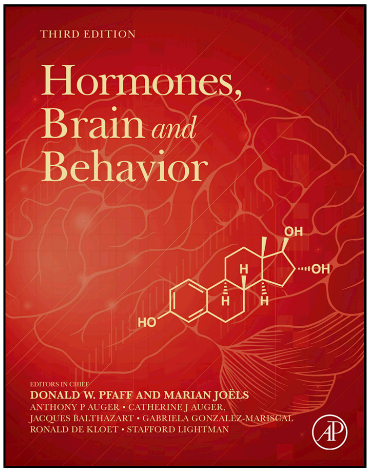

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2.01 Neuroendocrinology of Social Behavior in Teleost Fish

David Gonçalves, University of St. Joseph, Macao, China
Ana S Félix, Gulbenkian Institute of Science, Oeiras, Portugal; and ISPA – University Institute, Lisbon, Portugal
Rui F Oliveira, Gulbenkian Institute of Science, Oeiras, Portugal; ISPA – University Institute, Lisbon, Portugal; and Champalimaud Neuroscience Program, Lisbon, Portugal

2.01.1 Introduction

Animals need to interact with other members from the same species in order to survive and reproduce successfully, and the set of behaviors used in these social interactions are labeled social behaviors. From a functional perspective, these social behaviors can be classified into major groups according to the type of interaction in which they are expressed, namely, aggressive, mating, parental, and prosocial. Interestingly, despite their different functions, all these types of social behaviors seem to share a common underlying mechanism, composed of a neural network, recently named the social decision-making network (SDMN) (O'Connell and Hofmann, 2012a, 2011), whose overall state parallels the expression of the specific type of social behavior expressed in a given moment in time, such that the state of the network is a better predictor of social behavior than the activity of a specific brain region (Goodson and Kabelik, 2009; Teles et al., 2015). Moreover, the fact that all nodes in this network express receptors for steroid hormones and for neuropeptides opens the possibility for its neuromodulation and concomitantly for the regulation of its behavioral output by these agents. Thus, by acting on the SDMN, hormones can regulate the expression of social behavior and integrate it with the organismal state of the individual. Hormones can also regulate the social behavior of animals other than the one in which they are produced when they act as hormonal pheromones. In such cases, hormones are released into the environment and act on receptors located in sensory tissues of other individuals triggering changes on their behavior. In this chapter we will use the conceptual framework sketched above to illustrate how hormones regulate social behaviors in teleost fish.

2.01.2 The Social Decision-Making Network

2.01.2.1 Short History of the Concept

In 1999, Newman challenged the neuroscientific community by proposing the existence of a core set of brain areas that collectively regulate social behavior in mammals. Each one of these areas is reciprocally connected with the others, contains sex steroid hormone receptors, and it is involved in the activation or regulation of several social behaviors. It was designated as social behavior network (SBN), and it is composed of six limbic areas: the lateral septum (LS), the medial extended amygdala (medial amygdala, meAMY, and bed nucleus of the stria terminalis, BNST), the medial preoptic area (POA), the anterior hypothalamus (AH), the ventromedial and ventrolateral hypothalamus (VMH), all localized in the forebrain, and the midbrain periaqueductal gray and tegmentum (PAG/CG), lying in the midbrain. Her model was based on a considerable amount of behavioral, neuroanatomical, and neuroendocrine evidences from diverse studies in rodents and other mammals, which used electrical stimulation, neuropharmacological manipulations, specific brain lesions, and detection of immediate early gene (IEG) expression. Together, these data show that common areas jointly influence sexual, parental, or even aggressive behavior, counteracting the idea of one area (or even a separate minicircuit) is determining a specific behavior. Instead, all these areas represent the nodes of a neuroanatomical network, whose dynamic activation patterns are responsible for multiple behaviors. For instance, male sexual behavior would be the result of successive behavioral responses such as sniffing, mounting, ejaculation, or grooming, which altogether are activated by this integrated circuit and modulated by environmental stimuli and sex steroids. Newman also

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highlighted that species and sex differences in social behaviors are a consequence of brain organization and connectivity divergences, influenced by variations in hormone sensitivity along development, on this central network.

Later, Goodson (2005) expanded the same framework to other nonmammalian vertebrates describing important evidences for birds and teleost fish, and providing foundations for the evolutionarily conservation of the SBN in vertebrates. He also contributed to a better insight into this network by adding the role of peptidergic neuromodulation such as arginine vasotocin (AVT, homologue of mammalian arginine vasopressin) or isotocin (IT, homologue of oxytocin) on social behavior and specifically as an integrating component of SBN.

More recently, O'Connell and Hofmann (2012a, 2011) proposed that social behavior would be regulated by an even wider network. The SDMN would include SBN and the mesolimbic reward system. The latter system is the brain circuit responsible for the evaluation of the salience of a stimulus (via dopaminergic signaling) prior to the behavioral response, which in turn is elicited by the former network. Thus, the reinforcing/rewarding component of social behavior as a substantial feature of an individuals' adaptive response to the environment is the main argument of the authors. The mammalian mesolimbic reward system is constituted by the striatum (Str), the nucleus accumbens (NAcc), the ventral pallidum (VP), the basolateral amygdala (blAMY), the hippocampus (Hyp), the ventral tegmental area (VTA), and the LS and the meAMY/BNST, overlapping with nodes of the SBN. The authors performed a comparative analysis of the two neural circuits in five vertebrate lineages: mammals, birds, reptiles, amphibians, and teleost fish. Putative brain homologies were described based on neuronal connections, the presence of steroid hormone receptors, gene expression, neurochemistry, developmental and behavioral studies. Concurrently, they provided a very useful resource to study the neural substrates responsible for social behavior in vertebrates and a relevant framework to make species comparisons.

Nevertheless, attention must be drawn to the fact that some proposed homologies are not complete, instead they are only partial. In that sense, in a recent review, Goodson and Kingsbury (2013) proposed the inclusion of the paraventricular nucleus (PVN) of the hypothalamus within the mammalian POA node (i.e., POA/PVN), in order to comprehend vasopressin–oxytocin nonapeptide neurons crucial for the regulation of social behavior. With this incorporation the POA/PVN mammalian node would be similar to the anamniotes POA node.

On the other hand, for some nonmammalian species, homologies of the SDMN nodes are not clear, and functional studies are still missing, especially for the mesolimbic reward system (Goodson and Kingsbury, 2013). So, despite being strongly supported in mammals, for other taxa, the SDMN must be cautiously evaluated and tested.

2.01.2.2 Homologies between Teleost Fish and Mammalian Brain Areas in the SDMN

In teleosts, the SBN is assumed to be composed by the ventral (Vv) and lateral (Vl) part of ventral telencephalon, supracommisural part of the ventral pallium (Vs), POA, ventral tuberal region (vTn), anterior tuberal nucleus (aTn), all localized in the forebrain, in addition to the PAG, lying in the midbrain (O'Connell and Hofmann, 2011). On the other hand, the mesolimbic reward system is presumably constituted by the dorsal (Vd) and central (Vc) part of the ventral telencephalon, the medial part of the dorsal telencephalon (Dm), the lateral part of the dorsal telencephalon (Dl), the posterior tuberculum (TPp) on the midbrain, and also Vv/Vl and Vs, that are also nodes of the SBN (O'Connell and Hofmann, 2011; **Figure 1**).

Both Vv and Vl seem to be homologous of mammalian LS region. Cholinergic neurons were detected only in this telencephalic area. It is reciprocally connected to several important nuclei, and it expresses sex steroid receptors (see Wullimann and Mueller, 2004; O'Connell and Hofmann, 2011 for more details). It is also involved in reproductive behavior since electrical stimulation of Vv in Sockeye salmon, *Oncorhynchus nerka*, elicits females' digging and spawning while Vv and Vs ablation in the goldfish *Carassius auratus* impairs male ejaculation (Kyle and Peter, 1982; Satou et al., 1984). Vs is putatively homologous of meAMY/BNST based on developmental evidences, as well as neurochemical and connectivity similarities (see Wullimann and Mueller, 2004; O'Connell and Hofmann, 2011 for further details), even though some consider that ventral telencephalon (Vp) should also be included within this node (Goodson and Kingsbury, 2013). The teleost POA homology is well established. This node that is imperative for the regulation of sexual, parental, and aggressive behaviors (Demski and Knigge, 1971; Macey et al., 1974; Satou et al., 1984; Wong, 2000) is localized in the hypothalamus along the third ventricle, just like in mammals. It is divided into three subregions according to cell size: parvocellular, magnocellular, and gigantocellular, and it is reciprocally connected with the telencephalon and other hypothalamic regions (reviewed in O'Connell and Hofmann, 2011). vTn is the putative homologous of AH because it is localized between the POA and the ventral hypothalamus, it receives and sends projections to several hypothalamic regions, and it expresses sex steroid receptors (O'Connell and Hofmann, 2011 reviewed this information). However, functional studies are yet not available to confirm this homology. aTn was proposed to be the teleost equivalent of VMH, although only a subset of aTn cells are actually homologous (Goodson and Kingsbury, 2013). Lying in the ventrocaudal region of the hypothalamus, it is reciprocally connected with several parts of the telencephalon and contains sex steroid hormone receptors (reviewed in O'Connell and Hofmann, 2011) but functional studies are as well limited. PAG is also present in teleosts, located near the torus semicircularis and receiving and sending projections to several other nuclei (see O'Connell and Hofmann, 2011 for more information). Functionally, it is associated with social communication, specifically, in sound production of the plainfin midshipman *Porichthys notatus* (Kittelberger et al., 2006). Vc is comparable to Str in mammals, while Vd seems homologous to NAcc, but this is only supported by neurochemical studies and some hodological evidences (consider Wullimann and Mueller, 2004; O'Connell and Hofmann, 2011 for more details). Unfortunately, a homologous for the mammalian VP node has not yet been identified. Dm is the putative homologous of blAMY based on developmental, tract tracing, and lesions studies, demonstrating its implication in emotional

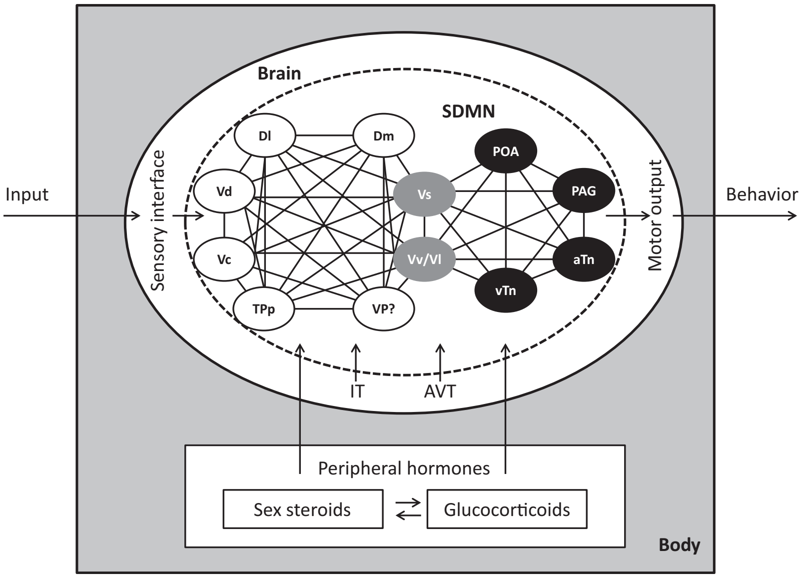

Figure 1 Representation of the interaction between hormones and the social decision-making network (SDMN) within teleosts' social behavior: putative nodes of the mesolimbic reward system in white – dorsal (Vd) and central (Vc) part of the ventral telencephalon, medial part of the dorsal telencephalon (Dm), lateral part of the dorsal telencephalon (Dl), posterior tuberculum (TPp) – and the social behavior network in black – medial preoptic area (POA), ventral tuberal region (vTn), anterior tuberal nucleus (aTn), and midbrain periaqueductal gray (PAG). Ventral and lateral (Vv/Vl) part of ventral telencephalon and supracommisural part of the ventral pallium (Vs), overlapping nodes of the social behavior network and the mesolimbic reward system, are in gray. A homologous for the mammalian ventral pallidum (VP) node has not yet been identified. AVT, arginine vasotocin; IT, isotocin.

learning, as shown in mammals (reviewed in O'Connell and Hofmann, 2011; Portavella et al., 2002). The homologous of Hyp is considered to be the Dl mainly because of its involvement in spatial learning (Dl lesions of *C. auratus* impair maplike memory representations, Rodríguez et al., 2002), besides some of its hodological features (reviewed in O'Connell and Hofmann, 2011). Finally, even though amphibians and teleosts lack a midbrain dopaminergic population, TPp, located in the ventral diencephalon, has been suggested to present homologies to VTA, the A10 dopaminergic cell group, because of its dopaminergic ascending projections to Vd and conserved neurochemical patterns (see O'Connell and Hofmann, 2011 for details). However, this seems to be refutable as a recent study on the zebrafish, *Danio rerio*, 'projectome' underlines that posterior tuberculum cells (DC2 and DC4–6 cell groups) seem homologous to A11 mammalian dopamine neurons based on transcription factor conservation and projection patterns (Tay et al., 2011). Actually ascending projections to telencephalon are scarce (and only from DC2 and DC4 neuronal cells), while the most important dopaminergic connections between the subpallium and the ventral diencephalon are descending (Tay et al., 2011). Consequently, the existence of a mesolimbic reward system in fish is questionable since the connection between the VTA and forebrain regions is considered the core of the dopaminergic reward system (Bromberg-Martin et al., 2010; Spanagel and Weiss, 1999).

2.01.2.3 Functional Analysis of the SDMN in Teleost Fish

A recent study in zebrafish functionally tested the SDMN concept. In this study, IEG expression was determined along selected nodes of the SDMN while animals were in different behavioral states (Teles et al., 2015). The aim of this work was to test for functional brain specialization or alternatively for functional connectivity and, for example, determine whether expression of social behavior is explained by the activation of a single node or by the overall combination of the activity in the various nodes. They quantified IEG expression in the brains of winners and losers of agonistic fights, as well as in individuals who only experienced mirror fights and compared them with a reference noninteracting group. IEG-transcription patterns of *c-fos* and *egr-1* as measured by qPCR were used as markers of neuronal activity in the Vv, Vs, POA, Dm, and Dl. The similarity of IEG activation between groups and areas showed that there were no patterns of localized activity in a specific nucleus. Instead socially driven behavioral states demonstrated patterns of functional connectivity across the nodes. The notion of an SDMN is therefore supported in a teleost fish.

On the other hand, a considerable number of studies centered on the behavioral responses of teleost fishes have documented the activation of specific SDMN nodes, hence establishing their involvement in the regulation of social behavior. For instance, Desjardins et al. (2010) focused on how mate information impacts female neural activity. In this work, they measured IEG (*c-fos* and *egr-1*) expression levels by qPCR in gravid females of the Burton's mouthbrooder cichlid, *Astatotilapia burtoni*, that saw their preferred males winning or losing a fight. They looked specifically to the Vv (LS), POA, vTn (AH), aTn (VMH), PAG, Dm, and Dl. Results demonstrate that the POA and VMH, two nuclei known to be involved in the control of reproduction, are highly activated when females see their preferred male winning, whereas IEG response in the mammalian LS homologue region (a nucleus associated with anxiety) is elicited when females see the male losing.

O'Connell et al. (2013) directed their interest to how individuals integrate social information. These researchers presented *A. burtoni* males with different social stimuli and discovered that visual information (seeing a female or a male) is sufficient to elicit *c-fos* transcription in dopaminergic neurons of Vc, and this transcription is significantly correlated to aggressive behavior in the case of exposure to an intruder male. These data suggest that Vc seems to be involved in assessing stimulus visual valence. Another interesting survey was also carried out in this species. Since *A. burtoni* males can reversibly switch between dominant and subordinate status and rapidly present distinct phenotypes, investigators examined IEG levels in several brain areas of males ascending or descending in social status, as compared with control individuals (Maruska et al., 2013a,b). In socially ascending males, both *c-fos* and *egr-1* levels were higher than in control males in all the SDMN nuclei (Vv, Vs, POA, vTn, aTn, Dm, and Dl) (Maruska et al., 2013b). Descending males presented different activation patterns for *c-fos* and *egr-1* across the same areas. *c-fos* expression levels were increased in the Vs, POA, and aTn by comparison with controls while *egr-1* mRNA levels were higher in the Vv, Vs, vTn, Dm, and Dl (Maruska et al., 2013a). Another relevant study used the monogamous cichlid *Amatitlania nigrofasciata* as a model to study the influence of IT in parental care (O'Connell et al., 2012). The authors compared males housed with their mate (control males), single fathers who had the mate removed or lone males (mate and offspring removed), and quantified *c-fos* expression in Vv, POA, and the central part of the dorsal telencephalon (Dc). At the behavioral level, only single fathers increased paternal care immediately after removal of their mate, and they also presented significantly higher IEG activity levels in Vv compared to lone males, as well as increased *c-fos* expression in the parvocellular POA IT neurons. Together these data suggest that IT promotes paternal care after mate removal and that Vv and POA are important brain areas in this process. Finally, a very interesting study with *P. notatus*, where reproductive behavior is intimately associated with social acoustic signals, measured *c-fos* activation in several brain nuclei including vTn, aTn, and TPp (Petersen et al., 2013). The authors report a significant increase of IEG expression in aTn and TPp of males exposed to acoustic signals of other males compared to control males, showing the importance of these nuclei in social reproductive communication in this species.

2.01.3 Endocrine Regulation of Social Behavior in Teleost Fish

The pioneering work of Arnold Berthold on the endocrine regulation of sexual behavior in animals demonstrated the influence of a 'blood-borne product' released in peripheral glands on behavior (Berthold, 1849). Likewise, early studies on the endocrine regulation of behavior in fish focused on the role of hormones produced in the periphery, mainly gonadal steroids, prostaglandins, and corticosteroids, and there is now substantive information on the role of these hormones as modulators of social behavior. However, in some cases, the expression of social behavior seems to be independent from hormones produced in the periphery, and the role of brain-synthesized hormones, in particular neurosteroids and neuropeptides, has been receiving increasing attention (for a review see Gonçalves and Oliveira, 2010; Oliveira and Gonçalves, 2008).

Regardless of the source, still little is known on how molecular and cellular mechanisms of hormonal action in the brain modify social behavior in fish. The recent concept of the SDMN is useful as it allows studies on the neuroendocrine modulation of social behavior to be focused in relevant brain areas. As described above, recent work has addressed the interplay between social environment and activation of the nodes of the SDMN using IEG as proxies of neuronal activity (e.g., Desjardins et al., 2010; Teles et al., 2015). However, studies investigating the regulatory role of hormones in the functionality of the SDMN are still scarce in spite of the fact that major modulatory effects of hormones in the SDMN are expected, as evidenced by the widespread distribution of hormone receptors in its nodes. In particular, estrogen (*P. notatus*, Forlano et al., 2005; *Micropogonias undulatus*, Hawkins et al., 2005; *D. rerio*, Menuet et al., 2002; *A. burtoni*, Munchrath and Hofmann, 2010; *Dicentrarchus labrax*, Muriach et al., 2008), progesterone (*A. burtoni*, Munchrath and Hofmann, 2010), androgen (*P. notatus*, Forlano et al., 2010; *C. auratus*, Gelinas and Callard, 1997; *A. burtoni*, Harbott et al., 2007; Munchrath and Hofmann, 2010), vasotocin (*A. burtoni*, Huffman et al., 2012; rock hind, *Epinephelus adscensionis*, Kline et al., 2011), and IT (*A. burtoni*, Huffman et al., 2012) receptors are widely distributed along the areas of the SDMN (see also Diotel et al., 2011).

Below we review the evidence for the endocrine modulation of different types of social behavior in fish, addressing their possible mechanisms of action at the brain level.

2.01.3.1 Aggressive Behavior

Different categories of hormones, notoriously gonadal steroids, corticosteroids, and nonapeptide hormones, have been associated with the regulation of aggressive behavior in fish. For gonadal steroids, early evidence demonstrated that male dominance correlated with circulating androgen levels, in particular with the nonaromatizable androgen 11-ketotestosterone (11KT; for a review, see Oliveira and Gonçalves, 2008; Oliveira et al., 2002). Classical castration–androgen replacement experiments suggested an effect of gonadal androgens in aggression, and a meta-analysis confirmed that exogenous administration of androgens promotes aggression in fish (Hirschenhauser and Oliveira, 2006). In one of the best studied models in this respect, the cichlid *A. burtoni*, a change from a submissive to a dominant status in males increases the expression of the GnRH1 gene and the concomitant production of its peptide in neurons of the POA, inducing gonadal development and a surge in plasma 11KT levels within 30 min (Francis et al., 1993; Maruska and Fernald, 2010; White et al., 2002). Interestingly, in this species a submissive experience seems to have more rapid and more profound physiological consequences than a dominant one as aggressive behaviors were reduced more promptly in males undergoing a descent in social status than they emerged in animals ascending in social status (White et al., 2002). Similarly, in zebrafish males, losing a fight induces a more pronounced change in future aggressive behavioral displays and in the neurogenomic state of the whole brain than winning (Oliveira et al., 2011, 2016).

Aggression in females has been much less investigated although, interestingly, the role of androgens in the modulation of aggressive displays seems to be more consistent than for males. In the Mozambique tilapia, plasma testosterone (T) levels in females peak during a phase of the reproductive cycle that matches increased aggression (Oliveira and Canário, 2000). In the cichlid *Neolamprologus pulcher*, females and males jointly defend a territory all year round and females were shown to be more aggressive than males in response to a territorial intrusion and to experience a higher increase in androgen levels (including 11KT, usually undetected in females, Desjardins et al., 2006). Similarly, in the blue acara, *Andinoacara pulcher*, T administration increased aggressive behavior in females (Munro and Pitcher, 1985) and daily injections of T to females of the Siamese fighting fish *Betta splendens* for a period of 9 weeks increased aggression directed toward males, although it decreased aggression directed toward females (Badura and Friedman, 1988). Finally, in all-female groups of *A. burtoni*, it was observed that females start to exhibit typical male behaviors, including territorial and aggressive displays (Renn et al., 2012). In this experiment, dominant females had higher T levels when compared with subordinates and T levels correlated with aggressive displays like chasing and threatening.

In birds and mammals, the central effects of androgens on aggressive behavior seem to depend on the aromatization of T into estradiol (E2) (Trainor et al., 2006). In fish, however, in spite of aromatase being abundant in nuclei of the SDMN (e.g., Forlano et al., 2001), there are conflicting results on the role of aromatization in aggression. Several lines of evidence suggest a direct action of androgens in the expression of aggressive behavior in fish: (1) androgen receptors are widely distributed in nuclei of the telencephalon and diencephalon, including in areas of the SDMN (e.g., Harbott et al., 2007); (2) differences in plasma androgen levels between aggressive and less aggressive phenotypes seem to be more evident for the nonaromatizable androgen 11KT than for T (Oliveira, 2005) and the peripheral administration of 11KT has been shown to promote aggression in teleosts (e.g., Rodgers et al., 2013); (3) in some species, peripheral administration of estrogens has an inhibitory effect on male aggression (e.g., three-spined stickleback, *Gasterosteus aculeatus*, Bell, 2001; *B. splendens*, Clotfelter and Rodriguez, 2006; *D. rerio*, Colman et al., 2009; Filby et al., 2012; peacock blenny, *Salaria pavo*, Gonçalves et al., 2007; *A. pulcher*, Munro and Pitcher, 1985; sand goby, *Pomatoschistus minutus*, Saaristo et al., 2010); and (4) whole brain aromatase activity was shown to be inversely correlated with aggression in females of the sex-changing blue-banded goby, *Lythrypnus dalli* (Black et al., 2005), suggesting that a higher availability of T (or a decrease in E2 synthesis) promotes aggression. Contrarily, in the cichlid *A. burtoni*, E2 administration increased male aggression (O'Connell and Hofmann, 2012b) and pharmacologically blocking aromatization with Fadrozole decreased these behaviors in the same species (Huffman et al., 2013) and also in the weakly electric fish *Gymnotus omarorum* (Jalabert et al., 2015). This would suggest that aromatization of T into E2 is needed to promote male aggressive displays in these species. Clearly, more data are needed to interpret the divergent results across species and understand what the general pattern in fish is.

The above data suggest that a dominance experience (e.g., winning fights) activates the hypothalamic–pituitary–gonadal axis, increasing the secretion of gonadal androgens that in turn act on different tissues to promote the expression of a dominant phenotype, including increased aggression, via effects on the brain (and the reverse for submissive experiences). This feedback between the environment and behavior, translated via neuroendocrine modulation by androgens, would allow animals to dynamically adjust their behavior and physiology to a particular social context (Oliveira, 2004). However, the hypothesis that high levels of aggression are maintained through a positive effect of gonadal androgens in the brain is contradicted by other studies. The majority of studies where males were gonadectomized during the breeding season, thus reducing the circulating levels of androgens, failed to find a significant effect on male aggression (reviewed in Gonçalves and Oliveira, 2010). As an example, in the Mozambique tilapia gonadectomy impaired the expression of reproductive behaviors in males, including nest building and courtship displays, but did not affect aggressive behavior toward a conspecific male (Almeida et al., 2014). Also, in the social sex-changing bluehead wrasse *Thalassoma bifasciatum*, gonadectomy did not prevent female-to-male behavioral change, including an increase in the expression of aggressive behavior, when females were given an opportunity to occupy a vacant territory (Godwin et al., 1996). Finally, variation in aggressive behavior has been shown to occur in immature individuals and animals outside the breeding season, questioning the hypothesis of aggression being modulated by gonadal androgens in these contexts. For example, in the *G. omarorum*, high levels of aggression were decoupled from 11KT levels outside the reproductive season (Jalabert et al., 2015) and in the damselfish *Stegastes nigricans*, also a year-round territorial species, androgen levels did not increase when an aggressive challenge was presented to males (Ros et al., 2014).

The contradictory results found for the effect of sex steroids on aggressive behavior have driven the search for alternative modulators of aggression. A pathway that has also been shown to relate with the neuroendocrine modulation of aggression in fishes is the hypothalamic–pituitary–interrenal axis. In the abovementioned study in *S. nigricans*, where androgens failed to respond to an aggressive challenge, cortisol levels in the plasma increased after males were presented with intra- and interspecific challenges, and its concentration was strongly correlated with aggressive behaviors (Ros et al., 2014). Also, in the cichlid *A. pulcher*, cortisol administration increased aggression toward a model intruder (albeit not toward a mirror image, Munro and Pitcher, 1985). In juvenile rainbow trout, *Oncorhynchus mykiss*, cortisol administration failed to promote aggression 1 h after being administered, but pharmacological blockage of GR and MR receptors reduced aggression levels, suggesting that basal levels of cortisol were contributing to aggressive behavior via activation of intracellular GR and MR receptors (Schjolden et al., 2009). Nevertheless, prolonged (48 h) exposure to cortisol reduced aggression, suggesting a complex time-dependent effect of this hormone in aggressive behavior (Øverli et al., 2002).

AVT and IT have also been implicated in the regulation of aggression, and more generally social behavior, in fishes (reviewed in Godwin and Thompson, 2012). AVT neurons occur in the POA and project to the neurohypophysis, releasing AVT into circulation when activated, but also project to many other brain regions, including the ventral telencephalon, thalamus, and mesencephalon (for details on the neuroanatomy of the AVT system in fish, see Godwin and Thompson, 2012; Huffman et al., 2012; Thompson and Walton, 2013). Within the POA, three subpopulations of AVT neurons can be identified; parvocellular, magnocellular, and gigantocellular, and they have been suggested to play different roles in osmoregulation and modulation of behavior (Greenwood et al., 2008). Receptors for both AVT and IT have been found throughout nuclei of the SDMN, suggesting a direct neuromodulatory action of these neuropeptides in nodes of this brain network (Huffman et al., 2012; Lema, 2010).

Following studies in mammals that associated AVP with increased expression of aggressive behavior, AVT has also been implicated in the regulation of aggression in fishes, although with inconsistent results between species. A positive effect of AVT on aggression has been described for some species, as, for example, nonterritorial phase males of *T. bifasciatum* (Semsar et al., 2001), males of the damselfish *Stegastes leucostictus* (Santangelo and Bass, 2006), and males of *A. nigrofasciata* (Oldfield and Hofmann, 2011) while a suppressive effect of AVT on aggression has been described for other species, as, for example, territorial phase males of *T. bifasciatum* (Semsar et al., 2001), males of the brown ghost knifefish, *Apteronotus leptorhynchus* (Bastian et al., 2001), males of Amargosa pupfish, *Cyprinodon nevadensis amargosae* (Lema and Nevitt, 2004; but see Lema et al., 2015), and males and females of *D. rerio* (Filby et al., 2010). These contradictory results may have different, but not necessarily exclusive, explanations. In studies with butterfly fish of the genus *Chaetodon*, it was shown that a territorial species had larger AVT-immunoreactive somata within the POA area and higher AVT fiber densities within a number of telencephalic nuclei than a nonterritorial species and that aggression correlated positively with the number of POA gigantocellular AVT cells and negatively with the number and size of POA parvocellular AVT cells (Dewan and Tricas, 2011; Dewan et al., 2008). In the *C. nevadensis amargosae*, telencephalic *pro*AVT mRNA levels were found to be elevated in subordinate males and to correlate with aggression. These males also had higher V1a$_1$ receptor transcript levels in the telencephalon and hypothalamus, as compared with dominant males. On the other hand, the levels of *pro*AVT mRNA were fourfold higher in the hypothalamus of dominant males, which also had higher levels of hypothalamic V1a$_2$ receptor transcript abundance (Lema et al., 2015). This may be interpreted as hypothalamic AVT playing a role in the expression of aggressive behavior in dominant males via the activation of the V1a$_2$ receptor, while AVT action in forebrain targets would promote aggression only in subordinate animals. Greenwood et al. (2008) showed an opposite pattern of AVT mRNA expression in *A. burtoni* parvocellular and magnocellular subpopulations of AVT cells, with territorial males having higher levels of expression of AVT in the gigantocellular layer but lower levels in the parvocellular layer, as compared with nonterritorial males. The authors suggested that gigantocellular neurons might be more related with the modulation of dominance-related traits, including the expression of aggressive behavior, while parvocellular cells may relate to the activation of the stress axis or submissive behaviors. Following this model, Godwin and Thompson (2012) suggest that AVT projections from the POA may regulate 'sociosexual circuits,' including those related with aggression, by modulating neuronal action in central brain regions, including nodes of the SDMN. On the other hand, AVT would also be able to promote submissive and escape behaviors by producing peripheral changes that feedback to the brain. These effects could be induced either directly, via modulation of hindbrain autonomic nuclei that regulate peripheral states, or indirectly, as, for example, through the demonstrated capacity of AVT to stimulate the stress axis (Baker et al., 1996). As a consequence, peripheral, or even central, administration of AVT may have variable effects in behavior as it activates the targets of multiple subpopulations of AVT neurons. In addition, and as demonstrated in mammalian models, the effects of AVP/AVT in behavior are greatly dependent on tissue sensitivity which may vary across phenotypes, developmental stages, or seasons due to variation in the abundance of its receptors (e.g., Walton et al., 2010). Future studies manipulating the AVT system using techniques such as optogenetics, transgenics, or others may offer an opportunity to investigate the exact function of the different subpopulations of AVT neurons and subtypes of receptors in the modulation of aggression, and other categories of social behavior, in fish.

The effect of IT on aggressive behavior in fish has been less investigated. In the plainfin midshipman, IT administered to the POA-AH elicited fictive aggressive vocalizations in a neurophysiological preparation of parasitic (sneaker) males but not of territorial males (Goodson and Bass, 2000). On the other hand, IT administered to males of the beaugregory damselfish had no effect in aggressive displays (Santangelo and Bass, 2006), and similar results were found in females and males of the cichlid *N. pulcher* (Reddon et al., 2012). Further studies are needed before a role for IT in the modulation of fish aggression can be established.

Finally, hormones involved in somatic growth, in particular the growth hormone (GH) and somatostatin (SS), have also been proposed as modulators of aggressive behavior in fish. These hormones are synthesized at the level of the hypothalamus projecting to somatotropes in the pituitary. In *A. burtoni*, SS seems to inhibit the expression of aggressive behavior in a dose-dependent fashion and independently of any potential effect in gonadal androgen secretion (Trainor and Hofmann, 2006). In the rainbow trout, peripheral administration of GH was shown to increase male aggression, but this was interpreted as an indirect effect as GH also increased swimming activity that promoted agonistic encounters (Jönsson et al., 1998). Later, Jönsson et al. (2003) confirmed this hypothesis by administering GH directly into the third ventricle of juvenile rainbow trout and observing also an increase in swimming activity. Interestingly, in the *A. burtoni* study, only chasing behavior, and not threatening behavior, was affected by SS. As SS is known to inhibit the release of GH, the inhibitory effects of SS in aggressive displays could be explained by a decrease in general locomotor activity induced by a reduction in GH levels. These data are also contradictory to the findings of Hofmann and Fernald (2000) showing that dominant males have larger SS immunoreactive neurons in the POA as compared with subordinate animals, suggesting that SS administration should increase aggression if it is directly related with the endocrine regulation of these behaviors.

2.01.3.2 Mating Behavior

The brain regions associated with the expression of sexual behaviors have been extensively described in vertebrates, including fish (for a related review, see Forlano and Bass, 2011). Notoriously, the POA and AH are known to be central brain regions for the control of reproduction as they contain the GnRH neurons that command the release of the gonadotropins LH and FSH from the pituitary, regulating gonadal development and secondarily gonadal steroid secretion. These regions also synthesize neuropeptides relevant for reproduction and are rich in sex steroid receptors. Early studies highlighted the role of this area in reproduction by showing that electrical stimulation of the POA induced reproductive behaviors in male bluegill sunfish *Lepomis macrochirus* (Demski and Knigge, 1971), results later confirmed in the hime salmon *O. nerka* (Satou et al., 1984). As mentioned above, females of the cichlid *A. burtoni*, observing their preferred male winning fights activated the POA (as measured by IEG expression) and also the Vm, another area implicated in female sexual displays in vertebrates (Desjardins and Fernald, 2010). In a study in female Medaka *Oryzias latipes*, mating induced widespread *c-fos* expression in the POA, telencephalon, optic tectum, and cerebellum (Okuyama et al., 2011), suggesting the implication of a widespread set of brain nuclei in female mating behavior. In addition to these central brain regions, hormones can also modulate reproductive displays by acting in sensory or effector systems. As an example, in female midshipman, E2 acts in the inner ear's sacculus to increase the degree of temporal encoding of the frequency content of male vocalizations (Sisneros et al., 2004), thus synchronizing female phonotaxis and receptivity with maturation of the ovaries (for a review, see Sisneros, 2009).

Both female and male reproductive behaviors are expected to be coordinated with gonadal function, and thus hormones of gonadal origin, in particular sex steroids for males and sex steroids and prostaglandins for females, have been seen as main candidates for endocrine regulation of reproductive behaviors in fish.

The main androgens detected in fish plasma are T, 11KT, and 11β-hydroxytestosterone (Borg, 1994). Males have usually higher plasma levels of 11KT than females while T levels often do not differ between sexes (Borg, 1994; Lokman et al., 2002). The impact of manipulating androgen levels in male reproductive displays is highly variable (see Oliveira and Gonçalves, 2008 for a review). While gonadectomy is effective in reducing plasma androgen levels (e.g., Almeida et al., 2014; Gonçalves et al., 2007; Salek et al., 2001), in some cases a concomitant reduction in reproductive behaviors occurs (e.g., *Oreochromis mossambicus*, Almeida et al., 2014; *G. aculeatus*, Hoar, 1962; *Morone americana*, Salek et al., 2001) while in others they are maintained (e.g., *G. aculeatus*, Páll et al., 2002; *T. bifasciatum*, Semsar and Godwin, 2003). Also, exogenous administration of androgens either to gonadectomized or to intact males has variable effects on male mating displays (for a list of studies, see Oliveira and Gonçalves, 2008). For example, androgen administration to gonadectomized males of *M. americana* restored sexual displays, with 11KT being more effective than T (Salek et al., 2001), while 11KT administration to intact males of the rock-pool blenny *Parablennius parvicornis* failed to promote sexual behavior (Ros et al., 2004). Finally, pharmacologically blocking androgen receptors decreased male nesting behavior in *G. aculeatus* (Sebire et al., 2008) and male courtship displays in the guppy *Poecilia reticulata* (Baatrup and Junge, 2001), in agreement with the hypothesis that male mating behaviors are directly facilitated by androgens. The administration of androgens to juveniles, parasitic 'sneaker' males or females, all phenotypes with lower plasma androgen levels than males, likewise produced variable results. In the peacock blenny, T implants inhibited female-like displays in castrated parasitic males but failed to promote nesting male behaviors (Gonçalves et al., 2007), while in *C. auratus* T and 11KT implants given to intact females induced the full-suite of male sexual behaviors (Stacey and Kobayashi, 1996).

The variable results obtained between studies of the effects of androgens on male sexual behavior surely have multiple causes, including differences in hormone concentrations, type of androgens and antiandrogens used, hormone delivery mode, species-specific differences, season when experiments were performed or duration of exposure to the hormone, just to mention a few. Nevertheless, the overall pattern suggests that androgens have a positive effect on male sexual displays also in fish.

The central effects of androgens on male displays and in particular their potential action in the nodes of the SDMN are still poorly understood. In mammals, aromatization of T into E2 in the brain plays a crucial role in the regulation of male sexual behavior (reviewed in Ball and Balthazart, 2004; Baum, 2003). However, although aromatase is abundant in the areas of the SDMN and partly colocalizes with androgen receptors (Forlano et al., 2010; e.g., Gelinas and Callard, 1997; Harbott et al., 2007), the evidence for aromatization playing a role in the activation of male sexual displays in fish via local conversion of T into E2 is less obvious than in birds or mammals. In fact, in some studies the nonaromatizable 11KT seems to have a more effective role in the induction or recovery of male sexual displays than the aromatizable T (e.g., Stacey and Kobayashi, 1996), and pharmacologically blocking aromatization with Fadrozole was shown to inhibit male displays in *P. reticulata* (Hallgren et al., 2006) but not in *A. burtoni* (Huffman et al., 2013). Also, exposure to estrogens or xenoestrogens generally reduces male sexual displays (e.g., *P. reticulata*, Bayley et al., 1999; *C. auratus*, Bjerselius et al., 2001; Colman et al., 2009; *D. rerio*, Pradhan and Olsson, 2015). Furthermore, while androgens masculinize the electric organ discharge signal in ghost knifefishes, estrogens feminize it (reviewed in Smith, 2013). In zebrafish, E2 seems to feminize the male brain and 11KT to masculinize the female brain, as assessed by gene transcriptomic profiling (Pradhan and Olsson, 2015), further supporting a direct action of androgens on male reproductive behavior.

Male sexual displays are often more elaborated than female displays, and consequentially there are more published studies testing the effect of endocrine manipulations in sexual behavior in males than in females. The regulation of female sexual behavior was initially hypothesized to be controlled by gonadal hormones and determined by the mode of reproduction (Stacey, 1981). In internal fertilizers, sexual behavior and fertilization are temporally dissociated, and sex steroids were proposed to regulate female displays. By contrast, in external fertilizers, female sexual behavior was considered to be mostly restricted to oviposition, which may be regarded as homologous to parturition. Thus ovarian prostaglandins, which induce uterine contractions in mammals and oviposition in fishes (Jalabert and Szöllösi, 1975), were proposed to modulate female spawning behaviors. This idea was originally proposed based mainly on data for *P. reticulata*, an internal fertilizer, and *C. auratus*, an external fertilizer, but new evidence suggests that the sex steroid and prostaglandin pathways may actually be complementary. In a sex-role reversed population of the peacock blenny, an external fertilizer, females court males with very elaborate displays (Gonçalves et al., 1996), providing an opportunity to test the effects of endocrine manipulations in female sexual behavior. Ovariectomy was effective in quantitatively reducing the expression of female courtship displays and nuptial coloration 2 weeks after the removal of the ovaries but still a majority of ovariectomized females (9 out of 13) courted at least once a nesting male, showing that removal of the ovaries does not completely suppress the expression of sexual behavior (Gonçalves et al., 2014). Interestingly, both the steroid E2 and the prostaglandin PGF2α restored female sexual displays (but not nuptial coloration), although PGF2α was more effective than E2 in this respect. In the same population, parasitic males that mimic female displays occur and the removal of the testes in these males has the paradoxical effect of promoting even further the expression of female-like behaviors (Gonçalves et al., 2007). This is probably explained by the fact that androgens suppress female-like displays in sneaker males (Gonçalves et al., 2007; Oliveira et al., 2001), and removing the testes reduces circulating androgen levels, releasing this inhibition (Gonçalves et al., 2007). Because E2 levels are very low in sneaker males and E2 administration does not promote female-like displays (Gonçalves et al., 2007), other neuroendocrine mechanisms are proposed to regulate these behaviors (see below).

Prostaglandins have been shown to promote female displays in other externally fertilizing species, including the paradise fish, *Macropodus opercularis* (Villars et al., 1985), the black acara *Cichlasoma bimaculatum* (Cole and Stacey, 1984), the barb *Puntius gonionotus* (Liley and Tan, 1985), the cichlid *A. burtoni* (Kidd et al., 2013) and, notoriously, the goldfish *C. auratus* (reviewed in Kobayashi et al., 2002). Recently, Juntti et al. (2016) confirmed this role of PGF2α in *A. burtoni* by showing that the expression of a putative PGF2α receptor in areas such as vagal lobe and POA increase during spawning and that the activation of this receptor is needed for spawning behavior to occur. This evidence suggests that ovarian prostaglandins act in external fertilizing teleost species, and probably also in amphibians, as a short-duration endogenous messenger to synchronize sexual behavior with the presence of mature oocytes in the ovaries. However, alternative explanations exist including the possibility of direct neural communication between the gonads and the brain via the vagal nerve, which would induce neural synthesis of PGF2α and the activation of female reproductive displays (Juntti et al., 2016), or the activation of brain PGF2α synthesis by other ovarian hormones. For example, in mammals, E2 has been found to promote the synthesis of prostaglandins both in the uterus (PGF, Ham et al., 1975) and in the POA (PGE2, Amateau and McCarthy, 2002). It seems possible that the above-described positive effects of both E2 and PGF2α in the activation of sexual displays in ovariectomized females of *S. pavo* could occur via a direct effect of PGF2α in the brain and to a stimulatory effect of E2 in the neural synthesis of PGF2α. Studies investigating in further detail the interconnection between sex steroids and prostaglandins in fish, in particular the effects of gonadal steroids in brain PGF2α synthesis and receptor expression, and the modulation by PGF2α of SDMN nodes look like promising venues for future research.

Nevertheless, evidence that the expression of sexual behavior in fish does not rely on hormones of gonadal origin was obtained by Godwin et al. (1996) who showed that, in the sex-changing wrasse *T. bifasciatum*, females could rapidly occupy a territory left vacant by the removal of the dominant male and express male courtship and spawning displays in the absence of gonads. Hypothalamic abundance of proAVT mRNA in the brain of these females during sex change increases fourfold when compared with nonchanging females (Godwin et al., 2000) and is higher in ovariectomized dominant females than in subordinate females (Semsar and Godwin, 2003), suggesting that AVT may be a key peptide regulating the transition into male sexual displays in this species. However, the effect of AVT seems to be context dependent as AVT administration failed to induce male sexual behaviors when a dominant male was present (Semsar and Godwin, 2004). Interestingly, 11KT administration also promoted male displays in subordinate ovariectomized females but did not change AVT hypothalamic levels (Semsar and Godwin, 2004, 2003), suggesting that gonadal androgens modulate male reproductive displays via a pathway independent from AVT. The positive effects of AVT on male sexual displays are confirmed by studies in other species (e.g., *A. leptorhynchus*, Bastian et al., 2001; white perch, *M. americana*, Salek et al., 2001). For example, in the gymnotiform *Brachyhypopomus gauderio*, AVT stimulated the production of electric signals used for courtship by direct action on the hindbrain pacemaker cells (Perrone et al., 2010). However, in the cichlid *A. burtoni*, blocking the V1a receptor inhibited aggression and stimulated courtship displays in subordinate males that ascended to become dominant, suggesting that AVT impairs male reproductive displays in this context, although the same manipulation did not produce any effects in stable dominant or subordinate fish (Huffman et al., 2015).

AVT has also been shown to promote female displays. In a sex-role reversed population of the peacock blenny *S. pavo*, AVT mRNA levels were higher in the courting morphs, i.e., in females and in female-mimicking parasitic males, than in noncourting nesting males (Grober et al., 2002). Accordingly, AVT administration promoted sexual displays in females and in parasitic males but not in nesting males (Carneiro et al., 2003).

Taken together, these results suggest that AVT promotes sexual behavior in fishes and, following the model proposed by Godwin and Thompson (2012), this is probably achieved via modulation of central brain areas, including nodes of the SDMN, by AVT projections from the POA.

2.01.3.3 Parental Care

The wide diversity of modes of reproduction in fishes extends to the patterns of care to eggs or juveniles, and examples of no care, paternal, maternal, biparental, or even alloparental care can be found (Breder and Rosen, 1966). This offers an excellent opportunity to study the proximal mechanisms of parental care in vertebrates but not much is known on the brain substrates of parental care in fish. In mammals, the POA, thalamus, BNST, and the LS have been associated with the expression of paternal care (for a review, see Dulac et al., 2014). In fish, the putative homologue for the LS is the Vv, but an equivalent area to the BNST is still ambiguous. Also, Dc, the central part of the dorsal telencephalon, has been suggested to relate with paternal care in bluegill sunfish (Demski and Knigge, 1971). In the only study so far investigating the neural substrates of parental care in fish using IEG, it was shown in the cichlid *A. nigrofasciata* that parental males have a higher activation of the Vv, but not of the POA or Dc, as compared with nonparental males (O'Connell et al., 2012).

Paternal care is more common than maternal care (Breder and Rosen, 1966), and thus the endocrine regulation of parental behavior has been mainly investigated in males. A conceptual framework for the relationship between androgens and parental care was proposed by Wingfield (1990), following the observation in birds that male androgen levels decrease during the parenting phase as compared with the mating phase, even in animals that continue to reproduce after the initiation of parental care (Wingfield, 1984). This hypothesis postulates that androgen levels should be lower during the paternal phase, when social instability is usually reduced, as compared to the mating phase, when males need to compete for territories and sexual partners. In fish, androgen levels drop during the parental phase thus supporting this prediction of the challenge hypothesis (Oliveira et al., 2002). However, there are many exceptions to this pattern (e.g., Rodgers et al., 2006; Ros et al., 2003), and exogenous administration of androgens to parenting males failed to have the expected suppressive effect in parental behavior in some species (T propionate implants in *L. macrochirus*, Rodgers et al., 2012; e.g., 11KT implants in *Parablennius sanguinolentus parvicornis*, Ros et al., 2004). In the context of the challenge hypothesis, the regulation of paternal behavior by androgens is interpreted as a trade-off between parental behavior and androgen-induced aggression. The decrease in androgen levels postulated to occur during the parental phase would decrease the frequency of aggressive behaviors, releasing more energy and time to parental duties. Androgens may thus be better seen as secondary modulators of parental behaviors, more related with aggressive displays, while other hormones are expected to have a more direct regulatory action on specific parental care displays.

Prolactin (PRL) has been suggested as a prime candidate for the endocrine modulation of both paternal and maternal behavior across vertebrates (e.g., Bachelot and Binart, 2007; Schradin and Anzenberger, 1999), including fish (reviewed in Whittington and Wilson, 2013). The first study on the effects of this hormone in fish paternal behavior was conducted in the ocellated wrasse *Symphodus ocellatus* where PRL administration was shown to promote egg fanning behavior in nesting males (Fiedler, 1962). These results were corroborated by studies in other species, both in males (e.g., blue discus, *Symphysodon aequifasciata*, Blüm and Fiedler, 1965; *L. macrochirus*, Kindler et al., 1991; *G. aculeatus*, Páll et al., 2004) and females (e.g., *S. aequifasciata*, Blüm and Fiedler, 1965). However, there are also studies where the expected positive effect of PRL on parental behavior was not observed. In the cooperatively breeding cichlid *N. pulcher*, PRL mRNA levels in the pituitary were not elevated in breeding females as compared with nonbreeding females, and PRL administration to both males and females did not promote parental behavior (Bender et al., 2008). In the Nile tilapia *Oreochromis niloticus*, pituitary and plasma levels of the two PRL isoforms described in fish also did not differ between female mouthbrooding eggs and nonincubating females (Tacon et al., 2000). Nevertheless, PRL II showed high variation during the mouthbrooding period, and the authors did not exclude a possible role of PRL in the regulation of maternal behavior. In a comparative study between a monogamous and a polygynous species of cichlids of the genus *Herichthys*, gene expression levels of PRL and of a PRL receptor in brain macroareas were not associated with paternal care (Oldfield et al., 2013).

Interestingly, sex steroids have been found to interact with PRL, raising the possibility of modulation of parental behavior by sex steroids occurring indirectly via effects in PRL. Estrogens have been found to promote the secretion of PRL from pituitary glands (e.g., *O. mossambicus* Barry and Grau, 1986; rainbow trout *O. mykiss*, Williams and Wigham, 1994). Onuma et al. (2005) report variable effects of E2, T, and 11KT in PRL mRNA expression levels in pituitary cell cultures of masu salmon depending on gender and time in the reproductive season. During the prespawning stage, E2, T, and 11KT increased the expression of PRL mRNA while opposite effects were detected during the spawning stage, suggesting that sex steroids may regulate both positively and negatively PRL secretion. This study also highlights the importance of integrating variation in tissue sensitivity to modulatory agents to understand their mode of action.

Similar to what has been described for oxytocin in mammals, IT has also been found to regulate paternal care in fish. In the monogamous cichlid, *A. nigrofasciata*, *c-fos* expression was higher in POA parvocellular IT neurons in fathers than in nonfathers, and the administration of an IT receptor antagonist blocked paternal care (O'Connell et al., 2012). Interestingly, IT fibers and IT receptors are present in the Vv, a brain area observed to be more activated in fathers than in nonfathers, raising the possibility of stimulatory effects of IT on parental behavior occurring via modulation of neuronal signals in this brain region (O'Connell et al., 2012).

2.01.3.4 Prosocial Behavior

The idea that social bonding, or affiliative behavior, can be regulated by evolutionary conserved brain and neurochemical systems across vertebrates is relatively new. In fact, since the ground-breaking research on the role of AVP and oxytocin in the regulation of social behavior in rodents (reviewed in Young et al., 2011), evidence has been accumulating showing that these nonapeptides, and their nonmammalian homologues, play an important role in social bonding, affiliative behavior, and attention to social stimuli also in other taxa, including fish (reviewed in Godwin and Thompson, 2012). In goldfish, intracerebroventricular administration of AVT and IT has opposite effects in social behavior, with AVT-reducing approach behavior toward a conspecific and IT increasing the duration of this behavior (Thompson and Walton, 2004). The inhibitory effects of AVT seemed to be mediated by AVT cell projections from the POA to the hindbrain (Thompson and Walton, 2009). This was confirmed by showing that the behavioral effects of AVT infusions into the fourth ventricle were more potent than the effects of infusions into the third ventricle (Thompson et al., 2008). Accordingly, it was demonstrated that seasonal changes in behavioral responsiveness to AVT are associated with changes in hindbrain sensitivity to AVT, as measured by the expression of the V1a AVT receptor in this brain region (Walton et al., 2010). In the cichlid *N. pulcher*, peripheral administration of IT seemed to increase responsiveness to socially relevant information during aggressive contests as IT-treated fish fought in accordance with the size of the opponent while control animals fought according to their intrinsic aggressive levels (Reddon et al., 2012). In the monogamous cichlid *A. nigrofasciata*, the peripheral administration of an AVP/IT receptor antagonist to males reduced affiliative behavior although it did not prevent pair bonding nor did it disrupt pair bonding after pairs had been established (Oldfield and Hofmann, 2011). In the cleaner wrasse, *Labroides dimidiatus*, AVT inhibited interspecific cleaning activities while it did not affect other social conspecific behaviors (Soares et al., 2012). In the same study, IT administration failed to affect social behavior. In contrast with previous studies, in *N. pulcher*, IT administered intraperitoneally reduced affiliative behavior and, in a second study, brain IT levels were found to be negatively correlated with these behaviors (Reddon et al., 2015).

Information on the brain areas targeted by AVT or IT to regulate social bonding is still very scarce but Godwin and Thompson (2012) suggest forebrain nodes of the SDMN to be likely candidates for AVT modulation; indeed motor output pathways descending from these regions show dense AVT innervation and project into multiple central targets. New studies selectively manipulating subpopulations of AVT cells will be able to test this hypothesis.

2.01.4 Hormones as Social Semiochemicals

When hormones are released into the environment, either actively or passively, they convey information about the sender that becomes potentially available to other conspecifics, and thus can be seen as social semiochemicals (i.e., chemical cues of conspecific origin). If released hormones have evolved to convey information about the sender and trigger a specific and adaptive response in the receivers, then they can be viewed as pheromones (Sorensen, 2014; Wyatt, 2010). Thus, the evolution of hormonal pheromones has been proposed to follow a cue-signal continuum, where different evolutionary states can be recognized (Sorensen and Scott, 1994; Sorensen and Stacey, 1999; Wisenden, 2014; **Figure 2**). In the ancestral state, senders release hormones into the environment, but potential receivers are unable to detect them. In a second state, receivers evolved the capacity to detect and respond adaptively to the hormone; hence they are now spying on senders based on the hormone that acts as a chemical cue for the internal state of senders. Finally, a third evolutionary state may evolve if the selective pressure imposed by spying on senders leads to the evolution of specialized production and/or release of the hormonal pheromones, which becomes a signal (i.e., true pheromone) according to animal communication terminology (Wisenden, 2014).

An apparently easy way to discriminate between spying and true signaling would be to look for the occurrence of specialized structures in the production and/or release of pheromones. Many such structures have been described among

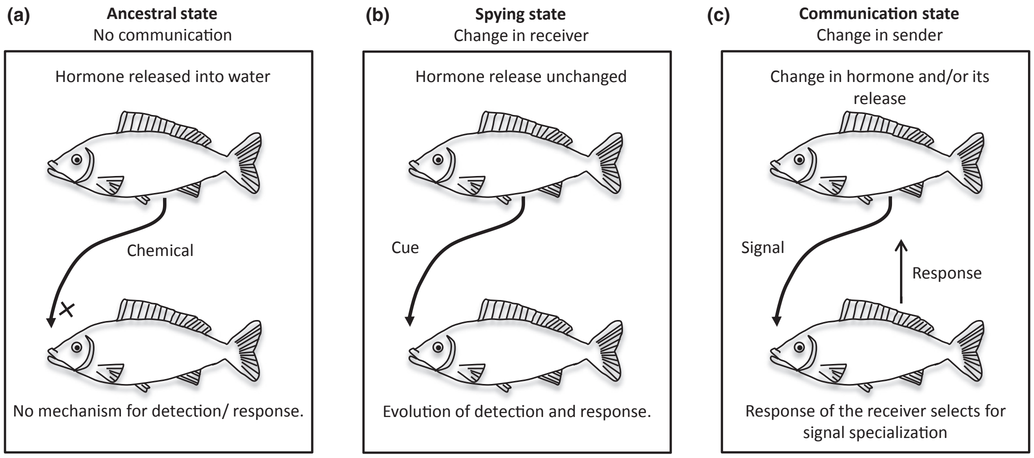

Figure 2 Stages in the evolution of chemical signaling in fish: (a) ancestral state, in which fish release a hormone that is not detected by conspecifics; (b) spying state, where conspecifics are able to detect and respond adaptively to the hormone; and (c) communication state, characterized by a response of the receiver which selects for signal specialization.

teleost fish, such as the seminal vesicles in catfish (*Clarias gariepinus*) that release female attractants (Resink et al., 1989), the hypertrophied mesorchial glands in the testes of gobies that secrete steroids that attract females (e.g., Colombo et al., 1980; Murphy et al., 2001), or anal glands in blennies, which consist of a transformation of the first rays of the anal fin into a sex pheromone-producing gland (Serrano et al., 2008a,b). Interestingly, in the case of both gobies and blennies, i.e., in species in which male alternative reproductive tactics occur and both territorial and sneaker males are present, only territorial males develop the glands that produce female attractants (blennies: Gonçalves et al., 1996; gobies: Locatello et al., 2002), suggesting a secondary loss of the pheromone-producing tissue in sneakers. However, the absence of such specialized structures cannot by itself rule out the ability to release/store pheromones, and thus apparent cases of chemical spying in fish may just reflect our failure to detect these more subtle specializations. A good example of such scenario is the goldfish (*C. auratus*), where, despite lacking any obvious specialization for production and release of pheromones, females release sequentially two hormonal pheromones: (1) a preovulatory pheromone, consisting of progestins (17,20-β-dihydroxy-4-pregen-3-one and its sulfated form) and androstenedione, that has a primer effect on sperm production in males; and (2) a postovulatory pheromone, consisting of prostaglandins (prostaglandin F2-α and 15-keto-PGF2-α), that triggers male courtship and makes ovulated females attractive to the males (reviewed in Stacey and Sorensen, 2002). Given that these female pheromones are the result of passive release into the water of sex hormones and their metabolites involved in female ovulation (progestins and androstenedione) and in the regulation of female reproductive behavior (prostaglandins), and there are no specialization for the production and/or their release in the scope of chemical communication, this system has initially been considered a classic example of males spying on reproductive state of females in order to increase their reproductive success (Stacey and Sorensen, 2002; Wisenden and Stacey, 2005). However, subsequently it has been found that these hormones are mainly released through the urine and that female goldfish increase the frequency of pulses of urine when in the presence of a male, in particular if in the presence of oviposition substrate (Appelt and Sorensen, 2007), indicating a specialization in the sender for the release of the signal, compatible with a true signaling scenario. This form of control of signal release is also present in other species where hormonal pheromones are released through the urine and males adjust the urination rate in response to the presence of receptive/preovulatory females (e.g., Mozambique tilapia, *O. mossambicus*, Almeida et al., 2005; Burton's mouthbrooder, *A. burtoni*, Maruska and Fernald, 2012; swordtail, *Xiphophorus birchmanni*, Rosenthal et al., 2011). Thus, the role of hormones as pheromones may be more common than initially thought.

Most of the examples of hormonal pheromones provided above are related to reproduction and to their effect on the behavior and physiology of the opposite sex. However, evidence has accumulated indicating a role for chemical cues in other aspects of fish social behavior such as intrasexual aggression, parental care, and affiliative behaviors (Keller-Costa et al., 2015; e.g., Sorensen and Baker, 2014). Unfortunately, for most of these other cases of chemical communication, the chemical identity of the cue/signal is not known, and thus hormones cannot be directly implicated. One particular function that has been the focus of recent research is the role of chemical communication in the regulation of male–male aggression in cichlids (Keller-Costa et al., 2015). In the Mozambique tilapia, males also release urine during agonistic interactions in pulses of short duration and those that become subordinate stop releasing urine (**Figure 3**; Barata et al., 2007). If urination is surgically prevented, agonistic interactions escalate and more overt

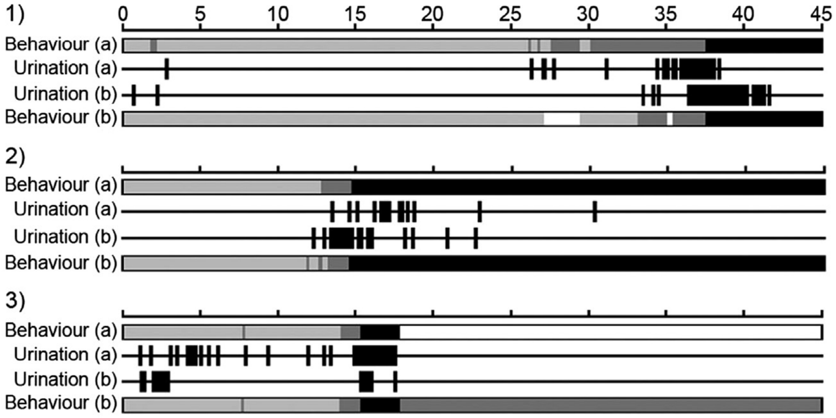

Figure 3 Examples (1–3) of behavior of two territorial tilapia males (a) and (b) interacting for 45 min (submissive: white; not aggressive: light gray; aggressive displays: dark gray; highly aggressive: black) and their corresponding release of urine pulses (urination). In (1), male (a) started aggressive behavior and urination (time point around 25 min), subsequently male (b) initiated aggressive displays and then agonistic interaction escalated to high symmetrical aggression. In (2), both males increased their urination frequency and aggressivity almost at the same time (within 10–15) and maintained agonistic behavior until the end of experiment, although urine pulses decreased significantly. In (3), after the release of several urine pulses from both males and a short period of symmetrical high aggression, male (a) became submissive whereas male (b) continued with agonistic displays; both males stopped urine release at this time point (around 18 min). Adapted from Barata, E.N., Hubbard, P.C., Almeida, O.G., Miranda, A., Canário, A.V.M., 2007. Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). BMC Biol. 5, 1–11.

aggressive behaviors are expressed (Keller-Costa et al., 2012). Moreover, in stable dominance hierarchies the olfactory potency of the urine is correlated with the male's social rank (Barata et al., 2007), and urine of dominant and subordinate males triggers different patterns of gene expression in olfactory brain regions of male receivers (Simões et al., 2015). Together these results strongly suggest the presence of a chemical signal in the urine used in social status assessment in this species. Interestingly, dominant males also store large volumes of urine (Barata et al., 2007), having hypertrophied urinary bladders (Keller-Costa et al., 2012), which indicates a specialization for urine release supportive of the evolution of a true dominance pheromone rather than just a dominance cue. The chemical identity of this putative dominance pheromone has not been established yet, but it is known to have multiple components, present both in polar and nonpolar urine fractions (Keller-Costa et al., 2016) and to be distinct from the sex pheromone that has primer physiological effects on females (Keller-Costa et al., 2014). Similar evidence for the occurrence of putative dominance pheromones has also been collected for two other cichlid species (Burton's mouthbrooder, Crapon de Caprona, 1980; Maruska and Fernald, 2012; Nile tilapia, Giaquinto and Volpato, 1997; Gonçalves-de-Freitas et al., 2008), suggesting that pheromones may be also a widespread phenomena in this teleost family.

2.01.5 Conclusions

To conclude, it is now clear that hormones exert powerful modulatory effects on social behavior by acting on a core of forebrain and midbrain areas that underlie the expression of these behaviors in fishes. However, the exact mechanism through which hormones change the functional connectivity of the SDMN to affect behavior remains poorly understood, and this is a promising area for research. Studies manipulating hormone levels and investigating the effect in the neurogenomic states and neuronal output of nodes of the SDMN will help to elucidate how hormones modulate the expression of social behaviors. Also, different hormonal systems are known to interact with each other, and studies addressing the cross-talk between endocrine systems are valuable. Finally, hormones may also act on social behavior by acting as pheromones, and their role in the regulation of social interactions has started to be unveiled.

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