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Social behavior in context: hormonal modulation of behavioral plasticity and social competence

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Synopsis In social species animals should fine-tune the expression of their social behavior to social environments in order to avoid the costs of engaging in costly social interactions. Therefore, social competence, defined as the ability of an animal to optimize the expression of its social behavior as a function of the available social information, should be considered as a performance trait that impacts on the Darwinian fitness of the animal. Social competence is based on behavioral plasticity which, in turn, can be achieved by different neural mechanisms of plasticity, namely by rewiring or by biochemically switching nodes of a putative neural network underlying social behavior. Since steroid hormones respond to social interactions and have receptors extensively expressed in the social behavioral neural network, it is proposed that steroids play a key role in the hormonal modulation of social plasticity. Here, we propose a reciprocal model for the action of androgens on short-term behavioral plasticity and review a set of studies conducted in our laboratory using an African cichlid fish (*Oreochromis mossambicus*) that provide support for it. Androgens are shown to be implicated as physiological mediators in a wide range of social phenomena that promote social competence, namely by adjusting the behavioral response to the nature of the intruder and the presence of third parties (dear enemy and audience effects), by anticipating territorial intrusions (bystander effect and conditioning of the territorial response), and by modifying future behavior according to prior experience of winning (winner effect). The rapid behavioral actions of socially induced short-term transient changes in androgens indicate that these effects are most likely mediated by nongenomic mechanisms. The fact that the modulation of rapid changes in behavior is open to the influence of circulating levels of androgens, and is not exclusively achieved by changes in central neuromodulators, suggests functional relevance of integrating body parameters in the behavioral response. Thus, the traditional view of seeing neural circuits as unique causal agents of behavior should be updated to a brain–body–environment perspective, in which these neural circuits are embodied and the behavioral performance (and outcomes as fitness) depends on a dynamic relationship between the different levels. In this view hormones play a major role as behavioral modulators.

Performing in a social environment: social competence as a performance trait

The "performance paradigm", originally proposed by Arnold (1983), assumes that the variation in the ability of organisms to perform ecologically relevant tasks (performance traits), such as sprint speed, biting force, or capacity for endurance, emerges from variation in underlying morphological and physiological traits (lower-level traits). On the other hand, since organisms interact with the environment through their functional capacities. natural selection is expected to operate primarily on performance traits and only indirectly on lower-level traits (Arnold 1983; Irschick and Garland 2001; Lailvaux and Irschick 2006). Therefore, performance should be correlated with the Darwinian fitness of the organism. Since the proposal of this paradigm, ~25 years ago, a large body of literature has supported the link between lower-level traits and performance traits showing the emergent functional properties of suites of morphological and physiological characters. However, establishing a link between performance of the whole organism and its fitness has proved to be a much more difficult task. Nevertheless, a recent review of the literature identified 23 published studies that have quantified selection on performance. From these studies it could be concluded

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that, in general, performance had a positive impact on fitness, but that there was no evidence for selection to act more strongly on performance than on morphological/physiological traits (Irschick et al. 2008).

In social species individuals interact frequently with each other and their behavior should be adjusted to a changing social environment by previous social experience and by social context. This fine-tuning of the expression of social behavior according to a changing social environment is a key ecological task. Therefore, we propose that apart from maximal dynamic performance traits relevant for social interactions, such as endurance and sprint speed, the ability of animals to regulate the expression of their social behavior in order to optimize their social relationships—social competence—should also be viewed as a performance trait (see Husak et al. this issue). There are several examples of this type of ecological performance from animals living in social networks. For example, animals that are bystanders can use information collected from observing an interaction between conspecifics in subsequent interactions with the observed individuals, so that they adjust their fighting behavior according to the assessed fighting ability of the putative opponent, therefore avoiding the costs of escalated fights (McGregor and Peake 2000). This phenomenon of eavesdropping has been demonstrated in Siamese fighting fish (*Betta splendens*), where bystanders responded more aggressively toward intruders that they have previously observed losing an interaction than toward intruders for which they have no previous information. Conversely, bystanders took longer to attack a previously observed winner (Oliveira et al. 1998). In this case the dynamic performance traits of our focal animal, such as speed of swimming or endurance are expected to be the same in both situations. We have not measured maximum performance in this study, but we have measured display rate in both interactions, which has been shown to be a good predictor of outcome of fights in this species (Simpson 1968) and can thus be seen as a measure of ecological performance; we found no difference between the two types of interactions (i.e., against previously seen versus unseen intruders). In summary, this study illustrates how fighting performance can be adjusted according to social context and independently of maximal performance traits. This social competence of adjusting behavior to social environment has an expected added-value in terms of fitness, since it allows animals to avoid, or to limit, the costs of risky social interactions with opponents of higher fighting ability.

A requisite for social performance (competence) is behavioral plasticity, so that the same individual may respond differently to the same social stimulus (e.g., presence of a territorial intruder), depending solely on variation in its internal state. Usually behavioral responses to social releasers vary according to the social status of the animal, the presence, or not, and nature of other conspecifics and the location where behavior is being expressed. Most social behaviors are status-dependent, with dominant and subordinate individuals displaying very different behavior in response to similar stimuli, such as expressing, or not, courtship behavior toward a putative mate. Also the social context modifies behavior, and many social phenomena have been described, such as audience effects (Matos and Schlupp 2005), bystander effects (McGregor and Peake 2000) and dear-enemy effects (i.e., when territory owners react more aggressively toward unfamiliar intruders than toward neighbors; Ydenberg et al. 1988). Finally, the spatial location where a social interaction occurs also modulates the expression of social behavior, with home-advantage occurring in territorial species (Huntingford and Turner 1986). All these examples of socially driven behavioral plasticity occur within a short time frame within the same life-history stage of the animal, with individuals quickly modifying their response to the same releaser. On the other hand, social behavior also changes over larger timescales according to the life stage of the animal, as in seasonally breeding species in which cyclic changes in social behavior occur between the breeding and nonbreeding season, particularly in aggressiveness and in courtship behavior. The distinction between these two extremes of behavioral plasticity is relevant in terms of identifying their most parsimonious underlying mechanisms.

Neural and endocrine mechanisms of behavioral plasticity

For changes in behavior to occur the neural networks underlying social behavior must exhibit the potential for neural plasticity, so that the same inputs to the network can produce different outputs depending on the motivational state of the animal. Two major neural mechanisms have been proposed to mediate these changes in behavior: structural reorganization of the neural circuits and biochemical switching of neural networks (Zupanc and Lamprecht 2000). Each of these two types of neural mechanisms underlying behavioral plasticity is expected to operate on

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different time scales. Structural rewiring of neural circuits is predicted when motivational changes are slow and long-lasting and induce dramatic behavioral changes (Zupanc and Lamprecht 2000). Modulation of existing neural networks is postulated to mediate fast and transient changes between motivational states that promote gradual changes in behavioral expression (Zupanc and Lamprecht 2000).

Structural reorganization

Structural reorganization may be accomplished by different forms of structural modifications that might require adding new cells or removing old cells from the circuit, modifying the connectivity between different components of the network, or changing the responsiveness of the circuit by modifying its molecular components.

Adult neurogenesis has now been described for most vertebrate taxa, from fish to mammals, and the generation and incorporation of new neurons in circuits or the generation of new glial cells involved in the regulation of the neural environment in which the circuit operates, would be a way to accomplish structural changes in behavior. Adult neurogenesis has been extensively studied in the mammalian hippocampus where it seems to contribute to learning and to memory formation (Abrous and Wojtowicz 2007). However, new neuronal cell production in adults has also been reported, although at lower levels, in other brain areas more directly involved in the control of social behavior such as the amygdala and the hypothalamus (Fowler et al. 2008). Interestingly, cell proliferation in adults and/or survival in these different areas of the brain is influenced by the social environment (Kempermann and Gage 1999; Kozorovitskiy and Gould 2004; Thomas et al. 2007) and by steroid hormone levels (Gould and Gross 2002). Also in teleosts, social status and social cues seem to modulate\\ proliferation of brain cells and cell survival (Dunlap et al. 2006, 2008; Sorensen et al. 2007).

Changes in connectivity between different nodes of the network can also explain behavioral plasticity and can be accomplished by changes in dendritic structure, such as density of dendritic spines and synapses, or by retraction or outgrowth of axons. For example, seasonal changes between breeding and nonbreeding life-history phases in chirping behavior of weakly electric fish are mediated by dendritic retraction of central posterior/prepacemaker nucleus neurons that leads to a reduction of the interface between the sensory and the motor components of this neural system (Zupanc and Heiligenberg 1989). As in the case of neurogenesis described above, also the morphology of dendrites and patterns of synaptic connectivity respond both to social interactions and to treatment by steroid hormones (McKittrick et al. 2000; Cooke and Woolley 2005).

Finally, a third possible mechanism of structural plasticity does not involve rewiring of the neural network but, rather, changes in its molecular constitution that would promote changes in its responsiveness. Therefore, changes in the inhibitory/excitatory balance of a given network can be achieved by increasing or reducing the expression of receptors for different neurotransmitter and/or neuromodulators in specific neurons. For example, exposure to adverse social conditions early in development increases the expression of corticotropin-releasing factor receptor and decreases the levels of GABA-A/CBZ and glucocorticoid receptors in neural systems that mediate stress reactivity, which may then serve to influence maternal behavior (Meaney 2001). Similarly, the responsiveness of neural networks underlying social behavior to circulating steroids can be modulated by differential expression of steroid receptors in a socially dependent fashion. This can be illustrated by recent results that show that dominant males of the cichlid fish *Astatotilapia burtoni* had higher mRNA expression of AR-α, AR-β, ER-β1, and ER-β2, but not of ER-α receptors, when compared to subordinate males (Burmeister et al. 2007).

Together these results suggest that socially induced changes in circulating steroid hormones have the potential to sculpt the neural mechanisms underlying social behavior.

Biochemical switching

Biochemical switching mechanisms allow for a variable response of the same neural network under similar stimulation regimes. This is achieved by different neuroactive molecules that interact with the circuit and alter its functional properties, therefore promoting either excitatory or inhibitory states. These neuromodulatory agents are released by neurons in a nonsynaptic fashion and interact with receptors at multiple sites in the neural system, therefore changing its functioning in a diffuse way and affecting multiple aspects of behavior in an integrated fashion. Thus, instead of promoting the expression of behavior *per se*, neuromodulators appear to tune ongoing activity to promote the occurrence of behaviors adapted to a given context (Libersat and Pflüger 2004). Catecholamines and

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neuropeptides are considered the two major classes of neuromodulators, and the action of both of them on social behavior has been extensively documented. Monoamines have been implicated in the regulation of motivated behaviors and among them the role of the serotonergic system on the control of aggressive motivation has been demonstrated both in vertebrates and in invertebrates, suggesting an ancient evolutionary emergence of serotonin as a signaling mechanism for transitions between motivational states (Kravitz 2000; Huber 2005). Nonapeptides from the arginine vasotocin family (AVT, arginine vasopressin, AVP in eutherian mammals) have also been implicated in the regulation of social behavior and sociality across all vertebrate taxa (Goodson and Bass 2001). Interestingly, the AVT/AVP system is regulated by gonadal steroids (Goodson and Bass 2001; De Vries and Panzica 2006), therefore allowing for the adjustment of behavioral expression to seasonal changes in social context (e.g., breeding versus nonbreeding) and to immediate behavioral context.

Finally, it has been proposed recently that estrogens should also be regarded as neuromodulators since they have direct nongenomic effects on neuronal membranes affecting neural activity, they can be produced locally (by aromatization of testosterone) in presynaptic terminals, and their production can be modulated within minutes by calcium-dependent phosphorylation (Balthazart and Ball 2006).

Thus, monoamines, neuropeptides, and sex steroids may act as neuromodulators producing context-appropriate behavior.

To promote an integrated response at the level of the whole organism, these neural mechanisms of behavioral plasticity would be expected to be orchestrated by an endocrine control mechanism. In fact, there is a parallel between these two neural mechanisms and the activational–organizational effects of hormones (Arnold and Breedlove 1985), depending on the time scale of the behavioral plasticity. Thus, by making a distinction between slower and long-lasting behavioral changes, usually corresponding to transitions between life-history stages (e.g., breeding versus nonbreeding) and rapid, but transient. Behavioral changes, usually occurring within the same life-history stage, an organizational role of hormones would be predicted in the former case and an activational role in the latter one. This rationale is an extension of the relative plasticity hypothesis proposed by Moore (1991) for the endocrine control of alternative reproductive tactics.

Steroid hormones are major candidates to play a role as indicators of internal state that regulate neural mechanisms of behavioral plasticity. On one hand steroids have pleiotropic-like effects that help to promote integrated responses by the whole organism, and on the other hand steroids respond to different aspects of the social environment: corticosteroids are a major component of the response to stress and respond to unpredictability and perception of risk (McEwen and Wingfield 2003) whereas androgens are known to respond to social challenges in many species (Wingfield et al. 1990; Hirschenhauser and Oliveira 2006). Moreover, steroids interact with the functioning of the nervous system at different levels and have known effects on all the mechanisms of neural plasticity as described above. In particular, steroids are known to target the neural network of social behavior originally proposed by Newman (1999) in mammals and recently confirmed to be conserved across different vertebrate classes (Goodson 2005). This social behavior network is composed of six nodes located in the basal forebrain and midbrain (i.e., the extended medial amygdala, the lateral septum, the preoptic area, the anterior hypothalamus, the ventromedial hypothalamus, and the periaqueductal gray in mammals, and in homologous structures in other vertebrates) that are reciprocally connected and that together regulate a wide repertoire of social behaviors including sexual behavior in both males and females, parental behavior, and different forms of aggressive behavior (Newman 1999; Goodson 2005). Steroid receptors are present in the different nodes of this network suggesting that plasticity in social behavior in response to changes in social environment are likely to be moderated by these hormones.

In summary, social information is translated into changes in levels of steroid hormones that in turn will modulate the neural network of social behavior so that behavioral output is tuned according to the perceived social environment. Depending on the time-frame of the exposure to relevant social signals, different forms of neural plasticity can be activated in the different nodes of the social behavioral network, resulting in transient or long-lasting changes in social behavior that will increase the fitness of the animal (Fig. 1).

In this article, we will focus on the role of androgens as physiological mediators of short-term behavioral plasticity.

Reciprocal model of androgen—behavior interactions

Several studies over the years have established an association between androgens and the expression

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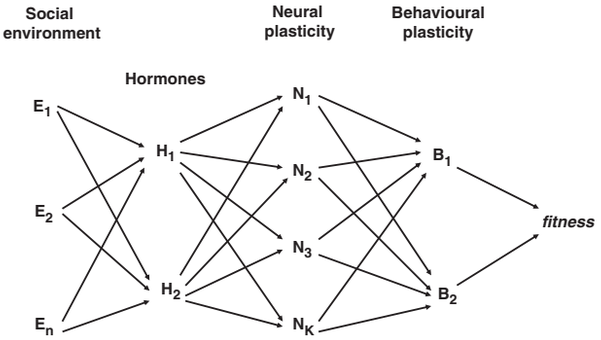

Fig. 1 Path diagram showing the proposed relationship between the social environment (E_1–E_n), steroid hormones (H_1; H_2), neural circuits (N_1–N_k), social behavior (B_1; B_2), and fitness. Variations in the social environment induce changes in steroid hormone levels that modulate the plasticity of the neural circuits underlying social behavior with consequences for fitness.

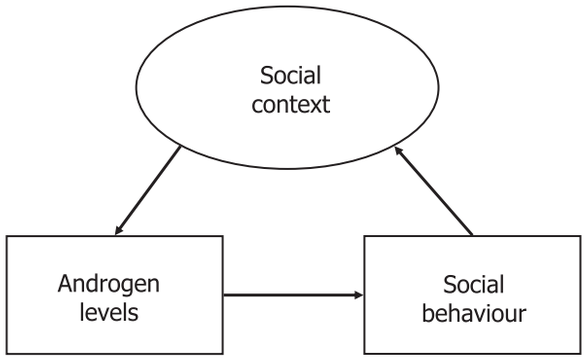

Fig. 2 Reciprocal model for the interaction between androgens and social behavior.

of aggressive and sexual behavior in male vertebrates. Overall, these studies show that although, *per se*, androgens are neither necessary nor sufficient to elicit the expression of social behavior, they increase the probability of its expression by acting as modulators of neural pathways of social behavior, thus acting as behavioral facilitators (Simon 2002; Oliveira 2004). Conversely, evidence has accumulated over the past two decades showing that levels of circulating androgens respond to the social environment, namely to territorial intrusions and to interactions with sexual partners (Wingfield et al. 1990; Oliveira 2004). Thus, androgens not only affect behavior but also respond to it. This reciprocity between androgens and social behavior led to the proposal of a reciprocal model according to which the feedback of behavior on the endocrine system has been interpreted as a way to coordinate an integrative response of the organism to changes in the social environment, and therefore to alter the expression of behavior in subsequent interactions (Mazur 1976; Leshner 1979). This reciprocal model was later expanded to a comparative context and re-named as "the challenge hypothesis" by John Wingfield and co-workers, who stressed the key role of different components of the mating system on the magnitude of the response by androgens to a social challenge (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 or to which he is exposed, influence its androgen levels, which in turn will modulate perceptive, motivational, and cognitive mechanisms that will affect its subsequent behavior in social interactions (Fig. 2). The response by androgens to social interactions is present across all vertebrate classes, but varies from species to species as a function of the characteristics of the mating system, such as the degree of male–male competition and investment in parental care (Hirschenhauser et al. 2003; Hirschenhauser and Oliveira 2006). In a number of species, androgens respond to the outcome of social interactions with elevated levels in winners and a drop in losers, resulting in dominant individuals usually having significantly higher androgen levels than do losers (Hirschenhauser and Oliveira 2006).

The function of the elevated androgen levels following a win and their decrease following a loss is not yet known. One possibility is that increased androgen levels will prepare winners for future challenges that they are more likely to face in order to maintain their dominant status, whereas the drop in testosterone experienced by losers may encourage withdrawal from subsequent interactions, thus preventing further costs of interacting in an adverse social environment (Oliveira et al. 2009).

The Mozambique tilapia as a model for the study of behavioral plasticity and social competence

In our laboratory, we have been using an African cichlid fish, the Mozambique tilapia (*Oreochromis mossambicus*), as a research model to investigate the role of androgens on social plasticity. Fish have sophisticated cognitive abilities that range from social learning, to transitive inference of social information and to the use of socially relevant information by eavesdropping on social interactions of third parties (Oliveira et al. 1998; Brown and Laland 2003; Grosenick et al. 2007), suggesting a degree of social sophistication comparable in some

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aspects to that of primates (Bshary et al. 2002). Cichlid fish, in particular, have complex mating systems with extensive plasticity in the expression of social behavior, which makes them a unique preparation for the study of social plasticity both at the proximate and the ultimate levels (Taborsky 2001; Desjardins and Fernald 2008; Renn et al. 2008). Moreover, their small size and the ease with which they can be kept and bred in captivity allows for precise manipulations of their social environment under laboratory conditions.

The Mozambique tilapia is an African maternal mouthbrooding cichlid that displays a lek mating system. Males can express one of two behavioral phenotypes depending on social status. At the start of the breeding season when males arrive into the breeding grounds, males fight with each other and dominant males establish breeding territories in the bottom where they dig spawning pits, assume a dark coloration, defend a breeding territory, and actively court females (Neil 1964; Oliveira et al. 1996; Oliveira and Almada 1998a). Spawning takes place in the pit and the female quickly takes eggs and sperm into her mouth where fertilization takes place. The embryos and fry are brooded in the female's mouth (Fryer and Iles 1972; Bruton and Boltt 1975). Subordinate males become nonterritorial and try to intrude into nests during spawning and engage in sneaking attempts (Oliveira and Almada 1998b). Territorial males were also observed to court subordinate males displaying the full courtship sequence found in this species. Courted males performed the typical female sexual behavior, which includes following the courting male to the nest, assuming a pivot position in the nest, while the other male circled them and in fewer cases putting their mouth close to the genital papillae of the courting male and performing chewing movements when the courting male released sperm, a behavior typical of females inhaling sperm to ensure the fertilization of the eggs inside the mouth (Oliveira and Almada 1998b). Thus, Mozambique tilapia males express a high degree of behavioral plasticity that involves transitions between life-history stages (breeding versus nonbreeding) and within the same life-history stage depending on social status (territorial versus nonterritorial) and social context (i.e. social information available).

Androgen modulation of social plasticity in cichlid fish

In cichlid fishes, males respond to social intrusions with an increase in androgen levels and the magnitude of this response varies with mating system and with the degree of paternal investment of the species (Hirschenhauser et al. 2004). This rapidly evolving group exhibits a great variety of breeding systems and types of parental care (Trewavas 1983; Sturmbauer et al. 2002), which offers an opportunity to test experimentally the predictions of the challenge hypothesis by comparing the magnitude of the androgen response to a simulated territorial intrusion in phylogenetically closely related species that differ in their mating systems. Thus, we compared two closely related pairs of haplochromine cichlids: (1) *Neolamprologus pulcher*, a monogamous species in which breeding pairs defend territories and have helpers at the nest, versus *Lamprologus callipterus*, a polygynous species with small parasitically breeding males; (2) *Tropheus moorii*, a polygynous species with temporal pair formation, versus *Pseudosimochromis curvifrons*, that is polygynous with explosive lek breeding. Males from all species sampled were highly responsive to territorial intrusions with larger androgen responses found among males from monogamous species or with more intense pair bonding in the specific mating system (*T. moorii*) (Hirschenhauser et al. 2004; Fig. 3A). Thus, the predictions of the challenge hypothesis postulated for male birds seem to be also fulfilled among cichlids.

In our model species (*O. mossambicus*), the two main androgens found in fish, testosterone (T), and 11-ketotestosterone (KT), increase in response to an interaction with a receptive female and both hormones further increase when the male is subsequently faced with a territorial intruder (Hirschenhauser et al. 2004; Fig. 3B). Furthermore, the magnitude of the response is typical of other lek-breeding cichlids (Hirschenhauser et al. 2004; Fig. 3A). A key to understanding the adaptive role of the androgen response to social challenges, is a knowledge of the crucial aspects of the interactions that are eliciting the response. The endocrine response can be either a way whereby individuals adjust current behavior to the dynamics of the ongoing interaction, in which case it should correlate with the escalation of fights, or a way of adjusting future behavior in subsequent interactions, in which case it should vary with the outcome of the interaction (i.e. winning/losing). In order to disentangle these alternative explanations, we took advantage of the fact that fish do not recognize their own image in a mirror and thus attack it as if it were an intruder (Rowland 1999). Thus, we set-up unsolved interactions, in which male tilapia fight with their own image on a mirror. In mirror-elicited contests

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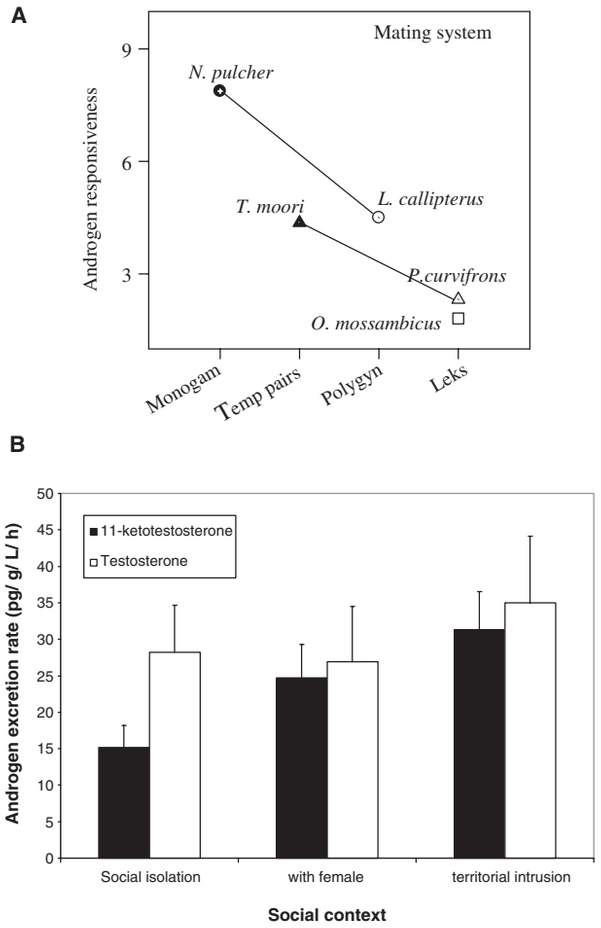

Fig. 3 Androgen response to social interactions in cichlid fish; (A) Comparison of 11-ketotestosterone responses to simulated territorial intrusions in pairs of closely related species with different mating systems; (B) response by 11-ketotestosterone and testosterone to interactions with a receptive female and to a subsequent territorial intrusion in males of the Mozambique tilapia (Fig. 3A reprinted with permission from Hirschenhauser et al. 2004 Anim Behav 68:741–50).

males extensively express aggressive behavior toward the mirror. After an initial phase of displaying toward the mirror they escalate the fights in an apparent attempt to solve the interaction (Fig. 4A–C) (Oliveira et al. 2005). The prediction is that if changes in androgen levels are targeting current behavior, they should respond to escalation and an endocrine response should be present in mirror-elicited fights. Alternatively, if the androgen changes serve to modify future behavior, they should respond mainly to the outcome of the fight, in which case unsolved mirror fights should not elicit an androgen response. Despite the behavioral response to the mirror we found no androgen response, a result that suggests that androgens are responding to the outcome of the contests, thereby allowing individuals to trigger an endocrine response only after having assessed their relative fighting ability (Fig. 4D). These results also show that the increase in androgens after fights is not a mere side-effect of exhaustion due to sustained physical exercise.

Thus, in this species, androgens are thus good candidates to act as endrocrine modulators of social plasticity. Several social phenomena have been described that require flexible behavioral responses from the performing animal, such as differential responses toward familiar individuals versus strangers (dear–enemy effect), altering the response to an intruder depending on the presence and nature of an audience of conspecifics (audience effect), using intrusions on neighboring territories, or other cues indicating the presence of potential intruders, to anticipate subsequent territorial intrusions (bystander effects), and finally modifying the expression of aggressive behavior according to prior experience, so that winners become more eager to interact again and losers to avoid future interactions (winner/loser effects). According to the reciprocal model presented above, androgens can be playing a major role as physiological mediators of these flexible social responses. In order to further explore the potential adaptive function of the androgen response to social interactions, we will address the role of androgens on each of these social phenomena.

Adjusting the response to the nature of the intruder and to the presence of third parties: "dear enemy" and audience effects

In many species, the response of territorial males toward familiar intruders is less intense than to intrusions by strangers. This differential response has been named as the "dear enemy effect" and allows the resident to adjust its territorial behavior according to the threat posed by the intruder, thus reducing the costs of territorial defense (Ydenberg et al. 1988; Temeles 1994). At a proximate level the "dear enemy effect" requires the animals to be able to discriminate conspecifics according to familiarity and to habituate to neighbors. For androgens to play a role as mediators of the "dear enemy effect", it is predicted that the androgen response to an intrusion should be higher toward a stranger than to a familiar intruder, and it should habituate to repeated intrusion. We have recently tested this hypothesis in the Mozambique tilapia by exposing territorial males to intrusions by either familiar (neighbors) or unfamiliar males for 4 consecutive days, and we found both an effect of intruder type and also habituation of the androgen response. Strangers elicited

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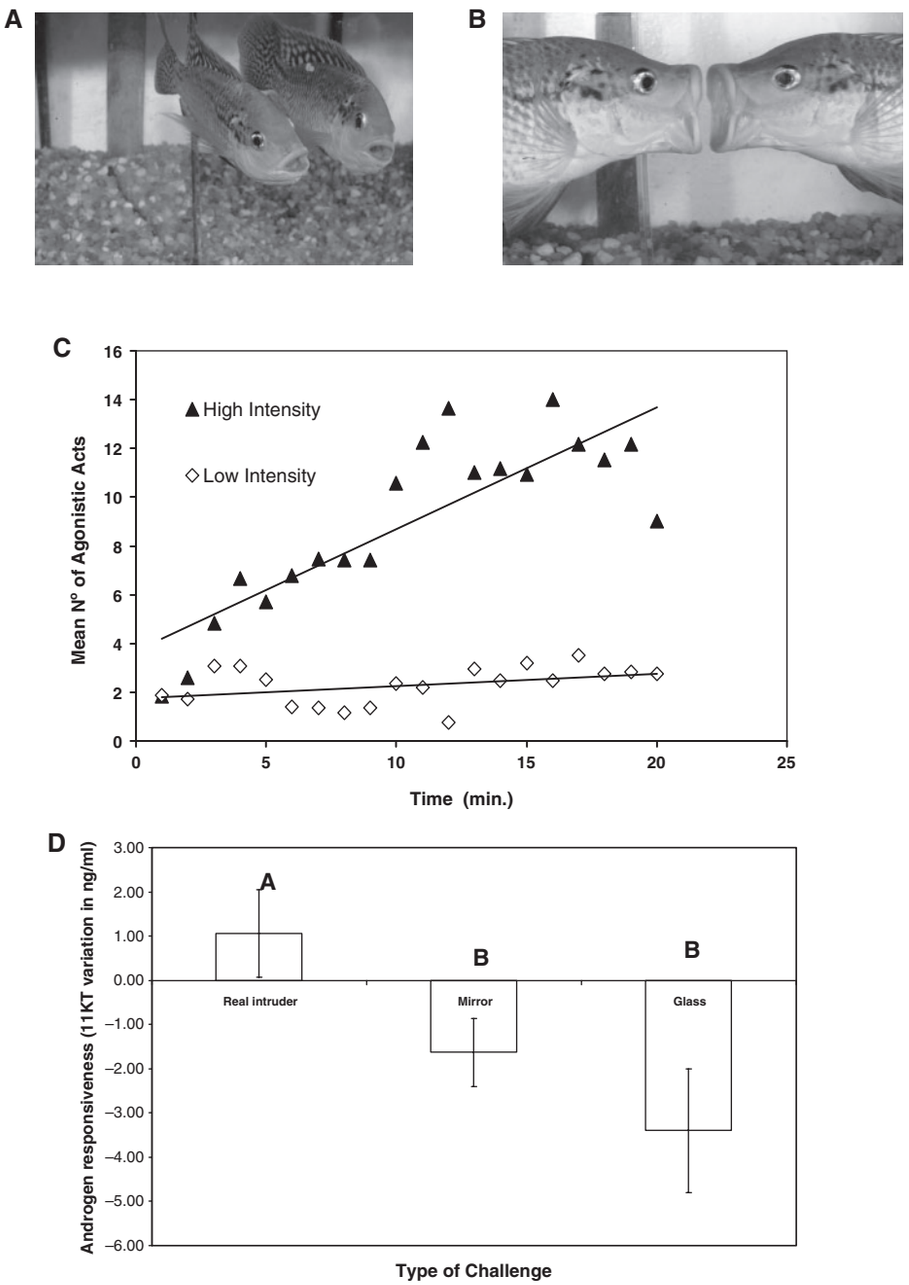

Fig. 4 Mirror-elicited aggression in Mozambique tilapia; (A) males displaying toward own image on a mirror; (B) Mouthfighting with mirror-image; (C) Variation in low intensity acts (i.e., displays) and high-intensity acts (i.e., overt aggression) toward the mirror along the interaction with the mirror; (D) responsiveness of 11-ketotestosterone under different conditions; interaction with a live intruder, mirror challenge, and when a transparent glass was used to control for the presence of a novel object in the tank (Fig. 4B reprinted with permission from Oliveira et al. 2005 *Nature* 437:207–8; Fig. 5D redrawn with data from Oliveira et al. 2005).

higher KT levels than did neighbors and there was a reduction in the response from the first to the fourth day (R.F. Aires, A.F.H. Ros and R.F. Oliveira, unpublished data). These changes in the endocrine response were paralleled by changes in the behavioral response toward intruders. Resident tilapia males exhibited lower latencies to attack unfamiliar intruders than toward neighbors, and the latency to attack the familiar intruder increased with the day of the experiment, suggesting habituation. Taken together, these results suggest a mediating role for androgens in the "dear enemy effect".

Depending on the spacing pattern of territories and on the transmittance range of the signals used in the interactions, many territorial intrusions occur in the presence of other conspecifics that are not

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directly involved in the interaction and that are called audiences. The presence of an audience potentially affects the pay-off matrix of the interaction by imposing additional costs and/or benefits on the contestants. For example, losing a fight in front of an audience may increase the chances of being more readily challenged by third parties that eavesdropped on the interaction (Oliveira et al. 1998). Therefore, the presence of an audience is expected to modulate signaling behavior, a phenomena that has been termed the "audience effect" (Matos and Schlupp 2005). Audience effects in the territorial context have been extensively studied in Siamese fighting fish (*B. splendens*), in whom the presence and nature of an audience modifies aggressive behavior (Doutreland et al. 2001; Matos et al. 2002, 2003; Dzieweczynski et al. 2005). Interestingly, the androgen response to the fight accompanies these audience-induced changes in behavior, with KT levels being higher in males fighting in front of a male audience, or when no audience was present, than in males with a female audience present (Dzieweczynski et al. 2006).

Anticipating territorial intrusions: bystander effect and conditioning of the territorial response

Watching a territorial contest between conspecifics may induce changes in the behavior of the observer, that can be due either to the acquisition of the available social information in the interaction (eavesdropping) or to an heightening of aggressive motivation as a result of this experience (priming) (Oliveira et al. 1998; Clotfelter and Paolino 2003). These two processes should not be confused. Eavesdropping involves gathering information from observing interactions and using this information in subsequent interactions with the observed individuals, and thus involves complex cognitive tasks. Priming of agonistic motivation in bystanders only involves motivational changes (Hogan and Bols 1980; Bronstein 1989) and is another social phenomenon that might be mediated by androgens. We have tested this hypothesis in the Mozambique tilapia, by having bystander males observing pairs of conspecifics through a one-way glass under one of the two conditions: fighting versus resting and/or performing maintenance activities (Fig. 5A). Both KT and T increased in bystanders exposed to fighting conspecifics while no significant changes in androgens levels were found in the control treatment (Oliveira et al. 2001; Fig. 5B), suggesting a mediator role for androgens in the priming effect of bystanders. This priming response seems to be adaptive

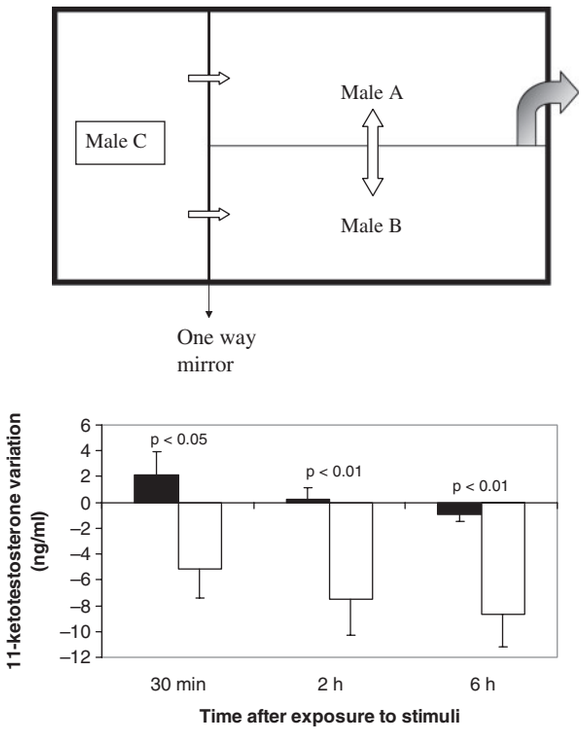

Fig. 5 Androgen response in bystanders of male Mozambique tilapia. (A) Experimental set-up to study the bystander effect: a focal male observes pairs of conspecifics through a one-way mirror; conspecifics are placed in compartments separated by an opaque partition (resting condition); in the experimental treatment this partition is removed (noted by the grey arrow) and the observed males are allowed to interact. (B) Changes in 11-ketotestosterone in bystanders following exposure to conspecific pairs (Fig. 5B reprinted with permission from Oliveira et al. 2001. Nature 409:475).

since it prepares the bystanders for forthcoming interactions in a context of social instability, that is, when agonistic interactions are already present in the social environment. Clotfelter and Paolino (2003) have recently shown that in Siamese fighting fish male bystanders have a greater probability of winning their next social interaction than do controls.

If the androgen response does, indeed, prepare the individual for subsequent interactions it can be predicted that animals should evolve associative learning mechanisms that would allow them to activate an anticipatory androgen response to environmental cues signaling the presence of a potential intruder. Classical conditioning has been suggested to recreate naturally occurring situations in which imminent social interactions are signaled through visual, chemical, or mechanical changes of the surrounding environment (Hollis 1997). In fact, in the territorial fish, *Trichogaster trichopterus*, it has

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been shown that males learn to associate environmental cues with territorial disputes, which translates into a competitive edge for conditioned males (Hollis 1999). However, little is known about the mechanisms whereby it occurs. Recently, we have shown that circulating androgens in territorial male tilapia rise in anticipation of territorial intrusions, in parallel with a decrease in latency of aggressive responses toward the putative intruder (R. Antunes and R.F. Oliveira, unpublished data). To test whether androgen levels respond to environmental cues signaling an imminent territorial intrusion, we used a Pavlovian trace conditioning paradigm to promote an association between a conditioned stimulus (CS, a light) and an unconditioned stimulus (US, the intruder male). After eight training trials, conditioned males showed an androgen response to CS in the test trial of a similar magnitude to that of trained males that on the test trial are also exposed to the intruder (CS + US treatment). Surprisingly, a control group where the presentation of the CS and US was unpaired (US followed CS only after an interval of 2 h, UCS treatment) showed a sharp decrease in androgen levels in the test trial where they were only exposed to the CS, suggesting the occurrence of conditioned inhibition of androgen levels (R. Antunes and R.F. Oliveira, unpublished data). Hence, androgen levels can be conditioned in either direction, enhancing agonistic motivation in the imminence of a challenge and relaxing defense in socially stable periods, thereby avoiding the costs of unnecessary high androgen levels. Thus, the endocrine anticipation of rival intrusions might optimize territorial defense in this species.

Modifying future behavior according to prior experience: winner and loser effects

If the functional significance of the androgen is to modulate the expression of social behavior in future interactions, as postulated above, then it can be hypothesized that socially induced transient changes in androgen levels could be the causal mediators of winner/loser effects. Previous studies conducted with California mice (*Peromyscus californicus*) have found an association between prior winning and both an increased likelihood of winning future fights and increased testosterone levels (Oyegbile and Marler 2005). Also, in human studies, increased androgen levels after a social interaction predict the willingness of subjects to engage in subsequent interactions (Mehta and Josephs 2006; Carré and McCormick 2008; Carré et al. 2008). Further support for this hypothesis came from a recent study of Mozambique tilapia in which circulating levels of androgen in winners and losers were manipulated and the implications for winning/losing a subsequent interaction were assessed (Oliveira et al. 2009). Winners of a first aggressive encounter were treated with the anti-androgen cyproterone acetate (CA) and losers with KT. As predicted, winners of the first encounter won the majority of the second interactions with a naïve male and the reverse situation occurred for losers. However, in CA-treated winners the winner effect was no longer detectable at the second fight, suggesting an involvement of androgens in the winner effect. Contrary to predictions, we could not reverse the loser effect in KT-treated males, suggesting that the observed drop in androgens in losers is not the only underlying mechanism for the loser effect (Oliveira et al. 2009). This result suggests that other neuroendocrine mechanisms must be involved in the loser effect. In particular, the serotonergic system seems to be a good candidate for mediating loser effects since a defeat increases brain levels of serotonin, and subordinates have chronically elevated serotonin levels in the brain (Winberg and Nilsson 1993a, 1993b; Winberg et al. 1997; Winberg and Lepage 1998). Furthermore, serotonin promotes behavioral inhibition in general and aggressive behavior in particular (Winberg and Nilsson 1993a, 1993b; Adams et al. 1996; Edwards and Kravitz 1997). These results also illustrate another important point, namely that similar phenomena at the functional levels, such as winner and loser effects, usually seen as the two sides of the same coin, may be mediated by different causal mechanisms.

The next step in terms of understanding the functional significance of the winning-driven raise in androgens is to unravel the mechanisms through which this transient increase in androgens increases the probability of winning future interactions. An obvious first answer to this question is that increased androgen levels promote an increase in aggressive motivation that will make winners more reactive to future challenges and more persistent once engaged in an interaction. Another possibility is that androgens influence the performance of animals in subsequent fights by acting on psychological traits that are highly relevant for the dynamics and outcome of contests, such as sensory abilities, selective attention to social threats, implicit learning of motor patterns relevant to fighting, and decreased fear leading to an increase in risk-taking. Most evidence supporting this possibility comes from research on humans in which administration of testosterone has been shown to increase visuo-spatial ability (Aleman et al. 2004)

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and selective attention to social threat (i.e., angry faces) (Van Honk et al. 1999) and to promote the activation to angry versus happy faces in areas of the brain involved in reactive aggression, such as the amygdala and hypothalamus (Hermans et al. 2008). Moreover, T has also been shown to reduce fear (van Honk et al. 2005; Hermans et al. 2006) and to reduce sensitivity to punishment and enhance dependency on rewards (van Honk et al. 2004). In animals the effects of T on cognitive traits relevant for social competence have been less studied and most studies concentrate on the effects of sex steroids on different mechanisms for memory in rodents, including social memory (Sawyer et al. 1984; Vazquez-Pereyra et al. 1995; Ceccarelli et al. 2001; Frye and Seliga 2001; Kritzer et al. 2001). In nonmammals, T has also been shown to facilitate discrimination of conspecific song in zebra finches (Cynx and Nottebhom 1992). In our laboratory, we are extending these studies to teleost fish. In a pilot study on Siamese fighting fish, we recently assessed the effects of T on selective attention to social interactions between conspecifics. In the behavioral paradigm used, the experimental subject is placed in a central compartment of a tank and two pairs of conspecifics are placed in the two end-compartments. The central compartment is separated from the end compartments by one-way mirrors so that the focal fish can observe the stimulus fish without being observed. In one of the end-compartments the pair is separated by an opaque partition, and therefore the individuals did not interact with each other, while in the other end-compartment the pair is separated by a transparent partition that allows them to engage in mutual agonistic displays. We scored the time our focal fish spent observing (i.e., within 10 cm from the end tank and oriented toward the conspecifics) the interacting conspecifics and used it as a measure of social attention (for more details on this paradigm see Oliveira et al. 1998). We compared focal fish injected with methyl-testosterone (MT) with focal fish injected with saline and found that although both groups of males spent more time near the interacting pair, MT-treated males did so significantly more often than did control males.

Social modulation of steroid receptors: beyond circulating levels

Varying the plasma concentrations of androgens is only one of the many ways of modifying signaling by these hormones. Changes in androgen-mediated effects on behavior can arise as well by changes at the different levels of the androgen signaling cascade, namely by changes in steroid binding proteins that regulate the availability of the hormone to intracellular receptors or in the density of hormone receptors at the target tissue. The androgen response can therefore be regulated at different levels, creating a differential response to the same concentration of circulating hormone (Ball and Balthazart 2008). Testosterone may also exert its behavioral effects via conversion to other biologically active steroids by specific enzymes, such as aromatase that leads to the production of estradiol, 5-α-reductase to 5-α-dihydrotestosterone (DHT), and 11-β-HSD and 11-b-hydroxylase to 11-ketotestosterone in the case of teleost fish (Kime 1993; Ball and Balthazart 2008). Variations in the activity of each of these enzymes would result in local variations in the available biologically active hormones in the target tissue. Finally, the response of the target tissue to the same levels of androgens can also be affected by transcription co-activators and co-repressors that alter the effectiveness of the genomic action of steroids (Ball and Balthazart 2008).

Although the social modulation of the androgen signaling system has been mainly studied at the levels of variations in circulating concentrations, several studies indicate that all these levels also can potentially respond to the social environment. The expression of androgen (AR) and estrogen (ER) receptors in cichlid fish are influenced by social status, with dominant *A. burtoni* males showing higher mRNA expression of AR-α, AR-β, ER-βa, and ER-βb, but not of ER-α, in the forebrain when compared to subordinates (Burmeister et al. 2007). Also, in the Mozambique tilapia dominant males have higher expression of ER-α and aromatase in the forebrain, suggesting a possible involvement of the aromatization pathway in status-related behaviors (J.M. Simões, D.M. Gonçalves, and R.F. Oliveira, unpublished data). These differences in gene expression in the brain between males of different social status can be an example of a reorganization mechanism underlying social plasticity on a longer time frame. However, the expression of steroid receptors can respond very rapidly to cues from the social environment, as can be illustrated by recent results from tilapia in which a single 90-min interaction was enough to elicit a response in the expression of AR-α in losers (J.M. Simões, D.M. Gonçalves, and R.F. Oliveira, unpublished data). Thus, the response of target tissues can itself be modulated over relatively short intervals of time (ca. 1 h), allowing for a continuum between very rapid response mechanisms (seconds to minutes), mediated by changing levels

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of circulating hormone acting on nongenomic mechanisms (see below) and by long-term mechanisms that involve more deep re-structural modifications of the neural networks.

Implications of the reciprocal model

The evidence presented above provides strong support for an activational role of circulating androgens on rapid behavioral responses to changes in social context or status. This has two implications that challenge the classic view of the mechanisms of steroid action.

First, the rapid increase in circulating levels of androgens in response to social stimuli (i.e., within minutes) may not be compatible with the time lag for the response to be mediated by the activation of the hypothalamic–pituitary–gonadal axis. For example, in the cichlid fish *A. burtoni* when a subordinate male detects an opportunity to ascend in status there are very rapid changes in aggressive behavior and in coloration; in contrast changes in the preoptic area in level of expression of GnRH-1, that will trigger the hormonal cascade in the HPG to culminate in increased androgen levels, lag behind (White et al. 2002; Burmeister et al. 2005). Therefore, alternative mechanisms for rapid changes in circulating levels of androgen driven by social factors must be in action. At least two alternative explanations are possible: (1) a rapid brain–gonadal pathway that controls production and release of testosterone by the gonads; or (2) the androgen response does not originate in the gonads but in the brain, and the changes in blood levels of androgens are a result of neurosteroids entering the circulation.

Evidence for both hypotheses is currently available but further research is needed to elucidate this point. A direct innervation of the gonad may provide a fast communication channel for rapid androgen responses. Nerve terminals have been identified in the testicular interstitial tissue of different teleost species, but its functional significance has never been assessed (Follenius 1964; Nilsson 1970; Gresik 1973). In rats, the administration of a selective-beta adrenergic antagonist reduces testosterone release from Leydig cells (Khan et al. 2004), suggesting that the nor-adrenergic innervation of the gonad may regulate circulating androgen levels. Moreover, it is known that rapid increases in blood glucocorticoid (GC) levels induced by stressors lead to correspondingly rapid declines in testosterone production by the testis that are mediated by GC membrane receptors and by suppression of cAMP (Hu et al. 2008). Thus, both the autonomic nervous system and stress-elicited changes in circulating GC levels may explain rapid changes in androgen levels. On the other hand, evidence for a rapid response of neurosteroids to social interactions is also available. In particular, brain levels of estradiol (synthesized locally from testosterone by the enzyme aromatase) have been shown to vary within minutes due to a rapid modulation of aromatase activity by phosphorilation (Balthazart et al. 2006; Cornil et al. 2006). Moreover, a recent study on male zebra finches has found that this rapid change in estradiol levels can be elicited in forebrains of males by social interactions with females or when exposed to other males' songs (Remage-Healey et al. 2008).

The second implication of the reciprocal model has to do with the rapid behavioral actions of steroids. The classical mode of action of steroids on behavior involves binding to an intracellular receptor that, in turn, leads to the formation of a hormone–receptor complex. This complex forms dimers that migrate to the cell nucleus where they bind to hormone-responsive elements located in the promoter region of specific genes, thus modulating the transcription of steroid-sensitive genes that encode a variety of proteins relevant for neurotransmission (McEwen and Alves 1999; Baker 2003). The latency for these genomic actions of steroids can range from 1 h to several days, and therefore provides a mechanism for relatively slow responses of behavioral plasticity, such as seasonal changes in behavior, but cannot explain effects of steroids that occur within seconds to minutes and are therefore too rapid to be mediated by changes in DNA transcription (McEwen and Alves 1999; Cornil et al. 2006; Remage-Healey and Bass 2006). Thus, surges in circulating steroid levels that shape rapid changes in social behavior (e.g., steroid modulation of calling behavior in vocalizing fish) (Remage-Healey et al. 2006) must do so through nongenomic actions on neural circuits that encode behavior involving the interaction of steroids with membrane receptors and/or with intracellular signaling pathways (Balthazart et al. 2006; Cornil et al. 2006). In the case of the rapid androgen responses to social cues reported here, nongenomic actions are the most plausible mechanism for the behavioral action of androgens. These can be acting indirectly via aromatization into estrogens in the case of testosterone, or directly in the case of the nonaromatizable 11-ketotestosterone. Both estrogen and androgen membrane receptors have been isolated and characterized in fish gonads (Thomas et al. 2006). The presence of membrane steroid receptors in fish

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brains and their potential behavioral role remain to be explored.

Conclusions

In this article, I reviewed the available evidence that supports a role for socially driven changes in androgen levels in rapid changes in behavior (Reciprocal model). This short-term behavioral plasticity allows for the adjustment of social behavior to changing conditions in the social environment, promoting social competence and with concomitant adaptive benefits for the individual. Therefore, social competence can be seen as a performance trait with expected impact on fitness.

The first question that comes to mind is why should sex steroids produced in the gonads be involved in the regulation of neural circuits underlying behavior, when central neuromodulators could do the job? For long-term changes in behavior the answer seems obvious since the pleiotropic-like effects of steroid hormones on different organismal compartments allow for a coordinated brain–body response to transitions between life-history changes, such that, for example, the expression of reproductive behavior is restricted to individuals with mature gonads and displaying secondary sex characters. For short-term changes in behavior this mechanism is less intuitive. The situated-embodied-dynamical (SED) framework that appeared in the mid-1980s in the computational cognitive sciences, that emphasizes the way in which an individual's behavior arises from the dynamical interaction between its brain, its body and its environment may provide an explanation (Beer 1995; Chiel and Beer 1997) (Fig. 6A). According to this framework the environment in which the animal is placed plays a central role in its behavior, since it imposes constraints and offers opportunities for the individual's actions and gives them meaning (situatedness), and individuals are seen as embodied agents whose behavior is better explained if the physical and physiological aspects of an agent's body are taken into account (embodiment). Hence, the animal's nervous system, its body and its environment are each viewed as dynamic systems that are in continuous interaction (Fig. 6A). As a consequence, the relationship between the parameters of the neural circuits underlying a specific action pattern and behavioral performance is very indirect, passing through several layers of transformations (Fig. 6B). Thus, the same neural parameters may translate into very different levels of performance (Beer 2009). Since evolution will only be acting on behavioral efficacy, all components

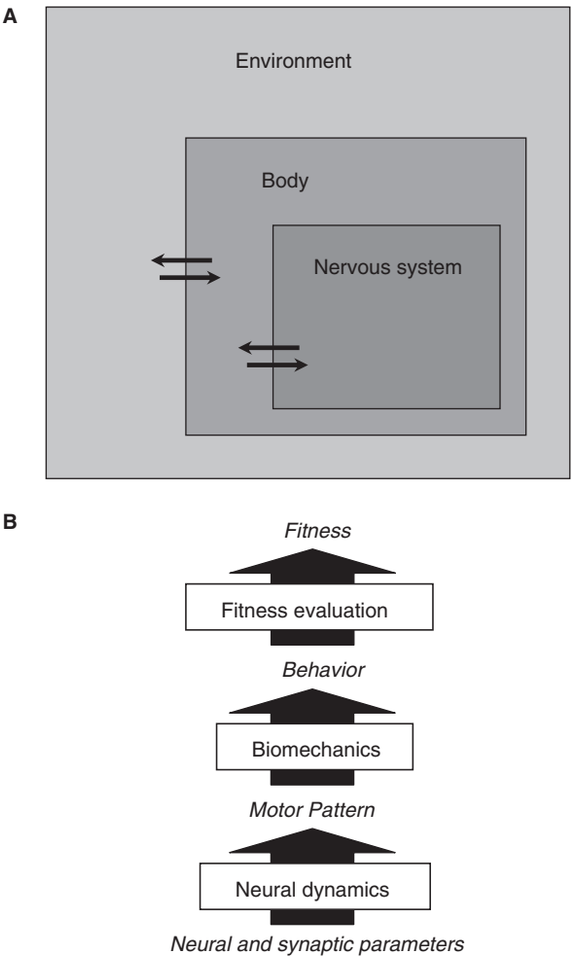

Fig. 6 The situated-embodied-dynamical (SED) framework. (A) Viewpoint of adaptive behavior emerging from an animal's nervous system that is embedded into a body that, in turn, is embedded into a situated environment. Each of these levels is considered a dynamic system that is coupled one to another; behavior is seen as resulting from the interaction between the three systems. (B) Neural parameters are linked to behavioral output by several layers of transformations occurring at the body level where effector systems translate motor programs into motor patterns. Therefore, a linear relationship between neural-dynamics and the outcome of fitness is not expected; the same fitness may result from different neural parameters [Redrawn with permission from Beer RD 2009. Beyond control: the dynamics of brain–body–environment interaction in motor systems. In: Sternad D, editor. Progress in motor control V: a multidisciplinary perspective. Springer. p. 7–24].

in the brain–body–environment system will contribute to the variation in behavioral outcome on which selection will act. Thus, any mechanisms that would couple the best parameters at each level to an optimized behavioral outcome, given a specific environment, should be selected. Hormones may play such a role, since pleiotropic effects of hormones will influence this dynamic system both

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at the neural-dynamics and biomechanical levels (Fig. 6B), thus having stabilizing properties that would channel the system into less variable fitnesses upon which evolution can act.

This approach has the assumption that socially induced transient changes in androgen levels must have an effect not only on neural circuits underlying behavior, but also on body compartments underlying motor patterns relevant for behavioral performance. Consequently, the existence of rapid effects of androgens on the musculo-skeletal system is a crucial condition for further consideration of this hypothesis. So far, the effects of androgens on muscular systems have been mostly restricted to the field of anabolic-androgenic steroid use in sports contexts (see Husak and Irschick, this issue). Most of these studies confirm a positive effect of androgens on the muscular biomechanical properties (i.e., increase in muscle mass and strength) that will promote behavioral performance (Evans 2004). Again, these effects are the result of prolonged hormonal exposure. Fewer studies have been carried out on rapid effects of androgens on muscle physiology. Tsai and Sapolsky (1996) have shown a rapid enhancement effect of small increases in testosterone on metabolism of cultured myotubules (i.e., increased 2-deoxyglucose uptake within 1 min). More recently, Estrada and co-workers (2003, 2004) have shown that administration of testosterone to rat myotubules induces a rapid (<1 min) increase in intracellular calcium levels followed by calcium oscillations, and identified the intracellular signaling mechanisms involved. The rapidity of these anabolic effects indicates again a role for nongenomic actions of androgens through membrane receptors that stimulate early intracellular signaling pathways through interaction with G proteins. Thus, transient changes in testosterone in response to social cues may also have consequences for subsequent muscle physiology, and the assumption of an androgen effect on muscle physiology seems to be fulfilled.

In summary, behavioral plasticity can occur in a continuum from short-term to long-term changes in behavior. In Table 1 a contrast of the characteristics of each type of plasticity at different levels is presented. The reciprocal model specifically applies to short-term behavioral plasticity. This encompasses rapid responses to changes in the social environment that lead to transitions between transient behavioral states that occur within the same life-history stage of the individual. These changes are promoted by activational effects of hormones that will switch the biochemical parameters of neural circuits and biomechanical systems underlying behavior, acting through nongenomic mechanisms. This brain–body coupling achieved by the pleiotropic effects of hormones that allow for fast responses to environmental change, impose constraints on evolutionary change since the action of selection will be limited to circulating levels of the hormone. In contrast, changes in behavior that occur when an animal goes from one life stage to another, as it happens when individuals become sexually mature or gain, or lose, status in stable social hierarchies, with consequences for their reproduction, are slow and resilient leading to the emergence of different behavioral traits between individuals in different stages (e.g., dominant versus subordinate) (e.g., Desjardins and Fernald 2008). These changes are promoted by organizational-like effects of hormones that reorganize, through genomic mechanisms, the structure of the underlying neural circuits and musculoskeletal systems involved in the behavior. Thus, at this level of behavioral plasticity the responses can be compartmentalized with selection being able to act on different levels of the hormone signaling pathway (e.g., target tissue sensitivity), which will increase evolutionary opportunity because different

Table 1 Mechanisms mediating behavioral changes at different levels of organization.

Behavioral plasticity	Short-term	Long-term
Latency of response	Rapid	Slow
Temporal expression	Transient (states)	Resilient (traits)
Type of variation	Behavioral plasticity (intra-individual)	Behavioral profiles (inter-individual)
Developmental scale	Within life-history stages	Between life-history stages
Hormonal mechanisms	Activational	Organizational
Cellular mechanisms	Nongenomic	Genomic
Neural and biomechanical mechanisms	Biochemical switching	Structural (re)organization
Evolutionary mechanisms	Selection acting on circulating levels ("evolutionary constraint hypothesis")	Selection acting on target tissue sensitivity ("evolutionary potential hypothesis")

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phenotypes will potentially result from the combination of different traits at each level (see Hau 2007 and McGlothlin and Ketterson 2008 for discussions on the role of hormone-mediated suites of characters as adaptations or evolutionary constraints).

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