

21

Hormones, social context and animal communication

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Introduction

The views on the role that hormones play in the control of behaviour have changed progressively with time. Hormones were classically seen as causal agents of behaviour, acting directly on the display of a given behaviour. This view was mainly supported by early studies of castration and hormone-replacement therapy, which showed that some behaviours were abolished by castration and restored by exogenous administration of androgens (Nelson, 2001). Later this view shifted towards a more probabilistic approach and hormones started to be seen more as facilitators of behaviour than as deterministic factors (Simon, 2002). According to this new view, hormones may increase the probability of the expression of a given behaviour by acting as modulators of the neural pathways underlying that behavioural pattern. For example, the effects of androgens on the expression of aggressive behaviours in mammals are mediated by modulatory effects on central serotonergic and vasopressin pathways (Simon, 2002). Yet, it is also known that the social environment (i.e. network of interacting individuals) also feeds back to influence hormone levels (Wingfield *et al.*, 1990), suggesting a two-way type of interaction between hormones and behaviour. In this chapter, I will develop the hypothesis that social modulation of androgens is an adaptive mechanism through which individuals adjust their motivation according to the social context that they are facing. Thus, the social interactions within a given social network would stimulate the production of androgens in the individuals and the individual levels of androgens would be a function of the perceived social status and the stability of the social environment in which the animal is living. According to this view, androgens may play a key role as endocrine mediators of the effects

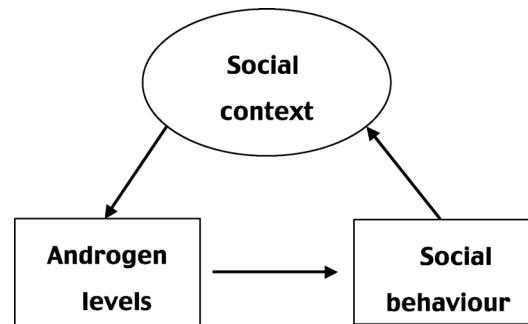


Fig. 21.1. Interplay between androgens, social behaviour and social context. Androgens influence the production of a number of social behaviours involved in communication interactions between animals. In turn, these social interactions among a network of individuals will shape the social context in which these animals live, which subsequently will modulate their androgen levels.

of social context on the expression of social behaviour, allowing the animal to adjust its social behaviour to the context by modulating sensory, cognitive and motor neural mechanisms underlying animal communication (Fig. 21.1).

In this chapter, I only consider vertebrates because they have a remarkably similar endocrine system, whereas that of invertebrates can be very different (e.g. the androgenic hormone in crustaceans is a peptide not a steroid as in vertebrates (Hasegawa *et al.*, 2002)). Within the vertebrates, I mainly use examples from bony fishes, a group with wide diversity in mating and parental care systems that makes up about half the existing vertebrate species (Nelson, 1994). I have also concentrated on androgens and male behaviour because I argue that the social network in which the individual lives modulates its neuroendocrine system, which, in turn, adjusts the expression of behaviour according to social context. Stress hormones are, by definition, affected by the social environment and a number of reviews on social stress and hypothalamus–pituitary–adrenal axis have been published since the early 1990s (e.g. Sapolsky, 1992). Consequently, an additional benefit of this chapter is to claim that, like stress hormones, androgens (and perhaps also other hormones) respond in an adaptive way to the social context, preparing the animal for the social interactions that it has to face in its everyday life.

Hormones and communication I: the dyadic view

Conceptually, the neurochemical pathways modulated by hormones can be part of one of three major functional compartments of the nervous system: sensory, central processing and effector systems (Nelson, 2001). If we translate this rationale to the communication paradigm, one can consider that hormones may affect communication by modulating the production of the signal in the

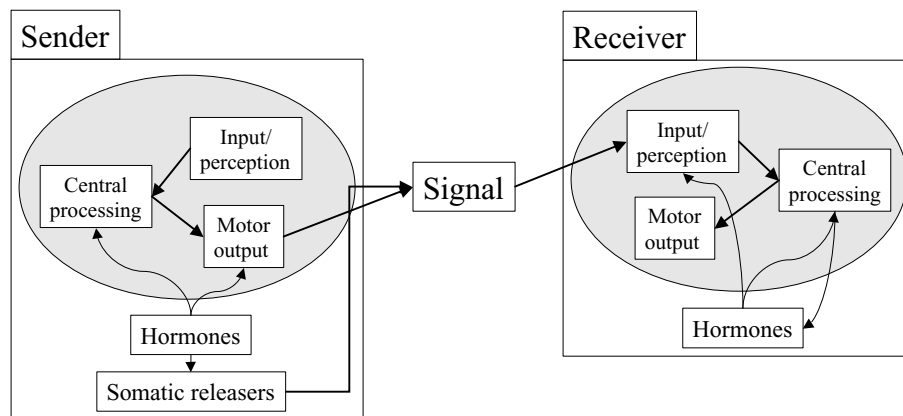


Fig. 21.2. Flow of information in a communication dyad. The arrows indicate the direction of circulation of the information within and between individuals. In the sender, sensory information received will influence central processing mechanisms in the central nervous system (CNS), which control, at a higher level, the behavioural motor output systems that produce the signals. Hormones may modulate signal production by the sender by acting on central mechanisms, on motor output mechanisms or by modifying somatic structures that affect the emission of the signal (i.e. somatic releasers). In the receiver, the signal will be detected by sensory systems and after peripheral processing will be forwarded to central processing systems in the CNS. Hormones may affect signal reception and processing in the receiver by acting directly on the sensory systems that perceive it and/or by acting at a higher level on the central processing mechanism of the CNS. The central processing of the signal by the limbic system (and other structures involved in motivational mechanism) may feed back on hormone levels. The boxes delimit the two organisms and within the boxes the grey elliptical areas represent the nervous system.

sender, the perception of the signal by the receiver or the central processing of the message in both senders and receivers (Fig. 21.2).

Hormonal modulation of effector pathways

In senders, hormones may modulate the effector pathways that are involved in the motor circuits underlying the production of the signal. In this way, hormones can affect the expression of visual displays, vocalizations or pheromone production and/or release. From the numerous examples in the literature, I have selected the following, which are intended to cover different communication channels in different vertebrate taxa.

Androgens and the production of acoustic signals

In songbirds, circulating levels of testosterone are higher at the peak of the breeding season when singing behaviour reaches its maximum (e.g. Rost, 1990,

1992; Smith *et al.*, 1997). Moreover, song production is substantially reduced after castration and is restored after androgen-replacement therapy (e.g. Arnold, 1975; Heid *et al.*, 1985). Finally, both androgen and oestrogen receptors have been localized in the song control nuclei of the bird brain: the former in the high vocal centre, the robust nucleus of the archistriatum, the lateral part of the magnocellular nucleus of the anterior neostriatum and the dorsomedial part of the intercollicular nucleus; the latter in the high vocal centre and the intercollicular nucleus (Balthazart *et al.*, 1992; Brenowitz & Arnold, 1989, 1992; Gahr *et al.*, 1987, 1993). Song is produced by the coordinated contraction of respiratory, syringeal and cranio-mandibular muscles (Suthers *et al.*, 1999). The activity of syringeal muscles regulates both the timing and the fundamental frequency of the sound (Suthers *et al.*, 1999). Therefore, by acting directly on the activity and development of syringeal muscles, hormones may affect song production. For example, in zebra finches *Taenopygia guttata*, androgens inhibit the activity of the enzyme cholinesterase, which breaks down the neurotransmitter acetylcholine in the neuromuscular junctions of the syrinx. This results in a longer lifetime for the neurotransmitter in the synaptic cleft, which will affect the syringeal contraction pattern and, subsequently, song output and/or structure (Luine *et al.*, 1980). Testosterone is also known to increase both syringeal muscle mass (Luine *et al.*, 1980) and the density of acetylcholine receptors in syringeal muscles, suggesting that circulating levels of testosterone may increase the size and number of endplates in neuromuscular junctions (Bleisch *et al.*, 1984). Also, in non-oscine birds, testosterone is effective in inducing changes in call structure by acting on the motor vocal structure underlying these calls. In grey partridges *Perdix perdix*, male mating calls used by females in mate choice are affected by testosterone treatment, which induces a thickening of the external tympanic membranes that are known to be the main sound source in galliforms (Beani *et al.*, 1995).

These effects of androgens on motor systems underlying the production of vocal signals are not exclusive to birds. Many fish species also use sounds to communicate. Male toadfish are among the most vocal fish, producing loud humming calls to attract females to their nest site (e.g. plainfin midshipman *Porichthys notatus*; Brantley & Bass, 1994). Also in toadfish, the exogenous administration of androgens promotes the development of the sonic muscles, for example the oyster toadfish *Opsanus tau* (Fine & Pennymaker, 1986) and the plantin midshipman (Brantley *et al.*, 1993). Another example comes from amphibians, in which vocal behaviour is sexually dimorphic in most species and thus potentially androgen dependent (Kelley, 2002). In the African frog *Xenopus laevis*, males produce mating calls characterized by fast trills that attract females (Wetzel & Kelley, 1983; Kelley, 2002). The call-production organ of *X. laevis* is the larynx and all sounds are produced underwater (Kelley, 2002). The sex differences in vocal behaviour observed in this species

are mostly a result of sex differences in adult laryngeal synapses. Male larynx motor neurons release less neurotransmitter, which will produce lower postsynaptic potentials than in females, allowing the fibres to reach a spike threshold (Tobias *et al.*, 1995). This synaptic facilitation in male motor neurons allows modulation of the amplitude of the trills, a characteristic of the call that is used by females when assessing the males as potential mates (Tobias *et al.*, 1995). Contrary to most cases of sexual dimorphism in which the default situation is female, the sex differences in postsynaptic response emerge in females under the influence of oestradiol, with the default being the slow neurotransmitter release typical of males (Tobias & Kelley, 1995). However, other sex differences in this vocal system are androgen dependent, namely the differentiation of laryngeal motor neurons, muscles fibres and laryngeal cartilage (Kelley, 2002).

Androgens and pheromone production and/or release

A very large number of mammals use chemical signals (i.e. pheromones) in intraspecific communication. These pheromones can be produced by specific scent glands or are released into the environment in the urine or in other body fluids (Bradbury & Vehrencamp, 1998). Most mammals use marking behaviour to release these pheromones, a behaviour that is sexually dimorphic (Johnson, 1973; Brown & McDonald, 1985; Chs. 11 and 16). There are classic examples of marking behaviour, such as the scent marking of reindeer *Rangifer tarandus*, with preorbital, caudal and tarsal glands as well as with urine (see Brown & MacDonald, (1985) for other examples and detailed references). Scent marks are also widespread in rodents such as mice *Mus musculus*, hamsters *Mesocricetus auratus* and rats *Ratus* sp. (Hurst, 1990 Chs. 11 and 16).

In general, both pheromone production and its release (i.e. scent marking) are androgen dependent in males, as shown by castration and testosterone-replacement therapy experiments for example hamsters *Mesocricetus auratus* (Gawienowsky *et al.*, 1976), meadow voles *Microtus pennsylvanicus* (Ferkin & Johnston, 1993), tree shrews *Tupaia belangeri* (Holst & Eichman, 1998) and (Wistar rats) Manzo *et al.*, 2002); however, see Lepri & Randall (1983) and Randall *et al.* (1986) for an exception regarding the endocrine control of sandbathing in male kangaroo rats *Dipodomys* spp. The scent-marking behaviour decreases after castration and is restored after treatment with testosterone (e.g. rats: Brown, 1978; Taylor *et al.*, 1987; Manzo *et al.*, 2002). Interestingly, in many species, testosterone is the prohormone for this effect, because it needs to be metabolized in specific brain areas into oestradiol or dihydrotestosterone in order to become biologically active, for example rabbits *Oryctolagus cuniculus* (González-Mariscal *et al.*, 1993), gerbils *Meriones unguiculatus* (Yahr & Stephens, 1987) and Wistar rats (Manzo *et al.*, 2002).

Chemical communication is also widespread in urodeles, playing a major role in sex recognition and mate attraction (e.g. European newts *Triturus spp.*: Cedrini & Fasolo, 1970; Malacarne *et al.*, 1984; Belvedere *et al.*, 1988). One of the best-studied species is the Japanese red-bellied newt *Cynops pyrrhogaster*. In this species, males produce a female-attracting pheromone (sodefrin) with the abdominal glands, which is released by the cloaca of the male (Kikuyama *et al.*, 1995, 1997). Both castration and hypophysectomy reduced the sodefrin content of the abdominal glands and testosterone administration restored it (Yamamoto *et al.*, 1996).

Androgens and visual displays

Many species of vertebrates use complex visual displays in intraspecific communication, both in the context of conflict resolution (i.e. aggressive displays) and for mate attraction (i.e. courtship displays) (Bradbury & Vehrencamp, 1998). The evolution of stereotypic species-specific movements suggests that specific neuromuscular systems (i.e. motoneurons and their target muscles) may have evolved specifically for the production of these behaviours.

In some bird species, courtship displays involve coordinated wing and leg movements with the individuals on the ground, on perches or in the air (Schlinger *et al.*, 2001). These visual displays are usually sexually dimorphic. Because sex steroids, including androgens, have been shown to play a major role in secondary sex differentiation in most vertebrate species studied so far, they are also potential candidates for a key role in the control of these displays. In wild golden-collared manakins *Manacus vitellinus*, a tropical arena bird, males perform a courtship display that consists of a sequence of jumps and wing snaps (i.e. upward flips of the bird's wings that produce an acoustic signal). The feathers involved in the production of these wing snaps are the primary and secondary wing feathers (Schlinger *et al.*, 2001), which are sexually dimorphic (Chapman, 1935). Also the muscles controlling the wing movements and/or feather position and the jump often associated with the wing snap are hypertrophied in male manakins (Lowe, 1942). The muscles involved in the wing-snap movement also show sex differences when examined in more detail (e.g. in fibre diameter, metabolic enzyme activity and myosin isoform expression), which suggests that they are specialized for greater force generation and speed of contraction (Schultz *et al.*, 2001). These sex differences in this neuromuscular system are not present in species in which males do not use these muscles in courtship displays (e.g. zebra finch), although they are still functional for other activities (e.g. for raising and lowering of the wings during flying). These muscles are innervated by motor neurons that accumulate [³H]-testosterone in their soma in the spinal cord, suggesting a role for androgens in the control of these behavioural mechanisms (Schultz & Schlinger, 1999).

Another example of an androgen-dependent display is the amplexus behaviour displayed by amphibian males to clasp females during mating. The forelimb muscle involved in this behaviour (i.e. the flexor carpi radialis), is androgen sensitive (Dorlöchter *et al.*, 1994). Castration induces atrophy and testosterone treatment of castrated males causes hypertrophy of some regions of this muscle; immunocytochemistry techniques have identified the presence of androgen receptors (Dorlöchter *et al.*, 1994). Adult males have slower acetylcholine receptor kinetics than females, which facilitates slow and tonic muscle contractions appropriate for the function of this behaviour (Brennan & Henderson, 1995). Moreover, testosterone has been shown to act both at the pre- and postsynaptic level in these neuromuscular junctions, which may be viewed as an adaptation for a more flexible modulation of this behaviour (Nagaya & Herrera, 1995).

Finally in fish, androgens induce the development of somatic structures used in visual signalling such as the elongation of the dorsal and anal fins used in lateral displays and the thickening of the jaw used in mouthfighting (e.g. Mozambique tilapia *Oreochromis mossambicus*: Oliveira & Almada, 1998).

Androgens and electrocommunication signals

There are two orders of fish that produce weak electric signals with an electric organ located in their tails: the Gymnotiformes from South America and the Mormyriiformes from Africa (Zakon & Smith, 2002). The evolution of these weak electric signals most probably occurred independently in the two orders because they are phylogenetically distant (Alves-Gomes, 1999). Nevertheless, in both orders, this electric sense is used for the same two functions: electrolocation (i.e. locating objects in the environment) and intraspecific communication (Zakon & Smith, 2002). Electrical signals are perceived by the receivers with specialized electroreceptors mainly located in the midline of the fish (Zakon & Smith, 2002). There are two types of electric organ discharges: pulse type and wave type. Each species only produces one or the other (Zakon & Smith, 2002). Within species, there are marked sex differences in the electric organ discharge. In most Gymnotiform species that generate wave-type discharges, the males produce signals of lower frequency than females. For example, in *Sternopygus macrurus* males produce an electric discharge of 50–90 Hz while female signals range from 100 to 150 Hz (Hopkins, 1972). Sex steroids, in particular androgens, seem to be important in the determination of electric organ discharge frequency. In male *S. macrurus*, circulating levels of androgens are negatively correlated with frequency (Zakon *et al.*, 1991) and when their reproductive axis was challenged with human chorionic gonadotrophin, they responded with an increase in circulating 11-ketotestosterone levels and a decrease in the frequency of the discharge from their electric organs

(Zakon *et al.*, 1990). Moreover, treatment of wave gymnotiforms with androgens induces a masculinization of the waveform (i.e. higher wave frequency and increased duration (Meyer, 1983; Mills & Zakon, 1987; Dunlap & Zakon, 1998)). Interestingly, 11-ketotestosterone increased the frequency of electric organ discharge (Meyer *et al.*, 1987) in species in which the discharge pattern is sex reversed, that is males generate higher-frequency discharges than females (e.g. brown ghost, *Apteronotus leptorhynchus*: Hagedorn & Heiligenberg, 1985). In all pulse-type species, both mormyriforms and gymnotiforms, the treatment of juveniles, females, castrated males or non-reproductive males with androgens masculinizes the pulse form (Bass & Hopkins, 1983, 1985; Hagedorn & Carr, 1985; Bass & Volman, 1987; Landsman & Moller, 1988; Freedman *et al.*, 1989; Landsman *et al.*, 1990; Herfeld & Moller, 1998). The effects of androgens on the frequency and/or duration of electric organ discharges may be mediated by their effects on the morphology of the electric organ (i.e. size and/or shape of electrocytes) or by an influence on the ionic currents of the electromotor system (e.g. Bass *et al.*, 1986; Bass & Volman, 1987; Mills & Zakon, 1991). Apart from its influence on electric organ discharge parameters, testosterone also activates the onset of electric signalling in weakly electric fish (Landsman & Moller, 1988).

Hormonal effects on signal reception

A literature search revealed fewer studies of androgen modulation of sensory perception than of the effects of androgens on effector mechanisms. The four studies below are examples of effects on perception.

In many cyprinid fishes, females produce a sex pheromone that elicits male courtship behaviour. The response of males to the female pheromones can be measured either behaviourally or electrophysiologically, by placing electrodes in the olfactory epithelium and measuring the potentials evoked by the exposure of the epithelium to different odorants (i.e. electroolfactograms: Stacey & Sorensen, 2002). In the tinfoil barb *Puntius schwanenfeldi*, females release a sex pheromone (15-ketoprostaglandin-2 α) that stimulates male courtship behaviour (Cardwell *et al.*, 1995). This response is greatest during the breeding season in sexually mature males; such males have visible breeding tubercles, dermal structures that are known to be androgen dependent (Smith, 1974). Moreover, juveniles implanted with androgens (either 11-ketotestosterone or methyltestosterone) show both an increased electroolfactogram response to 15-ketoprostaglandin-2 α and increased sexual behaviours directed towards stimuli fish (i.e. juveniles injected with 15-ketoprostaglandin-2 α (Cardwell *et al.*, 1995)). These results clearly demonstrate a peripheral effect of androgens on olfactory sensitivity. Other species also show increased olfactory sensitivity to such stimuli during the breeding season when androgen levels are also higher (e.g. electroolfactogram responsiveness to

testosterone in the Atlantic salmon *Salmo salar* (Moore & Scott, 1991)), which suggests that the effect described above may be a general phenomenon in fish olfaction.

In addition, electroreception in weakly electric fish seems to be modulated by androgens (Keller, 1986; Sisneros & Tricas, 2000). Testosterone not only affects the frequency of discharge from electric organs (as described above) but also shifts the maximum receptivity of the electroreceptor to the new frequency produced (Meyer & Zakon, 1982; Bass & Hopkins, 1984). Thus, androgens keep the electroreceptors of a given individual fine-tuned to its own electric organ discharge, which might be viewed as an adaptation for electrolocation.

A third example comes from studies of auditory sensitivity in the plainfin midshipman. As mentioned above, in this species type I males produce a humming call during the breeding season that is used to attract spawning females to their nests (Ibara *et al.*, 1983; Brantley & Bass, 1994). Male reproductive success must depend heavily on their calling behaviour because females are choosy regarding call parameters of the 'hum' signal (McKibben & Bass, 1998). Female reproductive success is also expected to depend on their ability to locate and choose males based on their acoustic signals. Recently, it has been demonstrated that, during the summer when females need to exert their mate choice preferences based on the male call, the auditory saccular units in the females increase their temporal encoding capacity up to 340 Hz, compared with only 100 Hz in winter females (Sisneros & Bass, 2003). This seasonal plasticity of the peripheral auditory system is most probably driven by sex steroids, because it follows the seasonal variation in steroid profiles (Forlano *et al.*, 2003) and because expression of the oestrogen receptor β has been identified recently in auditory hair cells (P. M. Forlano & A. H. Bass, unpublished data). Therefore, an increase in sex steroids at the beginning of the breeding season may induce changes in the frequency sensitivity of these hair cells in a similar way to androgen-dependent changes in electroreceptor tuning described above.

Finally, there are suggestions that sex steroids may also be involved in the modulation of visual perception in teleost fish. In the three-spined stickleback *Gasterosteus aculeatus*, sexually active females prefer to mate with males with redder bellies (e.g. Milinski & Bakker, 1990). Using optomotor responses, Cronley-Dillon & Sharma (1968) have demonstrated that the sensitivity of the female visual system to red wavelengths increases during the breeding season, suggesting a potential role for female sex hormones. In this example, it can be argued that the effect found could be acting either at the level of the sensory organ or at the level of visual information processing by the central nervous system (i.e. optic tectum). Interestingly, aromatase activity has been found in fish retina, indicating that these cells are actively metabolizing sex steroids (Callard *et al.*, 1993) and supporting

the idea that the steroid modulation of visual sensitivity to key colours may occur in the periphery.

These four studies taken together suggest that sex steroid modulation of sensory perception is a common phenomenon in different sensory modalities.

Hormonal modulation of motivational and memory mechanisms

Androgens can also affect central mechanisms of information processing both in senders and receivers. At this level, the modulatory action of hormones may affect signalling behaviour by acting either on motivational neural circuits underlying decision-making mechanisms, or on learning and memory systems (Schulkin, 2002; Dohanich, 2002). By acting on central mechanisms, androgens may set up the subject to perceive stimuli and to behave in particular ways, for example by increasing the likelihood of the expression of a given behaviour, ranging from food ingestion to maternal behaviour or aggression. For example, androgens modulate central mechanisms of chemical perception in male hamsters. In this species, vaginal secretions stimulate male sexual behaviour after male anogenital investigation of the female (Johnston, 1975; Ch. 16). These secretions are detected by two different sensory systems, the olfactory mucosa and the vomeronasal organ, that use different neural pathways converging in three central areas: the medial nucleus of the amygdala, the bed nucleus of the stria terminalis and the medial preoptic area (Scalia & Winans, 1975). Androgen receptors are found in all these three areas (Wood *et al.*, 1992) and direct androgen implantation here restores sexual behaviour in castrated males (Lisk & Bezier, 1980).

Usually the effects of steroids, including androgens, on motivational mechanisms involves the regulation of neuropeptide gene expression in the limbic system, namely of arginine-vasopressin (or its homologue arginine-vasotocin in non-mammalian vertebrates), which subsequently influence central states that control the behavioural output (Herbert, 1993). There are numerous examples of this principle. In hamsters, testosterone enhances the effects of arginine-vasopressin infused in the bed nucleus of the stria terminalis on scent-marking behaviour (Albers *et al.*, 1988). In male prairie voles, testosterone also promotes the expression of parental behaviour by increasing arginine-vasopressin synthesis and by preventing the apoptosis of responsive neurons (De Vries, 1995). Finally, in amphibians, sex steroids control both female egg-laying behaviour and male courtship via arginine-vasotocin modulation (Moore *et al.*, 1992).

The potential effects of sex steroids on learning, memory and other cognitive functions have been addressed using two main approaches: (a) by documenting the distribution of androgen and oestrogen receptors in brain areas known to be involved in these functions, and (b) by testing hormone-treated subjects in

cognitive tasks. There is a much larger body of literature on oestrogens than on androgens regarding this topic. The available data on androgens will be summarized below.

Androgen receptors are found in the hippocampus of mammals and birds (Kerr *et al.*, 1995; Saldanha *et al.*, 1999) and in the homologue dorsolateral telencephalon of fish (Northcutt & Davis, 1983; Gelinas & Callard, 1997). These brain areas are involved in relational memory processes, namely in spatial memory (Eichenbaum *et al.*, 1992; Squire, 1992). Androgen receptors have also been found in pyramidal cells of the cortex in rats, monkeys and humans (Pomerantz & Sholl, 1987; Kerr *et al.*, 1995; Tohgi *et al.*, 1995). These results set the stage for a potential functional direct effect of androgens on memory mechanisms. The occurrence of oestrogen receptors together with aromatase (an enzyme that metabolizes androgens into oestrogens) also suggests a potential alternative route for aromatizable androgens to affect cognitive function (e.g. Gelinas & Callard, 1997).

There are numerous examples of sex differences in spatial memory tasks, with males outperforming females, which suggests a role for sex steroids in spatial memory mechanisms (reviewed by Dohanich, 2002). Early androgen exposure apparently has organizational effects on adult spatial abilities, and the masculinization of spatial learning involves the aromatization of androgens into oestrogens in rodents (Williams *et al.*, 1990; Roof & Havens, 1992; Roof, 1993). In humans, early exposure to androgens masculinizes spatial function, as is suggested by data on girls suffering from congenital adrenal hyperplasia. These girls are exposed to androgens in utero as a result of hypertrophy of the adrenal glands and are born with virilized genitalia. When compared with their unaffected sisters, girls with congenital adrenal hyperplasia have better performances in mental object-rotation tests designed to measure spatial ability (Resnick *et al.*, 1986; see Kimura (1996) for further references). In adults, the relationship between circulating androgen levels and spatial ability is not linear. Lower testosterone levels in males, and higher testosterone levels in females, are associated with better performances in an object-rotation task, which suggests an optimum circulating level of testosterone to excel in this task (Moffat & Hampson, 1996). As regards other cognitive mechanisms, in general the administration of androgens to birds and mammals outside the critical period of development fails to affect learning and memory tasks (Dohanich, 2002). However, social memory is an exception to this rule in rats and zebra finches (Sawyer *et al.*, 1984; Cynx & Nottebohm, 1992).

Hormones and somatic releasers

There are a number of somatic structures that act as sign stimuli (*sensu* Tinbergen, 1951) evoking a behavioural response in conspecifics. The classic

example of these releasers is the red belly of the male three-spined stickleback, which elicits aggressive responses in other male sticklebacks (Tinbergen, 1951). Since initially proposed by Tinbergen, these social releasers have been described in many other species and can range from nuptial colouration patterns in fish and birds to dermal appendages in fish (e.g. dermal tubercles), birds (e.g. combs, elongated tail feathers) and reptiles (e.g. dewlap membrane in *Anolis* sp.). The development of at least some of these somatic structures with a releaser function is under hormonal control. There are various examples in the teleosts. First, male nuptial colouration in African cichlids is suppressed in castrated males and restored in castrates and females by exogenous administration of testosterone (Levy & Aronson, 1955; Reinboth & Rixner, 1972; Wapler-Leong & Reinboth, 1974; Fernald, 1976). Also in male sticklebacks, the nuptial colouration can be suppressed by castration (Ikeda, 1933) or by the exogenous administration of an anti-androgen (cyproterone acetate) (Rouse *et al.*, 1977). Finally, in the sex-role-reversed peacock blenny *Salaria pavo*, in which some 'sneaker' males mimic female nuptial colouration, androgens (i.e. 11-ketotestosterone) inhibit the expression of female nuptial colouration in these sneaker males (Oliveira *et al.*, 2001a).

However, nuptial colouration is not the only releaser to be androgen dependent in fish. The development of the sword as an extension of the caudal fin in male swordtail fish *Xiphophorus helleri* and the development of the dermal breeding tubercles in male cyprinids are both also induced by testosterone (Baldwin & Goldin, 1939; Smith, 1974). Therefore, another way for hormones to affect communication is by affecting the expression of somatic releasers in senders.

Social modulation of androgen levels

As shown above, androgens can be viewed, on the one hand, as causal agents of behaviour, including signalling behaviour among animals in a communication network. On the other hand, the endocrine system is responsive to the network of social relationships in which the animal is involved. Several studies have shown effects of social interactions on the short-term modulation of androgen levels. In the early 1940s, it was established that male mice that lost an agonistic interaction had lower levels of androgens than winners (Ginsberg & Allee, 1942). This pattern has been found repeatedly in other vertebrate taxa from fish (e.g. Hannes, 1984, 1986) to primates, including humans (e.g. Rose *et al.*, 1971, 1975; Bernstein *et al.*, 1974; Booth *et al.*, 1989; see Mazur & Booth, 1998 for more references). This set of results led to the proposal of the 'challenge hypothesis' by John Wingfield and co-workers (Wingfield, 1984; Wingfield *et al.*, 1987, 1990), according to which the social interactions involving the subject determine androgen levels. This hypothesis gives a conceptual framework for the study of the interplay

between social factors and endocrine responses and generates a number of testable predictions.

1. Androgen levels should be higher during periods of social instability when social interactions are more frequent and more intense. In fact, in bird species in which a clear breeding cycle can be recognized, testosterone levels are higher during the period of territory establishment than when territories are established (Hegner & Wingfield, 1987a; see Wingfield *et al.*, 1999, 2000 for more examples).
2. Territorial and dominant males are expected to show higher androgen levels than non-territorial or subordinate males because territorial males have to defend their territories from intruders and dominant males have actively to maintain their status. Again the available evidence supports this hypothesis (e.g. see Oliveira *et al.* (2002) for a review of teleost fish and Wingfield *et al.* (1999, 2000) for reviews of birds).
3. Populations of the same species breeding under different population-density regimes should also show differences in the average androgen levels of breeding males as a result of a different probability of territory intrusions. This prediction should be taken with caution because in a population with increased density, physiological and/or behavioural mechanisms may be present to avoid aggression. Nevertheless, positive correlations have been found between density of breeding territories and androgen levels both in fish and in birds (e.g. Ball & Wingfield, 1987; Beletsky *et al.*, 1990, 1992; Pankhurst & Barnett, 1993).

Interestingly, during periods of social inertia, the levels of social interaction fall to a baseline and androgen levels become decoupled from social behaviour. These results have been interpreted as an adaptation (or an exaptation *sensu* Gould and Vrba (1982), depending on the underlying historical evolutionary pathway) for the individuals to adjust their behaviour (motivation) to the social milieu that they are currently experiencing. Thus, social interactions would stimulate the production of androgens and androgen levels would be a function of the stability of the social environment in which the animal is living (Wingfield *et al.*, 1990, 1999, 2000; Oliveira *et al.*, 2002).

It is interesting to note here that it is the perception that the individual has of the interaction in which it is involved or which it is observing that activates the endocrine response and not the objective structure of the situation *per se*. To investigate this idea we have recently tested the effect of mirror-elicited aggression on androgen levels in a cichlid fish (L. Carneiro & R. F. Oliveira, unpublished data). The mirror image stimulation test is widely used in fish ethology to assess

aggressiveness (Rowland, 1999), but some inconsistencies have been found in the relationship between social status and the aggressive score of an individual in this test (Ruzzante, 1992). In Mozambique tilapia, we showed that androgen levels before the fish were grouped were not good predictors of social status, but androgens levels at the end of the time spent in a group were highly correlated with the social status of each individual, suggesting that androgens are being modulated by the social interactions experienced by the grouped individuals (Oliveira *et al.*, 1996). In the mirror image stimulation test, the individual is placed in a very peculiar situation. Because fish do not recognize as themselves the image reflected by the mirror, they respond to it as an intruder and attack. In our experiment, males reacted aggressively to their own images in the mirror and escalated the interaction using more overt aggressive behaviours (e.g. biting) as time went by. However, because the mirror reflects exactly the same behaviours that the experimental fish is displaying, the interaction has no outcome (winning versus losing). Therefore, if the endocrine response to the social interaction is triggered by the behavioural output during the interaction (e.g. number of displays or time spent displaying), a variation in androgen levels is predicted. However, if it depends on behavioural feedback received from the opponent, then no androgen variation is predicted in the test. In our mirror image stimulation experiment with Mozambique tilapia, we found a strong behavioural response but a complete lack of an androgen response (L. Carneiro & R. F. Oliveira, unpublished data), which suggests that the endocrine system responds to a clear perception of the outcome of the social interaction. This result is also interesting because it shows that it is the communication component of the social interaction that may affect hormone levels.

Hormones and communication II: the network view

In the previous section, the interrelationship between hormones (i.e. androgens) and social behaviour was considered at the dyadic level. First, the mechanisms through which androgens may affect communication between a pair of individuals were described. Second, the ways in which these androgen levels might be modulated by the social environment (network) in which the animal is living were described.

If we now consider an interaction that occurs within a social network (or a communication network *sensu* McGregor (1993)), with possibilities for other individuals in the network to eavesdrop on the interaction (e.g. Ch. 2) and for the interacting pair to adjust their behaviour according to the presence of an audience (Ch. 4), the complexity of the interrelationship between hormones and behaviour/communication mechanisms could increase substantially. The presence

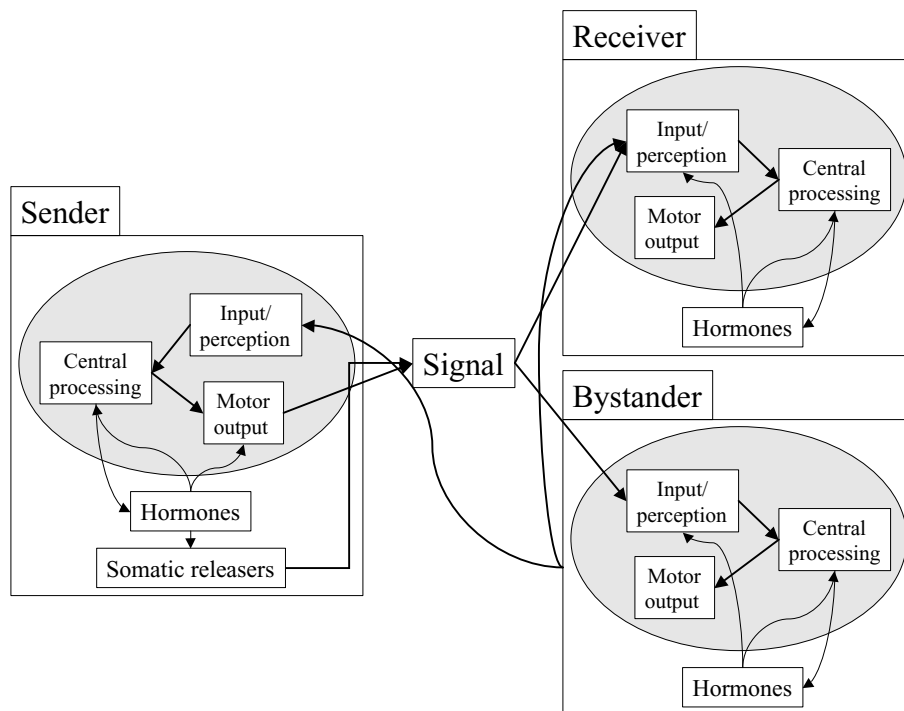


Fig. 21.3. Flow of information in a communication network. This figure is similar to Fig. 21.2 with the following extra elements. The presence of a third individual (the bystander) may be perceived by both the sender and the receiver and affect their signal production and signal reception mechanisms, respectively. The perception of the presence of the bystander may also affect central (motivational) mechanisms in the central nervous system in both senders and receivers, which may, in turn, modulate hormone levels in both individuals. The perception of the signal by the bystander would also affect its central processing of information at the level of motivational mechanisms, which could affect its hormone levels.

of a bystander that could act both as an eavesdropper and as an audience (Fig. 21.3), may affect androgen levels in both the sender and the receiver and subsequently affect their androgen-modulated communication behaviour in the same ways as described above (see also Fig. 21.2). The androgen levels of the bystander itself may respond to the observed interaction, which, in turn, will affect its own subsequent social behaviour.

Consequently, androgens may play a key role as physiological mediators of the modulation of behaviour by the social context. A number of social phenomena (e.g. winner–loser effects, bystander effect, dear enemy effect) that have been described in social networks may then be physiologically mediated by changes in hormone levels, especially androgens.

Adjusting behaviour to the social context: a role for androgens?

Winner–loser effects

There is an extensive literature (including most of the chapters of this book) that clearly shows that animals use information on relative competitive abilities in the social network in which they are placed to adjust their behaviour accordingly. They may obtain this information by direct assessment of their peers by interacting with one another in a dyadic fashion and then adjusting their behaviour in subsequent interactions depending on the outcome of previous interactions. For example, individuals that win an interaction increase their probability of winning a subsequent interaction and vice versa for losers. In this case, although only two individuals have to be present during the initial interaction, unless there were other individuals with whom the interactants subsequently interacted, there would be no winner–loser effect. Therefore, this effect is better understood within the framework of social networks than with a dyadic approach. This winner–loser effect may last from a few minutes up to several hours or even days and has been reported for several taxa, for example invertebrates (Alexander, 1961; Otronen, 1990; Whitehouse, 1997), fish (McDonald *et al.*, 1968; Frey & Miller, 1972; Bakker & Sevenster, 1983; Francis, 1983, 1987; Abbott *et al.*, 1985; Beaugrand & Zayan, 1985; Beacham & Newman, 1987; Franck & Ribowski, 1987; Beacham, 1988; Bakker *et al.*, 1989; Beaugrand *et al.*, 1991, 1996; Chase *et al.*, 1994; Hsu & Wolf, 1999), reptiles (Schuett, 1997) and birds (Drummond & Osório, 1992). The winner effect is usually of shorter duration than the loser effect (e.g. Chase *et al.*, 1994), and when integrating prior social experiences more recent outcomes are more effective in predicting the probability of winning a subsequent interaction than previous ones (Hsu & Wolf, 1999). Another interesting characteristic of this effect is that it is more effective when winning or losing against a well-matched opponent than when there is a large asymmetry in resource-holding potential (*sensu* Parker, 1974) between the two individuals (Beaugrand & Goulet, 2000).

The behavioural mechanism proposed to explain the winner effect is based on the fact that initiators of interactions have higher probabilities of winning and that winners of recent encounters become more likely to initiate future interactions (Jackson, 1991). This is especially true for the initiators of attacks (Hsu & Wolf, 2001).

It is conceivable that by winning an interaction an individual raises its androgen levels, which, in turn, increases its willingness to initiate future interactions and the probability of winning the next interaction in which it participates. The reverse would be predicted for losers.

We are conducting an ongoing literature survey to collect data on the two steps of this endocrine hypothesis for the winner–loser effect: (a) that winners

Hormones, social context and animal communication 497

Table 21.1. Literature survey of reported differences in male androgen levels among vertebrates according to social status and the phase of the sexual cycle and of the effects of androgen treatment on aggressive behaviour

Taxa	Androgens and social status			Androgens and phase of sexual cycle			Effect of androgen treatment on aggressive behaviour		
	No.	D = S or		No.	MP < PP or		No.	Effect	No effect
		D > S	D < S		MP > PP	MP = PP			
Fish	12	9	3	9	8	1	12	7	5
Amphibians	1	0	1	2	2	0	0	-	-
Reptiles	3	2	1	0	-	-	3	3	0
Birds	10	4	6	48	47	1	10	6	4
Mammals	18	15	3	4	3	1	9	5	4
Total	44	30	14	63	58	5	34	21	13

Male androgen levels in; D, dominant; S, subordinate; MP, mating phase; PP, parental care phase. K. Hirschenhauser & R. F. Oliveira, unpublished data.

have higher androgen levels than losers; (b) that androgens increase aggressive behaviour and hence the probability of victory in a subsequent interaction. As there are not enough studies that we can find that measured the androgen variations in response to a social interaction to address the first step, it was decided to search for correlational data in the form of reported androgen differences between dominant and subordinate individuals. We found 44 published studies, 68% of which confirmed that androgen levels were higher in dominants than in subordinates (Table 21.1). Our literature survey revealed that 62% of the studies confirmed that administration of androgens increased aggressive behaviour in different taxa (Table 21.1), thereby supporting the second step of the endocrine hypothesis. Although the majority of the studies supported the assumptions of the proposed hypothesis, the percentages do not provide overwhelming support and so we decided to test this hypothesis experimentally with the Mozambique tilapia (A. Silva & R. F. Oliveira, unpublished data). After staging a first fight between two males, the winner and the loser fought two independent, naive individuals (i.e. males that have not been involved in social interactions recently) (Fig. 21.4a). As expected, our preliminary data showed that winners of the first encounter won the majority of the interactions with the naive fish and vice versa for losers (Fig. 21.4b). When winners were treated with an anti-androgen (cyproterone acetate) between the two interactions (which were two hours apart), the winner effect was no longer detectable in the second fight with the neutral fish, suggesting an involvement

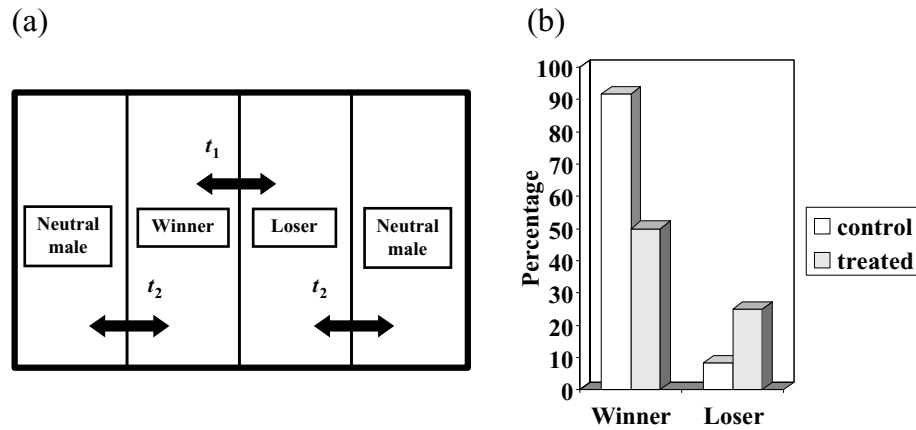


Fig. 21.4. Androgens and the winner–loser effect. (a) Experimental-set up: four Mozambique tilapia *Oreochromis mossambicus* males were introduced to individual compartments separated by opaque partitions in an aquarium. After a period of acclimation (t_1), the central partition was removed and the two individuals in the central compartments were allowed to interact until a winner and a loser could be recognized. Then the partition was put back in place. Two hours later (t_2), the two lateral partitions were simultaneously removed and the winner and the loser of the previous interaction were allowed to interact with the neutral males that were placed in the end compartments. This second interaction went on until a winner and a loser could be recognized. (b) Percentage of second interactions won by winners or losers of the first interaction. Four groups of experimental animals were compared: t_1 winners treated with an androgen inhibitor (cyproterone acetate); control t_1 winners (treated with a placebo saline solution); t_1 losers treated with an androgen (11-ketotestosterone); control t_1 losers (treated with a placebo saline solution). Twelve replicates of the experiment were run. (A. Silva & R. F. Oliveira, unpublished data.)

of androgens in the winner effect (Fig. 21.4b). However, the loser effect was not inhibited in the second interaction by treating losers with exogenous androgens, which suggests that, although a fall in androgens is observed in losers, it is not the underlying causal mechanism for the loser effect. Although this result may seem paradoxical at first sight, it makes some sense; androgen variations induced by social interactions occur in the short term and so do winner effect; however, the loser effect may last up to several days depending on a number of factors. Consequently, other neuroendocrine mechanisms must be involved in the loser effect. One of the best candidates for this role is the serotonergic system. The following evidence from studies using different fish species seems to support this hypothesis: (a) losers experience increased brain levels of serotonin and subordinate individuals have chronically elevated brain levels of serotonin (Winberg &

Nilsson, 1993a,b; Winberg *et al.*, 1997; Winberg & Lepage, 1998); and (b) serotonin appears to be inhibitory to behavioural responsiveness in general and to inhibit aggressive behaviour in particular (Winberg & Nilsson, 1993a,b; Adams *et al.*, 1996; Edwards & Kravitz, 1997). Therefore, losers would display a marked behavioural inhibition, with increased attack latencies in subsequent interactions, which would prevent them from winning these interactions and would reinforce their subordinate role. Interestingly, the administration of a precursor of dopamine (L-dopa) to individuals that had lost an interaction two days before induced lower serotonergic activity and reduced the attack latency in subsequent interactions, suggesting that the dopaminergic system counteracts the serotonin-mediated effects of social subordination (Höglund *et al.*, 2001).

Bystander effects

Information on the relative competitive ability of conspecifics within a social network can also be gathered using indirect methods, namely by extracting information from watching conspecific interactions that the subject uses in subsequent interactions with the observed individuals (eavesdropping (McGregor, 1993; McGregor & Peake, 2000) and social eavesdropping *sensu* Peake, Ch. 2). This sort of information gathering on the relative ability of conspecifics has been demonstrated in a number of species (see Ch. 2), for example fish (Johnsson & Akerman, 1998; Oliveira *et al.*, 1998; Earley & Dugatkin, 2002; Ch. 5) and birds (Hogue *et al.*, 1996; McGregor *et al.*, 1997; Naguib *et al.*, 1999; Peake *et al.*, 2001), and has the advantage of avoiding the costs associated with fighting (e.g. McGregor, 1993; McGregor & Peake, 2000; Dugatkin, 2001). Some authors consider that there is a difference between bystander and eavesdropping effects: eavesdropping implies an active gathering of information by bystander individuals that will be used in future interactions within the social network (McGregor, 1993; McGregor & Peake, 2000), while the bystander effect was originally described as a priming of aggressive motivation in bystanders of agonistic interactions (Hogan & Bols, 1980; Bronstein, 1989). Therefore, from the point of view of the required cognitive abilities, eavesdropping is expected to be more demanding than a mere priming response. However, both phenomena are adaptive because they might increase the probability of eavesdroppers/bystanders of winning their next social interaction (Clotfelter & Paolino, 2003; Hollis *et al.*, 1995; Peake & McGregor, 2004).

The priming response associated with the bystander effect is another phenomenon that could be mediated by androgens. To investigate if bystanders experience an increase in their androgen levels, we conducted an experiment with Mozambique tilapia in which a bystander fish had visual access through a one-way mirror to two conspecific neighbours separated by an opaque partition

500 R. F. Oliveira

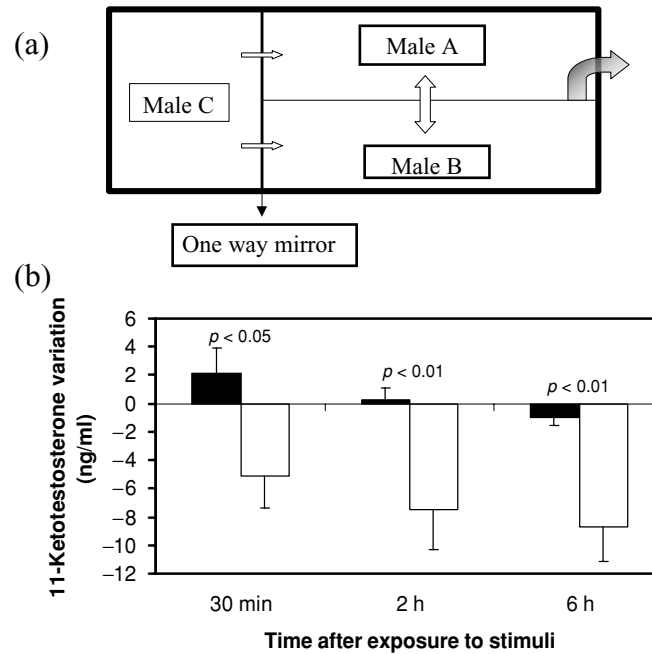


Fig. 21.5. Social modulation of androgen levels in bystander male Mozambique tilapia *Oreochromis mossambicus*. (a) Experimental-set up: three males were introduced to individual compartments in an aquarium. Males A and B were separated by an opaque partition and male C was separated from the other two males by a one-way mirror that allow it to observe the other two males without being observed. After a period of acclimation, two conditions were created. (i) In the experimental group, the opaque partition separating males A and B was removed (grey arrow) and the two individuals were allowed to interact for 20 minutes while male C observed the interaction (bystander). (ii) In the control group, the opaque partition separating males A and B was not removed and the bystander individual observed its two neighbours resting or swimming around for 20 minutes. Urine samples were collected from male C at regular intervals (just before the start of the test, 30 minutes after, two hours after and six hours after the experiential situation) and assayed for androgens using radioimmunoassays. (b) Androgen (11-ketotestosterone) variation (i.e. urine concentrations after the experiential situation minus the urine concentrations just before the experiential situation) in bystander males of the experimental (black bars) and control (white bars) groups. (Adapted from Oliveira *et al.* (2001b).)

(Fig. 21.5; Oliveira *et al.*, 2001b). After a period of familiarization, in the experimental treatment the opaque partition between neighbours was removed and the bystander was allowed to observe the agonistic interaction between its neighbours. In the control group after the same period of familiarization, the opaque partition between neighbours remained in place and the bystander could see its

two neighbours resting or swimming around in their respective compartments. As predicted, androgen levels (both 11-ketotestosterone and testosterone) increased significantly in the experimental group of bystanders after watching their neighbours fighting and no effect was detected in the control group (Oliveira *et al.*, 2001b). This result has an interesting parallel in humans. It has been demonstrated that sport fans experience variations in testosterone levels depending on the outcome of the game they have attended, both for college basketball and for soccer. Fans of the winning team display an increase in salivary testosterone levels and there is a decrease in testosterone levels in fans of the losing team (Bernhardt *et al.*, 1998).

Audience effects

The term audience effect was first used in the ethological literature to describe the facilitation effect of the presence of other individuals on the production of food calls or alarm calls in response to food items or a predator, respectively (Cyger *et al.*, 1986; Marler *et al.*, 1986; Evans & Marler, 1994). Here the term will be used in a more restricted way, following the definitions provided by McGregor & Peake (2000) and by Matos (2002) (see also Ch. 4): individuals participating in an interaction may also manipulate the information available to others and adjust their signalling behaviour according to the presence and composition of an audience of conspecifics. These audience effects have been demonstrated in different vertebrate taxa, including fish (e.g. Doutrelant *et al.*, 2001; Matos & McGregor, 2002), birds (e.g. Searcy *et al.*, 1991; Baltz & Clark, 1997) and mammals (e.g. Hector *et al.*, 1989), and have involved different social contexts, from agonistic interactions in Siamese fighting fish *Betta splendens* (Doutrelant *et al.*, 2001; Matos & McGregor, 2002) to extra-pair copulations in male budgerigars *Melopsittacus undulatus* (Baltz & Clark, 1997).

The audience effect has been interpreted as a way for the individual to manipulate the information broadcast to its social network, which may influence subsequent social interactions in which it will have to participate. Therefore, it can be predicted that subjects behave more promptly and aggressively towards an intruder when a male audience is present. Again it is predicted that this effect may be mediated by increased androgen levels in the interacting individuals induced by the presence of the audience. This aggressive priming effect of an audience has already been established in Siamese fighting fish (Matos, 2002) but its androgen-mediation remains to be tested.

Dear enemy effects

In territorial systems, residents react less aggressively towards familiar opponents than to intrusions by strangers, a phenomenon called the dear

502 R. F. Oliveira

enemy effect (Ydenberg *et al.*, 1988; Temeles, 1994). In evolutionary terms, this phenomenon can be viewed as an adaptation for the individual to adjust its territorial behaviour according to the threat posed by the intruder (Temeles, 1994): having a dear enemy neighbour allows the resident individual to defend its territory against unfamiliar intruders with the same efficiency as if they were the only competitors in the area, which reduces the costs of territory defence (Leiser & Itzkowitz, 1999; Whiting, 1999).

The dear enemy phenomenon can be explained in terms of proximate mechanisms by an ability of the resident male to discriminate between familiar and unfamiliar intruders together with a habituation to the neighbours, which would explain the lower response that they elicit, for example visual habituation to neighbours in Siamese fighting fish (Bronstein, 1994) and habituation to neighbours' calls in frogs (Owen & Perrill, 1998). Therefore, it can be predicted that resident males will react more aggressively towards strangers than towards familiar intruders and that the increase in androgen levels expected from the social challenge experienced will be higher in the case of intrusions by strangers. Moreover, it is also predicted that, for repeated intrusions by neighbouring males, the androgen response should be higher in the first trials and decrease with the number of trials (i.e. habituation). These two predictions remain to be tested.

The adaptive value of social modulation of hormones: a cost-benefit analysis of androgen levels

As stated above, the main adaptive reason for androgens to respond to the social environment is to allow individuals to fine-tune the expression of their behaviours in a context-dependent fashion. For example, this mechanism would allow subordinate individuals to downregulate the expression of their aggressive behaviour and thus avoid the initiation of agonistic encounters that they have low probabilities of winning. In the long run, this mechanism can be seen as an opportunity for individuals to adopt a behavioural tactic that suits best their relative competitive ability. As a result, androgen-mediated behavioural tuning to the social environment may result in either a continuous or a discrete variation of behavioural phenotypes. For example, even small changes in androgen levels induced by social interactions in electric fish, can affect the pulse duration, resulting in dominant males with more masculinized discharges from their electric organs than subordinates (e.g. *Brienomyrus brachyistius*: Carlson *et al.*, 2000). Also, in the Mozambique tilapia, the acquisition of dominant status induces the exaggeration of male morphological traits, an effect that has been shown to be mediated by androgens (Oliveira & Almada, 1998). By comparison, in a number

of teleost species, individuals of lower competitive ability can adopt frequency- or condition-dependent alternative reproductive tactics (Taborsky, 1994) or even change sex (Grober, 1998).

However, it can be argued that, instead of having their androgen levels open to social influences, selection could have favoured animals that permanently keep their androgen levels at an optimum high value in order to optimize their social behaviour at all times. It follows that there must be costs associated with maintaining high levels of androgens that counteract the social benefits of high androgen levels. Therefore, a cost-benefit analysis is needed to establish the adaptive value of the social modulation of androgens.

Potential benefits of high androgen levels

Among the potential benefits of increasing androgen levels at periods of social challenge, one can think of androgen effects both on aggressive motivation and on cognitive tasks that would promote the success of the animals in social interactions.

The available data on the effects of androgens on aggressive motivation has already been review above, and in most studies an effect has been found (Table 21.1). Sex steroids, including androgens, are known to play a major role in cognitive processes such as social attention, learning and memory in a variety of vertebrate taxa (e.g. Andrew, 1991; Cynx & Nottebohm, 1992) and so they may help the animal to be prepared for a competitive context (see text above for more references).

We have recently tested the effects of androgens on social attention in Siamese fighting fish. Eavesdropping has already been demonstrated in this species and male Siamese fighting fish are known to spend time observing conspecific interactions (Oliveira *et al.*, 1998). So we designed an experiment to assess the effect of the administration of exogenous androgens on the time males spend observing social interactions between conspecific males. Not surprisingly, androgen-treated males spent more time observing social interactions than controls, suggesting an effect of androgens on selective attention to the social environment (R. F. Oliveira & L. Carneiro, unpublished data).

Another potential benefit that androgens may convey in a competitive situation is an increased probability of the expression of risk-taking behaviours, which might be adaptive in a competitive situation. A nice example of this phenomenon has recently been published (Kavaliers *et al.*, 2001). Male mice were pre-exposed to the odour of an oestrous female and subsequently exposed to the odours of predators (cat and weasel). Mice that were only exposed to the predator odour, simulating a situation of increased predation risk, showed increased circulating levels of corticosterone and decreased levels of testosterone. The pre-exposure to

504 R. F. Oliveira

the female odour attenuated this response to predator odour, which might reflect a greater tendency for risk taking in the presence of predators (Kavaliers *et al.*, 2001).

Potential costs of high androgen levels

Elevated androgen levels have been shown to have associated costs; consequently, one would expect high circulating levels to be restricted to periods of social challenge. The following potential costs have been discussed in the literature: (a) increased energy consumption; (b) impairment of immunocompetence; (c) higher rates of injuries and reduced survival; (d) interference with parental care; and (e) potential oncogenic effects (Wingfield *et al.*, 1999). Of all these potential costs, two will be analysed in more detail below: the potential negative effects of androgens on metabolic rate and on parental behaviour.

Metabolic costs of high androgen levels

Studies of the metabolic effects of androgens have produced contradictory results. In bird species, testosterone treatment increased the basal metabolic rate in house sparrows *Passer domesticus* (Buchanan *et al.*, 2001), reduced it in white-crowned sparrows *Zonotrichia leucophrys* (Wikelsky *et al.*, 1999) and had no effect in dark-eyed juncos *Junco hyemalis* (Deviche, 1992). However, in juncos, an independent study found an association between high testosterone levels and increased lipid catabolism and nocturnal body temperature (Vezina & Thomas, 2000). In the lizard *Sceloporus jarrovi*, testosterone treatment increased the maximal metabolic rate but had no effect on basal metabolic rate (Marler *et al.*, 1995) and male tilapia treated with 11-ketotestosterone showed an increase in the resting metabolic rate and in metabolic scope but a non-significant increase in the basal metabolic rate (K. Becker, A. Ros & R. F. Oliveira, unpublished data). This discrepancy in the results can be attributed to methodological variations among studies, including the choice of the measures taken, the timespan of the experiment, the season, etc. Nevertheless, androgens failed to affect the metabolic measure used in only two studies, and in one case the data are contradicted by a subsequent study on the same species. In the other four studies, androgens affected different metabolic measures. Consequently, it can be said that androgens may affect metabolism in a non-linear way and a metabolic cost associated with higher levels of androgens should not be excluded.

Parental care trade-off with androgens

One of the predictions of the challenge hypothesis is that male androgen levels above a breeding baseline are incompatible with male parental care

(Wingfield *et al.*, 1990). If androgen levels increase as a result of social challenges, males will invest less time in paternal activities, and thus a trade-off between social interactions and paternal care, mediated by androgens emerges. In many bird species with male parental care, the experimental increase of circulating testosterone in parental males suppressed paternal behaviour and promoted agonist interactions (Silverin, 1980; Hegner & Wingfield, 1987b; Ketterson *et al.*, 1992; Beletsky *et al.*, 1995). Moreover, several studies on the seasonal variation of androgen levels in birds show that during the breeding season male androgen levels are higher during the mating phase than during the parental phase (Wingfield *et al.*, 1987). To document this trade-off further, we have gathered published data on androgen levels in vertebrate species with respect to paternal care: out of the 63 species of vertebrates for which data are available, 92% show the expected pattern of lower circulating androgen concentrations during the parental phase (Table 21.1). In summary, keeping high levels of androgens at all times is detrimental to the individual in many ways and so the stage was set for the evolution of a flexible system modulated by the social environment.

Summary and future directions

Androgen modulation by social context and the subsequent role of androgens in the activation of expression of social behaviour have been proposed in this chapter to explain the mechanisms underlying experiential effects. However, this hypothesis does not exclude explanations of the phenomena described, in terms of associative learning mechanisms. Cognitive abilities such as individual recognition and discrimination would explain some of the described behavioural responses to social context (e.g. McDonald *et al.*, 1968) and winning or losing can be seen as having reinforcing properties. For instance, male Siamese fighting fish will perform an operant response to have access to an opponent that they can subsequently fight (Hogan, 1967; Bols, 1977). Similar results have been reported for mice (Tellegen *et al.*, 1969), suggesting that the opportunity to interact with an opponent may be a universal positive reinforcer in vertebrates. However, the two explanations (i.e. endocrine modulation and associative learning) should not be seen as mutually exclusive but as complementary, and it is even possible that they represent two levels of analysis that are tightly interconnected. Conditioning of the endocrine response by social stimuli is a possibility that remains to be tested, and there are already examples of androgen modulation of learning mechanisms (e.g. in castrated zebra finches testosterone facilitates conspecific song discrimination (Cynx & Nottebohm, 1992)). Therefore, the interrelationship between androgens and associative learning mechanisms is certainly a key topic for future research in this area.

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520 R. F. Oliveira

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