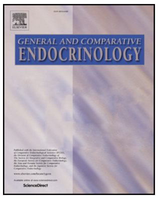
General and Comparative Endocrinology 273 (2019) 67–72

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen



Review article

Vasotocinergic control of agonistic behavior told by Neotropical fishes

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ARTICLE INFO

Keywords:
Vasotocin
Pre-optic area
Electric fish
Cichlids
Agonistic behavior
Dominant-subordinate status

ABSTRACT

The hypothalamic neuropeptides of the vasopressin-oxytocin family (and their homologs for non-mammalian species) are key modulators of the Social Brain Network, acting via specific receptors reported in all the nuclei of this network. Different conclusive examples have proven the context-dependency actions of hypothalamic nonapeptides on social behavior in several vertebrate taxa. Teleost fishes provide endless possibilities of experimental model systems to explore the underlying mechanisms of nonapeptide actions on social behavior given that they are the most diverse group of vertebrates. Although it has been difficult to identify commonalities of nonapeptide actions across species, indisputable evidence in many teleost species have demonstrated a clear role of vasotocin in the modulation of aggressive and sexual behaviors. Though Neotropical South American fish contribute an important percentage of teleost diversity, most native species remain unexplored as model systems for the study of the neuroendocrine bases of social behavior. In this review, we will revise recent data on the two model systems of Neotropical fish, South American cichlids and weakly electric fish that have contributed to this issue.

1. Introduction

Social behavior in vertebrates can be considered as an emergent property of a network of brain nuclei, the social behavior network (SBN), that includes the medial preoptic area, lateral septum, anterior hypothalamus, ventromedial hypothalamus, periaqueductal grey, medial amygdala, and bed nucleus of the stria terminalis (Nelson and Trainor, 2007; Newman, 1999). 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 (Goodson and Kabelik, 2009; Newman, 1999). 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). Multiple neuromodulators, acting both via 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 (Goodson et al., 2012; Johnson and Young, 2017; Newman, 1999; O'Connell and Hofmann, 2011). The hypothalamic neuropeptides of the vasopressin-oxytocin family (and their homologs for non-mammalian species) are key modulators of the SBN, acting via specific receptors reported in all the nuclei of this network. Different conclusive examples have proven the context dependency actions of hypothalamic nonapeptides on social behavior in several vertebrate taxa. Extensive evidence support the idea that social behavior in vertebrates has evolved in close association to the evolution of these hypothalamic nonapeptides (Goodson, 2008; Goodson et al., 2012; Goodson and Bass, 2001; Insel and Young, 2000).

Given the extraordinary diversity of teleost species with different social organizations and reproductive tactics, it will be unlikely to reach a comprehensive view of the general strategies of the context-dependent actions of hypothalamic neuropeptides within this group. However, several studies have contributed new insights to confirm the complexity and importance of nonapeptide modulation of social behavior in different teleost species (Godwin and Thompson, 2012; Thompson and Walton, 2013). Vasotocin (AVT) systems have been especially studied associated to social aggression in several teleost species (Table 1, Semsar et al., 2001; Ramallo et al., 2012; Perrone and Silva, 2016, 2018). In some species, the importance of AVT pathways for the regulation of interspecific cooperative behavior has also been analyzed (Cardoso et al., 2015).

In this review, we will focus on the description of the morphological

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https://doi.org/10.1016/j.ygcen.2018.04.025
Received 29 December 2017; Received in revised form 23 March 2018; Accepted 23 April 2018

arrangement of teleost AVT neuronal populations giving also clear examples of context dependent actions of AVT. In particular, we will revise recent data on the two groups of Neotropical fish, South American cichlids and weakly electric fish that have contributed to this issue. It is important to remark that we will focus in the relation of AVT neuronal systems with social aggression, because the referred species do not show cooperative behavior.

2. Neotropical teleosts as novel model systems for the study of the neuroendocrine bases of social behavior

As mentioned above, teleost fishes provide endless possibilities of experimental approaches to explore the underlying mechanisms of nonapeptide actions on social behavior. It has been difficult to identify commonalities of nonapeptide actions across taxa, but indisputable evidence in many teleost species have demonstrated a clear role of AVT in the modulation of aggressive and sexual behaviors (revised in Godwin and Thompson, 2012). Though Neotropical South American fish contribute an important percentage of teleost diversity, most native species remain unexplored for the study of the neuroendocrine bases of social behavior.

Cichlid fishes (Cichliformes) are intensively studied in the field of social control of reproduction. In particular, two African species have been deeply explored: *Astatotilapia burtoni* and *Oreochromis mossambicus* (Fox et al., 1997; Ogawa et al., 2006). *Cichlasoma dimerus* (Cichliformes, Cichlidae), locally known as chanchita in Argentina, Bolivia, Paraguay, and Uruguay (Fig. 1A), is a serially monogamous Neotropical cichlid with a hierarchical social system established and sustained through agonistic interactions (revised in Pandolfi et al., 2009; Ramallo et al., 2014). This highly social fish offers an ideal opportunity for the study of hormone-behavior relationships within a rich social context. Chanchitas are found in one of two basic and interchangeable social phenotypes that are linked to social and reproductive status. Non-territorial (subordinate, NT) chanchitas have dark background body coloration and are socially denied immediate access to reproduction by the brightly colored territorial (dominant, T) conspecifics (Alonso et al., 2011). Male–female pairs occupying top ranked positions aggressively guard territory, an asset that is critical for reproduction in this species, as it offers a substrate where fish can first spawn and afterwards provide bi-parental care to the eggs and larvae (Fig. 1A right, Ramallo et al., 2015).

Weakly electric fish are traditional neuroethological model systems that combine both locomotor and electric displays for their behavioral performance. The electric organ discharge (EOD) is generated by a very well-known electromotor circuit and carries information about an individual's species identity, sex, and physiological state, coded both by the rate and wave form of the EOD (Caputi et al., 2005; Stoddard, 2002).

Brachyhypopomus gauderio (Gymnotiformes; Hypopomidae, Giora and Malabarba, 2009*)* is a South American freshwater weakly electric fish that belongs to the Order Gymnotiformes (Fig. 1B). *B. gauderio* is gregarious, presents a polygynous breeding system, strong morphological and electrophysiological sexual dimorphism during the breeding season and displays a typical intrasexual reproduction-related aggression (Zubizarreta et al., 2012). Agonistic interactions in this species occurs among courting males and include the signaling of dominance by increasing EOD basal rate (electric dominance, Perrone and Silva, 2016) and, more rarely, by the emission of threat chirps (Perrone et al., 2009). Subordinates signal submission by locomotor displays and by the sporadic emission of chirps and EOD cessations (Zubizarreta et al., 2012).

Gymnotus omarorum (Gymnotiformes, Gymnotidae, Richer-de-Forges et al., 2009) is the most abundant species of weakly electric fish at the southern boundary of the continental distribution of Gymnotiformes in South America (Fig. 1C). *G. omarorum* displays a clear-cut example of pure territorial aggression (Batista et al., 2012; Jalabert et al., 2015; Perrone and Silva, 2018; Quintana et al., 2016; Silva et al., 2013; Zubizarreta et al., 2015). During the non-breeding season, when gonads are regressed and no reproductive motivation is expected to drive competition, males and females of this sexually monomorphic species fiercely defend territories in intrasexual and intersexual dyadic encounters. While dominants are highly aggressive even after the conflict is clearly solved, subordinates signal submission in a precise sequence of locomotor and electric traits using transient offs and chirps, and a persistent decrease in EOD rate (electric subordination; Batista et al., 2012; Perrone and Silva, 2018; Quintana et al., 2016).

3. AVT neurons morphology and distribution in Neotropical teleost species

3.1. *Cichlasoma dimerus*

3.1.1. *Cell bodies*

In adult males, AVT-ir neurons are localized exclusively within the Preoptic Area (POA). Vasotocinergic cell populations extend from behind the anterior commissure (AC) to the posterior POA, above the optic chiasm (OC), forming an arch-like structure (Ramallo et al., 2012). Immunoreactivity can be observed in all three cell populations forming the POA: parvocellular nucleus (P-cells), magnocellular nucleus (M-cells), and gigantocellular nucleus (G-cells), with all the three nuclei facing the border of the third ventricle (3V) (Fig. 2A and B). The most anterior and ventral AVT-ir somata are those of the P-cells, located immediately posterior to the anterior commissure (Fig. 2A and B). These neurons are small rounded or oval in shape, and densely packed against the border of the 3 V.M-cells are the most numerous type of AVT neurons and extend dorsal and posteriorly from the anterior POA (Fig. 2A and B). M-cells are round or pyriform in shape, with eccentric spherical nucleus, and larger soma diameter than P-cells. The G-cell population exhibits the largest somata and occupies the most caudal position within the POA (Fig. 2A and B). G-cells are generally irregular in shape, with spherical eccentric nuclei.

3.1.2. *Axonal projections*

The greatest density of AVT-ir axons observed occurred within the

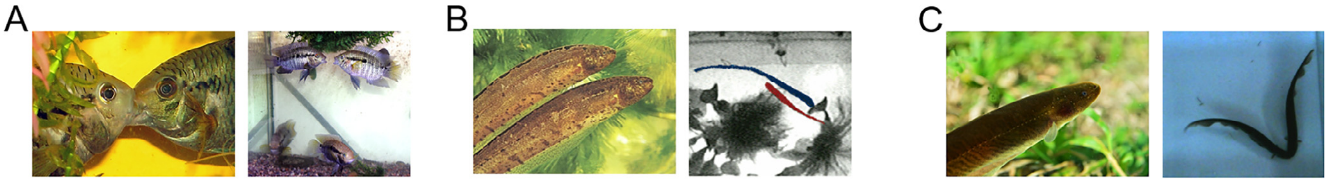

Fig. 1. Neotropical teleosts as model systems for the study of the neuroendocrine bases of social behavior. (A) The South American cichlid, *Cichlasoma dimerus*. Left: male-male dyadic agonistic interactions. Right: communal aquarium exhibiting the typical social hierarchies with two territorial (dominant) males in the top, and one non-territorial male and one female in the bottom. Credits: Felipe Alonso. (B) The South American weakly electric fish, *Brachyhypopomus gauderio.* Left: resting male-male dyad during daytime. Right: nocturnal recordings of a male-male encounter in which individuals adopt the typical agonistic antiparallel position. Credits: Matías Galeano. (C) The South American weakly electric fish, *Gymnotus omarorum.* Left: resting individual during daytime. Right: nocturnal recordings of a dyadic encounter in which individuals adopt the typical agonistic jaw-locking display. Credits: Pablo Vaz.

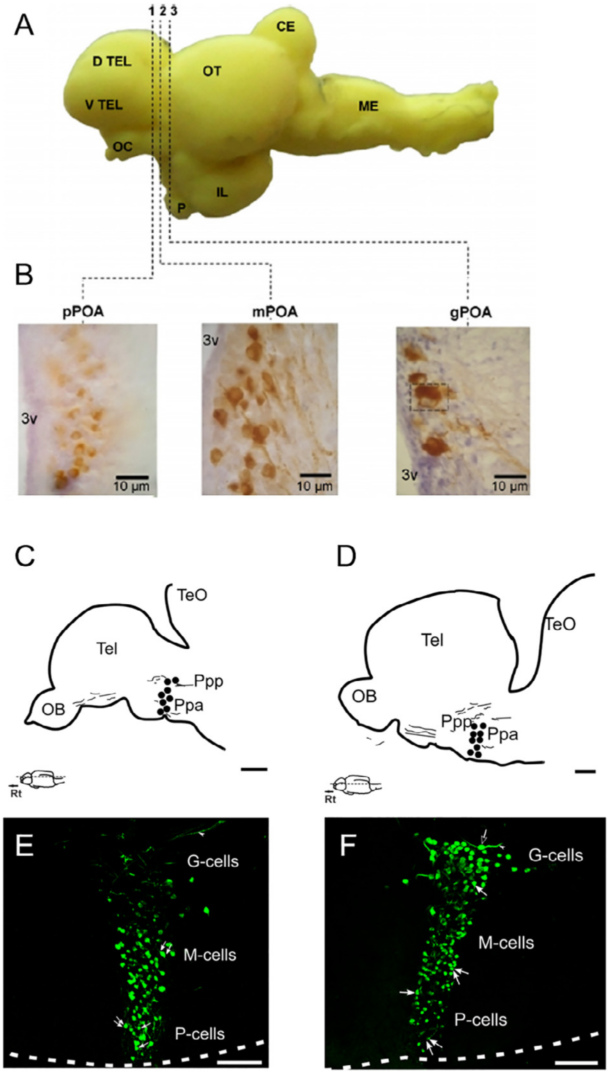

Fig. 2. Vasotoninergic neurons: Morphology and distribution in Neotropical teleost species. (A) Lateral view of *C. dimerus* brain. Dashed lines show the position of transverse sections shown on b. The series 1, 2 and 3 correspond to the anterior, medium and posterior POA, respectively. (B) Microphotograph of transverse sections from pPOA (1), mPOA (2) and gPOA (3), where typical cell size and morphology of the three cell populations are shown. Enclosed within the dashed box lies a gPOA cell intercalated between mPOAcells. CE: cerebellum; D TEL: dorsal telencephalon; IL: inferior lobe; ME: medulla; OC: optic chiasm; OT: optic tectum; P: pituitary; TEL: telencephalon; V TEL: ventral telencephalon. Scale bar: in image. Modified from Ramallo et al. (2012). (C) Distribution of vasotocin-immunoreactive (AVT-ir) cells and fibers in the preoptic area (POA) of *Gymnotus omarorum*. Diagram show AVT-ir cells (dots); parvocells (P-cells), magnocells (M-cells), gigantocells (G-cells) and fibers (lines) Scale bar = 500 um. D) Microphotographs of AVT-ir P-cells, M-cells and G-cells and fibers in a sagittal section. Scale bar = 60 um. Modified from Pouso et al. (2017). (E) Distribution of vasotocin-immunoreactive (AVT-ir) cells and fibers in the preoptic area (POA) of *Brachyhypopomus gauderio*. Diagram show AVTir cells (dots); parvocells (P-cells), magnocells (M-cells), gigantocells (G-cells) and fibers (lines) Scale bar = 500 um. F) Microphotographs of AVT-ir P-cells, M-cells and G-cells and fibers in a sagittal section. Scale bar = 60 um. Modified from Pouso et al. (2017).

POA, where fibers form a dense preoptic-hypophyseal tract that enters the pituitary through the anterior and posterior infundibular stalks (Ramallo et al., 2012). At the pituitary level, AVT-ir fibers are observed at the proximal *pars distalis* and mainly at the *pars intermedia*. AVT-ir-fibers can be also observed in association to the pineal stalk of the pineal organ and to cells of the dorsal sac, which is also part of the pineal complex (Ramallo et al., 2012).

3.2. *Gymnotus omarorum and Brachyhypopomus gauderio*

3.2.1. *Cell bodies*

In non-breeding adult males of *G. omarorum* and *B. gauderio* AVT immunoreactive (ir) cells have been exclusively reported within the POA with a similar anatomical distribution between species (Pouso et al., 2017). AVT-ir cell bodies form a large periventricular band extended from behind the AC to the posterior POA, above the OC. The typical three types of AVT-ir cells mentioned above can be identified in coronal (not shown) and sagittal sections of the POA: (Fig. 2C–F) following the same pattern of distribution as in other teleosts. No qualitative differences in the position or distribution of AVT-ir cells were found between both species (Fig. 2C–F).

3.2.2. *Axonal projections*

AVT-ir fibers scarcely innervate basal telencephalic regions outside the POA. AVT-ir fibers course through the ventral sub-division of the ventral telencephalon (Vv) facing both the ventricle and the proximity of the forebrain bundle (Pouso et al., 2017). In the diencephalon, AVT-ir fibers are densely distributed across the OC and the anterior hypothalamus (Ha). In the POA, AVT-ir fibers extend in a lateral direction. The descending fibers from the POA follow two paths. The first path runs ventro-caudally to the pituitary and to the hypothalamus lateral and ventral. The second path courses dorso-caudally from the diencephalon and continues into the midbrain (Pouso et al., 2017). AVT-ir fibers also occur in areas related to the control of electromotor behavior in the proximity of the pacemaker nucleus (PN) in both species (Perrone et al., 2014; Pouso et al., 2017). At this level, transverse fibers are scattered and more abundant than longitudinal ones. Mostly longitudinal AVT-ir fibers run dorsally and laterally to the dorsal pole of the PN

4. Context-dependent actions of AVT

The agonistic behavior, (i.e., any combative behavior involving struggle among individuals of the same species over limited resources, King, 1973), is a very advantageous example of social behavior to explore context-dependent actions of the AVT system. In agonistic encounters, the distinctive behavior of contestants towards the emergence of the dominant-subordinate status is evident. It is thus clear as well, that both phenotypes shall arise by plastic context-dependent brain control; and that AVT is an excellent candidate to be involved in signaling the valence of this hierarchy. Interestingly, there are at least two different time scales in which this status-dependent brain plasticity becomes evident: 1) In the short-term, i.e., in the moment of the emergence of the dominant-subordination status, which can be as short as seconds; and 2) In the consolidation of dominance, particularly in rank-group species, in which dominance can be quite permanent and remain for months. Though a general rule respect to AVT actions on teleost agonistic phenotypes has remained elusive, several studies have proven the involvement of AVT in both the acquisition and consolidation of dominance. Two general predictions arise respect to these processes: 1) In the consolidation of the dominant-subordinate status, for example, after one week of group ranking without reversion, AVT cells traits should parallel somehow behavioral phenotypic differences between dominants and subordinates; and 2) In the emergence of the dominant-subordinate status, for example, in the moment of dyadic contest resolution, AVT actions should be different between dominants and subordinates.

4.1. *Long term: Dominant-subordinate phenotypes impact on AVT cellular morphology*

Vasopressin/AVT have been related to very different context-

Table 1
Dominant (territorial)-dependent changes in AVT cells located in the preoptic area of the teleost brain. Revision of studies in which significant changes among AVT cells subpopulations were found. Reported variations include changes in cell number (n), size (s), signal intensity, presence of granules (g), and/or their association with behavioral traits of dominance. IHC: immunohistochemistry; ISH: in situ hybridization;*: Neotropical species; ↑: increase; ↓: decrease. Modified and updated from Greenwood et al. (2008).

Species	References	Technique	Phenotype	AVT neurons POA		
				P-cells	M-cells	G-cells
Peacock blenny *Salaria pavo*	Grober et al. (2002)	IHC	territorial	↓ (s)	–	–
Zebrafish Danio rerio	Larson et al. (2006)	IHC	dominant	↓ (n)	↑	↑
Multiband butterflyfish *Chaetodon multicinctus*	Dewan and Tricas (2011)	IHC	territorial	↓ (n,s)		↑ (n)
Cichlid Astatotilapia burtoni	Greenwood et al. (2008)	ISH	territorial	↓ (g)		↑
clown anemonefish Amphiprionocellaris	Iwata et al. (2010)	IHC	territorial	–	↓(n)	–
Cichlid Cichlasoma dimerus*	Ramallo et al. (2012)	IHC	territorial	↓ (s)	–	–
Cichlid Oreochromis mossambicus	Almeida and Oliveira (2015)	IHC	territorial	–	–	↑ (n) ↓ (s)

dependent aspects of the agonistic behavior in vertebrates. Across species, for example, Goodson and Bass (2001) postulate in their spacing hypothesis, that AVP/AVT exert a differential modulation between territorial and gregarious species. Within species, phenotype differences between dominants and subordinates have been found in differences in AVP/AVT neurons as well as in the distribution of AVP-AVT receptors (Albers, 2015).

In teleosts, several studies have pointed out the role of AVT neurons in agonistic phenotypic asymmetries (revised in Table 1). When dominance is established and maintained without reversion, changes in the number and/or size of AVT neurons have been reported by immunohistochemistry and in situ hybridization techniques (Greenwood et al., 2008; Godwin and Thompson, 2012). Table 1 summarizes evidence from the teleost species in which the dominant phenotype has been associated to significant changes in AVT cells subpopulations. Despite the differences in experimental approaches among these studies, it is clear that the consolidation of dominance is associated to enduring morphological changes in AVT neurons, and that these changes do not affect the all the subpopulations of AVT cells in a homogeneous way.

It is not easy to visualize a general strategy among teleosts from these diverse examples of AVT neurons phenotype-dependent plasticity. However, Greenwood et al. (2008) posed the conciliation hypothesis of a dual organization of teleost AVT neurons that has received support from varied species. It has been postulated that two subsystems of AVT neurons alternatively activate and control distinct aspects of social behavior (Godwin and Thompson, 2012; Greenwood et al., 2008). The M-G AVT populations produce and release AVT in circuits that stimulate courtship and/or aggressive behaviors, whereas P-neurons most likely release AVT in circuits that induce behaviors related to social subordination, particularly social withdrawal. According to this model, 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. Thus, the diversity of the data presented in Table 1 gains consistency given that in any of the reported species, there is always a different pattern of cellular changes between the P-cells with respect to M- and/or G-cells; as well as a general decrease in either the number or the size or the signal intensity in P-cells of territorial (dominant) fish.

In *Cichlasoma dimerus,* 48 h after hierarchy establishment, social status correlated with soma size but had no effect on the number or nuclear size of AVT-ir neurons in the preoptic area (Table 1). Dominant T males had P-cells 23% smaller than those present in NT males (subordinates) while no differences were observed in M-cells and G-cells size between T and NT males (Ramallo et al., 2012). Therefore, these data on *C. dimerus* add evidence for a putative role of P-cells in the activation/modulation of submissive neural circuits or inhibition of aggressive/dominance neural networks. As NT males also have higher levels of cortisol than T males (Alonso et al., 2012), it has been postulated that AVT, through its actions on the hypothalamus–pituitary–adrenal axis, could act in concert with cortisol at the SBN to induce the typical subordinate behavior.

4.2. Short term: The emergence of the dominant-subordinate status relies on distinctive AVT actions

Pharmacological manipulations of the AVT system in teleosts have contributed indirect evidence for status-dependent actions of AVT in the attainment of social hierarchies (Backstrom and Winberg, 2009; Goodson and Bass, 2000). However, only few studies in teleosts have explored these actions by comparing the same treatments on both dominants and subordinates. For example, in the bluehead wrasse, AVT inhibits aggression of territorial dominant males but enhances aggression of non-territorial subordinate ones (Semsar et al., 2001). Overall, these studies still provide inconsistent evidence that prevent the emergence of a general hypothesis of the role of AVT/AVP in the moment of establishment of social dominance.

Weakly electric fish are valuable model systems for the study of agonistic behavior and its neuromodulation, given that they readily display conspicuous context- and status-dependent electro communication signals. Among South American freshwater electric fish, agonistic electric displays are known to contribute to the behavioral repertoire of both dominants and subordinates. In particular, EOD rate has been traditionally reported as indicator of dominance and EOD cessations as submissive hiding displays (Hagedorn and Carr, 1985; Hopkins, 1974; Westby, 1975a,b). Chirps (brief, transient EOD modulations) in *Brachyhypopomus gauderio* (Perrone et al., 2009) have been interpreted as threat signals while in *Gymnotus omarorum* as submissive signals (Batista et al., 2012).

The non-breeding territorial aggression of *Gymnotus omarorum* provides the clearest example of non-overlapping status-dependent effects of AVT among teleosts: while in dominants AVT promotes aggression without affecting their electric displays; in subordinates, AVT induces an increase in the emission of electric submissive displays without affecting their locomotor aggression levels (Perrone and Silva, 2018). In other words, AVT modulation of agonistic behavior in *Gymnotus omarorum* acts in a non-overlapping status-dependent manner. The administration of exogenous AVT, and probably the liberation of endogenous AVT, in both dominants and subordinates, during the agonistic encounter consolidate each phenotype acting very specifically on the relevant traits that characterize either dominants' or subordinates' behavior. In contrast to *Gymnotus omarorum*, AVT does not modify aggression levels in dominants of the reproduction-related intermale aggression displayed by *Brachyhypopomus gauderio* (Perrone and Silva, 2016; Zubizarreta et al., 2012). However, and also in contrast to *G. omarorum*, AVT role in dominants' agonistic behavior of *B. gauderio* seems to be restricted to the modulation of EOD rate. The emergence of the EOD rate rank, electric dominance, is abolished by the administration of MC (Manning compound) (Perrone and Silva, 2016). AVT probably acts directly on the medullary PN to modulate the electric dominance, as suggested by the existence of AVT fibers in the proximity of the PN (Perrone et al., 2014; Pouso et al., 2017), and by its effects on the firing rate of the PN in *in vitro* preparations (Perrone et al., 2010). Previous studies have demonstrated other context dependent actions of AVT on EOD rate in this species, such as the increase of nocturnal EOD rate observed in social interacting breeding pairs but not in isolated animals (Perrone et al., 2010; Silva et al., 2007).

In contrast to previous reports (Ferris, 1992; Huffman et al., 2015), the pharmacological manipulation of the AVTergic system did not cause changes in contest timing nor outcome reversion in any of the studied species of weakly electric fish. In other words, the agonistic encounter occurs fairly alike when AVT actions are impeded by MC blockage in both species. We can thus speculate that though AVT is very important to direct the configuration of the brain towards a dominant or a subordinate configuration, this happens after the decision of winning or losing the contest is already made.

One way of acknowledging the importance of neuropeptidergic modulation of agonistic encounters is to evaluate if one contender can interpret the effects of pharmacological treatments applied to the other member of the dyad. The fact that AVT sole action of increasing EOD rate in dominants of *Brachyhypopomus gauderio* promotes the emergence of a more robust repertoire of submissive electric signals in subordinates gives an account of how important this effect is and how it is unequivocally interpreted by contenders (Perrone and Silva, 2016). If we consider the agonistic dyad as a unit, data obtained from *B. gauderio* and *G. omarorum* agree with the hypothesis of AVP/AVT as general promoters of aggression across vertebrates. Consistently in both species, AVT-treated dominants produce an intimidating effect on subordinates, whereas MC-treated dominants produce an encouraging effect in their contenders.

5. Concluding remarks

This review was focused on three examples of Neotropical teleost species in which several AVT context-dependent modulations of the agonistic behavior have been approached.

In the Neotropical cichlid, *Cichlasoma dimerus,* P- cells in the POA are differentially related to distinct social classes in which increased AVT expression may be associated with behavioral and physiological changes typical of NT males.

In South American weakly electric fish, the distinctive actions of AVT on the modulation of the dominant behavior between the two species with different social organization, add evidence to the context-dependent way of action of neuropeptidergic modulation acting at different levels of the brain. In the case of the dominants of *Gymnotus omarorum*, AVT most probably directs its actions to the SBN nuclei responsible for aggressive displays, whereas in dominants of *Brachyhypopomus gauderio*, the only likely target of AVT actions is the medullary command nucleus of the electric displays. Overall, challenging the AVTergic system by this comparative pharmacological approach between species, puts forth clear evidence of phenotypic-dependent actions of AVT within species, and of interspecific-dependent actions of AVT between dominants of both species.

The final purpose of this review was to show how underrepresented neotropical fish are in the study of AVT modulation of social aggresion. We therefore highlight the three species of Neotropical fish that have been used for this kind of studies in the last decade.

6. Declaration of interest

None.

Acknowledgments

We wish to thank Rossana Perrone and Paula Pouso for their generous revision and suggestions to our manuscript. This research was supported by ANII, project FCE2007 569, project FCE2009 2472, PEDECIBA, Agencia de Promoción Científica y Tecnológica (PICT 2016-1614) and Universidad deBuenos Aires (UBACyT 2016-0038)

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