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Electric organ discharges and near-field spatiotemporal patterns of the electromotive force in a sympatric assemblage of Neotropical electric knifefish

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ABSTRACT

Descriptions of the head-to-tail electric organ discharge (ht-EOD) waveform – typically recorded with electrodes at a distance of approximately 1–2 body lengths from the center of the subject – have traditionally been used to characterize species diversity in gymnotiform electric fish. However, even taxa with relatively simple ht-EODs show spatiotemporally complex fields near the body surface that are determined by site-specific electrogenic properties of the electric organ and electric filtering properties of adjacent tissues and skin. In *Brachyhypopomus*, a pulse-discharging genus in the family Hypopomidae, the regional characteristics of the electric organ and the role that the complex 'near field' plays in communication and/or electrolocation are not well known. Here we describe, compare, and discuss the functional significance of diversity in the ht-EOD waveforms and near-field spatiotemporal patterns of the electromotive force (emf-EODs) among a species-rich sympatric community of *Brachyhypopomus* from the upper Amazon.

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1. Introduction

The pulse-generating Neotropical gymnotiform electric fish of the families Gymnotidae, Hypopomidae, and Rhamphichthyidae generate weak pulsed electric organ discharges (EODs) for locating objects in the dark (electrolocation) and for electrocommunication. These pulses are generated at variable rates, and are typically represented as a 'head-to-tail' EOD (ht-EOD) – the time-voltage waveform recorded in the longitudinal axis at a distance of approximately one to two body lengths from the center of the fish. The ht-EOD is thought to approximate the 'far field' discharge that an electroreceptive receiver detects at a distance of more than one body length from a sender (Aguilera et al., 2001). The ht-EOD has

also been shown to encode information regarding species identity, sex, and reproductive condition (e.g. Caputi et al., 1998; Crampton et al., 2011; Gavassa et al., 2013; Hopkins, 1977; Silva et al., 2008; Stoddard, 2002a, 2002b), and has consequently formed the basis for most evolutionary and behavioral studies of electric signal diversity to date (e.g. Crampton, 1998a; Crampton and Albert, 2006; Crampton et al., 2011, 2013; Curtis and Stoddard, 2003; Hopkins and Heiligenberg, 1978).

The pulse-type gymnotiforms possess a morphologically heterogeneous hypaxial electric organ (EO) that extends along most of the body (Bennett, 1971). The timing and activity of the electromotive force EOD (emf-EOD) pattern (Caputi et al., 1993) along the length of the body, combined with the filtering properties of the skin and tissue and the load of the surrounding water, determine in ensemble a species-specific spatiotemporally complex field (Aguilera et al., 2001; Caputi and Budelli, 1995; Pedraja et al., 2014; Rodríguez-Cattáneo et al., 2008; Sanguinetti-Scheck et al., 2011). The lack of synchronization between localized emf-EOD waveforms that are generated by different regions of the fish body, and the presence of generators of opposite polarity, means that the amplitude and complexity of the field diminishes with dis-

Abbreviations: EO, electric organ; EOD, electric organ discharge; emf-EOD, electromotive force EOD; FDFT, fast discrete Fourier transform; FFT, fast Fourier transform; ht-EOD, head-to-tail electric organ discharge; PPF, peak power frequency; PSD, power spectral density.

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tance. Consequently, much of the 'near field' complexity of the field is not recovered in ht-EOD recordings. The spatiotemporally complex emf-EOD pattern can instead be documented using the 'multiple air gap' procedure of Caputi et al. (1993, see methods) in which the fish is suspended in air on a grill-like array of fine wire electrodes, and the electromotive force recorded across discrete portions of the body. Unlike in recordings taken from electrodes submerged in the water, in multiple air gap recordings the load of the water itself is eliminated, and each body section is also relatively unaffected by adjacent ones. Voltage recordings taken from a multiple air gap array are therefore considered to be a proxy for the equivalent electromotive forces generated by the corresponding portions of the fish's body.

There is a developing understanding that heterogeneity in the spatiotemporal pattern of electromotive force along the gymnotiform body underlies specialization of posterior and anterior portions of the EO and adjacent body tissue for different functions (Aguilera et al., 2001; Rodríguez-Cattáneo et al., 2013, 2008); here we use the terms anterior and posterior to refer to 'rostral' and 'caudal' portions of the EO, sensu Aguilera et al., 2001. The central (mid-body) and posterior (including caudal filament) regions of the EO generate relatively high-voltage, long-range emf-EODs that are mostly projected outward – indicating that their primary function is to carry an electrocommunication signal (Aguilera et al., 2001; Castello et al., 2000, 2009). In contrast, the emf-EODs generated in the anterior (abdominal) region of the EO appear to function primarily as an electrolocation carrier. The emf-EODs generated in the anterior region are significantly less powerful, and the internal resistance and geometric shape of the fish's body and EO 'funnel' locally-generated discharges toward the head into an electrosensory 'fovea' of high tuberosity and ampullary electroreceptor density around the mouth and snout (Aguilera et al., 2001; Castello et al., 2000, 2009). The emf-EODs generated in the anterior region are also reported to be characterized by low-frequency spectral energy (Aguilera et al. 2001; Rodríguez-Cattáneo et al., 2013; Stoddard et al., 1999), raising the possibility that ampullary electroreceptors (which are tuned to low frequencies) may be used in active electroreception, in addition to tuberosity electroreceptors.

The heterogeneity of localized emf-EOD waveforms generated along the length of the gymnotiform body has been relatively well described for several species of the family Gymnotidae, including the neurobiology model species *Gymnotus omarorum* (Caputi et al., 1993; Richer-de-Forges et al., 2009; Rodríguez-Cattáneo and Caputi, 2009), *Gymnotus carapo* SU and *G. coropinae* (Castello et al., 2009), *G. sp. ITU* (Rodríguez-Cattáneo and Caputi, 2009), *G. carapo* PE, *G. curupira*, *G. javari*, *G. obscurus*, *G. sylvius*, *G. tigre*, and *G. varzea* (Rodríguez-Cattáneo et al., 2013), and *Electrophorus electricus* (Albe-Fessard and Martins-Ferreira, 1953; Cox and Coates, 1938). Outside the Gymnotidae, emf-EODs have only been described for one species of Rhamphichthyidae – *Rhamphichthys rostratus* (Caputi et al., 1994), and one species of Hypopomidae – *Brachyhypopomus gauderio* (Caputi et al., 1998).

Although the emf-EOD has been characterized in only one species of *Brachyhypopomus* (*B. gauderio*), the genus is an attractive subject for comparative species-level studies of emf-EOD diversity. First, *Brachyhypopomus* is a species-rich genus with at least 28 species (Crampton et al., 2016) – the second most diverse pulse-type gymnotiform genus after *Gymnotus*, which includes 40 species (Crampton et al., 2013; Giora and Malabarba, 2016). Second, *Brachyhypopomus* is known to include considerable interspecific diversity of the ht-EOD (Crampton and Albert, 2006). Third, studies of the genus benefit from the resources available for the model species *B. gauderio*, which is now well-known from the perspectives of electrogenesis, neuroethology, and neuroendocrinology (Caputi et al., 1998; Markham, 2013; Salazar et al., 2013; Silva et al., 2013). Finally, detailed three-dimensional maps of the

near-field EOD, recorded from arrays of electrodes in the water, have been characterized for *B. gauderio* and two other congeners: *B. beebei* and *B. walteri* (Assad et al., 1999; Stoddard et al., 1999). These studies demonstrate considerable complexity and interspecific variation in the near-field EOD, despite the fact that all three species generate relatively simple biphasic ht-EODs. However, unlike emf-EOD descriptions derived from the multiple air gap approach, the studies of Assad et al. (1999) and Stoddard et al. (1999) do not provide detailed information about which areas of the fish's body produce the observed near-field features (primarily due to the filtering effects of skin and tissue along the fish's body, and the water).

Here we use the multiple air gap approach and additional procedures to explore the diversity of electrogenesis in a species-rich local assemblage of *Brachyhypopomus* species from the Upper Amazon of Peru. The nine congeners in this assemblage generate a wide diversity of ht-EOD waveform structures, including approximately monophasic, biphasic, triphasic, and tetraphasic representatives. We complement descriptions of emf-EOD diversity with classical descriptions of ht-EOD waveforms and EOD pulse rates. We discuss the extent to which anterior and posterior regions of the EO may be specialized for different functions, and the potential role of low-frequency fields in active electrolocation. Additionally, we raise the possibility that anteriorly-generated components of the emf-EOD of some species may carry information that facilitates species recognition in close encounters.

2. Materials and methods

2.1. Field sites

Brachyhypopomus specimens were collected during the non-breeding season in terra firme rainforest streams and seasonally inundated whitewater floodplain systems of the Ucayali River (a major tributary of the Amazon River), within 5 km of Jenaro Herrera, Loreto, Peru (04°54'S, 073°39'W); habitat classifications follow Crampton (2011). Sampling was undertaken with dipnets and electric fish finders (Crampton et al., 2007; Lambert and Crampton, 2010) along the margins of terra firme streams (mostly in leaf litter and roots) and in the root mats of floating rafts of aquatic macrophytes along the edge of floodplain lakes and channels.

2.2. ht-EOD waveforms recordings

Head-to-tail EODs were recorded in a field camp, within five minutes of capture, from individual fish placed in a tank (cooler) filled with water of ambient conductivity and pH from the capture locality and adjusted to a standardized temperature of 27 ± 0.1 °C. All recordings were taken during the period of peak nocturnal activity between 19:00 (approximately one hour after sunset) and 02:00. The tank was 80 cm long by 40 cm wide and filled with water to 36 cm depth. Individual fish were placed within a nylon-mesh sock supported by a mesh cradle suspended in mid-water, and positioned equidistant from the tank ends and sides, with the longitudinal body axis of the fish parallel to the tank sides. Signals were captured using nickel-chromium electrodes placed at the center of the tank ends, amplified differentially with a wide-band amplifier (Signal Recovery model 5113, with low-pass filtering set to 30 kHz cutoff), digitized at 200 ksamples s⁻¹ and 16-bit resolution using a National Instruments NI-USB 6216 data acquisition device, and saved as an array of voltages within a 2048-sample ASCII file. The ht-EOD of a single specimen was characterized by sampling 100 successive pulses and saving the averaged waveform. This averaging procedure was undertaken for noise reduction purposes. Here we do not report intra- or inter-specific compar-

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