REVIEW

Neuromodulation of the agonistic behavior in two species of weakly electric fish that display different types of aggression

Ana C. Silva[1,2,*], Rossana Perrone[1], Lucía Zubizarreta[1], Gervasio Batista[1] and Philip K. Stoddard[3]

[1]Unidad Bases Neurales de la Conducta, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo 11600, Uruguay,
[2]Laboratorio de Neurociencias, Facultad de Ciencias, Universidad de la Republica, Montevideo 11400, Uruguay and [3]Department of
Biological Sciences, Florida International University, Miami, FL 33199, USA

*Author for correspondence (asilva@iibce.edu.uy)

Summary

Agonistic behavior has shaped sociality across evolution. Though extremely diverse in types of displays and timing, agonistic encounters always follow the same conserved phases (evaluation, contest and post-resolution) and depend on homologous neural circuits modulated by the same neuroendocrine mediators across vertebrates. Among neuromodulators, serotonin (5-HT) is the main inhibitor of aggression, and arginine vasotocin (AVT) underlies sexual, individual and social context differences in behavior across vertebrate taxa. We aim to demonstrate that a distinct spatio-temporal pattern of activation of the social behavior network characterizes each type of aggression by exploring its modulation by both the 5-HT and AVT systems. We analyze the neuromodulation of aggression between the intermale reproduction-related aggression displayed by the gregarious *Brachyhypopomus gauderio* and the non-breeding intrasexual and intersexual territorial aggression displayed by the solitary *Gymnotus omarorum*. Differences in the telencephalic activity of 5-HT between species were paralleled by a differential serotonergic modulation through 1A receptors that inhibited aggression in the territorial aggression of *G. omarorum* but not in the reproduction-related aggression of *B. gauderio*. AVT injection increased the motivation towards aggression in the territorial aggression of *G. omarorum* but not in the reproduction-related aggression of *B. gauderio*, whereas the electric submission and dominance observed in *G. omarorum* and *B. gauderio*, respectively, were both AVT-dependent in a distinctive way. The advantages of our model species allowed us to identify precise target areas and mechanisms of the neuromodulation of two types of aggression that may represent more general and conserved strategies of the control of social behavior among vertebrates.

Introduction

Agonistic behaviors that regulate conflict situations between conspecifics have shaped sociality across evolution (Lorenz, 1963; King, 1973). Conflicts arise because animals compete for different resources (territory, food, mates, breeding sites, etc.) and they are solved when one individual keeps the resource in struggle (dominant) and the other loses it (subordinate). Though the resources individuals compete for may be different and the behavioral patterns involved may be extremely diverse, agonistic encounters always follow the same phases (evaluation, contest and post-conflict resolution). Conflicts may be solved without escalated contests, but animals usually have to fight to elucidate which will become the winner or the loser. Therefore, aggression, defined as an overt behavior that leads to displacing, dominating or harming another individual (Nelson, 2006), is part of the contest phase of agonistic encounters. Given the diversity of aggressive behaviors and the variety of contexts in which aggression is expressed, it has not been possible to reach a general consensus in the definition of aggression and its classification, though several authors have provided useful theoretical frameworks in this concern (Moyer, 1968; Brain, 1979; Wingfield et al., 2006). Within the agonistic context, individuals can aggressively compete either for space or for a mate, or aggressively establish hierarchies in a flock. Thus,

depending on the resources individuals compete for and the motivation towards combat, at least three distinctive types of aggression can be observed during agonistic encounters: territorial aggression, reproduction-related aggression and rank-related aggression (Wingfield et al., 2006). The type or types of aggression displayed by one species are correlated with its social structure. For example, it is not likely for gregarious species to display exclusive territorial aggression, nor for solitary species to display rank-related aggression. However, it is not always easy to discern between types of aggression, and to obtain model systems to test clear-cut examples of a distinctive type of aggression. Besides, both in natural performing animals and in laboratory settings, different types of aggression often intermingle, resulting, for example, in territorial aggression only observed between males during breeding while they are competing for mates, or rank-related aggression established by territory defense (Brown, 1964).

Several brain areas are known to control aggression, though it has not been possible to dissect a fixed neural circuit responsible for aggressive behavior. Rather, following Newman's hypothesis (Newman, 1999), we interpret aggressive behaviors as emergent properties of a complex social behavior network (SBN) that includes the medial preoptic area, lateral septum, anterior hypothalamus, ventromedial hypothalamus, periaqueductal gray,

medial amygdala and bed nucleus of the stria terminalis (Newman, 1999; Nelson and Trainor, 2007). From this perspective, the distributed pattern of neural activity among the interconnected nodes of the SBN controls social behavior and the diversity in social behavior would be achieved by plasticity in the weighting of activity across the network (Newman, 1999; Goodson and Kabelik, 2009). These neural circuits, initially described in mammals, appear to be highly conserved, and putative homologs have been identified for all classes of vertebrates (Goodson, 2005; O'Connell and Hofmann, 2011). Also conserved among vertebrates are the modulators that shape the activity of the SBN. Several signaling molecules, including hormones (steroid hormones, hypothalamic neuropeptides) and neurotransmitters (serotonin, dopamine, GABA), have been linked to aggression (Goodson and Bass, 2001; Miczek et al., 2002; Summers and Winberg, 2006; Nelson and Trainor, 2007). The SBN hypothesis predicts that each behavior, context and/or phenotype will arise from distinct spatio-temporal patterns of activation of the SBN, product of a precise orchestration of neuroanatomical pathways and neuroendocrine messengers.

Among neuromodulators of aggression, serotonin (5-hydroxytryptamine, or 5-HT) exerts the principal inhibitory control upon aggression (Nelson and Chiavegatto, 2001; Trainor et al., 2009). In several species in which the serotonergic system has been analyzed during agonistic interactions, serotonergic activity increases consistently in subordinates (Yodyingyuad et al., 1985; Blanchard et al., 1991; Summers and Greenberg, 1995; Overli et al., 1999; Summers et al., 2005b) and decreases or remains unchanged in dominants (van Erp and Miczek, 2000; Ferrari et al., 2003; Summers et al., 2003). The activation of $5\text{-}HT_{1A}$ receptors has been involved in the inhibitory effect of 5-HT on aggression in all vertebrate classes (Deckel and Fuqua, 1998; Sperry et al., 2003; Miczek and Fish, 2006; Clotfelter et al., 2007; Allee et al., 2008; Ten Eyck, 2008). In addition, the 5-HT deficiency hypothesis was formulated based on the correlation between low levels of the 5-HT metabolite 5-hydroxyindoleacetic acid and aggressive or violent behavior in humans and other primates (Krakowski, 2003). Although it is generally accepted that high levels of 5-HT inhibit aggression, there have been no attempts so far to determine whether the serotonergic system is differentially involved in the regulation of the different types of aggression displayed during agonistic interactions.

The hypothalamic nonapeptide arginine vasotocin (AVT) and its mammalian homolog, vasopressin, are key integrators underlying interspecific, sexual, individual and social context differences in behavior in vertebrates (Insel and Young, 2000; Goodson and Bass, 2001; Goodson, 2008; Goodson et al., 2012). Consistent patterns of activation of the vasopressin and AVT systems have emerged in mammals and birds, respectively. Differential central vasopressin signaling parallels differences in the social organization of closely related species of voles (Young et al., 1997). In estrildid finches, the AVT system encodes the valence of social stimuli and group-size preferences between species independently of other aspects of social organization (Goodson and Kingsbury, 2011). Vasotocin modulation of aggression has been demonstrated in several vertebrate classes (Stribley and Carter, 1999; Semsar et al., 2001; Lema and Nevitt, 2004b; Semsar and Godwin, 2004; Larson et al., 2006; Santangelo and Bass, 2006; Greenwood et al., 2008; Goodson and Kabelik, 2009; Filby et al., 2010). In birds, it has been reported that the AVT modulation of aggression depends on the type of aggression displayed (Goodson and Kabelik, 2009; Kabelik et al., 2009). In teleosts, though numerous studies have addressed the influence of the AVT system on agonistic behavior, no

consistent patterns across species have yet emerged, probably due (at least in part) to the extremely diverse approaches and procedures used among species (Godwin and Thompson, 2012).

Teleost fishes provide valuable models to explore neuroendocrine bases of behavior as they are the most taxonomically diverse infraclass of vertebrates, they inhabit a wide range of environments, and they display an extraordinary diversity of social systems, features that offer almost endless possibilities of experimental models. However, these advantages of fish models may raise difficulties in the interpretation of data as it is difficult to identify generalities or conserved strategies across teleosts, which are an older and more diverse group than either birds or mammals.

We present a comparative analysis of the neuromodulation of aggression between two species of gymnotiform electric fish with different social structure that display different types of aggression. As a particular case of the theoretical prediction raised by Newman (Newman, 1999), we hypothesize that each type of aggression will have a distinctive spatio-temporal pattern of activation across the network. To approach this issue, we selected two clear-cut examples of different types of aggression: the non-breeding intrasexual and intersexual territorial aggression of *Gymnotus omarorum* (Batista et al., 2012) and the intermale reproduction-related aggression of *Brachyhypopomus gauderio* (Zubizarreta et al., 2012). We then explored the emergence of distinctive patterns by analyzing the modulation of the serotonin and AVT systems upon these two types of aggression.

The non-breeding territorial aggression of *Gymnotus omarorum* and the reproduction-related aggression of *Brachyhypopomus gauderio*

Gymnotus omarorum (Richer-de-Forges et al., 2009) and *B. gauderio* (Giora and Malabarba, 2009) cohabit Uruguayan freshwater habitats at the southern boundary of the gymnotiform continental distribution (30–35°S) (Silva et al., 2003). As shown in Fig. 1, the solitary *G. omarorum* emits sexually monomorphic triphasic electric pulses at around 25 Hz at 20°C (Caputi, 1999; Richer-de-Forges et al., 2009), whereas the gregarious *B. gauderio* emits sexually dimorphic biphasic electric pulses at around 15 Hz at 20°C (Hopkins et al., 1990; Caputi et al., 1998). In both species, a medullary pacemaker nucleus (PN) controls the timing of the electric organ discharge (EOD) (Bennett et al., 1967). The spatial organization and innervation pattern of the peripheral electric organ are responsible for the species-specific EOD waveform (Trujillo-Cenóz et al., 1984; Stoddard, 2002). *Brachyhypopomus gauderio*, but not *G. omarorum*, exhibits a sustained nocturnal increase of EOD rate (Fig. 1), along with a circadian rhythmicity of EOD waveform, both of which vary seasonally and are dependent on social context (Franchina and Stoddard, 1998; Franchina et al., 2001; Silva et al., 2007; Gavassa et al., 2013).

Though male and female *G. omarorum* display aggression all year round in intrasexual and intersexual interactions, we focused on the non-breeding dyadic agonistic encounters as a remarkable example of non-sex-biased territorial aggression (Batista et al., 2012). Several considerations must be taken into account to reliably diagnose this distinctive type of aggression and to exclude other possible interfering types. During the non-breeding season, resource value is not expected to depend on individuals' reproductive status and should thus be equal for males and females in this sexually monomorphic species in which interaction costs can also be considered to be symmetric between sexes. We designed controlled behavioral experiments to ensure that territory is the only resource animals fight for, by placing two fish (with the same
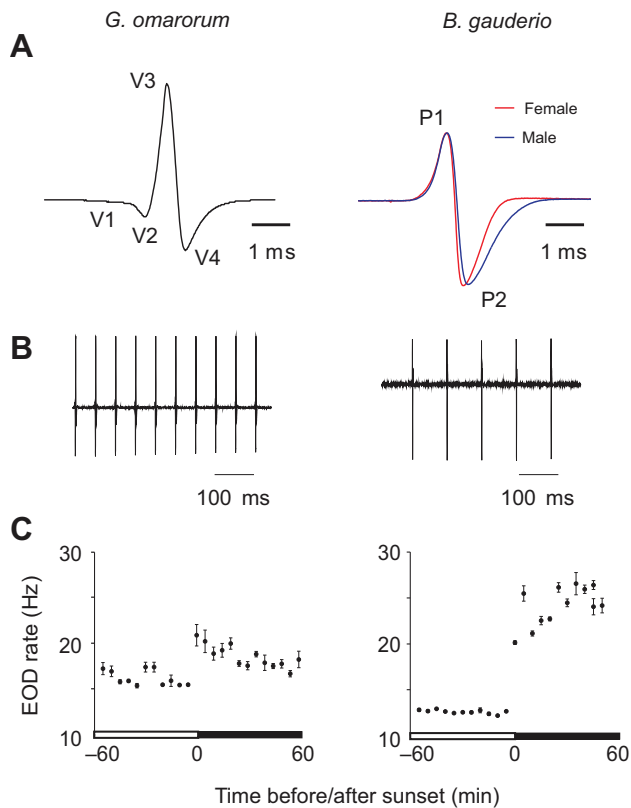
Fig. 1. Species-specific characteristics of the electric organ discharge (EOD) in the solitary *Gymnotus omarorum* (left) and in the gregarious *Brachyhypopomus gauderio* (right) recorded at 20°C. (A) EOD waveform: averaged head-to tail recordings of the EOD obtained from individual fish showing four sexually monomorphic components in *G. omarorum* (V1–V4) (Richer-de-Forges et al., 2009) and two components in *B. gauderio* (P1, P2) (Hopkins et al., 1990) with a remarkable sexual dimorphism in the P2 phase. (B) EOD rate: raw head-to-tail recordings of the EOD displayed at a lower time scale indicate differences in the discharge rhythm among species. (C) Day–night EOD rate: mean (±s.d.) EOD rates values recorded 60 min before and 60 min after sunset in isolated non-breeding adults (adapted from Migliaro and Silva, 2012). *Brachyhypopomus gauderio* exhibits a persistent nocturnal increase in EOD rate that is only transiently observed in *G. omarorum.*

previous experience and residence time) in equal-sized plain compartments separated by a removable glass gate. When the gate was removed, all fish (from either female–female, male–male or male–female dyads) defended this space vigorously and a clear dominance was established (Fig. 2). Theoretical asymmetric contest models (Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981) predict that when sex asymmetries in resource holding potential (RHP) or in the resource value itself are not expected between contenders, the contest outcome should be sex-independent. However, until now, this prediction had not been demonstrated, mainly because in monomorphic species the value of the resource often differs between male and female contestants (Dunham, 2008). *Gymnotus omarorum* fits perfectly in this model, as dominance is not influenced by individuals' sex, and only weight asymmetry, the most direct indicator of RHP, influenced the contest outcome (Batista et al., 2012).

The reproduction-related intermale aggression displayed by *B. gauderio* (Zubizarreta et al., 2012) is probably part of the natural behavioral repertoire of this gregarious species, which has a polygynous breeding system in which males hold consistent home

ranges typical of exploded lek polygyny (Miranda et al., 2008). Territory itself is not a sufficient incentive to elicit aggression in this species, but long-term residents aggressively defend their courting sites against intruders, and become dominants if size asymmetry favors them (Fig. 2).

As shown in Fig. 2, both species followed the three standard phases of agonistic encounters (evaluation, contest and post resolution) but with different timing: *G. omarorum* resolved contests in less than 3 min, whereas *B. gauderio* took around 15 min to establish dominance. Within the contest phase, both species interacted aggressively, though displays of overt aggressive behaviors were species-specific. For example, only *G. omarorum* displayed highly aggressive jaw locks and bites directed to the opponent's abdomen, whereas *B. gauderio* showed milder displays such as mutual attempts to bite the opponent's tail in an antiparallel position. *Gymnotus omarorum* produced submissive electric signals (offs and chirps) that showed a consistent temporal pattern (Fig. 2) (Batista et al., 2012). During the contest phase, only offs (electric silence) were produced as an early sign of submission. After contest resolution, the subordinate continued to produce more and longer-lasting offs, and added chirps, probably as a more unambiguous submissive signal (Fig. 2). The clear submissive information encoded by chirps in *G. omarorum* contrasts with previous findings in *Apteronotus leptorhynchus* (Zupanc et al., 2006; Triefenbach and Zakon, 2008; Hupé and Lewis, 2008), in which chirps were interpreted as threat signals associated to aggression. *Brachyhypopomus gauderio* produced chirps (either dominants or subordinates) and offs (only subordinates) but they did not seem to follow a predictable temporal pattern (Zubizarreta et al., 2012).

As in other gymnotiforms (Hopkins, 1974; Hagedorn and Heiligenberg, 1985; Zakon et al., 1991; Fugère et al., 2011), both species establish ranks of EOD rate after contest resolution, in which dominants display higher discharge rates than subordinates (Perrone, 2012). Interestingly, we see interspecific differences in the way this post-resolution EOD rate rank is attained (Fig. 2). In the reproduction-related aggression of *B. gauderio*, the dominant fish increases its EOD rate during the contest to signal its dominance status. In contrast, in the non-breeding territorial aggression of *G. omarorum*, the subordinate fish decreases its EOD rate, adding a persistent signal of electric submission. We assume fish find advantage in advertising either dominance or subordination status *via* electric cues, thus avoiding extra time-consuming contests and injuries derived from fights. Each species establishes its post-resolution EOD rate rank in coherence with its social structure. In exploded lek systems (*B. gauderio*), it may be crucial for males to signal dominance to discourage other neighbor males to invade their home ranges, whereas in highly aggressive solitary species in which individuals rarely interact (*G. omarorum*), it may be more important to signal subordination unambiguously.

In summary, two clear-cut types of aggression displayed by two species with different social structure can be reliably tested in laboratory settings using distinct experimental protocols that simulate the natural conditions in which agonistic behaviors arise in each species. This approach, which allows a precise characterization of the agonistic encounter in each species (Fig. 2), also opens the possibility for a comparative evaluation of its modulation.

Differential serotonergic modulation of two types of aggression

Though indisputable and ubiquitous across evolution, the 5-HT inhibitory control of aggression is now conceived to be much more
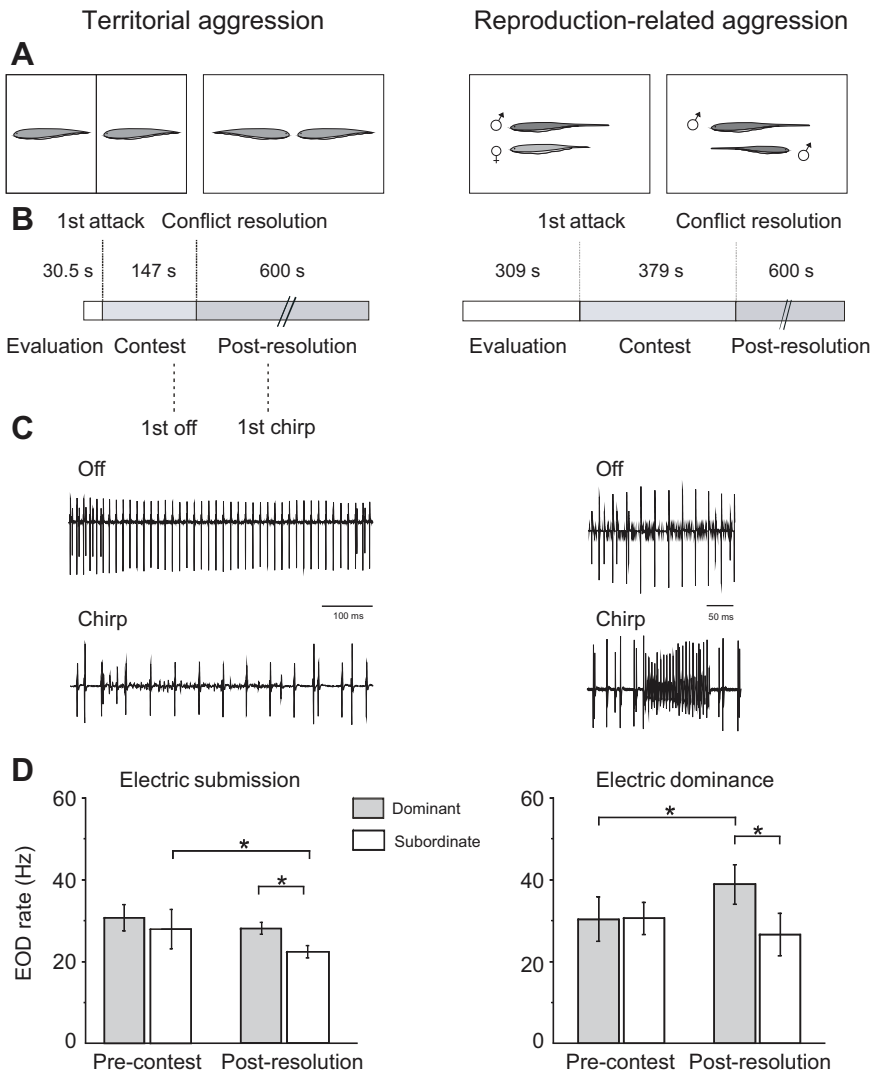
Territorial aggression   Reproduction-related aggression

Fig. 2. Agonistic encounters in *Gymnotus omarorum* (left) and *Brachyhypopomus gauderio* (right). (A) Behavioral protocol: dyads of *G. omarorum* (0–50% weight asymmetry, *N*=33) were placed in equal-sized compartments separated by a glass gate that was removed 10 min after sunset. The agonistic behavior of *B. gauderio* was tested using a 2-day protocol: on day 1, sexually mature male–female dyads were placed in the recording tank; only the males that courted the female during the first night (Perrone et al., 2009) were tested during the second night; 30 min after sunset, the female was removed and a smaller intruder male (0–34% weight asymmetry, *N*=8) was added to the tank 5 min later. (B) Dynamics: phases of agonistic encounters; (1) evaluation: from time 0 (gate removal in gate protocols and intruder addition in resident–intruder protocols) to the occurrence of the first attack; (2) contest: from the occurrence of the first attack to conflict resolution (resolution time, third consecutive retreat of one fish without retaliating); and (3) post-resolution: 10 min after conflict resolution. (C) Social electric signals: cessations of the EOD (offs) and transient increases in EOD rate with waveform distortion (chirps) were observed in both species, but only in *G. omarorum* did these occur in a consistent temporal pattern. (D) Rank-related EOD rate (electric submission in *G. omarorum* and electric dominance in *B. gauderio*): median (±m.a.d.) EOD rates values recorded during the pre-contest and post-resolution phases in dominants and subordinates of both species; *N*=10 dyads for each species (Wilcoxon matched pairs test; *P<0.05) (adapted from Batista et al., 2012; Zubizarreta et al., 2012; Perrone, 2012).

complex than expected, as it appears to be dependent on brain region, time and context (Summers et al., 2005b). For example, the differential involvement of 5-HT in different behavioral phenotypes within a same species has been reported in lizards and mice (Summers et al., 2005b; Caramaschi et al., 2008; de Boer et al., 2009). However, no attempts to identify distinct patterns of activation of the serotonergic system among different types of aggression have been reported so far. Only one previous study in macaques compared the activity of the serotonergic system between species with different social structure (Westergaard et al., 1999).

Neurochemical data support the existence of a differential pattern of activation of the serotonergic system between the non-breeding territorial aggression of *G. omarorum* and the reproduction-related aggression of *B. gauderio*. In *B. gauderio*, as expected, the telencephalic serotonergic activity increases in subordinate males following a contest; however, in *G. omarorum*, 5-HT levels exhibited by both subordinates and dominants after territorial aggression were significantly lower than those exhibited by controls (Zubizarreta et al., 2012). Taken together, the conventional 5-HT profile found in *B. gauderio* and the unexpected 5-HT profile found in *G. omarorum* constitute the first evidence of the differential activation of the serotonergic system between types of aggression.

As the involvement of 5-HT_{1A} receptors in the serotonergic inhibition of aggression is well known across vertebrates (Nelson and Trainor, 2007), we tested the effects of the administration of the 5-HT_{1A} agonist 8-hydroxy-2-(di-*n*-propylamino)tetralin (8-OH-DPAT) to potential dominants prior to the contest. As expected, 8-OH-DPAT decreased aggression in *G. omarorum* (Fig. 3). This treatment reversed the expected contest outcome in seven of 12 dyads, a phenomenon that in other vertebrates has been associated with 5-HT changes (Summers et al., 2005a). These results confirm that the inhibition of aggression by pharmacological manipulation of 5-HT levels shown in a previous report in *G. omarorum* (Capurro et al., 1997) is mediated at least partially by the activation of 5-HT_{1A} receptors. However, the resident male *B. gauderio* failed to show consistent effects on any aspect of the agonistic encounter after the administration of 8-OH-DPAT. Pharmacological stimulation of the 5HT_{1A} receptors in *B. gauderio* did not affect contest outcome (seven out of eight injected residents won the contest), aggression levels or motivation towards combat (Fig. 3). Previous reports in *B. gauderio* showed that 8-OH-DPAT diminishes amplitude and duration of the EOD waveform (Allee et al., 2008), which is an important proxy of male body size and endocrine status (Gavassa et al., 2011). The lack of effect of the 5-HT_{1A} agonist in *B. gauderio* is relevant because this is the first species in which the administration of 5-HT_{1A} receptor agonists
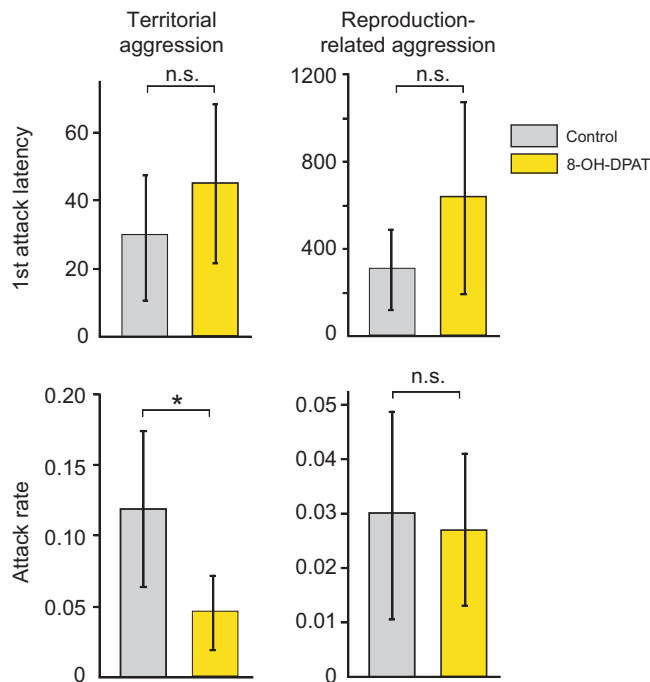
Fig. 3. Effects of 8-OH-DPAT upon motivation (first attack latency) and aggression (attack rate) in the non-breeding territorial aggression of *G. omarorum* and in the reproduction-related aggression of *B. gauderio*. One hour before the encounter, predicted dominants (larger individuals in *G. omarorum*, *N*=12, and resident males in *B. gauderio*, *N*=8) were injected either intraperitoneally or intramuscularly with 1 µl g^{-1} body mass of a 2.5 mmol l^{-1} 8-OH-DPAT solution. Values are expressed as medians ± m.a.d. (Mann–Whitney *U*-test; *P<0.05; n.s., not significant) (adapted from Zubizarreta et al., 2012).
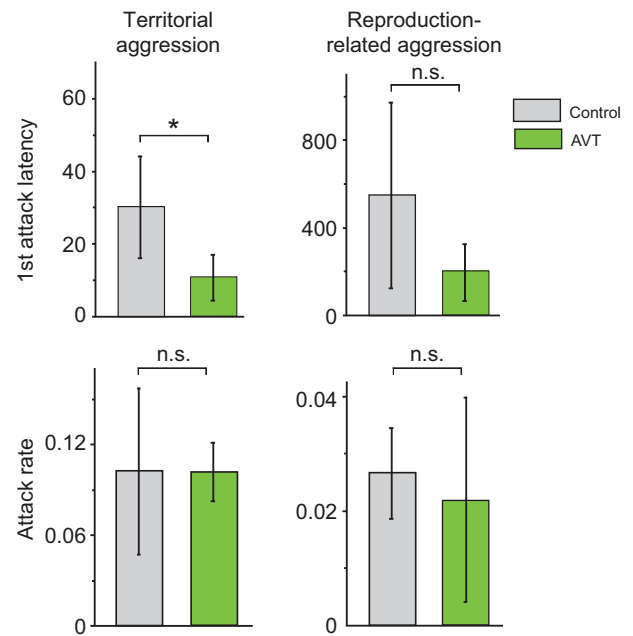

Fig. 4. Effects of arginine vasotocin (AVT) upon motivation (first attack latency) and aggression (attack rate) in the non-breeding territorial aggression of *G. omarorum* and in the reproduction-related aggression of *B. gauderio*. Predicted dominants of *B. gauderio* (residents, *N*=8) and *G. omarorum* (larger individuals, *N*=8) were intraperitoneally injected 40 min before the encounter with 1 µg g^{-1} body mass of a 1 µg µl^{-1} solution of AVT. Predicted subordinates were intraperitoneally injected with the same volume of a physiological saline solution. Values are expressed as medians ± m.a.d. (Mann–Whitney *U*-test; *P<0.05; n.s., not significant) (adapted from Perrone, 2012).

does not clearly diminish aggression in realistic dyadic encounters. These results demonstrate interspecific differences in the organization of the 5-HT system in two species that display different types of aggression.

In summary, *G. omarorum* is characterized by a low basal serotonergic activity and, after agonistic encounters, shows a slow recovery of 5-HT levels. This is consistent with the clear anti-aggressive effect of the 5-HT$_{1A}$ agonist obtained with the pharmacological manipulation in this species. The reproduction-related aggression of *B. gauderio* shows a dynamic response of the serotonergic system, in which subordinates exhibit the expected 5-HT levels higher than controls. *Brachyhypopomus gauderio* shows a high basal serotonergic activity, which may explain the non-responsiveness of reproduction-related aggression after 5-HT$_{1A}$ agonist administration.

Differential AVT modulation of two types of aggression

Three populations of AVT neurons in fish brains are distributed along the third ventricle in the ventral portion of the preoptic area in the anterior hypothalamus (Lema and Nevitt, 2004a; Dewan et al., 2008; Thompson and Walton, 2009). The parvocellular AVT neuron population (homologous to the supraoptic nucleus in tetrapods) is located at the rostral and ventral portion of the preoptic area; magnocellular and gigantocellular AVT neuron groups (homologous to the paraventricular nucleus in tetrapods) are found more caudally and dorsally (Kapsimali et al., 2001; Urano and Ando, 2011; Godwin and Thompson, 2012). The projections of these neurons reach the neurohypophysis, where

AVT is released into the bloodstream to exert peripheral effects, and several widespread brain areas (from telencephalon to hindbrain) where AVT is postulated to modulate social behavior (Goodson and Bass, 2001; Saito et al., 2004). As recently reviewed, several studies have demonstrated the involvement of the AVT system in the modulation of the aggressive behavior in different species of teleosts (Godwin and Thompson, 2012). Given the heterogeneity in both the social structure of fish species studied and the experimental approaches used, it has been difficult to identify general strategies in the AVT control of aggression in teleosts so far. However, based on pharmacological and neuroanatomical data, it has been postulated that two subsystems of AVT neurons alternatively activate and control different aspects of social behavior (Greenwood et al., 2008; Godwin and Thompson, 2012). The magno-gigantocellular AVT populations produce and release AVT in circuits that stimulate courtship and/or aggressive behaviors, whereas parvocellular neurons most likely release AVT in circuits that induce behaviors related to social subordination, particularly social withdrawal. According to this model, different types of aggression, and the responses dominants and subordinates display, would depend on both the relative development of these different two subsystems across species and phenotypes, and their relative activation in particular social contexts. For example, greater levels of AVT expression were found in territorial males of *Astatotilapia burtoni* than in non-territorial males (Greenwood et al., 2008). Territorial butterflyfish (*Chaetodon multicinctus*) show larger magnocellular and gigantocellular AVT neurons and greater density of AVT
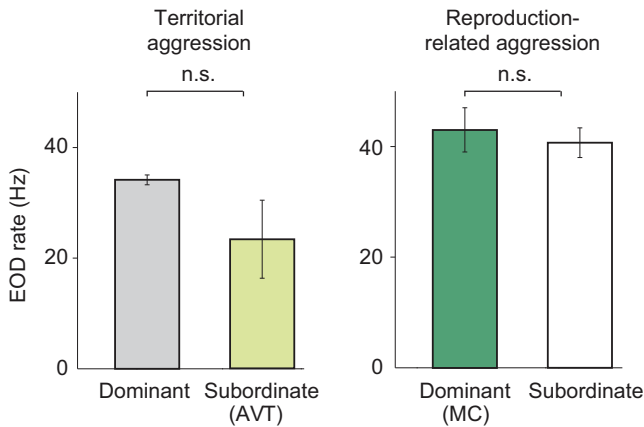
Fig. 5. AVT-dependent rank-related EOD rate: the electric submission of the territorial aggression of *G. omarorum* and the electric dominance of the reproduction-related aggression of *B. gauderio*. EOD rates were recorded during the post-resolution phases in dyads of both species after treatment. Predicted subordinates of *G. omarorum* (smaller individuals, $N=6$) were intraperitoneally injected 40 min before the encounter with 1 µg g^{-1} body mass of a 1 µg µl^{-1} solution of AVT. Predicted dominants of *B. gauderio* (residents, $N=6$) were intraperitoneally injected 40 min before the encounter with 2 µg g^{-1} of a 1 µg µl^{-1} solution of Manning compound (MC). The other animal of the dyad of both species was intraperitoneally injected with the same volume of a physiological saline solution. Values are expressed as medians ± m.a.d. (Wilcoxon matched-pairs test; n.s., not significant) (adapted from Perrone, 2012).

projections than the non-territorial species *Chaetodon miliaris* (Dewan et al., 2008). In *Cichlasoma dimerus*, non-territorial males show larger parvocellular AVT neurons than the territorial males (Ramallo et al., 2012). In the peacock blenny (*Salaria pavo*), territorial males present smaller parvocellular neurons than non-territorial ones (Grober et al., 2002). In zebrafish (*Danio rerio*), dominants express AVT in magnocellular neurons whereas subordinates express AVT in parvocellular preoptic neurons (Larson et al., 2006).

Vasotocin is probably acting directly by influencing the activity of SBN nodes and descending motor output pathways, and indirectly by changing peripheral body states that feed back to the brain, but it has been challenging to determine the precise target areas of AVT effects in teleosts. As the pattern of emission of the electromotor output in electric fish is itself a social display [as it signals species, sex, season, status, male quality and social context (Silva et al., 2007; Perrone et al., 2009; Gavassa et al., 2012)], which relies on the activity of a well-known and accessible medullary medial nucleus (the PN) (Pouso et al., 2010; Quintana et al., 2011a; Quintana et al., 2011b), electric fish appear as a good model system to target specific brain areas of AVT actions. In a previous study, Perrone et al. (Perrone et al., 2010) demonstrated that AVT induced a long-lasting and progressive increase of EOD rate in isolated *B. gauderio*, but had no effects in *G. omarorum*. The administration of AVT in an *in vitro* preparation of the isolated PN of *B. gauderio* also induced a long-lasting increase in its firing rate, strongly suggesting that the PN is a direct target of AVT projections (Perrone et al., 2010).

Gymnotus omarorum and *B. gauderio* differed in the effects of the administration of AVT to potential dominants prior to the contest. In the non-breeding territorial aggression of *G. omarorum*, AVT injection increased the motivation towards aggression revealed by a decrease in the first attack latency and a marginal decrease in contest duration, but no changes in aggression levels (Fig. 4) (Perrone, 2012). Vasotocin injection in the resident male had no consistent effects on aggression levels or motivation towards combat of *B. gauderio* (Fig. 4) (Perrone, 2012). More interestingly, the electric submission and dominance observed in *G. omarorum* and *B. gauderio*, respectively, were both AVT-dependent in a distinctive way (Fig. 5) (Perrone, 2012). In the territorial aggression displayed by *G. omarorum*, AVT injected into the predicted subordinate prevented the electric submission observed after conflict resolution, suggesting that the sustained decrease in EOD rate observed in intact subordinates is achieved by the inhibition of an AVT input to the PN. In the reproduction-related aggression, the AVT receptor V1a antagonist Manning
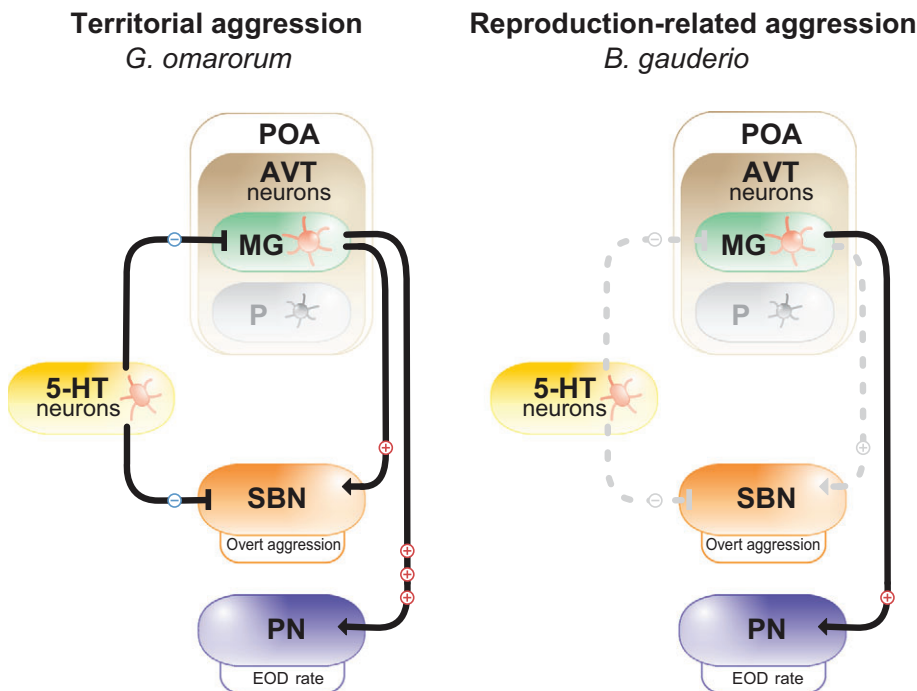

Fig. 6. Putative model of interactions of 5-HT and AVT systems in the modulation of the territorial aggression of *G. omarorum* and of the reproduction-related aggression of *B. gauderio* in dominants. MG, magno-gigantocellular population of AVT neurons, which is highly active in dominants; P, parvocellular population of AVT neurons, which is relatively inactive (gray) in dominants; PN, pacemaker nucleus, responsible of the modulation of EOD rate; POA, preoptic area; SBN, social behavior network, spatio-temporal characteristic pattern modulating the activity of descendent locomotor pathways involved in overt aggression; +, excitatory pathways; –, inhibitory pathways; solid black lines, activated pathways; dashed gray lines, non-activated pathways.

compound administered to the predicted dominant male *B. gauderio* prevented the electric dominance display, allowing us to hypothesize that the sustained increase in EOD rate observed in intact dominants is caused by direct stimulation of the PN *via* AVT fibers.

As observed in teleost-related species with different social structure (Dewan et al., 2008) and among dominants and subordinates within the same species (Greenwood et al., 2008; Filby et al., 2010; Ramallo et al., 2012), there is a differential pattern of activation of the AVT system between the non-breeding territorial aggression of *G. omarorum* and the reproduction-related aggression of *B. gauderio*. Our results match coherently with the above-described hypothesis that AVT's control of social behavior in teleosts relies on the balanced activity of the magno-gigantocellular and parvocellular subsystems of AVT neurons (Greenwood et al., 2008; Godwin and Thompson, 2012). Assuming that AVT fibers reach the PN in both species (an assumption that will be investigated shortly by immunohistochemical techniques), an excitatory AVT-ergic input, probably from the magno-gigantocellular subsystem, can exert a tonic control of EOD rate that is expected to be stronger in *G. omarorum* than in *B. gauderio* (Fig. 6). As the administration of AVT to resting isolated *G. omarorum* (Perrone et al., 2010) or putative dominants (Perrone, 2012) does not affect EOD rate, we assume there is a permanent input of AVT to the PN in this species that occupies all the binding sites of AVT receptors (saturated). In contrast, in *B. gauderio* the non-saturated AVT input to the PN may be further activated in dominants after conflicts and thus explains their electric dominance (Fig. 5). In subordinates, the prevalence of the activation of the parvocellular subsystem of AVT neurons may result in the inhibition of the AVT input to the PN, a hypothesis confirmed in *G. omarorum* in which the injection of AVT prevented the establishment of their electric submission behavior (Fig. 5). Another interesting difference in the activation of the AVT system among dominants of both species is that only in *G. omarorum* (but not in *B. gauderio*) does activation of the magno-gigantocellular subsystem of AVT neurons appear to enhance overt aggression (Fig. 6). This global picture of the distinct activation patterns of the AVT system between species may be part of a more general strategy; i.e. our results indicate the existence of specific spatio-temporal patterns of activation of the SBN that may characterize different types of aggression in concert with the social structure of each species.

Conclusions and speculations

Multiple neuromodulators, acting *via* both fast wired circuits and slow global diffusive ways, shape the spatio-temporal pattern of activity of the network controlling social behavior, thus providing the emergence of environmental-, ontogenic-, social-context- and phenotype-dependent behaviors (Newman, 1999; O'Connell and Hofmann, 2011; Goodson et al., 2012). Our study provides an interesting contribution to assess the complexity of the control of social behavior showing distinctive patterns of activation of both the 5-HT and the AVT systems in the modulation of different types of aggression in species with different social structure. We have demonstrated that these different patterns of activation arise not only between dominants and subordinates of each species but also among dominants, depending on the type of aggression they have displayed (Fig. 6). For example, the activation of the serotonergic system *via* 5-HT$_{1A}$ receptors inhibits overt aggression of dominants in the territorial aggression but not in the reproduction-related aggression. Conversely, AVT induces electric dominance in the reproduction-related aggression but not in the territorial aggression. In addition, we have identified different target areas in which these modulatory actions are taking place (Fig. 6). Besides the effects of 5-HT and AVT on SBN nodes that control the locomotor pathways involved in overt aggression, AVT is also acting on the PN (shaping either electric dominance or submission).

In mammals, 5-HT and vasopressin are known to act as functionally opposed neurotransmitter systems in the control of aggressive behavior, and we have considerable evidence of direct and indirect connections between neurons of both systems (reviewed in Ferris, 2006; Trainor et al., 2009). Though the interaction between 5-HT and AVT has not been extensively analyzed in teleosts, raphe neurons expressing AVT receptors have been recently described (Kline et al., 2011). Following the same trend reported in mammals, we observed opposing actions of 5-HT and AVT upon overt aggression in the territorial aggression of *G. omarorum*, probably acting by enhancing and decreasing the activity of the same target areas across the SBN (Fig. 6). However, we failed to find opposing effects of both systems on the overt aggression of *B. gauderio*, as neither 5-HT nor AVT affected dominants' aggression. Interestingly, an asymmetric control of 5-HT and AVT systems was evidenced at the level of the PN (Fig. 6). Our data suggest an important excitatory function for AVT in both species (even stronger in *G. omarorum*, as discussed above), but provide no evidence that 5-HT modulates EOD rate. Previous studies in both species evaluating the effects of the activation of the 5-HT system on locomotor and electric behaviors did not report 5-HT actions on EOD rate in *Brachyhypopomus* (Allee et al., 2008), whereas pharmacologically increased levels of 5-HT evoked a decrease in EOD rate in *Gymnotus* (Capurro et al., 1997).

The advantages of our model species allowed us to combine behavioral, neurochemical and pharmacological techniques to identify precise target areas and mechanisms of the neuromodulation of different types of aggression that may represent more general strategies of the control of social organization across vertebrates.

List of abbreviations

5-HT	5-hydroxytryptamine (serotonin)
8-OH-DPAT	8-hydroxy-2-(di-*n*-propylamino)tetralin
AVT	arginine vasotocin
EOD	electric organ discharge
PN	pacemaker nucleus
RHP	resource holding potential
SBN	social behavior network

Funding

References

Allee, S. J., Markham, M. R., Salazar, V. L. and Stoddard, P. K. (2008). Opposing actions of 5HT1A and 5HT2-like serotonin receptors on modulations of the electric signal waveform in the electric fish *Brachyhypopomus pinnicaudatus*. *Horm. Behav.* **53**, 481-488.

Batista, G., Zubizarreta, L., Perrone, R. and Silva, A. (2012). Non-sex-biased dominance in a sexually monomorphic electric fish: fight structure and submissive electric signalling. *Ethology* **118**, 398-410.

Bennett, M. V., Pappas, G. D., Giménez, M. and Nakajima, Y. (1967). Physiology and ultrastructure of electrotonic junctions. IV. Medullary electromotor nuclei in gymnotid fish. *J. Neurophysiol.* **30**, 236-300.

Blanchard, D. C., Cholvanich, P., Blanchard, R. J., Clow, D. W., Hammer, R. P., Jr, Rowlett, J. K. and Bardo, M. T. (1991). Serotonin, but not dopamine, metabolites are increased in selected brain regions of subordinate male rats in a colony environment. *Brain Res.* **568**, 61-66.

Brain, P. (1979). Hormones, drugs and aggression. *Ann. Res. Rev.* **3**, 1-38.

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bull.* **76**, 160-169.

Capurro, A., Reyes-Parada, M., Olazabal, D., Perrone, R., Silveira, R. and Macadar, O. (1997). Aggressive behavior and jamming avoidance response in the weakly electric fish *Gymnotus carapo*: effects of 3,4-methylenedioxymethamphetamine (MDMA). *Comp. Biochem. Physiol.* **118A**, 831-840.

Caputi, A. A. (1999). The electric organ discharge of pulse gymnotiforms: the transformation of a simple impulse into a complex spatio-temporal electromotor pattern. *J. Exp. Biol.* **202**, 1229-1241.

Caputi, A. A., Silva, A. C. and Macadar, O. (1998). The electric organ discharge of *Brachyhypopomus pinnicaudatus*. The effects of environmental variables on waveform generation. *Brain Behav. Evol.* **52**, 148-158.

Caramaschi, D., de Boer, S. F., de Vries, H. and Koolhaas, J. M. (2008). Development of violence in mice through repeated victory along with changes in prefrontal cortex neurochemistry. *Behav. Brain Res.* **189**, 263-272.

Clotfelter, E. D., O'Hare, E. P., McNitt, M. M., Carpenter, R. E. and Summers, C. H. (2007). Serotonin decreases aggression via 5-HT1A receptors in the fighting fish *Betta splendens. Pharmacol. Biochem. Behav.* **87**, 222-231.

de Boer, S. F., Caramaschi, D., Natarajan, D. and Koolhaas, J. M. (2009). The vicious cycle towards violence: focus on the negative feedback mechanisms of brain serotonin neurotransmission. *Front Behav Neurosci* **3**, 52.

Deckel, A. W. and Fuqua, L. (1998). Effects of serotonergic drugs on lateralized aggression and aggressive displays in *Anolis carolinensis. Behav. Brain Res.* **95**, 227-232.

Dewan, A. K., Maruska, K. P. and Tricas, T. C. (2008). Arginine vasotocin neuronal phenotypes among congeneric territorial and shoaling reef butterflyfishes: species, sex and reproductive season comparisons. *J. Neuroendocrinol.* **20**, 1382-1394.

Dunham, A. (2008). Battle of the sexes: cost asymmetry explains female dominance in lemurs. *Anim. Behav.* **76**, 1435-1439.

Ferrari, P. F., van Erp, A. M., Tornatzky, W. and Miczek, K. A. (2003). Accumbal dopamine and serotonin in anticipation of the next aggressive episode in rats. *Eur. J. Neurosci.* **17**, 371-378.

Ferris, C. (2006). Neuroplasticity and aggression: an interaction between vasopressin and serotonin. In *Biology of Aggression* (ed. R. J. Nelson), pp. 163-175. New York: Oxford University Press.

Filby, A. L., Paull, G. C., Hickmore, T. F. and Tyler, C. R. (2010). Unravelling the neurophysiological basis of aggression in a fish model. *BMC Genomics* **11**, 498.

Franchina, C. R. and Stoddard, P. K. (1998). Plasticity of the electric organ discharge waveform of the electric fish Brachyhypopomus pinnicaudatus. I. Quantification of day-night changes. *J. Comp. Physiol. A* **183**, 759-768.

Franchina, C. R., Salazar, V. L., Volmar, C. H. and Stoddard, P. K. (2001). Plasticity of the electric organ discharge waveform of male *Brachyhypopomus pinnicaudatus*. II. Social effects. *J. Comp. Physiol. A* **187**, 45-52.

Fugère, V., Ortega, H. and Krahe, R. (2011). Electrical signalling of dominance in a wild population of electric fish. *Biol. Lett.* **7**, 197-200.

Gavassa, S., Silva, A. C. and Stoddard, P. K. (2011). Tight hormonal phenotypic integration ensures honesty of the electric signal of male and female *Brachyhypopomus gauderio. Horm. Behav.* **60**, 420-426.

Gavassa, S., Silva, A. C., Gonzalez, E. and Stoddard, P. K. (2012). Signal modulation as a mechanism for handicap disposal. *Anim. Behav.* **83**, 935-944.

Gavassa, S., Goldina, A., Silva, A. C. and Stoddard, P. K. (2013). Behavioral ecology, endocrinology and signal reliability of electric communication. *J. Exp. Biol.* **216**, 2403-2411.

Giora, J. and Malabarba, L. R. (2009). *Brachyhypopomus gauderio*, new species, a new example of underestimated species diversity of electric fishes in the southern South America (Gymnotiformes: Hypopomidae). *Zootaxa* **2093**, 60-68.

Godwin, J. and Thompson, R. (2012). Nonapeptides and social behavior in fishes. *Horm. Behav.* **61**, 230-238.

Goodson, J. L. (2005). The vertebrate social behavior network: evolutionary themes and variations. *Horm. Behav.* **48**, 11-22.

Goodson, J. L. (2008). Nonapeptides and the evolutionary patterning of sociality. *Prog. Brain Res.* **170**, 3-15.

Goodson, J. L. and Bass, A. H. (2001). Social behavior functions and related anatomical characteristics of vasotocin/vasopressin systems in vertebrates. *Brain Res. Brain Res. Rev.* **35**, 246-265.

Goodson, J. L. and Kabelik, D. (2009). Dynamic limbic networks and social diversity in vertebrates: from neural context to neuromodulatory patterning. *Front. Neuroendocrinol.* **30**, 429-441.

Goodson, J. L. and Kingsbury, M. A. (2011). Nonapeptides and the evolution of social group sizes in birds. *Front. Neuroanat.* **5**, 13.

Goodson, J. L., Kelly, A. M. and Kingsbury, M. A. (2012). Evolving nonapeptide mechanisms of gregariousness and social diversity in birds. *Horm. Behav.* **61**, 239-250.

Greenwood, A. K., Wark, A. R., Fernald, R. D. and Hofmann, H. A. (2008). Expression of arginine vasotocin in distinct preoptic regions is associated with dominant and subordinate behaviour in an African cichlid fish. *Proc. Biol. Sci.* **275**, 2393-2402.

Grober, M. S., George, A. A., Watkins, K. K., Carneiro, L. A. and Oliveira, R. F. (2002). Forebrain AVT and courtship in a fish with male alternative reproductive tactics. *Brain Res. Bull.* **57**, 423-425.

Hagedorn, M. and Heiligenberg, W. (1985). Court and spark: electric signals in the courtship and mating of gymnotoid fish. *Anim. Behav.* **33**, 254-265.

Hopkins, C. D. (1974). Electric communication in the reproductive behavior of *Sternopygus macrurus* (Gymnotoidei). *Z. Tierpsychol.* **35**, 518-535.

Hopkins, C. D., Comfort, N. C., Bastian, J. and Bass, A. H. (1990). Functional analysis of sexual dimorphism in an electric fish, *Hypopomus pinnicaudatus*, order Gymnotiformes. *Brain Behav. Evol.* **35**, 350-367.

Hupé, G. J. and Lewis, J. E. (2008). Electrocommunication signals in free swimming brown ghost knifefish, *Apteronotus leptorhynchus. J. Exp. Biol.* **211**, 1657-1667.

Insel, T. R. and Young, L. J. (2000). Neuropeptides and the evolution of social behavior. *Curr. Opin. Neurobiol.* **10**, 784-789.

Kabelik, D., Klatt, J. D., Kingsbury, M. A. and Goodson, J. L. (2009). Endogenous vasotocin exerts context-dependent behavioral effects in a semi-naturalistic colony environment. *Horm. Behav.* **56**, 101-107.

Kapsimali, M., Bourrat, F. and Vernier, P. (2001). Distribution of the orphan nuclear receptor Nurr1 in medaka (*Oryzias latipes*): cues to the definition of homologous cell groups in the vertebrate brain. *J. Comp. Neurol.* **431**, 276-292.

King, J. A. (1973). The ecology of aggressive behavior. *Annu. Rev. Ecol. Syst.* **4**, 117-138.

Kline, R. J., O'Connell, L. A., Hofmann, H. A., Holt, G. J. and Khan, I. A. (2011). The distribution of an AVT V1a receptor in the brain of a sex changing fish, *Epinephelus adscensionis. J. Chem. Neuroanat.* **42**, 72-88.

Krakowski, M. (2003). Violence and serotonin: influence of impulse control, affect regulation, and social functioning. *J. Neuropsych. Clin. Neurosci.* **15**, 294-305.

Larson, E. T., O'Malley, D. M. and Melloni, R. H., Jr (2006). Aggression and vasotocin are associated with dominant-subordinate relationships in zebrafish. *Behav. Brain Res.* **167**, 94-102.

Lema, S. C. and Nevitt, G. A. (2004a). Variation in vasotocin immunoreactivity in the brain of recently isolated populations of a death valley pupfish, *Cyprinodon nevadensis. Gen. Comp. Endocrinol.* **135**, 300-309.

Lema, S. C. and Nevitt, G. A. (2004b). Exogenous vasotocin alters aggression during agonistic exchanges in male Amargosa River pupfish (*Cyprinodon nevadensis amargosae*). *Horm. Behav.* **46**, 628-637.

Lorenz, K. (1963). *On Aggression.* New York, NY: Harcourt, Brace and World.

Maynard Smith, J. and Parker, G. A. (1976). The logic of asymmetric contests. *Anim. Behav.* **24**, 159-175.

Miczek, K. A. and Fish, E. (2006). Monoamines, GABA, glutamate and aggression. In *Biology of Aggression* (ed. R. J. Nelson), pp. 114-149. New York, NY: Oxford University Press.

Miczek, K. A., Fish, E. W., De Bold, J. F. and De Almeida, R. M. (2002). Social and neural determinants of aggressive behavior: pharmacotherapeutic targets at serotonin, dopamine and γ-aminobutyric acid systems. *Psychopharmacology* **163**, 434-458.

Migliaro, A. and Silva, A. C. (2012). The role of AVT in the modulation of the circadian rhythmicity of EOD basal rate in South American weakly electric fish. In *10th International Congress of Neuroethology*. University of Maryland: International Society for Neuroethology. www.icn2012.umd.edu

Miranda, M., Silva, A. C. and Stoddard, P. (2008). Use of space as an indicator of social behavior and breeding systems in the gymnotiform electric fish *Brachyhypopomus pinnicaudatus. Environ. Biol. Fishes* **83**, 379-389.

Moyer, K. E. (1968). Kinds of aggression and their physiological basis. *Commun. Behav. Biol.* **2**, 65-87.

Nelson, R. J. (2006). *Biology of Aggression.* Oxford University Press.

Nelson, R. J. and Chiavegatto, S. (2001). Molecular basis of aggression. *Trends Neurosci.* **24**, 713-719.

Nelson, R. J. and Trainor, B. C. (2007). Neural mechanisms of aggression. *Nat. Rev. Neurosci.* **8**, 536-546.

Newman, S. W. (1999). The medial extended amygdala in male reproductive behavior. A node in the mammalian social behavior network. *Ann. New York Acad. Sci.* **877**, 242-257.

O'Connell, L. A. and Hofmann, H. A. (2011). The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. *J. Comp. Neurol.* **519**, 3599-3639.

Øverli, Ø., Harris, C. A. and Winberg, S. (1999). Short-term effects of fights for social dominance and the establishment of dominant-subordinate relationships on brain monoamines and cortisol in rainbow trout. *Brain Behav. Evol.* **54**, 263-275.

Parker, G. A. and Rubenstein, D. I. (1981). Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Anim. Behav.* **29**, 221-240.

Perrone, R. (2012). *Acción Diferencial de la Vasotocina en la Modulación del Comportamiento Social en dos Especies de Peces Eléctricos con Diferente Socialidad.* PhD thesis, PEDECIBA, Uruguay.

Perrone, R., Macadar, O. and Silva, A. (2009). Social electric signals in freely moving dyads of *Brachyhypopomus pinnicaudatus. J. Comp. Physiol. A* **195**, 501-514.

Perrone, R., Batista, R., Batista, G., Lorenzo, D., Macadar, O. and Silva, A. C. (2010). Vasotocin actions on electric behavior: interspecific, seasonal, and social context-dependent differences. *Front. Behav. Neurosci.* **4**, 52.

Pouso, P., Quintana, L., Bolatto, C. and Silva, A. C. (2010). Brain androgen receptor expression correlates with seasonal changes in the behavior of a weakly electric fish, *Brachyhypopomus gauderio. Horm. Behav.* **58**, 729-736.

Quintana, L., Pouso, P., Fabbiani, G. and Macadar, O. (2011a). A central pacemaker that underlies the production of seasonal and sexually dimorphic social signals: anatomical and electrophysiological aspects. *J. Comp. Physiol. A* **197**, 75-88.

Quintana, L., Sierra, F., Silva, A. C. and Macadar, O. (2011b). A central pacemaker that underlies the production of seasonal and sexually dimorphic social signals: functional aspects revealed by glutamate stimulation. *J. Comp. Physiol. A* **197**, 211-225.

Ramallo, M. R., Grober, M., Cánepa, M. M., Morandini, L. and Pandolfi, M. (2012). Arginine-vasotocin expression and participation in reproduction and social behavior in males of the cichlid fish *Cichlasoma dimerus. Gen. Comp. Endocrinol.* **179**, 221-231.

Richer-de-Forges, M. M., Crampton, W. G. R. and Albert, J. S. (2009). A new species of *Gymnotus* (Gymnotiformes, Gymnotidae) from Uruguay: description of a model species in neurophysiological research. *Copeia* **2009**, 538-544.

Saito, D., Komatsuda, M. and Urano, A. (2004). Functional organization of preoptic vasotocin and isotocin neurons in the brain of rainbow trout: central and neurohypophysial projections of single neurons. *Neuroscience* **124**, 973-984.

Santangelo, N. and Bass, A. H. (2006). New insights into neuropeptide modulation of aggression: field studies of arginine vasotocin in a territorial tropical damselfish. *Proc. Biol. Sci.* **273**, 3085-3092.

Semsar, K. and Godwin, J. (2004). Multiple mechanisms of phenotype development in the bluehead wrasse. *Horm. Behav.* **45**, 345-353.

Semsar, K., Kandel, F. L. and Godwin, J. (2001). Manipulations of the AVT system shift social status and related courtship and aggressive behavior in the bluehead wrasse. *Horm. Behav.* **40**, 21-31.

Silva, A., Quintana, L., Galeano, M. and Errandonea, P. (2003). Biogeography and breeding in Gymnotiformes from Uruguay. *Environ. Biol. Fishes* **66**, 329-338.

Silva, A., Perrone, R. and Macadar, O. (2007). Environmental, seasonal, and social modulations of basal activity in a weakly electric fish. *Physiol. Behav.* **90**, 525-536.

Sperry, T. S., Thompson, C. K. and Wingfield, J. C. (2003). Effects of acute treatment with 8-OH-DPAT and fluoxetine on aggressive behaviour in male song sparrows (*Melospiza melodia morphna*). *J. Neuroendocrinol.* **15**, 150-160.

Stoddard, P. K. (2002). Electric signals: predation, sex, and environmental constraints. *Adv. Stud. Behav.* **31**, 201-242.

Stribley, J. M. and Carter, C. S. (1999). Developmental exposure to vasopressin increases aggression in adult prairie voles. *Proc. Natl. Acad. Sci. USA* **96**, 12601-12604.

Summers, C. H. and Greenberg, N. (1995). Activation of central biogenic amines following aggressive interaction in male lizards, *Anolis carolinensis. Brain Behav. Evol.* **45**, 339-349.

Summers, C. H. and Winberg, S. (2006). Interactions between the neural regulation of stress and aggression. *J. Exp. Biol.* **209**, 4581-4589.

Summers, C. H., Summers, T. R., Moore, M. C., Korzan, W. J., Woodley, S. K., Ronan, P. J., Höglund, E., Watt, M. J. and Greenberg, N. (2003). Temporal patterns of limbic monoamine and plasma corticosterone response during social stress. *Neuroscience* **116**, 553-563.

Summers, C. H., Forster, G. L., Korzan, W. J., Watt, M. J., Larson, E. T., Øverli, Ø., Höglund, E., Ronan, P. J., Summers, T. R., Renner, K. J. et al. (2005a). Dynamics and mechanics of social rank reversal. *J. Comp. Physiol. A* **191**, 241-252.

Summers, C. H., Korzan, W. J., Lukkes, J. L., Watt, M. J., Forster, G. L., Øverli, O., Höglund, E., Larson, E. T., Ronan, P. J., Matter, J. M. et al. (2005b). Does serotonin influence aggression? comparing regional activity before and during social interaction. *Physiol. Biochem. Zool.* **78**, 679-694.

Ten Eyck, G. R. (2008). Serotonin modulates vocalizations and territorial behavior in an amphibian. *Behav. Brain Res.* **193**, 144-147.

Thompson, R. R. and Walton, J. C. (2009). Vasotocin immunoreactivity in goldfish brains: characterizing primitive circuits associated with social regulation. *Brain Behav. Evol.* **73**, 153-164.

Trainor, B. C., Sisk, C. L. and Nelson, R. J. (2009). Hormones and the development and expression of aggressive behavior. In *Hormones, Brain and Behavior*, Vol. 1 (ed. D. W. Pfaff, A. P. Arnold, A. M. Etgen, S. E. Fahrbach and R. T. Rubin), pp. 167-203. San Diego, CA: Academic Press.

Triefenbach, F. A. and Zakon, H. H. (2008). Changes in signalling during agonistic interactions between male weakly electric knifefish, *Apteronotus leptorhynchus. Anim. Behav.* **75**, 1263-1272.

Trujillo-Cenóz, O., Echagüe, J. A. and Macadar, O. (1984). Innervation pattern and electric organ discharge waveform in *Gymnotus carapo* (Teleostei; Gymnotiformes). *J. Neurobiol.* **15**, 273-281.

Urano, A. and Ando, H. (2011). Diversity of the hypothalamo-neurohypophysial system and its hormonal genes. *Gen. Comp. Endocrinol.* **170**, 41-56.

van Erp, A. M. and Miczek, K. A. (2000). Aggressive behavior, increased accumbal dopamine, and decreased cortical serotonin in rats. *J. Neurosci.* **20**, 9320-9325.

Westergaard, G. C., Suomi, S. J., Higley, J. D. and Mehlman, P. T. (1999). CSF 5-HIAA and aggression in female macaque monkeys: species and interindividual differences. *Psychopharmacology* **146**, 440-446.

Wingfield, J. C., Moore, I. T., Goymann, W., Wacker, D. W. and Sperry, T. (2006). Contexts and ethology of vertebrate aggression: implications for the evolution of hormone–behavior interactions. In *Biology of Aggression* (ed. R. J. Nelson), pp. 179-210. New York: Oxford University Press.

Yodyingyuad, U., de la Riva, C., Abbott, D. H., Herbert, J. and Keverne, E. B. (1985). Relationship between dominance hierarchy, cerebrospinal fluid levels of amine transmitter metabolites (5-hydroxyindole acetic acid and homovanillic acid) and plasma cortisol in monkeys. *Neuroscience* **111**, 851-858.

Young, L. J., Winslow, J. T., Nilsen, R. and Insel, T. R. (1997). Species differences in V1a receptor gene expression in monogamous and nonmonogamous voles: behavioral consequences. *Behav. Neurosci.* **111**, 599-605.

Zakon, H. H., Thomas, P. and Yan, H.-Y. (1991). Electric organ discharge frequency and plasma sex steroid levels during gonadal recrudescence in a natural population of the weakly electric fish *Sternopygus macrurus. J. Comp. Physiol. A* **169**, 493-499.

Zubizarreta, L., Perrone, R., Stoddard, P. K., Costa, G. and Silva, A. (2012). Differential serotonergic modulation of two types of aggression in weakly electric fish. *Front Behav Neurosci.* **6**, 77.

Zupanc, G. K., Sîrbulescu, R. F., Nichols, A. and Ilies, I. (2006). Electric interactions through chirping behavior in the weakly electric fish, *Apteronotus leptorhynchus. J. Comp. Physiol. A* **192**, 159-173.