



# Local vasotocin modulation of the pacemaker nucleus resembles distinct electric behaviors in two species of weakly electric fish



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## ABSTRACT

The neural bases of social behavior diversity in vertebrates have evolved in close association with hypothalamic neuropeptides. In particular, arginine-vasotocin (AVT) is a key integrator underlying differences in behavior across vertebrate taxa. Behavioral displays in weakly electric fish are channeled through specific patterns in their electric organ discharges (EODs), whose rate is ultimately controlled by a medullary pacemaker nucleus (PN). We first explored interspecific differences in the role of AVT as modulator of electric behavior in terms of EOD rate between the solitary *Gymnotus omarorum* and the gregarious *Brachyhyppopomus gauderio*. In both species, AVT IP injection (10 µg/gbw) caused a progressive increase of EOD rate of about 30%, which was persistent in *B. gauderio*, and attenuated after 30 min in *G. omarorum*. Secondly, we demonstrated by *in vitro* electrophysiological experiments that these behavioral differences can be accounted by dissimilar effects of AVT upon the PN in itself. AVT administration (1 µM) to the perfusion bath of brainstem slices containing the PN produced a small and transient increase of PN activity rate in *G. omarorum* vs the larger and persistent increase previously reported in *B. gauderio*. We also identified AVT neurons, for the first time in electric fish, using immunohistochemistry techniques and confirmed the presence of hindbrain AVT projections close to the PN that might constitute the anatomical substrate for AVT influences on PN activity. Taken together, our data reinforce the view of the PN as an extremely plastic medullary central pattern generator that not only responds to higher influences to adapt its function to diverse contexts, but also is able to intrinsically shape its response to neuropeptide actions, thus adding a hindbrain target level to the complexity of the global integration of central neuromodulation of electric behavior.

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## 1. Introduction

Complexity and diversity of social organization patterns in vertebrates have evolved in close association with hypothalamic neuropeptides of the vasopressin-oxytocin family including the ancestral arginine-vasotocin (AVT) (Goodson, 2008; Goodson and Bass, 2001; Goodson et al., 2012; Insel and Young, 2000). Fundamental mechanisms through which these peptides influence social

behaviors have emerged from multi-species studies involving mammals and birds. For example, differences in the social organization of closely related species of voles have been demonstrated to be paralleled by differential central vasopressin signaling (Young et al., 1997). In estrildid finches, Goodson and Kingsbury (2011) have shown that the valence of social stimuli and group size preferences between species are encoded by the AVT system. As fish are the most ancient and diverse class of vertebrates, teleosts arise as advantageous model systems to test the role of AVT in shaping social behavior across evolution. Fish species have been intensively studied in the last years to understand the role of neuropeptide control of social behavior, but no consensual general patterns have yet emerged (Godwin and Thompson, 2012; Thompson and Walton, 2013). However, previous reports did succeed in demonstrating how evolutionary adaptations in AVT hindbrain descending pathways have evolved in fish in response to unique social pressures to control, for example, vocal behavior in the pla-

**Abbreviations:** AVT, arginine-vasotocin; EOD, electric organ discharge; MC, Manning Compound; PN, pacemaker nucleus.

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infin midshipman (Goodson and Bass, 2000a,b), or social approach in goldfish (Thompson et al., 2008).

The electric organ discharge (EOD) and its modulations displayed by South American electric fish (Order Gymnotiformes) constitute easily measurable, conspicuous, and distinctive social behaviors that depend on a well-known neural circuit. The peculiarities of electric behavior, the tractability of its underlying neural circuit, and the possibility of conducting comparative studies among related species with different social structures, make electric fish excellent model systems to explore the neuroendocrine bases of social behavior. The EOD carries information about an individual's species identity, sex, and physiological state, which is coded both by discharge rate and EOD waveform (Caputi et al., 2005). Each EOD is triggered by the command discharge of a medullary structure, the pacemaker nucleus (PN), which is composed of two different neuronal types: intrinsic autorhythmic pacemaker cells and projecting bulbospinal relay neurons (Caputi et al., 2005). The rhythmic command for the EOD is initiated at the pacemaker cells, which fire in synchrony, and then transmitted to relay cells in a 1:1 manner (Bennett et al., 1967; Curti et al., 2006). The PN itself commands the regular basal rhythm of the EOD, whereas modulations arise from higher centers (pre-pacemaker structures) to continuously adapt PN rate to environmental, physiological, and social contexts (Comas and Borde, 2010; Kawasaki and Heiligenberg, 1989, 1990; Keller et al., 1991; Stoddard, 2002). EOD rate varies by season, time of day, temperature, sex, social status, locomotor activity, and presence of novel stimuli (Silva et al., 2007). In addition, fish also produce transient communication signals (rapid modulations of the EOD such as chirps, accelerations, and interruptions) that are displayed in different behavioral scenarios (Lorenzo et al., 2006; Perrone et al., 2009).

Our group has been recently interested in the study of AVT modulation of social behavior in two species of weakly electric fish that exhibit different social organization and display different types of aggression (Silva et al., 2013). *Gymnotus omarorum* is a sexually monomorphic solitary, highly aggressive species that displays a unique form of non-sexually biased territorial aggression (Batista et al., 2012). *Brachyhyppomus gauderio* is a sexually dimorphic gregarious species with a polygynous breeding system that displays a reproduction-related intermale aggression (Zubizarreta et al., 2012). Our first approach was to explore interspecific differences in the effect of AVT on the basic unit of electric behavior, i.e. the EOD basal rate of isolated individuals during their resting diurnal phase of the non-breeding season. We found that the administration of AVT induced a large and long-lasting increase in the EOD basal rate of *B. gauderio*, but had no persistent effect in *G. omarorum* (Perrone et al., 2010). The firing rate of the PN of *B. gauderio*, when tested in an *in vitro* preparation, also increased persistently (lasting > 60 min) after the addition of AVT (for 20 min) to the bathing solution, suggesting that the electric behavior observed *in vivo* (Perrone et al., 2010) is due to the direct effect of AVT on the PN. More recently, in a more realistic approach during agonistic encounters, AVT has been confirmed to be distinctively involved in the modulation of electric behavior in both species, responsible for the electrical dominance of *B. gauderio* and involved in the electrical submission of *G. omarorum* (Silva et al., 2013). The PN thus arises as an accessible target nucleus to explore precise mechanisms of interspecific differences in AVT modulation of behavior.

In this study, we aim to deepen the exploration of the diverse actions of AVT on the modulation of electric behavior between the solitary *G. omarorum* and the gregarious *B. gauderio*. We first analyzed early effects of AVT (<30 min) on the EOD basal rate of isolated individuals of both species and identified that AVT induces a small transient increase in sexually monomorphic adults of *G. omarorum* and a large progressive increase in males of *B. gauderio*.

Secondly, we focused on the PN to explore to what extent these behavioral differences can be accounted for by dissimilar effects of AVT upon the command nucleus in itself. In this respect, we demonstrate that AVT modulation of the spontaneous activity of the PN in brainstem slices of *G. omarorum* is different than the effect previously reported in *B. gauderio* (Perrone et al., 2010). We also identify (by immunodetection) the presence of AVT fibers in close proximity to the PN in males of both species. We finally speculate on how these findings contribute to the understanding of the role of the PN as an integrator of multiple influences that shape the diversity and plasticity of social electric behavior.

## 2. Materials and methods

### 2.1. Animals

Individuals of *B. gauderio* (Giora and Malabarba, 2009), and of *G. omarorum* (Richer-de-Forges et al., 2009) were detected and collected using a “fish detector”, an electronic audio amplifier connected to a pair of electrodes, as described elsewhere (Silva et al., 2003). *B. gauderio* were obtained from Laguna Lavalle (31°48'S, 55°13'W, Department of Tacuarembó, Uruguay), and *G. omarorum* were collected from Laguna del Sauce (34°51'S, 55°07'W, Department of Maldonado, Uruguay). As previously described (Perrone et al., 2010), and in accordance with their different social structure, *G. omarorum* were housed in individual compartments within 500 l-outdoor tanks, whereas *B. gauderio* were housed in social groups with the sex ratio of natural breeding colonies containing 3 females per male (Miranda et al., 2008). Fish were fed *Tubifex tubifex ad libitum*. As *B. gauderio* is a sexually dimorphic species (Giora and Malabarba, 2009), we selected males to carry out this study. In the case of the sexually monomorphic *G. omarorum* (Richer-de-Forges et al., 2009), in which sex can only be identified by gonadal inspection, we used males for immunohistochemical experiments and a mixed population (sex ratio 1:1) of adults for behavioral and *in vitro* experiments. To achieve reliable and repeatable behaviors, our collection, transportation, housing, and recording conditions were adjusted to minimize stress on the animals. All research procedures complied with ASAP.ABS Guidelines for the Use of Animals in Research and were approved by the Institutional Ethical Committee (Comisión de Ética en el Uso de Animales, Instituto Clemente Estable, MEC, 07-28-2008 and 007/02/2010) and Comisión de Ética en el Uso de Animales, Facultad de Medicina, UdelaR, 071140-000092-13).

### 2.2. Behavioral experiments

Fish were placed in an experimental setup (40 l-glass tanks) that allowed simultaneous video and electric recordings as described elsewhere (Silva et al., 2007). Fish were recorded during daytime (10–12 AM) in the non-breeding season after being in the recording tank at constant temperature (20–22 °C) for 12 h before the beginning of the experiment. The EODs of freely moving fish were detected by two pairs of fixed electrodes, connected to two high-input impedance amplifiers (FLA-01, Cygnus Technologies Inc.). The electric signals were captured by an audio card (Encore Electronics, ENM 232-8VIA), and images were captured by a video card (Pinnacle Systems, PCTV-HD pro stick) and stored in the computer. Following Perrone et al. (2010), we tested the effects of AVT (IP, 10 µg/gbw) on EOD rate against saline controls (IP administration of equivalent volumes of saline solution,  $n = 6$ ) in resting conditions (freely moving isolated males during daytime in the non-breeding season) in *B. gauderio* ( $n = 6$ ) and *G. omarorum* ( $n = 7$ ).

We took 10 s EOD recordings every 10 min, and calculated the mean EOD interval in each sample using Clampfit (Axon,

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