

REVIEW

The energetics of electric organ discharge generation in gymnotiform weakly electric fish

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Summary

Gymnotiform weakly electric fish produce an electric signal to sense their environment and communicate with conspecifics. Although the generation of such relatively large electric signals over an entire lifetime is expected to be energetically costly, supporting evidence to date is equivocal. In this article, we first provide a theoretical analysis of the energy budget underlying signal production. Our analysis suggests that wave-type and pulse-type species invest a similar fraction of metabolic resources into electric signal generation, supporting previous evidence of a trade-off between signal amplitude and frequency. We then consider a comparative and evolutionary framework in which to interpret and guide future studies. We suggest that species differences in signal generation and plasticity, when considered in an energetics context, will not only help to evaluate the role of energetic constraints in the evolution of signal diversity but also lead to important general insights into the energetics of bioelectric signal generation.

Key words: signal evolution, action potential, bioelectric signalling, electric field, electrosensory system, energetic cost, neuroenergetics, metabolic rate, oxygen consumption.

Received 6 November 2012; Accepted 4 March 2013

Introduction

Brain activity is thought to account for a significant fraction of the whole-animal resting metabolic rate: estimated at 5–7% in fish to 20% in humans (Mink et al., 1981). The high energetic cost is primarily due to the maintenance of membrane potentials, generation of action potentials and synaptic transmission (e.g. Attwell and Laughlin, 2001; Lennie, 2003; Niven and Laughlin, 2008; Harris et al., 2012). Weakly electric fish generate an electric signal to sense their environment and communicate with conspecifics over their entire lifetime. Because these signals are large relative to a typical neuronal action potential, it is reasonable to hypothesize that they would be metabolically costly. In fact, one previous study suggests that signalling in one species of electric fish is responsible for 60% of resting energy consumption (Nilsson, 1996). That said, other studies of these fish have not found a strong association between energy consumption and electric discharge properties (e.g. Julian et al., 2003). To better understand these apparent contradictions, as well as the role energetics may have played in the evolution of bioelectrogenesis and electrosensory processing in weakly electric fish, we present a bottom-up analysis of the associated energetic costs, followed by a comparative analysis of electric signal features.

Weakly electric fishes

The defining feature of weakly electric fish is that they generate an electric field around their body by discharging a specialized electric organ (EO) and sense perturbations of their self-generated electric field with electroreceptor organs distributed over their skin. They use this active electrosense to detect objects in their environment

as well as the electric organ discharges (EODs) of conspecifics (Lissmann, 1958; Lissmann and Machin, 1958; Hopkins, 1988). As a prime example of convergent evolution, active electrosensation has evolved independently in two groups of teleost fishes, the African Mormyriiformes and the South and Central American Gymnotiformes (Bullock et al., 2005). Depending on whether their EOD is a quasi-sinusoidal oscillating signal or whether the EOD pulses are separated by pauses that can be of variable duration, species of both the African and American clades are assigned to one of two categories, wave-type and pulse-type electric fishes, respectively (Fig. 1). Our review focuses on the gymnotiform fishes, for which considerably more data on energetics are available.

Control and generation of the EOD

The EOD of weakly electric fish is under the control of a pacemaker nucleus (PN) in the hindbrain whose action potential output shows a one-to-one relationship to the electrical pulses generated by the EO (Fig. 2) (see Markham, 2013). The PN consists of pacemaker neurons, which are intrinsic to the nucleus, and relay neurons, whose axons transmit action potentials down the spinal cord, where they activate spinal motor neurons. Pacemaker neurons and relay neurons are electrotonically coupled *via* gap junctions supporting synchronous firing among all PN neurons (Moortgat et al., 2000a). The activity of the PN is under the control of two prepacemaker nuclei, the sublemniscal prepacemaker nucleus (SPPN) and the prepacemaker nucleus (PPN), whose input can gradually or rapidly accelerate EOD frequency and, in some species, decelerate EOD frequency or even cause cessation of EO firing (Heiligenberg et al.,

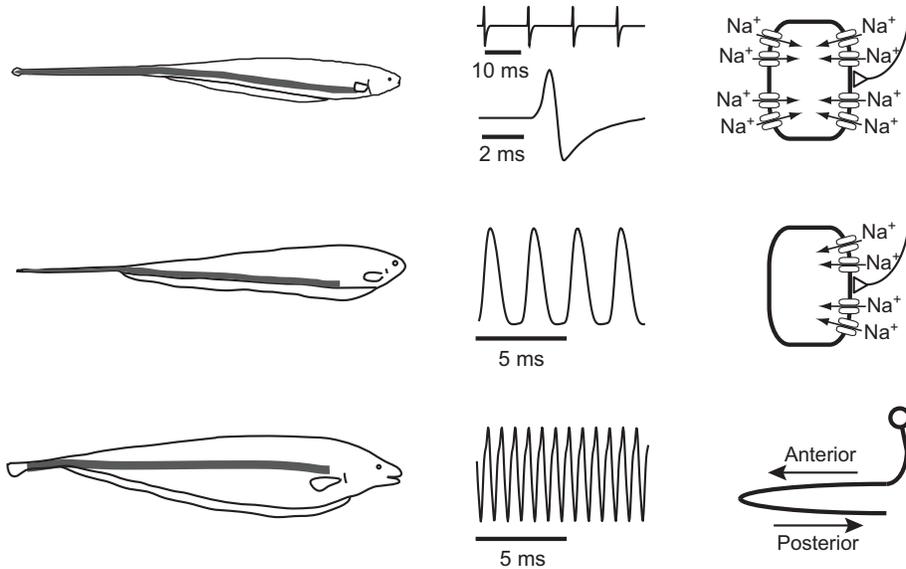


Fig. 1. Electric organs (EOs), electric organ discharges (EODs) and electrocytes for three genera of gymnotiform fish. Top row: *Brachyhyppopomus gauderio* (a pulse-type electric fish); middle row: *Eigenmannia* sp. (a wave-type electric fish); bottom row: *Aptereronotus albifrons* (a wave-type electric fish). Left column: outlines of fish body and approximate location of EO (grey); centre column: EOD trace with time scale (for *B. gauderio*, the upper trace shows a pulse train and the lower trace a single EOD pulse). Right column: sketch of an electrocyte indicating the location of Na⁺ channels for *B. gauderio* and *Eigenmannia* sp.; for *A. albifrons*, the hairpin shape of the axon of the spinal motor neuron inside the EO is shown schematically, with the direction of current flow indicated by arrows.

1981; Heiligenberg et al., 1996; Kawasaki and Heiligenberg, 1989; Keller et al., 1991; Metzner, 1993; Metzner, 1999).

In the gymnotiform family Apterontidae, the EO is composed of the specialized terminals of spinal motor neurons. In all the remaining gymnotiforms and in the African mormyrids, the EO consists of electrocytes that are derived from muscle tissue, and these muscle-derived electrocytes are innervated by spinal motor neurons. Accordingly, the apteronotid EOD is called neurogenic and the EOD of all the remaining weakly electric fishes is called myogenic (Table 1) (Bennett, 1971).

In the simplest case of myogenic electric organs, only the posterior face of the electrocyte is equipped with voltage-gated Na⁺ channels and able to fire an action potential leading to a head-positive, monophasic EOD. This is the case for the electric eel, *Electrophorus electricus*, and several pulse-type and wave-type gymnotiform species (e.g. *Eigenmannia*; Fig. 1). If both faces of the electrocytes contain voltage-gated sodium channels, then the depolarization resulting from firing the posterior face may spread to the anterior face, causing an action potential there. In this case, the EOD is biphasic with an initial head-positive phase caused by the action potential of the posterior face followed by a head-negative phase due to the action potential of the anterior face (e.g. *Brachyhyppopomus*; Fig. 1). More elaborate EOD waveforms can arise in some groups of gymnotiform fish because of the presence of accessory EOs as well as variation in electrocyte size and innervation within the EO (e.g. Bennett, 1971; Caputi et al., 2005).

In *Aptereronotus*, the EO is situated just ventral of the spinal cord (Fig. 1). Upon entering the EO, each electromotor neuron axon turns anterior and then makes a hairpin turn to terminate at approximately the same rostrocaudal level at which it entered the EO. The head-positive and head-negative phases of the EOD are produced by current flowing along the part of the hairpin pointing in the anterior direction and by current flowing along the hairpin part pointing in the posterior direction, respectively (see sketch in Fig. 1) (Bennett, 1971; Waxman et al., 1972).

The cost of generating the EOD we are interested in for the purpose of this article is the performance cost. We therefore disregard any differences between fish in the cost of developing or maintaining the electrogenerating mechanism. Immediately relevant costs are incurred through, first, the ionic flows across the cell membranes of neurons in the PN, spinal cord and EO, all of which fire action potentials at the rate of the EOD; second, the action potentials of the sensory neurons driven by the EOD and its perturbations; and third, synaptic mechanisms in both the electromotor and electrosensory circuits.

Electrosensory circuitry

The self-generated electric field and its perturbations are sensed by ~15,000 tuberous electroreceptor organs distributed over the surface of the fish (Carr et al., 1982). The axons of the corresponding primary afferent neurons project to the electrosensory lateral line lobe (ELL)

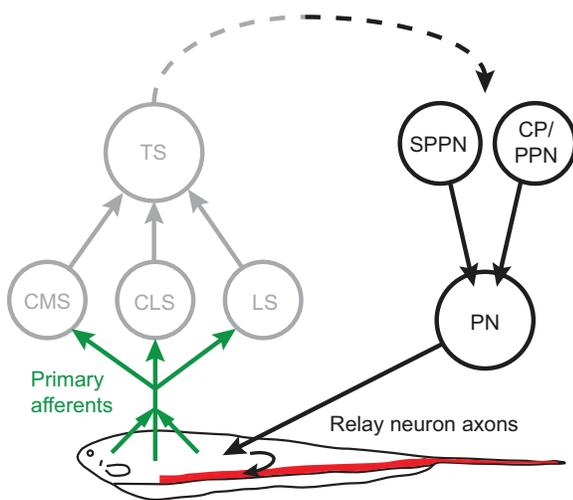


Fig. 2. Simplified electrosensory and electromotor circuitry. Primary electrosensory afferent fibres (green) carry information about perturbations of the fish's electric field to the hindbrain, where each fibre trifurcates to terminate in each of the three topographic electrosensory lateral line lobe (ELL) maps of the body surface: centromedial segment (CMS), centrolateral segment (CLS) and lateral segment (LS) (grey). The output neurons of the three maps project to the torus semicircularis (TS) (grey). Additional electrosensory and feedback nuclei have been omitted. The activity of the pacemaker nucleus (PN) is controlled by two prepacemaker nuclei, the sublemniscal prepacemaker nucleus (SPPN) and the central posterior/prepacemaker nucleus (CP/PPN). The axons of the PN relay cells project to the spinal cord, where they activate spinal motor neurons (small black arrow), which, in turn, innervate the EO (red). Black, motor circuitry.

Table 1. Summary of our current knowledge of the relationships between signal characteristics, habitat preferences and mass-adjusted oxygen consumption rates (\dot{M}_{O_2}) from representative species of the five recognized gymnotiform families

Family ^{a,b} (approx. EODf range) ^{b,v}	Species ^a	Sexually dimorphic		Short-term		Habitat preference(s) ^g	Routine \dot{M}_{O_2} ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$)
		EO type ^{a,b}	EOD waveform	EOD rate	EOD waveform plasticity		
Pulse-type gymnotiforms Gymnotidae (20–80 Hz)	<i>Gymnotus carapo</i> n. sp.	My	Mostly no ^{c,e}	No ^d	No ^o	Lowland <i>terra firme</i> streams and small rivers; floodplains (none found in deep river channels)	2.25 ^s
	<i>Gymnotus cylindricus</i>	My			No ^o		–
	<i>Gymnotus ucayara</i>	My			No ^o		–
	<i>Gymnotus</i> sp. nov.	My			–		4.37 ^s
Rhampichthyidae (10–120 Hz)	<i>Gymnorhampichthys cf. rondoni</i>	My	No ^f	–	Yes ^o	Deep river channels; lowland <i>terra firme</i> streams and small rivers; floodplains	2.49 ^s
	<i>Rhampichthys</i> sp. A	My			–		4.78–6.03 (N=2) ^s
	<i>Rhampichthys marmoratus</i>	My			Yes ^o		–
	<i>Hypopygus lepturus</i>	My			–		6.92–11.51 (N=2) ^s
	<i>Steatogenys elegans</i>	My			Yes ^o		2.97–8.80 (N=2) ^s
Hypopomidae (2–115 Hz)	<i>Brachyhypopomus beebei</i>	My	Yes ^{c,f,g}	No ^h	–	Lowland <i>terra firme</i> streams and small rivers; floodplains (none found in deep river channels)	7.20 ^e
	<i>Brachyhypopomus bennetti</i>	My			Yes ^o		–
	<i>Brachyhypopomus breviostris</i>	My			–		5.65 (mean; N=4) ^s
	<i>Brachyhypopomus gauderio</i> (male)	My			–		3.74 (mean; N=10) ^l
	<i>Brachyhypopomus gauderio</i> (female)	My			Yes ^{h,p,q}		2.47 (mean; N=10) ^l
	<i>Eigenmannia cf. virescens</i> (male)	My	Yes ^{i,j}	Yes ^l	Yes ^o		7.00 (mean; N=5) ^u
Wave-type gymnotiforms Sternopygidae (24–900 Hz)	<i>Eigenmannia cf. virescens</i> (female)	My			–		3.10–3.80 (N=2) ^s
	<i>Sternopygus macrurus</i>	My			Yes ^f	Deep river channels	5.86 (mean; N=6) ^u 1.59 ^s
Apterontidae (700–2200 Hz)	<i>Adontosternarchus balaenops</i>	N	Mostly Yes ⁿ	Mostly yes ^{n,t}	–	Deep river channels	4.11 ^s
	<i>Apterontus albifrons</i>	N			No ^o		2.10–4.25 (N=2) ^s
	<i>Apterontus bonaparti</i>	N			–		1.96 ^s
	<i>Apterontus leptorhynchus</i> (male)	N			–		5.85 (mean; N=6) ^u
	<i>Apterontus leptorhynchus</i> (female)	N			No ^o		6.05 (mean; N=5) ^u
	<i>Magosternarchus duccis</i>	N			–		2.69 ^s
	<i>Magosternarchus raptor</i>	N			–		3.67 ^s
	<i>Orthosternarchus tamandua</i>	N			–		6.45–9.74 (N=2) ^s
	<i>Parapterontus hasemani</i>	N			–		3.63–15.60 (N=2) ^s
	<i>Platyrosteronarchus macrostomus</i>	N			–		1.77 ^s
	<i>Sternarchella schotti</i>	N			–		2.55 ^s
	<i>Sternarchogiton nattereri</i>	N			–		4.10 ^s
	<i>Sternarchorhynchus</i> sp. A	N			–		3.41 ^s
	<i>Sternarchorhynchus curvirostris</i>	N			–		11.27 ^s
<i>Sternarchorhynchus mormyrus</i>	N			–		2.82 ^s	

EO, electric organ; EOD, electric organ discharge; My, myogenic; N, neurogenic. –, data not available.

^aBased on Crampton's (Crampton, 2011) revised classification and generalized habitat categories, where deep river channels are characterized by fast flow rates and high dissolved oxygen, and lowland *terra firme* streams, small rivers and floodplains are characterized by slow flow rates and low dissolved oxygen; ^bAlbert and Crampton, 2005; ^cWestby, 1988; ^dCrampton and Hopkins, 2005; ^eCrampton et al., 2011; ^fStoddard, 2002; ^gKawasaki and Heiligenberg, 1989; ^hStoddard et al., 2003; ⁱMcAnelly et al., 2003; ^jHopkins, 1972; ^kDunlap et al., 1998; ^lZakon, 1993; ^mZhou and Smith, 2006; ⁿGoldina, 2011; ^oSilva et al., 1999; ^pFranchina and Stoddard, 1998; ^qMarkham et al., 2009; ^rJulian et al., 2003; ^sSalazar and Stoddard, 2008; ^tReardon et al., 2011; ^uCrampton, 1998.

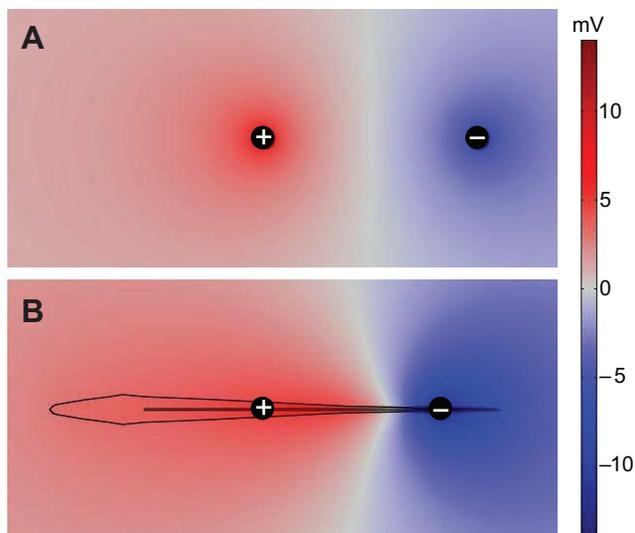


Fig. 3. Dipole-like electric fields. (A) Voltage map for electric dipole scaled to match that for the fish in B. Schematic point charges are indicated by black circles. The voltage map for the fish is based on the model described previously (Babineau et al., 2006; Babineau et al., 2007) for *Apteronotus leptorhynchus*.

of the hindbrain, where each fibre trifurcates to terminate in each of three somatotopic maps (Fig. 2) (Carr et al., 1982; Heiligenberg and Dye, 1982). In addition to the afferent input, the ELL receives a vast amount of feedback from higher areas including the cerebellum. The ELL output neurons project to the midbrain torus semicircularis from where further projections reach the optic tectum and other higher processing centres (for reviews, see Berman and Maler, 1999; Bell and Maler, 2005).

EOD-related energy budget: theoretical considerations

In this section, we consider some of the individual factors involved in EOD-related energy consumption, beginning with the electric field itself and then followed by the energetics of action potential generation in cells involved in electrogenesis and electrosensory processing.

The electric field

Although the temporal features of electric fish EODs differ significantly among species (e.g. pulse-type and wave-type; see Fig. 1), the spatial aspects of the resulting electric fields all resemble those of a distorted dipole (Fig. 3). At the most basic level, one can ask how much energy is required to assemble the charge necessary to produce a three-dimensional electric field similar to that of an electric fish. From electrostatics, we can calculate the energy of a simple dipole directly (Griffiths, 1981); the minimum energy (or work) required to bring two point charges Q (one positive, one negative) within a distance d of one another is proportional to Q^2/d . For an electric field strength similar to that of the wave-type electric fish, *Apteronotus leptorhynchus*, with a peak voltage of ~ 10 mV (measured near the head with respect to distant ground) (Assad et al., 1999), the dipole energy is of the order 10^{-13} J (note that this is in water; a similar calculation in a vacuum would be two orders of magnitude larger because of the much larger dielectric constant of water). In a biological context, 10^{-13} J is equivalent to the energy released when a phosphate is cleaved from each of 10^6 molecules of ATP (6×10^{23} ATP molecules provide about 50 kJ) (Horton,

2006). Note that the dipole energy scales with the square of the dipole charge, so a doubling of Q (which is proportional to the dipole potential) requires four times the energy. Thus, for EODs of higher amplitude, the energy demand is expected to be disproportionately greater. For example, the energy required for a dipole field similar to that of the pulse-type fish *Gymnotus carapo*, with an EOD amplitude of 40 mV (Assad et al., 1999), is almost 10^{-11} J, or about 10^8 ATP molecules. There is also a wide range of EOD frequencies across species. If we assume our energy estimates pertain to each EOD cycle and that each cycle is independent, then the energetic cost is also expected to increase proportionately with EOD frequency.

Similar estimates of energy are found for more realistic multipole electric field models (Chen et al., 2005) (J.E.L., unpublished observations). But more important is the fact that we have only considered one phase of the EOD waveform, and so the estimates do not reflect the cost of the entire EOD cycle nor do they consider the efficiency of the underlying biophysical processes generating current. Nonetheless, they provide a reference point for the energetic cost of an EOD cycle.

Action potential energetics

As mentioned earlier, each EOD waveform is associated with the synchronous firing of action potentials by cells in the PN, spinal cord and EO. Thus, to provide a biological context for the electric field estimates, we next consider the energetic cost of action potential generation in neurons. It is generally agreed that this cost arises primarily from the Na^+/K^+ -ATPase, which hydrolyzes one molecule of ATP to pump three Na^+ ions out for every two K^+ ions into the cell, thus maintaining the ion gradients that drive Na^+ and K^+ flux during membrane depolarization and repolarization (Laughlin et al., 1998; Attwell and Laughlin, 2001; Lennie, 2003). Although direct measurements of energy use can be problematic, estimates are typically based on Na^+ flux during an action potential, a quantity that can be measured electrophysiologically; this Na^+ current determines how much activity is required by the Na^+/K^+ -ATPase, and thus is directly related to energetic cost (e.g. Alle et al., 2009; Sengupta et al., 2010). Such estimates suggest that each action potential consumes between 10^7 and 10^9 ATP molecules depending on neuron type (Attwell and Laughlin, 2001; Lennie, 2003; Sengupta et al., 2010; Hallermann et al., 2012; Harris et al., 2012). Thus, an action potential in just a single neuron can consume an order of magnitude more energy than the minimal amount required to assemble the electric field, suggesting that the actual cost of EOD generation must be several orders of magnitude higher than this theoretical lower bound.

Electromotor networks: pacemaker nucleus

Next, we consider the energy required by the central brain region that sets the timing of the EOD: the PN. To estimate energy consumption by the neurons of the PN, we must consider their Na^+ currents, but data are lacking in this area. However, in the case of *A. leptorhynchus*, we can take advantage of the ionic-based model of the PN developed by Moortgat and colleagues (Moortgat et al., 2000a; Moortgat et al., 2000b). This model adopts the Hodgkin–Huxley formalism to describe the ionic currents underlying action potential generation in this network.

The PN comprises ~ 120 pacemaker (P) neurons and 30 relay (R) neurons in *A. leptorhynchus* (Moortgat et al., 2000a) with some variation of the P/R ratio between species (Ellis and Szabo, 1980). These neurons form a gap junction-coupled network and fire synchronous action potentials that propagate *via* the R axons

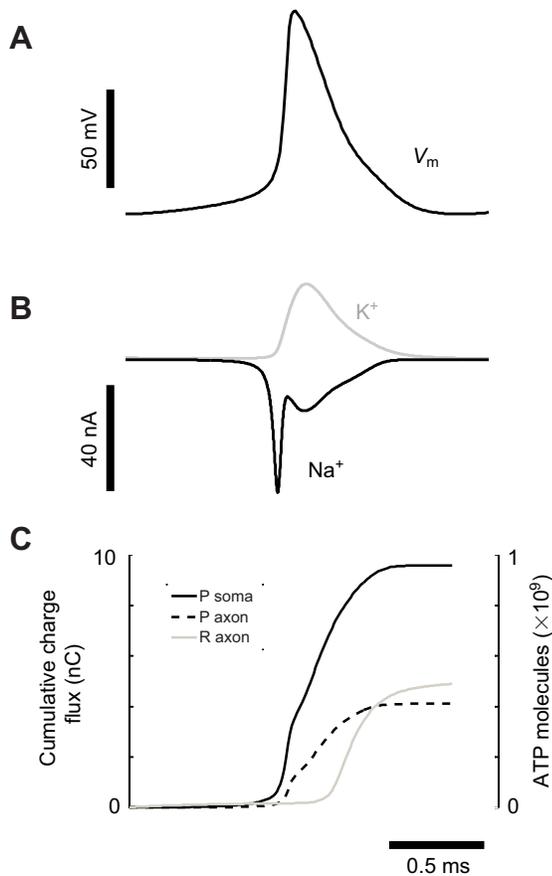


Fig. 4. Pacemaker nucleus energetics based on a previously published model network (Moortgat et al., 2000b). (A) Action potential trace from single pacemaker neuron (somatic compartment). V_m , membrane potential. (B) Na^+ (black trace) and K^+ (grey trace) currents underlying the pacemaker neuron action potential. (C) Cumulative Na^+ current over a single action potential in a pacemaker neuron soma (solid black line), pacemaker neuron axon (dashed black line) and relay cell axon (grey line). Also shown is the equivalent energetic cost in terms of ATP molecules, calculated using standard methods (see 'Electromotor networks: pacemaker nucleus'). P, pacemaker; R, relay.

to drive the EOD in a one-to-one manner. The Moortgat model describes the full network of 150 P and R neurons, with each neuron modelled by a soma and an axon compartment, as well as a distribution of Na^+ , K^+ and leak currents (Moortgat et al., 2000b). Fig. 4A,B shows an example action potential trace and associated Na^+ and K^+ currents for one P neuron (soma compartment). From the total Na^+ flux during an action potential in both somatic and axonic compartments, and using standard methods (e.g. Alle et al., 2009; Sengupta et al., 2010), we calculate the cost of a single action potential in a P neuron to be about 10^9 ATP molecules (Fig. 4C); this is similar to, but on the high end of the range of, previous estimates for other neurons (Attwell and Laughlin, 2001; Lennie, 2003; Hallermann et al., 2012). Note that such estimates depend strongly on the relative gating kinetics of the Na^+ and K^+ channels and can vary significantly between neurons (Sengupta et al., 2010). Of particular interest in the present context is the energy consumed by the entire PN: calculating Na^+ flux over all the P and R neurons in the model network results in a cost of 2×10^{11} ATP molecules per action potential (i.e. per EOD cycle).

Electromotor networks: electrocytes

The PN drives production of the EOD through activation of the EO, which comprises electrocytes that fire action potentials in synchrony with the PN neuron population. Electrocyte action potentials involve Na^+ currents in the μA range (McAnelly and Zakon, 1996; Markham et al., 2009), 20 times larger than that estimated for the model P neuron (peak Na^+ currents near 50 nA). As energetic cost is expected to scale similarly, an electrocyte action potential should consume about 2×10^{10} ATP molecules (Markham et al., 2013). Given EO and electrocyte morphology, there are probably almost 1000 electrocytes in the *Eigenmannia* EO (Schwartz et al., 1975); this translates to about 2×10^{13} ATP molecules per EOD cycle, or 8×10^{15} ATP s^{-1} (1.7×10^{-6} J s^{-1}) for an EOD frequency of 400 Hz.

Electrosensory networks

The neural circuitry involved in the production of the EOD is not the only energy consumer. Sensory pathways may also be a significant contributor to overall energy consumption. For example, in high-frequency wave-type fish (e.g. *A. leptorhynchus* with EOD frequencies near 1000 Hz), electroreceptor afferents have very high firing rates: T-units fire at the EOD frequency and P-units on average at 1/3 the EOD frequency (Scheich et al., 1973; Bastian, 1981; Nelson et al., 1997; Gussin et al., 2007). There are relatively few T-units, so we can consider the 15,000 or so P-units alone (Hopkins, 1976; Carr et al., 1982), firing on average at around 300 Hz. If we assume a conservative cost per action potential of 10^7 ATP molecules, this electroreceptor subpopulation alone could nonetheless use more than 10^{10} ATP molecules per EOD cycle.

In addition, other neurons in the early sensory pathways will also fire at high rates. For example, the population of spherical cells (~600 in total) (Maler, 1979) of the ELL firing at the EOD frequency could play a significant role in action potential-related costs. Other neurons involved in electrosensation fire action potentials at much lower rates than spherical cells. The spontaneous firing rates of the ~5000 pyramidal cells in the ELL (Maler, 2009) range from 3 to 50 Hz (Bastian and Nguyenkim, 2001; Krahe et al., 2008). The torus semicircularis, in particular, is a large and cell-rich structure, but many of its neurons display extremely sparse response properties (Chacron et al., 2011). Therefore, even though a large percentage of the brain of gymnotiforms seems to be dedicated to electrosensory processing, the performance cost of higher electrosensory processing may be relatively modest. Further, action potential production is not the only energy-consuming process. Indeed, recent estimates suggest that synaptic processing comprises as much as half of the nervous system energy budget (Lennie, 2003; Niven and Laughlin, 2008; Harris et al., 2012). Relatively little is known about the synaptic processing involved in EOD generation, though comparing species with neurogenic and myogenic mechanisms could provide insights if it is possible to control for differences in EOD frequency. That said, accounting for synaptic processing could effectively double the estimates of overall cost made through consideration of action potential firing alone.

EOD energetics and the whole-animal energy budget

So far, we have discussed energetic costs in terms of ATP consumed, which is common in the field of neuroenergetics (e.g. Attwell and Laughlin, 2001; Sengupta et al., 2010; Harris et al., 2012). In contrast, whole-animal studies typically involve measures of oxygen consumption (Julian et al., 2003; Salazar and Stoddard,

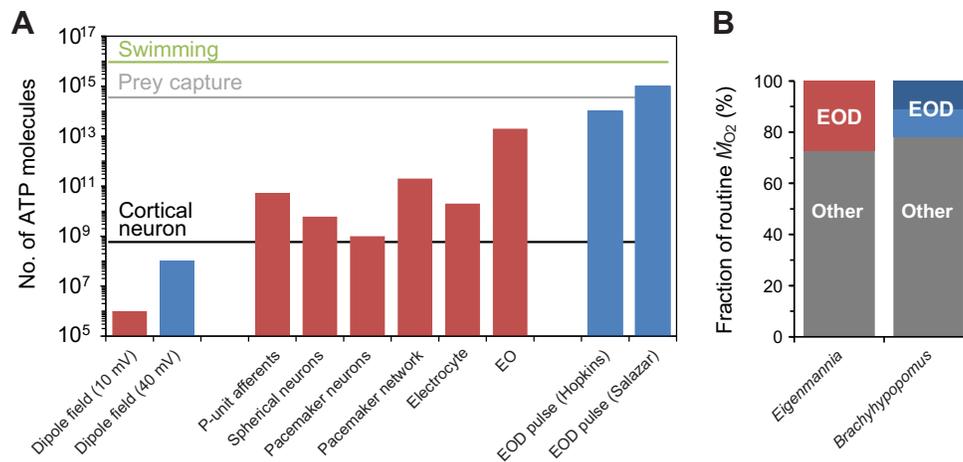


Fig. 5. Components of an EOD-related energy budget. (A) Summary of the energetic cost in ATP equivalents for the different components discussed in the text: dipole electric field at two different field strengths (red similar to wave-type fish, blue similar to pulse-type fish); P-unit cost based on a population of 15,000 cells firing on average at 1/3 of the EOD frequency, with each cell consuming 10^7 ATP spike $^{-1}$; ELL spherical cell cost based on a population of 600 cells firing at the EOD frequency, with each cell consuming 10^7 ATP spike $^{-1}$; costs for the pacemaker neuron and entire pacemaker network are based on a previously published model (Moortgat et al., 2000b) (see 'Electromotor networks: pacemaker nucleus' for details); costs for electrocyte and EO are explained in the text (and expressed per EOD cycle). Note that all cellular and population estimates are for wave-type species and are indicated in red. Values for a single EOD pulse (pulse-type fish, blue) are based on an estimate by Hopkins (Hopkins, 1999) and previous measurements (Salazar and Stoddard, 2008). Horizontal lines provide reference values: the black line shows the cost of a cortical neuron action potential (from Hallermann et al., 2012), intermediate value (equivalent to 4.2×10^{-11} J spike $^{-1}$); the grey line shows the energy required to capture a single prey item (see Maclver et al., 2010), equivalent to 25×10^{-6} J; the green line shows the energy required during scan swimming, as estimated by the 3-fold increase from routine consumption (Julian et al., 2003), equivalent to 7.3×10^{-3} J s $^{-1}$. (B) Fraction of routine \dot{M}_{O_2} used for EOD production for a wave-type species (*Eigenmannia* cf. *virescens*) and a pulse-type species (*Brachyhyppopomus gauderio*). Values for wave-type are based on estimates described in the text, and shown in A (EOD fraction in red); values for pulse-type are based on previous measurements (Salazar and Stoddard, 2008), with two different shades of blue indicating the range from day (lower cost) to night (higher cost, entire blue region).

2008; Reardon et al., 2011). By making a few assumptions, we can convert oxygen consumption (\dot{M}_{O_2}) into the equivalent breakdown of ATP molecules. First, we assume that the dominant fuel source is glucose, and its availability is not limited. Next, we assume that oxidative phosphorylation is the dominant energy system involved, with relatively little contribution from anaerobic processes. Oxidation of a single molecule of glucose requires six molecules of O_2 and yields about 30 molecules of ATP; thus five ATP molecules are provided for every molecule of O_2 consumed (e.g. Harris and Attwell, 2012; Horton, 2006). From this, we can convert \dot{M}_{O_2} from the typical units (e.g. $\mu\text{mol g}^{-1} \text{h}^{-1}$) to O_2 molecules s $^{-1}$ (assuming the appropriate fish mass) and then multiply this by 5 ATP O_2^{-1} to get the rate of ATP use. Oxygen consumption varies widely depending on species and body mass (Julian et al., 2003) (see Table 1), but here we consider the two species for which we have the most data, the wave-type *Eigenmannia* cf. *virescens* (Moorhead, 2010; Reardon et al., 2011) and the pulse-type *Brachyhyppopomus gauderio* (Salazar and Stoddard, 2008). Under routine conditions with a continuously active EOD, \dot{M}_{O_2} for a male *Eigenmannia* is about $7 \mu\text{mol g}^{-1} \text{h}^{-1}$ (Table 1); for a 5 g fish with an EOD frequency of 400 Hz that translates to 3×10^{16} ATP s $^{-1}$ (2.5×10^{-3} J s $^{-1}$) or 7×10^{13} ATP cycle $^{-1}$. For *Brachyhyppopomus*, routine \dot{M}_{O_2} with EOD is $3.7 \mu\text{mol g}^{-1} \text{h}^{-1}$, translating to about 4×10^{16} ATP s $^{-1}$ (3.5×10^{-3} J s $^{-1}$) for a 14 g fish; assuming a 25 Hz pulse frequency, the cost would be 1.7×10^{15} ATP pulse $^{-1}$. Note that although the routine energy consumption per pulse or cycle differs by more than an order of magnitude between the two species, the energy use per unit time is very similar. This suggests there may be a trade-off between EOD amplitude and frequency, with higher amplitude signals balanced by lower discharge rates.

These estimates will vary depending on the actual fuel source utilized; the oxidation of fatty acids can play an important role in powering moderate swimming in fish (e.g. Magnoni and Weber, 2007). As the ATP yield per unit time for fat metabolism is about 65% of that from carbohydrate metabolism (Weber, 2011), more accurate fuel source combinations may reduce estimates of ATP consumption accordingly.

We now consider how EOD-specific costs fit in with the whole-animal energy budget for weakly electric fish. In their study of *Brachyhyppopomus*, Salazar and Stoddard have provided the most detailed experimental breakdown to date of the energy budget in an electric fish (Salazar and Stoddard, 2008). By pharmacologically partitioning the energy budget, they estimated that a male fish spends 11–22% of its energy on EOD-related signalling over a 24 h period (reductions in EOD amplitude reduce costs during the daytime). Although similar studies have not yet been possible in a wave-type fish, we can consider the theoretical estimates in previous sections and add up all EOD-related components (Fig. 5). Remarkably, the result for all EOD-related components is about 30% of routine consumption. This suggests that the EOD comes at a relatively high cost. It is important to note that this is relative to routine levels, which in gymnotiforms are about 50% lower than in temperate teleosts (Julian et al., 2003). Julian and colleagues also showed that much of the variation in metabolic cost could be explained by scan swimming (exhibited only by wave-type fish) rather than EOD type (Julian et al., 2003). Such moderate swimming (about 1–1.5 body lengths s $^{-1}$) results in a 3- to 5-fold increase in \dot{M}_{O_2} from routine levels (Julian et al., 2003; Moorhead 2010). In the context of this higher level of energy expenditure, the fractional costs of the EOD may be closer to 5–10%. Regardless,

this comparison between species at routine levels suggests that wave- and pulse-type fish invest similar energetic effort to produce their EODs. It also provides evidence for energetic trade-offs between EOD amplitude and frequency.

Electromotor–sensory costs: evolutionary and ecological implications

In our final section, we consider the relationship between EOD-specific costs and the whole-animal energy budget with the environmental demands and evolutionary and ecological constraints acting upon weakly electric gymnotiform fish. Based on the latest phylogenetic analyses using molecular and morphological characters from over 215 documented species, gymnotiform fish constitute a clade of three pulse-type families (Gymnotidae, Rhamphichthyidae and Hypopomidae), and two wave-type families (Sternopygidae and Apterontidae) (Table 1) (Albert, 2001; Albert and Crampton, 2005; Crampton, 2011). Evidence from anatomical and phylogenetic studies suggests that the wave-type EOD strategy is a derived trait that evolved from a pulse-type ancestor (Bennett, 1971; Albert and Campos-da-Paz, 1998; Albert, 2001; Albert and Crampton, 2005). In addition, EOD waveform and baseline frequency vary significantly across the different gymnotiform families. For instance, the EOD waveforms of pulse-type gymnotiform families display high diversity in the number of phases (Crampton, 1998b; Stoddard, 2002b). Although phylogenetic evidence indicates that multiphasic pulse-type EODs evolved from a monophasic pulse-type ancestor, several species within the *Gymnotus* clade, the most speciose pulse-type gymnotiform genus, have followed the opposite evolutionary trend, displaying EOD waveforms with fewer phases (Lovejoy et al., 2010). Predation pressure has been hypothesized to be a strong driving force in the evolution of multiphasic pulse-type EODs, because they shift the spectral content of the signal to higher frequencies and out of the range of sensitivity of certain electroreceptive predators (Stoddard, 1999; Stoddard, 2002a; Stoddard, 2002b). Evidence for a role of predation in shaping EOD waveform has also been reported for African weakly electric fish (Hanika and Kramer, 1999; Hanika and Kramer, 2000). As the monophasic *Gymnotus cylindricus* lives in habitats that are relatively free of predators, Lovejoy and colleagues (Lovejoy et al., 2010) speculated that monophasy in *Gymnotus* may have evolved to save energy costs associated with EOD multiphasy when predation pressure is relaxed. When looking at the diversity in EOD baseline frequencies, some clear differences also emerge across gymnotiform families (Table 1). For instance, within the pulse-type gymnotiform species, members of the family Rhamphichthyidae display the highest EOD frequencies (up to ~120 Hz) (Crampton, 1998a; Albert, 2001). Within the wave-type gymnotiform species, however, members of the family Apterontidae display EOD frequencies as high as 2200 Hz (Crampton, 1998a; Albert, 2001; Albert and Crampton, 2005). Interestingly, the gymnotiform species with the highest EOD baseline frequencies dominate in well-oxygenated, fast-flowing water habitats such as large, deep river channels, and display little to no tolerance to experimental severe hypoxia and anoxia (Table 1) (Crampton, 1998a; Crampton, 1998b). Higher EOD frequencies may confer higher temporal acuity, an advantage when living in fast-flowing water habitats. Although it is not clear whether EOD frequencies exceeding a few hundred Hz can be exploited by individual electrosensory neurons, population-level computations could play a role, as in the well-studied jamming-avoidance response (Heiligenberg, 1991). Based on our calculations, high EOD frequencies are also energetically

costly and may come at the expense of a reduction in other EOD properties, such as EOD amplitude. In fact, when compared with other gymnotiform families, apteronotids generate EODs at higher frequencies but smaller amplitudes (Hopkins, 1976; Rasnow et al., 1993; Rasnow and Bower, 1996; Assad et al., 1999), perhaps sacrificing their detection range for higher temporal resolution. Although predation pressure seems like a plausible explanation for the evolution of high EOD frequencies, there is no sufficient evidence to date to strongly support this connection. For instance, analyses of the stomach contents of several electroreceptive catfish showed not only that gymnotiforms are a common prey item for these catfish but also that gymnotiform species with either low or high EOD frequencies are equally preyed upon (Barbarino Duque and Winemiller, 2003). Taken together, this wide taxonomic EOD waveform and frequency diversity seems to reflect the combined adaptive responses to energetic demands, predation pressure and electroreceptive demands associated with foraging and habitat characteristics.

To fully understand the extent to which the energetic costs of electromotor and electrosensory processing differ across weakly electric gymnotiform species, a comparative approach is necessary while measuring this relationship (1) in breeding individuals, (2) in males and females for species with sexually dimorphic EODs, (3) across the low and high states of EOD plasticity for species capable of short-term rapid EOD changes, and (4) within a framework that compares species with extreme habitat constraints, foraging behaviours and predation pressures as it pertains to the particular respiratory physiology and metabolic needs. As previously mentioned, Julian and colleagues (Julian et al., 2003) found no significant relationship between routine \dot{M}_{O_2} and EOD-related properties across gymnotiform species. Although this study represents the most exhaustive dataset measuring routine \dot{M}_{O_2} in 33 individuals from 23 species across all five gymnotiform families, two additional aspects related to EOD plasticity in gymnotiform fish need to be considered to advance our understanding of the interspecific differences in the energetic cost of bioelectrogenic properties, such as EOD amplitude, duration and baseline frequency. First, we need to consider the effect of breeding state on the EOD. In many gymnotiform species, when compared with non-breeding individuals, the EOD waveform's amplitude and duration and the EOD baseline frequency are significantly increased in breeding individuals (Meyer et al., 1987; Westby, 1988; Zakon, 1993; Stoddard, 2002a; Stoddard, 2002b; Crampton and Hopkins, 2005; Cuddy et al., 2012). In addition, a comparison between the EOD-related energetic cost of non-breeding and breeding individuals can help us to understand differences between the energetics of electrolocation and electrocommunication. Previous studies suggest that such a distinction can be made in the pulse-type species *Brachyhypopomus pinnicaudatus* (Salazar and Stoddard, 2008). Although in this species the enhanced EOD waveforms associated with breeding state are significantly more pronounced in males than in females (Hopkins et al., 1990; Silva et al., 1999; Stoddard, 2002a), this difference does not translate to males having better electrolocating capabilities (Stoddard, 2002b). Because the focus of the study by Julian and colleagues (Julian et al., 2003) was to sample as many species as possible, individuals in both non-breeding and breeding states were probably involved, possibly contributing to the high variance in the routine \dot{M}_{O_2} values within species (Table 1) (Julian et al., 2003). Accordingly, this approach could potentially underestimate differences in routine \dot{M}_{O_2} between species with different bioelectrogenic properties. Second, we also need to consider the role of sexual dimorphism

and short-term signal plasticity in the EOD waveform and frequency across gymnotiform species. Sexual dimorphism in EOD waveform and frequency is pervasive in species of three of the five gymnotiform families, Hypopomidae, Sternopygidae and Aptereronotidae (Table 1). For instance, in the brachyhypopomid species *Brachyhypopomus occidentalis*, *B. pinnicaudatus* and *B. gauderio*, breeding males produce larger and longer EOD waveforms than females (Hagedorn, 1988; Hopkins et al., 1990; Silva et al., 1999; Stoddard, 2002a). And in the wave-type species *Sternopygus macrurus*, *Eigenmannia* cf. *virescens* and *Aptereronotus albifrons*, females display higher EOD baseline frequencies than males (Hopkins, 1972; Hopkins, 1974; Dunlap et al., 1998), and the opposite is true in *A. leptorhynchus* (Dunlap et al., 1998). In addition, in several gymnotiform species from the Rhamphichthyidae, Hypopomidae and Sternopygidae families, individuals can alter their EOD waveforms reversibly within minutes to hours (Table 1) (Silva et al., 1999; Franchina and Stoddard, 1998; Markham et al., 2009; Goldina, 2011). For instance, the EOD waveforms of *B. gauderio* are enhanced from day to night, following a circadian rhythm (Franchina and Stoddard, 1998; Stoddard et al., 2007). This EOD circadian plasticity is also sexually dimorphic, with males displaying larger and longer EOD waveforms at night when compared with females (Franchina and Stoddard, 1998; Stoddard et al., 2007). Moreover, males enhance the magnitude of the circadian swing of their EOD waveforms even more in the presence of competing males, and suppress these enhancements if they are socially isolated for a few days (Franchina et al., 2001). Whereas apteronotids are not known to display circadian rhythms of EOD amplitude or waveform, they are able to increase their EOD frequency by several Hz and maintain this elevated frequency for several hours in response to extended exposure to a conspecific EOD mimic of similar frequency (Oestreich and Zakon, 2002).

Accordingly, studies that have examined the energetic cost of electric signals within the context of EOD plasticity have found a significant relationship between EOD-related \dot{M}_{O_2} or metabolic stress and specific EOD properties (Salazar and Stoddard, 2008; Reardon et al., 2011; Stoddard and Salazar, 2011). Salazar and Stoddard found that the night-time EODs of *B. gauderio* males are energetically expensive when compared with their daytime counterpart, and with other components of their energy budget (Salazar and Stoddard, 2008). Females do not display such extreme day-to-night increases in their EOD-related energetic costs. As such, when compared with females, male *B. gauderio* have far more expensive EODs. The occurrence of a marked circadian EOD change in males and its associated reduction in energetic expense may be an adaptive response that ensures the signal's waveform and frequency are enhanced at night to facilitate foraging, mate attraction and intrasexual competition, and reduced by day to maintain basal electrolocation and electrocommunication (Hopkins, 1999). In addition, the enhanced nocturnal EOD of male *B. gauderio* may incur other costs as it is more conspicuous across the detection range of natural electroreceptive predators, such as the electric eel (*E. electricus*) and catfishes, who track their prey's electric signals (Westby, 1988; Stoddard, 1999; Stoddard, 2002b). These electroreceptive predators can readily detect the low-frequency (DC) components of the EOD power spectrum of weakly electric fish (Hanika and Kramer, 1999; Hanika and Kramer, 2000; Stoddard, 1999). For instance, the African catfish *Clarias* sp., an electroreceptive predator, more readily detected EODs with longer durations, and to a lesser extent with higher pulse frequencies, of the only wave-type mormyrid fish, *Gymnarchus niloticus*

(Lissmann and Machin, 1963). In the case of *B. gauderio*, the nocturnal EOD duration increase, but not the nocturnal EOD amplitude or pulse frequency enhancement, exaggerates the second phase of their biphasic EODs making them significantly asymmetrical around zero voltage (Franchina and Stoddard, 1998; Stoddard, 2002b). This asymmetry will increase the low-frequency spectral properties of the male EODs, potentially making them more detectable by the ampullary electroreceptors of Neotropical catfish, such as *Pseudoplatystoma tigrinum* (reviewed by Stoddard and Markham, 2008). If predation pressure is the major driving force for the existence of EOD circadian rhythms in male *B. gauderio*, we would not expect to find pronounced EOD amplitude and frequency rhythms, as these two parameters do not seem to be major contributors to the increased risk of detection by predators. Thus, we can hypothesize that only the daytime reduction of the EOD duration seems to be a direct response to predation risk while the daytime reduction of EOD amplitude and frequency may be a response to energetic constraints and, to a lesser extent, predation. Reardon and colleagues used a different strategy to evaluate the relationship between EOD plasticity and EOD-related metabolic demands (Reardon et al., 2011). They measured changes to the EOD amplitude and frequency of individuals from two wave-type species, *E. cf. virescens* and *A. leptorhynchus*, during incremental hypoxic stress. In both species, the EOD amplitude and, to a much lesser extent, EOD frequency decreased in response to a gradual drop from normoxia to hypoxia. Yet, when compared with *A. leptorhynchus*, *E. cf. virescens* displayed higher tolerance to hypoxic stress, and greater EOD amplitude reduction. Reardon and colleagues' study highlighted how gymnotiform species with plastic EODs, such as *Eigenmannia*, can use this to their advantage to meet metabolic demands (Reardon et al., 2011). Understanding the energetic costs associated with different signal components, the detectability of these components by electric fish predators, and the female preference for such signal components should ultimately help us to understand the selective advantage of EOD plasticity across the gymnotiform clade.

Conclusion

We have deconstructed the various factors that contribute to EOD-related energy costs. Using our current knowledge on the anatomy and physiology of the electromotor/electrosensory processing pathways in gymnotiform fish, we calculated estimates of energy consumption for some of the main structures involved. We then compared the combined estimate of energy consumption for all energetically salient electromotor/electrosensory structures with whole-animal \dot{M}_{O_2} values for the various gymnotiform species where data are available. Such a comparison highlights the mismatch in \dot{M}_{O_2} values, where higher estimates result from our bottom-up reconstruction of energy costs when compared with empirically measured EOD-related \dot{M}_{O_2} values. Performance-related costs of EOD generation are surprisingly high, at up to 30% of routine \dot{M}_{O_2} . Our comparative analysis also highlights the need for future studies to identify anatomical substrates and physiological processes that may account for energy consumption efficiencies in the electromotor/electrosensory pathways. The dependence between EOD-specific features and routine \dot{M}_{O_2} remains unclear, and a trade-off between EOD amplitude and frequency may make this relationship difficult to characterize. Indeed, a complete understanding may require characterization of the full cost-benefit relationship in terms of bioenergetics, detection range, conspicuousness to predators, and communication (among other factors) (Nelson and MacIver, 2006; MacIver et al.,

2010). Nevertheless, we emphasize how current knowledge on EOD plasticity and the metabolic constraints of the various preferred habitats of gymnotiform species can stimulate future comparative studies looking at such trade-offs. For instance, additional research looking at (1) hypoxia-induced changes in EOD waveform, frequency, and communication-related modulations of EOD frequency across hypoxia-tolerant and hypoxia-intolerant gymnotiform species, and (2) changes in routine \dot{M}_{O_2} due to changes in EOD amplitude and frequency in highly plastic gymnotiform species can help us to further understand the role of EOD plasticity in energy conservation.

Acknowledgements

We gratefully acknowledge the work of our colleagues and students, without which this article would not have been possible: Lauren Chapman, Katie Gilmour, Michael Markham, Mayron Moorhead, Alana Parisi, Steve Perry, Erin Reardon and Philip Stoddard. We also thank Len Maler for valuable comments.

Author contributions

V.L.S., R.K. and J.E.L. conceived and co-wrote the manuscript. J.E.L. performed the calculations for the estimates of the EOD-related energy costs.

Competing interests

No competing interests declared.

Funding

This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants to V.L.S., R.K. and J.E.L.

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