are higher during the mating phase than during the parental phase (for reviews, see Wingfield et al., 1987, on birds; Ziegler, 2000, on mammals; and Oliveira et al., 2002, on fish; selected examples are given in Table II). Among birds the trade-off between parental care and androgens is larger during incubation than during later brooding phases (Hirschhorshuet et al., 2003). In many bird species an experimental increase in circulating T in parental males suppresses paternal behavior and promotes agonistic interactions (e.g., Beletsky et al., 1995; Hegner and Wingfield, 1987; Ketterson et al., 1992; Silverin, 1980). However, the use of castration to reduce T levels has yielded inconsistent results in mammals. Castration increases paternal behaviors in Mongolian gerbils (Clark and Galef, 1999), has produced mixed results in prairie voles (Microtus ochrogaster) (Lomstein and De Vries, 1999; Wang and De Vries, 1993), and in the biparental California mouse (Peromyscus californicus) it decreases parental care while androgen replacement restores it (Trainor and Marler, 2001). These results are in accordance with the fact that, in some species, males keep high T levels after the birth of offspring despite the fact that they still display high levels of paternal care (e.g., Djungarian hamsters Phodopus campbellii) (Jones and Wynne-Edwards, 2000; cotton-top tamarins Saguinus oedipus): Ziegler and Snowdon, 2000). This apparent contradiction may result from the fact that T action on parental behavior is mediated by its conversion to E2, which is likely to be the active steroid promoting paternal behaviors, as was shown in the California mouse (Trainor and Marler, 2002).

In fish species in which the mating and the parental phase overlap, a trade-off between androgen levels and paternal care has not been found. For example, in a facultative biparental cichlid, the St. Peter’s fish Sarotherodon galilaeus, there were no differences in androgen levels between brooding and non-brooding males (Ros et al., 2003). Also in the
rock-pool blenny, a promiscuous species with exclusive male parental care, although an incompatibility between defense of a breeding territory and high levels of parental behavior exists, KT implants failed to suppress paternal behavior (Ros et al., 2004b). In this case the trade-off between androgen-dependent behaviors (territorial defense/mating) and parental behaviors may not be regulated by androgens but may instead result from a time constraint in the individual’s activity budget (Ros et al., 2004b).

Interestingly, there is an inverse pattern on the variation of prolactin levels with androgen levels during periods of male parental care (for a review see Ziegler, 2000), and prolactin has been found to be involved in the expression of paternal care in a wide range of vertebrates, from fish to mammals (for a review, see Schrader and Anzenbacher, 1999). It is also known that prolactin is involved in the regulation of T secretion (e.g., Huang et al., 1999), and that in humans there is an orgasm-induced prolactin peak, which inhibits sexual arousal following an orgasm (Krüger et al., 2002). Moreover, multiorgasmic males, lacking a refractory period after ejaculation, also lack an orgasm-induced prolactin peak (Haake et al., 2002). Thus, prolactin seems to have a negative effect on androgen production and on the expression of androgen-dependent sexual behaviors. Therefore, the pattern of a T decrease during the parental phase may be due to a physiological constraint imposed by a rise in prolactin associated with the expression of paternal behaviors.

In summary, there are a number of potential costs, associated with keeping high levels of androgens for long periods of time, that may be avoided by the social modulation of androgens.

B. EVOLUTIONARY SCENARIOS FOR THE SELECTION OF ANDROGEN RESPONSIVENESS TO THE SOCIAL ENVIRONMENT

Since hormones act on different target tissues, many traits may have a common underlying physiological mechanism and thus be phenotypically linked (Ketterson and Nolan, 1999; Ketterson et al., 2001), as is the case with androgen-dependent traits such as the expression of male morphological characters, muscle hypertrophy, and the expression of aggressive and sexual behavior. Thus, it is likely that selection acting on any one of these traits will affect the others, so that beneficial traits may evolve indirectly as exaptations (in the sense of Gould and Vrba, 1982). According to Ketterson and Nolan (1999) one way to distinguish between adaptations and exaptations in hormone-dependent traits would be to assess whether these traits arose either in response to selection on circulating hormone levels (in which case selection probably did not act on all correlated traits and thus
the ones that subsequently conferred an advantage to its carriers are expatations), or whether they arose in response to variation in the responsiveness of the target tissues to invariable hormone levels (in which case selection probably acted independently of target tissue sensitivity to constant hormone levels). Although this dichotomy is simplistic (i.e., a mixed scenario may occur in which both circulating levels and target tissue sensitivity are under selection) it provides us with a framework to address the issue of endocrine-mediated adaptive traits. In this respect, androgen responsiveness to the social environment may be seen as a physiological mechanism that allows the organism to avoid the costs of high androgen levels at times when they are not crucial, thus suggesting that it might have evolved as an expatation in the context of fixed target tissue sensitivity to circulating androgens.

Independently of the question of whether androgen responsiveness to the social environment emerged as an adaptation or as an expatation it is important to try to identify the selective pressures on this mechanism. Since a large data set on androgen levels in wild avian populations is available, together with an established phylogeny, which allows for the control of phylogenetic bias in the comparative analysis, the approaches to this question have been restricted to birds. We tested the effects of the mating system (specifically, the intensity of social challenges that the males are exposed to and the investment in paternal care) on the evolution of androgen responsiveness to the social environment (Hirschenhauser et al., 2003; Fig. 12). When controlling for phylogenetic relatedness among the sampled species, an effect of the degree of male-male competition on

![Diagram](image)

**Fig. 12.** The evolution of androgen responsiveness to social challenges in male birds. Scatterplots of low androgen responsiveness varies with the degree of male-male aggression (right) and the degree of male investment in parental care (left); the lines represent a linear regression with phylogenetic distances.
androgen responsiveness was detected, whereas the degree of male investment in paternal care had no significant effect (Hirschenhauer et al., 2003; Fig. 12).

To further investigate this lack of effect of paternal care on shaping androgen responsiveness, the analysis was repeated on a subset of australopithecine species, using a quantitative scale of the degree of male incubation and feeding of offspring. This reanalysis showed an effect of the male contribution to incubation but no effect of the degree of offspring feeding (Hirschenhauer et al., 2003). Thus, the degree of male–female competition, rather than changes in parental investment, emerged as the most relevant factor for an evolutionary change in androgen responsiveness in birds. Further comparative studies will allow us to test which of these factors shaped the androgen response to social stimuli in other vertebrate taxa.

VIII. Social Modulation of Androgens in Men

During the evolution of the primate brain, different regions have developed differentially. Over primate phylogeny, the neocortex and the striatum, which correspond to the “executive” brain, have increased considerably in relative size, at the cost of a reduction in the relative size of the “emotional” brain, that is, the hypothalamus and the septum (Keverne et al., 1996). Since the “emotional” brain is the major neural target tissue for sex steroids, this differential development of different areas of the primate forebrain has progressively emancipated primate sexual and social behaviors from the influences of gonadal hormones over phylogenetic time (Keverne et al., 1996). A major selective pressure for this trade-off between the relative development of the “executive” versus the “emotional” brain may have stemmed from strong social constraints imposed on reproductive decision-making in large-brained anthropoids, which requires the evolution of more flexible behavioral strategies (Keverne et al., 1996).

Emancipation of sexual behavior from hormonal regulation is confirmed in behavioral studies of sexual behavior in humans and other primates (Waller, 2001). For example, eliminating T in adult male primitives, including humans, decreases sexual motivation but does not eliminate sexual behavior. Moreover, the effects of androgens in nonhuman primates vary with social context, and cognition is shown to play a major role in primate sexual behavior (Waller, 1999, 2001). Thus, androgen responsiveness to social stimuli, if present in humans, seems to have reduced or no behavioral significance. Nevertheless, a consistent body of literature on social modulation of androgen levels in humans, already presented in other parts of
this review (see Sections IV.B and V.A for numerous examples; and Mazur and Booth, 1998, for a general review), suggests that it is a common phenomenon in our species. Adaptive androgen responsiveness to the social environment has also been described for other primates. For example, increases in male circulating T levels correlated with male–male aggression have been documented in rhesus macaques (Lemur catta; Cavalli and Pereira, 2000), in rhesus monkeys (Macaca mulatta; Higley et al., 1996; Mehlerman et al., 1997), and mores notably also in free-living common chimpanzees (Pan troglodytes; Mulder and Wrangham, 2004).

In humans, the androgen response to stress in a social challenge has been interpreted as an adaptive mechanism that reinforces the instrumental behavior(s) associated with winning the interaction (Mazur, 1985). The finding that T administration has rewarding and mood-enhancing effects in agreement with this hypothesis (Fackard et al., 1998; Rubkin et al., 1996). However, the evidence for winning/losing effects on T in humans is equivocal, with some studies failing to detect such a pattern (e.g., Gonzales-Bono et al., 1999; Salvador et al., 1987; Susy et al., 1999; R. F. Oliveira, M. J. Gouveia, P. Almeida, and T. Oliveira, unpublished data on soccer players). It has been proposed that individual variations in motivational dispositions would explain these contrasting results (Schultheiss et al., 1990). According to the theory of implicit motives of human motivation, individuals may have unconscious enduring preferences for power or affiliation (McClelland, 1987). These implicit motives may influence behavior if activated by relevant situational cues. Individuals high in implicit power motivation, which is an indicator of the subject's need for dominance or status, responded with a T increase to winning a dominance contest, while individuals with a low implicit power motive did not show an androgen response to either winning or losing the context (Schultheiss et al., 1999). Furthermore, postvictory increases in T facilitated implicit learning of the instrumental behaviors associated with winning the contest, thus having a reinforcing role in winners with a high power motivation (Schultheiss and Rhode, 2002).

Thus, androgen responsiveness to social challenges seems to be an adaptive trait in humans in individuals with a particular social motivation style. Androgen responsiveness per se may represent an ancestral state in our evolutionary history since it is widespread in other vertebrate taxa, and it may have proved beneficial in the environment of our hominin ancestors, as it would have reinforced behaviors leading to dominance status, which is associated with reproductive success in most animal species (Ellis, 1995). However, it may have become maladaptive in the setting of modern life. As mentioned above, an increase in T levels is seen in fans of sports teams when their team wins a game (Bernhardt et al., 1998). An independent
study on the relationship between the outcome of American football games and the frequency of violent assaults on women has found a positive association between the victory of the favorite team and the frequency of admissions of women victims of violent assaults in the local hospital (White et al., 1993). Taken together these studies suggest that experiencing a team victory in response to perceived dominance success in men with high power motivation might act as a trigger for violent behavior.

In conclusion, social modulation of androgens is clearly also present in humans although its current adaptive value is questionable.

IX. SUMMARY

The social modulation of androgen levels seems to be a widespread phenomenon in vertebrates. It allows the individual to adjust its behavioral output to the context-dependent condition imposed by social constraints. The perception that the individual has of its social environment is needed to activate the androgen response. Animals can use different sensory channels to perceive the key social signals that trigger the response. The transduction of these stimuli into a neuroendocrine response involves the efferent projections from sensory areas of the central nervous system to the preoptic area/hypothalamus that controls the androgen response through the HPG axis. The development of this response during ontogeny can be primed by early exposure to androgens through maternal effects, and the androgen response to social challenges can be present early in the ontogeny of altricial species. The adaptive value (i.e., function) of having circulating androgen levels open to the influence of the social environment is to allow the individuals to adjust their competitive behavior to the social context according to their relative competitive ability, and this flexibility has advantages over an optimal fixed value of androgen levels, because of the high costs associated with high androgen levels (e.g., mismatched expression of behavior, trade-off with parental care; metabolic costs; immunosuppression; survival; etc.). A phylogenetic analysis in birds suggests that the evolutionary scenario in which the social modulation of androgens has evolved was characterized for selective pressures imposed by male-male competition regimes that vary with mating system.

In future the social modulation of hormones as an adaptive mechanism to adjust female behavior to social context should also be investigated. So far investigations using the conceptual framework provided by the challenge hypothesis have been mainly limited to androgen responses in males. In females, hormones other than androgens may be relevant in such a role, as is suggested by the less clear relationship between T and agonistic
behavior in females (e.g., Floody, 1983) and by the known effects of E2 on female aggression (e.g., Toda et al., 2001). A rise in progesterone has been described in female California mice as a response to a social challenge in a resident-intruder paradigm, while no changes were observed in T levels (Davis and Marler, 2003). These results suggest that in females different hormonal mechanisms may mediate behavioral responses to social challenges. The study of endocrine responses in females to social challenges is therefore a promising avenue for future research in this area.

Acknowledgments

I thank the following people with whom I have discussed over the years some of the ideas presented in this chapter: Katharina Hirschenhimer, Albert Ros, Luís Casavento, David González, Adelino Carreira, Vitor Almeida, and John Wingfield. Tim Roper, Peter Slater, and Asalita Kertz provided very helpful comments on an early version of this manuscript. Thanks are also due to the staff of ISPA’s library for help in finding the most obscure primary sources that I have requested, and to Teresa Garcia Marques for input on social psychology sources. Unpublished data reported in this review are part of an ongoing research project funded by the Portuguese Foundation for Science and Technology (FCT; grant ref. POCI/BES/58484/2003). The laboratory of R.E.G. is funded by the FCT Phare Program (Research Unit no. 331/94). I would like to express my gratitude to my lifetime partner Alexandra Lopes for her unconditional support during the writing of this chapter and to my two young children, João and Catarina, who are ever-vigilant observers of that work in Daddy’s favorite hobby.

References


Goudet, C., and Beauchard, J. P. (2004). Inversion of initial dominance relationships following the interexchange of roles of resident and intruder within pairs of male swordtail fish (Xiphophorus helleri). *Behav. Process.* in press.


