



Food deprivation reduces and leptin increases the amplitude of an active sensory and communication signal in a weakly electric fish



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ABSTRACT

Energetic demands of social communication signals can constrain signal duration, repetition, and magnitude. The metabolic costs of communication signals are further magnified when they are coupled to active sensory systems that require constant signal generation. Under such circumstances, metabolic stress incurs additional risk because energy shortfalls could degrade sensory system performance as well as the social functions of the communication signal. The weakly electric fish *Eigenmannia virescens* generates electric organ discharges (EODs) that serve as both active sensory and communication signals. These EODs are maintained at steady frequencies of 200–600 Hz throughout the lifespan, and thus represent a substantial metabolic investment. We investigated the effects of metabolic stress (food deprivation) on EOD amplitude (EODa) and EOD frequency (EODf) in *E. virescens* and found that only EODa decreases during food deprivation and recovers after restoration of feeding. Cortisol did not alter EODa under any conditions, and plasma cortisol levels were not changed by food deprivation. Both melanocortin hormones and social challenges caused transient EODa increases in both food-deprived and well-fed fish. Intramuscular injections of leptin increased EODa in food-deprived fish but not well-fed fish, identifying leptin as a novel regulator of EODa and suggesting that leptin mediates EODa responses to metabolic stress. The sensitivity of EODa to dietary energy availability likely arises because of the extreme energetic costs of EOD production in *E. virescens* and also could reflect reproductive strategies of iteroparous species that reduce social signaling and reproduction during periods of stress to later resume reproductive efforts when conditions improve.

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Introduction

The moment-to-moment metabolic costs of animal communication signals range from insignificant to staggering (reviewed by Stoddard and Salazar, 2011). Communication signals with the highest instantaneous costs, such as the vocal calls of Carolina wrens and the mechanical trilling of orthopteran katydids are typically intermittent in nature and can be stopped entirely to reduce their ongoing metabolic demands. During metabolic stress, reducing or ceasing signaling in these cases means losing only the benefits associated with signaling (e.g., territorial defense, mate attraction) while allowing a shift to other beneficial activities such as foraging. When metabolically expensive communication signals are coupled to active sensory systems, however, reducing or ceasing signaling effort in response to metabolic stress would incur the additional cost of degrading or eliminating sensory performance, potentially interfering with navigation and foraging for food or prey items.

This is the case for weakly electric fish that both sense and communicate with brief electric organ discharges (EODs). The EOD is produced by summation of synchronized action potentials from ~1000 electric organ cells (electrocytes) within the electric organ. Electric fish analyze distortions of the resulting electric fields caused by nearby objects to image their surroundings (Caputi and Budelli, 2006; Caputi et al., 1998; Marsat et al., 2012; von der Emde, 1999, 2006). These fish also communicate with transient changes in EODf (Hagedorn and Heiligenberg, 1985; Hopkins, 1974; Hupé and Lewis, 2008). EOD waveform can encode information such as species (Hopkins and Bass, 1981), sex (Hopkins, 1972), and even individual identity (McGregor and Westby, 1992). Additionally, in some species EOD waveform and rate indicate social status, reproductive status, and body condition (Gavassa et al., 2011, 2013).

The metabolic cost of each EOD is driven primarily by the costs associated with producing the electrocyte action potentials, specifically the energy required by the Na^+/K^+ ATPases to restore the necessary ionic gradients after each action potential (Lewis et al., 2014). The ongoing cost of EOD production is then a function of the cost per discharge and the discharge frequency. Pulse-type electric fish generate EODs at relatively low frequencies (1–100 Hz) with long irregular intervals between each EOD, while wave-type fish produce higher

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frequency EODs at regular uniform intervals (~100–2000 Hz) (Crampton and Albert, 2006). Under normal conditions, both pulse fish and wave fish control the metabolic demands of EOD production by circadian reductions in EODa (Markham et al., 2009b; Salazar and Stoddard, 2008). Pulse fish achieve additional energetic savings by large circadian reductions in EODf (Silva et al., 2007; Stoddard et al., 2007).

The high and steady discharge frequencies of wave fish create significant energetic demands (Lewis et al., 2014), likely making the EODs of these fish sensitive to metabolic stress. Consistent with this hypothesis, wave fish tend to occupy high-oxygen habitats whereas pulse fish generally are more tolerant of low-oxygen environments (Crampton, 1998). Reducing either EODa or EODf could reduce metabolic demand during periods of metabolic stress. Under acute metabolic stress (hypoxia) the wave species *Apteronotus leptorhynchus* and *Eigenmannia virescens* diminish EODa, but not EODf, to reduce the energetic costs of EOD production (Reardon et al., 2011), suggesting that, during short-term metabolic stress, wave fish may be unable to rapidly reduce EODf or that reductions in EODa are more effective in reducing EOD costs. It is not known if wave fish would respond similarly during longer periods of metabolic stress such as that would occur during food deprivation over several days.

In the pulse gymnotiform *Brachyhypopomus gauderio*, metabolic stress associated with food restriction does not cause measurable changes in EODa, and fish subjected to food restriction actually show larger socially-induced increases in EODa (Gavassa and Stoddard, 2012). These authors further found that exogenous cortisol reduces EODa, though food restriction does not alter levels of circulating endogenous cortisol. Here we report direct experimental tests investigating the effects of food deprivation on EODa and EODf in the high-frequency wave-type fish *E. virescens* (~250–600 Hz). We also investigated the endocrine mechanisms coupling food deprivation to changes in the EOD. Comparing *E. virescens* to *B. gauderio* in this regard is important both because of their different EOD rates and patterns, but also because of their different reproductive strategies. *B. gauderio* are semelparous single-season breeders (Silva et al., 2003), while *E. virescens* are longer-lived iteroparous breeders (Hagedorn and Heiligenberg, 1985; Kramer, 1987) that continue to reproduce for at least three years in laboratory conditions (Kirschbaum, 1979). Semelparous species typically continue reproductive behaviors (including costly advertisement signals) during periods of stress, while iteroparous species typically reduce reproductive efforts during stressful periods to survive then resume reproduction when environmental conditions are again favorable (Wingfield and Sapolsky, 2003). Given both the higher energetic demand of EOD production in *E. virescens* and their iteroparous life history, we predicted that *E. virescens* would reduce signaling effort during food restriction and restore signal strength when dietary energy sources are again available.

Materials and methods

Animals

Fish were wild-caught male and female *E. virescens* (Glass knife fish) from tropical South America (Fig. 1), obtained through tropical fish importers. In some experiments *E. virescens* were exposed to male and female *B. gauderio* taken from breeding colonies maintained at The University of Oklahoma. Because animals were not in reproductive condition we could not determine sex non-lethally. Fish were housed in groups of 4–10 in 40-liter or 10-liter tanks and fed live oligochaete blackworms *ad libitum* in a recirculating aquarium system at $28 \pm 1^\circ\text{C}$ with water conductivity of 200–400 $\mu\text{S}/\text{cm}$. In *E. virescens*, each EOD is a positive-going pulse approximately 1–2 ms in duration, and these EODs occur at regular intervals under the control of a medullary pacemaker nucleus, producing a 200–600 Hz sinusoidal wave (Hopkins, 1974) (Figs. 1B–D). All experimental methods were approved by the Institutional Animal Care and Use Committee of The University of Oklahoma, and have complied with the guidelines given in the Public

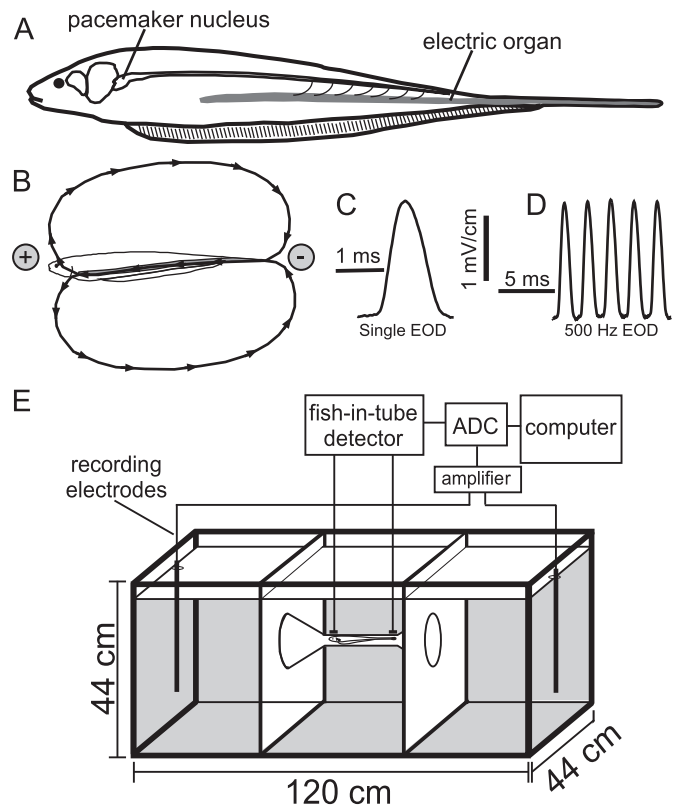


Fig. 1. The electric organ discharge in *Eigenmannia virescens* and experimental tank configuration. A) The electric organ discharge (EOD) is produced by the coordinated action potentials of the electrocytes in the electric organ. A medullary pacemaker nucleus synchronizes electrocyte action potentials via spinal electromotor neurons that innervate each electrocyte. B) The simultaneous action potentials of all electrocytes sum to produce current that moves forward toward the head, following a return path through the water to the tail. By convention, current toward the head measured as positive (upward). C) A single EOD is a positive-going voltage pulse approximately 1 ms in duration. D) The EOD waveform is a sinusoidal wave with frequency set by the pacemaker nucleus. E) Experimental preparation for recording calibrated EODs of free-swimming fish. EODs were digitized from nichrome recording electrodes at the ends of the tank only when custom circuitry detected that the fish was centered within an electrically transparent mesh tube and therefore centered between the recording electrodes at the ends of the tank. ADC: analog-to-digital-converter.

Health Service policy on humane care and use of laboratory animals (National Institutes of Health (U.S.) et al., 2002)

Solutions and reagents

The physiological saline for injections contained (in mM): 114 NaCl, 2 KCl, 4 $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$, 2 $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, 5 HEPES and 6 glucose; pH to 7.2 with NaOH. We purchased adrenocorticotrophic hormone (ACTH 1–39 from porcine pituitary) and hydrocortisone (98% HPLC grade) from Sigma-Aldrich (St. Louis, MO), and purchased leptin (human recombinant) from Enzo Life Sciences (Farmingdale, NY). We dissolved ACTH in water at a stock concentration of 1 M, and then stored this solution in single-use aliquots at -20°C . Stock solutions were thawed and diluted in saline to working concentrations immediately before use. Hydrocortisone was dissolved in 90% ethanol to a concentration of 15 mg ml^{-1} at the time of use. We dissolved leptin in saline at the working concentration of 1 mg/ml then stored it at -20°C in single-use aliquots that were thawed to room temperature just before use.

EOD recordings

Our automated system for recording calibrated EODs from freely swimming fish and procedures for injecting fish are described in detail

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