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# The evolutionary origins of electric signal complexity

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**Abstract**

This study explores the evolutionary origins of waveform complexity in electric organ discharges (EODs) of weakly electric fish. I attempt to answer the basic question of what selective forces led to the transition from the simplest signal to the second simplest signal in the gymnotiform electric fishes. The simplest electric signal is a monophasic pulse and the second simplest is a biphasic pulse. I consider five adaptive hypotheses for the evolutionary transition from a monophasic to a biphasic EOD: (i) electrolocation, (ii) sexual selection, (iii) species isolation, (iv) territory defense, (v) crypsis from electroreceptive predators. Evaluating these hypotheses with data drawn largely from the literature, I find best support for predation. Predation is typically viewed as a restraining force on evolution of communication signals, but among the electric fishes, predation appears to have served as a creative catalyst. In suppressing spectral energy in the sensitivity range of predators (a spectral simplification), the EOD waveforms have become more complex in their time domain structure. Complexity in the time domain is readily discernable by the high frequency electroreceptor systems of gymnotiform and mormyrid electric fish. The addition of phases to the EOD can cloak the EOD from predators, but also provides a substrate for subsequent modification by sexual selection. But, while juveniles and females remain protected from predators, breeding males modify their EODs in ways that enhance their conspicuousness to predators.


*Keywords:* Electric fish; Evolution; Communication; Gymnotiformes

## 1. Introduction

The structures of electric communication signals are sufficiently simple that we stand a reasonable chance of being able to uncover and connect every aspect of their evolution. Processes tractable to study include the ecological and behavioral forces that select among phenotypes, the physiological and biophysical processes that create and control the electric waveforms, and the molecular targets of signal evolution. This paper reviews and summarizes the evidence bearing on a question of origins: what forces drove the simplest electric signal waveform to the next stage of complexity, i.e., why did ancestral monophasic waveforms of the weakly electric fish give way to biphasic waveforms and other more complex forms? In this foray, I focus on the order Gymnotiformes, the New World electric fish, though the story could be worked out with equal success for Mormyroidei, the African superfamily of electric fish.

## 2. Primitive monophasy

Before looking at forces promoting complexity, one must establish that the original electric waveforms were in fact simpler than extant forms. The idea that natural forms evolve from simple to complex is consistent, but not sufficient evidence upon which to base an argument. Taking a broadly comparative approach, one can compare fish with independently derived electrogenesis. Monophasic EODs (electric organ discharges) are the norm within the torpedoes, skates, stargazers, and electric catfish [6]. However, the independently derived EOD waveforms of some freshwater synodontid catfish are not monophasic but rather biphasic, [26]. In *Synodontis* the EOD could be biphasic owing to its possible generation by a modified swim-bladder (C. Hopkins, pers. com.) instead of the linear arrays of electrogenic cells more typical of electrogenic fish—action potential propagation down a curving array of cells can produce a biphasic EOD as the ion flux changes direction with respect to the animal's body. Ideally, mapping EOD waveforms onto a phylogenetic analysis would reveal the primordial signal state. A molecular phylogeny of the mormyroidei shows the basal EODs in this group to be monophasic as predicted [50], but cladograms of the

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order Gymnotiformes [1,3] lack sufficient basal taxa to inform us on this question.

To support primitive monophasy in the Gymnotiformes, I turn instead to studies of anatomy, physiology, and development. In every gymnotiform studied, larval electrocytes develop from the fusion of muscle cells and the subsequent loss of contractile proteins [20,35,52]. The resulting electrocytes are fusiform in shape, with voltage-gated ion channels concentrated at the posterior end, producing upon depolarization inward, forward-flowing sodium currents. The resulting EOD is necessarily monophasic. In adult gymnotiforms, further modification of those larval cells into a derived, boxlike shape can (but does not always) result in a cell with two opposing excitable faces. When these two faces depolarize in alternation the resulting waveform is biphasic, and thus more complex in its temporal characteristics [8,9]. In the family Apteronotidae, adult electrocytes are J-shaped electromotoneurons—propagation of an action potential around the loop of the J produces the two phases of the EOD [9]. In every case, however, the electrocytes of larval and young juvenile fish are fusiform cells that produce monophasic EODs [20,35]. Thus the diverse electrocyte shapes that generate more complex waveforms can only be interpreted as derived structures.

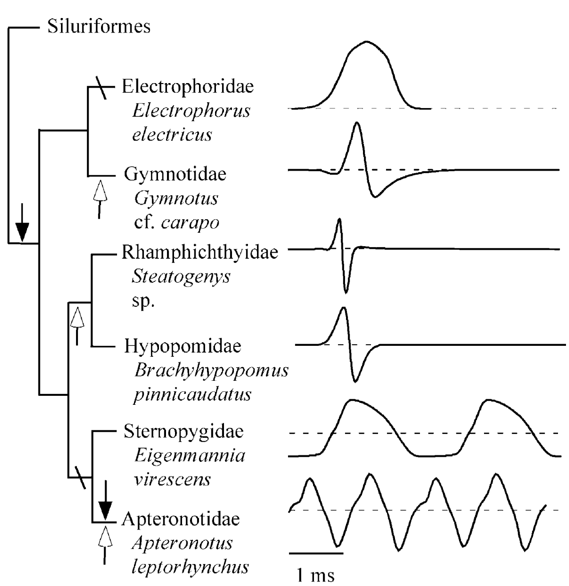


Fig. 1. Phylogeny of the Neotropical electric fish order Gymnotiformes [1] with representative EOD waveforms from each family. The outgroup Siluriformes (catfishes) root the tree. Solid and open-headed arrows show two alternate hypotheses for independent origins of the multiphasic EODs. Under one hypothesis (solid arrow), biphasy evolved twice, but was lost in Electrophoridae (slash). Under the other hypothesis (open arrow), biphasy evolved independently in the Gymnotidae. The independent origin of biphasy in the Apteronotidae is inferred from its novel, neurogenic electric organ [8,9,35]. Most EODs shown here have equal amounts of energy above and below zero volts (dashed line), which nulls the DC in the EOD spectrum and reduces energy that may be readily detected by predators with ampullary electroreceptors.

## 3. Non-adaptive hypotheses

Taking the monophasic EOD as the primitive condition among the Gymnotiformes, I can now ask what forces could have driven the transition to a biphasic EOD waveform. I consider first the possibility that the transition was not adaptive at all, but rather an epiphenomenon of other changes. Among the pulse gymnotiforms with multiphasic EODs, electrocytes resemble a shallow cylinder or cuboid in shape, and are arrayed in series with spaces between them. Linear stacking of electrocytes results in ion flow that is orthogonal to the membranes and in axis with the body, thus is maximally efficient. But this shape also lends itself to the support of opposing excitable membranes within individual electrocytes that produce biphasic EODs. So perhaps biphasic EODs arose as a side-effect of stacking flattened electrocytes. Yet flattened and stacked electrocytes need not and do not always produce biphasic EODs. In the genus *Brachyhypopomus*, such electrocytes in the anterior portion of the electric organ produce monophasic EODs; biphasic electrocytes are restricted to the tail, their spatial extent varying within the genus [14,47]. Likewise, the primitive mormyroid electric fish with monophasic EODs have the same stacked, biplanar electrocytes as their counterparts with biphasic EODs [31].

Among the Gymnotiformes, multiphasic EODs appear in two or possibly three independent lineages (Fig. 1) and in no lineage is monophasy clearly a primitive condition. The Apteronotidae evolved biphasic EODs independently of other taxa, concordant with their independently derived neural electric organs. Multiphasic EODs appear within all the pulse fishes (those with discontinuous EODs) except the electric eel (*Electrophorus electricus* L.). Sister families Hypopomidae and Rhamphichthyidae appear to share a common EOD structure in the two central phases, though members of both groups often produce additional phases from accessory electric organs [9,11]. The Gymnotidae generate multiphasic EODs in which the dominant head-positive and head-negative phases are produced by similar structures and mechanisms as those of the hypopomid-rhamphychthid clade, suggesting, though not proving, a common origin. The electric eel has a monophasic EOD, a condition common to all strongly electric fish, possibly adaptive for high current generation. Thus while the monophasic EOD of *Electrophorus* might represent the ancestral condition, it has such a specialized electric organ system that its ancestor could well have had and lost a multiphasic EOD, although this is purely conjecture. In the Sternopygids (e.g. *Eigenmannia*) the EOD is a modified monophasic form. The rise is caused by headward sodium ion flux in the electrocytes [18], but the entire EOD is offset to the negative of zero volts by a tail-positive DC potential

[8,9]. A few isolated gymnotiform species have monophasic signals resulting from loss of other phases [45].

Throughout the remainder of the discussion, the term "second phase" will be used to represent the second (head-negative) phase of the hypopomid biphasic EOD, and its analog or homolog in the Rhamphichthyidae and Gymnotidae.

## 4. Alternate adaptive hypotheses

Given that a conversion from monophasy to biphasy is not a necessary epiphenomenon of electrocyte membrane geometry we can consider a suite of adaptive hypotheses along the lines of those proposed to guide the evolution of visual signals [17]. These include navigation, recognition, mate attraction, territory defense, and predator avoidance.

### 4.1. Active electrolocation

Electric signals of weakly electric fish function for communication and navigation (i.e., active electrolocation). If a biphasic EOD serves active electrolocation, one should expect to find the EOD biphasic in the regions of greatest sensory acuity. Gymnotiforms have the greatest density of electroreceptors on and around their heads, as has been shown in the genus *Brachyhypopomus* [51,55]. Although some gymnotiforms use their tails for electrosensory exploration of objects, *Brachyhypopomus* explores exclusively with its head [38] (personal observation). But the EODs of *Brachyhypopomus, Rhamphichthys*, and *Gymnotus* lack the second phase at the head [11–13, 48]. Thus it seems unlikely that EODs evolved a second phase to heighten sensitivity for electrolocation.

### 4.2. Sexual selection—mate attraction and intrasexual competition

The second phase of the EOD is sexually dimorphic among several clades of pulse fish [30,37]. If the second phase of the EOD evolved to enhance sexual signaling, then one of two conditions should be met: (1) the second phase should have appeared only in the displaying sex or (2) if the 2nd phase evolved at the same time in both sexes, it should have been sexually dimorphic from the start.

Among gymnotiforms with multiphasic EODs, both males and females have second phases in their EODs. In the pulse gymnotiforms, a monomorphic second phase appears basal to sexual dimorphism in the second phase (Fig. 1): extended duration of the second phase of male EODs is common throughout the Hypopomidae, but neither Gymnotidae nor Rhamphichthyidae show clear sexual dimorphism in the second phase. Recent experiments have shown that the homologous phase in polyphasic *Gymnotus carapo* can be altered slightly by testosterone [5], but the effect is subtle. Thus while the second phase appears to have been modified by sexual selection in some clades, had sexual selection produced the second phase, say in the Hypopomidae-Rhamphicthyidae clade, then one would expect to see sexual differences occurring throughout the lineage, which one does not. Sexual selection does not provide strong support for the origin of the second phase, though it appears to have exploited the second phase later on in some lineages.

### 4.3. Territory defense

Among territorial species, enhancing signal amplitude would be useful for commanding greater active space [10,36]. Adding a second phase to a monophasic signal would provide a simple mechanism for doubling the amplitude. So, we would predict that territorial species should be more likely to have second phases than non-territorial species, and that high amplitude in EODs used for communication should be associated with the presence of a second phase. To address this question, we would want to compare EODs of territorial and non-territorial species within the same group, or conversely, to compare territorial behavior of closely related species with monophasic and multiphasic EODs. We don't have published data for either of these comparisons, so we might look to the weaker prediction that if the second phase evolved to increase amplitude of the signal, monophasic EODs should be lower in amplitude than biphasic EODs of closely related species.

In the one clade where I have obtained calibrated amplitude data for all members (*Brachyhypopomus* in part), the species with a monophasic EOD has far greater amplitude than its biphasic congeners, possibly to facilitate mimicry of the electric eel [45] (Fig. 2). Likewise, in none of the strongly electric fish is the EOD anything other than monophasic. Hanika and Kramer [27] reported extremely low amplitude EODs for a monophasic mormyrid, *Hyppopotamyrus* s. nov. The genus *Hyppopotamyrus* is not close to the base of the mormyrid clade [50] and so the monophasy is probably derived. In summary, I find no support for evolution of the second phase as a mechanism to enhance EOD amplitude, though our evidence against this hypothesis could be stronger.

### 4.4. Reproductive isolation

Distinctive EOD waveforms reveal extreme taxonomic radiation within the mormyrid electric fish of West Africa [50]. EODs must play a significant role in the selection of genetically compatible mates, just as vocalizations do in cryptic species of anurans [23,42].

The more complex the EOD waveform, the greater is the potential for producing taxonomically distinctive signals. Thus the second phase could serve the function of reproductive isolation within taxonomically related groups. Within two genera with biphasic EODs, the gymnotiform *Brachyhypopomus* (Fig. 3) and the mormyrid *Brienomyrus* [2], the first phase is the more distinctive among species while the second phase differs more between the sexes. So, we don't see compelling evidence that species isolation drove the evolution of the second phase, though it may have contributed to further differentiation of EODs and evolution of waveform complexity beyond the second phase.

### 4.5. Predation avoidance

Modern gymnotiforms in the South American tropics are preyed upon by a variety of electroreceptive predators, including various catfishes and some gymnotiforms themselves [4,15,39,41]. Because Gymnotiformes split with the Siluriformes (catfish) after the evolution of electroreception [19], they have probably always shared the water with electroreceptive predators. To make a case that survival benefits of electric crypsis have driven the EOD from monophasy to biphasy, one would want to see that biphasic EODs are less detectable by ancestral predators, and lacking those, one might settle for modern predators. Theoretical and empirical evidence supports this latter line of reason. All modern electroreceptive teleosts have ampullary electroreceptors, highly sensitive to low frequency electric fields (1–10 μV/cm) [56]. The amount of low frequency energy present in a signal is a function of the asymmetry in the net signal. For instance, signals with equal amounts of energy above and below zero volts (Fig. 1) show much reduced energy close to zero Hz (DC). In contrast, signals with highly asymmetric distribution of energy with respect to DC display enhanced energy in the low frequencies. Monophasic EODs represent the extreme in asymmetric energy distribution. They show a "low-pass" power spectrum, flat from zero Hz up to some frequency where the spectrum attenuates (Fig. 4). Thus ampullary electroreceptors are well suited to detect monophasic EODs. Gymnotiformes also have tuberous electroreceptors of lesser absolute sensitivity (> 1 mV/cm), tuned with varying degrees of precision to the spectrum of the EOD [7,29,34,43,53]. The electric eel (*Electrophorus electricus*) is a strongly electric piscivore, anecdotally known for its depredations on weakly electric gymnotiforms [54] (M. Hagedorn personal communication). Marina Olman and I tested the predatory response of one medium-sized electric eel, presenting it playbacks of biphasic and monophasic electric stimuli at natural intensities from at least 60 cm away [45]. For biphasic stimuli we used the EODs of female *Brachyhypopomus pinnicaudatus* and for monophasic

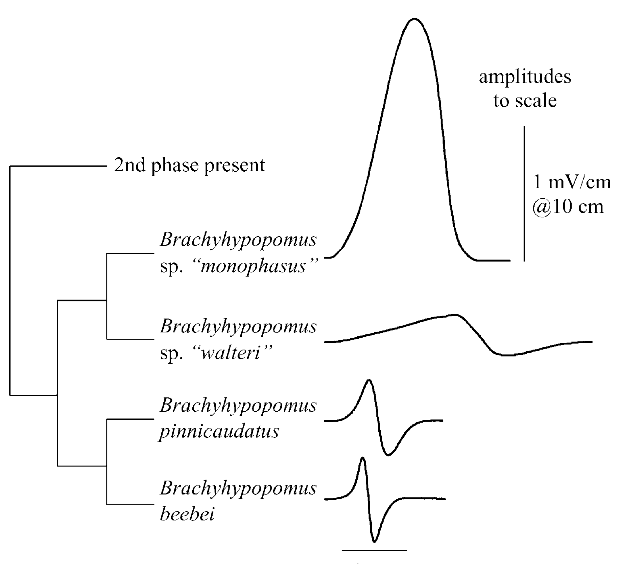


Fig. 2. Partial phylogeny of the genus *Brachyhypopomus* (Gymnotiformes, Hypopomidae) with representative EODs of identically sized mature females. Electric field strengths were calibrated with previously published calibration methods [22]. This figure shows that a large amplitude EOD can be generated by weakly electric fish without adding a second phase to the EOD. Phylogeny and proposed names of new species after Sullivan [49].

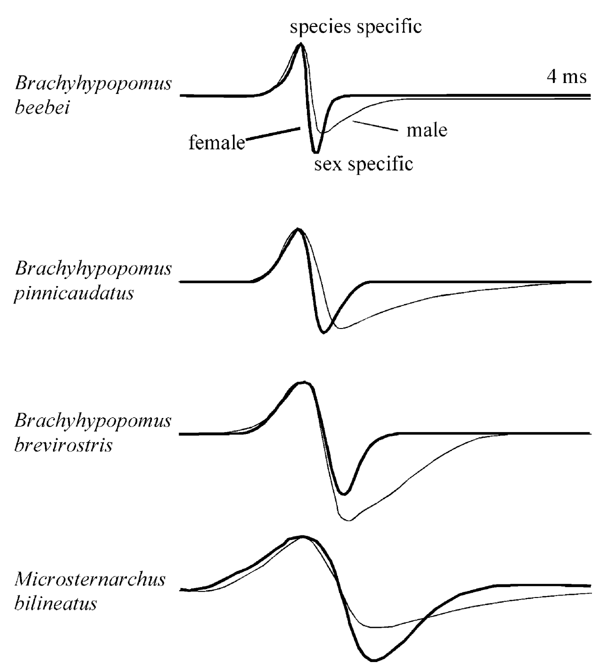


Fig. 3. EOD waveforms of male and female species in the gymnotiform family Hypopomidae. Random samples were taken from my EOD library where I had EODs of both sexes digitized, in some cases only one individual of a sex. I rescaled the waveforms to equate amplitude of the first peak to facilitate comparison of relative shape. In hypopomids, the first phase of the EOD is consistent between sexes but differs between species. Duration of the second phase differs between the sexes, and varies considerably over the course of the night [22,24,44]. This pattern is inconsistent with the hypothesis that the second phase evolved to serve as a species isolating mechanism.

stimuli the first phases of the same EODs (Fig. 4). Thus the biphasic stimuli were of twice the amplitude as the monophasic EODs so that if the eel were to sense the EODs with its tuberous electroreceptors, its responses would have been biased towards the biphasic EODs. The relative insensitivity of tuberous electroreceptors made this outcome unlikely, and indeed, as predicted, the eel was significantly more attracted to playback of the monophasic EODs. Hanika and Kramer [27] have shown the same bias towards monophasic EODs in detection thresholds of predatory catfish of the genus *Clarias*, a group known to prey on mormyrid electric fish [40]. Their lab playbacks fielded a respectable sample size of experimental subjects and a wide variety of electric signals, both synthetic and digitized EODs from a variety of mormyrids.

## 5. Discussion

We have seen no evidence of a continuing evolutionary arms race between weakly electric fish and their electroreceptive predators, but that may be because we have not looked. Some of the pimelodid catfishes of South America prey heavily on gymnotiforms with wave EODs in spite of their high frequency EOD spectra [41]. Perhaps the wave EODs go undetected while the catfish cue on scent or electric fields from muscle action, but perhaps not; nobody has looked at spectral sensitivity of the more specialized predators. One small Neotropical catfish [4] has some electroreceptors that resemble in their anatomy the tuberous electroreceptors of gymnotiforms. The physiology of these receptors has not been described.

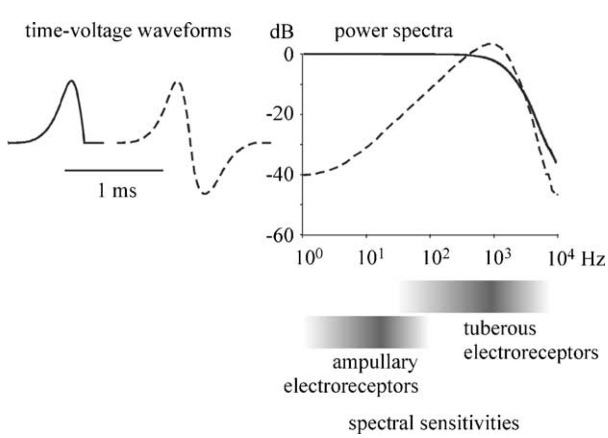


Fig. 4. Time voltage waveforms and power spectra of the first phase and complete EOD from a female *Brachyhypopomus pinnicaudatus*. Monophasic waveforms have a flat power spectrum throughout the lower frequencies whereas polyphasic EODs have much reduced power at the lower frequencies. Ampullary electroreceptors of Gymnotiformes and Siluriformes are maximally sensitive below 100 Hz and these fish detect monophasic EODs much more readily than biphasic EODs [27,45]. Thus monophasic EODs make the signaler more detectable by electroreceptive predators.

Pulse gymnotiforms of the genus *Brachyhypopomus* have sexually dimorphic EODs, a difference that results from organizing effects of androgens on the electrocytes [25]. *Brachyhypopomus* change their EODs between day and night in ways that enhance the sexually dimorphic characters [21,22,24]. Males maximize their masculine EOD characters in the early evening, around the peak spawning hours. In *Brachyhypopomus pinnicaudatus* the nightly increase in duration of the second phase also increases energy in the part of the spectrum detectable by the ampullary electroreceptors by about 15 dB [46]. So, while the second phase may confer juveniles and females with some degree of protection from predators, males have secondary adaptations to remove their electric crypsis during the spawning hours. When spawning is over, the male reduces the magnitude of sexually dimorphic EOD characters, partially restoring electric crypsis. X-rays of wild-caught *B. pinnicaudatus* revealed that about half the breeding males had regenerated tails, whereas virtually all the females had their original tails [33]. These authors could not determine whether damage was inflicted by predators or in fights with conspecifics. In our captive breeding colony, we find similar proportions of regenerated tails among mature male *B. pinnicaudatus*. Though we have never seen mature males with freshly bitten tails, it may happen when males are young. Captive male *B. brevirostris* bite off each other's tails routinely. Ongoing predation pressure on *B. pinnicaudatus* males remains unresolved.

## 6. Conclusion

The best-supported hypothesis for the evolution of the second phase of the EOD is electric crypsis to avoid electroreceptive predators. Hostile eavesdroppers exert directional selection on the signal spectra in many different prey groups in the acoustic and visual sensory modalities, and prey have responded by shifting emitted spectra or suppressing emissions in vulnerable frequencies [57]. It should be no surprise that the same phenomenon exists in the electric signal modality as well. What may be more unique to the electric sense, however, is that selection for electric crypsis should serve as a generative force. Addition of a second phase to a monophasic signal narrows the signal spectrum (a simplification perhaps), but significantly increases complexity in the time domain. The proposed ability of electric fish to detect and resolve signals in the time domain [28,32] may have allowed them to capitalize on this signal addition for other purposes including sexual selection and species isolation. Once a species adapts to escape predation, it may undergo rapid adaptive radiation [16]. Thus the evolution of a biphasic EOD may have contributed to the abundance and diversity of weakly electric fishes in the Neotropics and West Africa.

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## References

[1] J.S. Albert, Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei), Miscellaneous Publications, Museum of Zoology, University of Michigan, 2001.

[2] J. Alves-Gomes, C.D. Hopkins, Molecular insights into the phylogeny of mormyriform fishes and the evolution of their electric organs, Brain Behav. Evol 49 (1997) 324–350.

[3] J.A. Alves-Gomes, G. Orti, M. Haygood, W. Heiligenberg, A. Meyer, Phylogenetic analysis of the South American electric fishes (order Gymnotiformes) and the evolution of their electrogenic system: a synthesis based on morphology, electrophysiology, and mitochondrial sequence data, Mol. Biol. Evol 12 (1995) 298–318.

[4] K.H. Andres, M. von Düring, E. Petrasch, The fine structure of ampullary and tuberous electroreceptors in the South American blind catfish *Pseudocetopsis spec*, Anat. Embryol 177 (1988) 523–535.

[5] J.L. Ardanaz, A. Silva, O. Macadar, Temperature sensitivity of the electric organ discharge waveform in *Gymnotus carapo*, J. Comp. Physiol. A 187 (2001) 853–864.

[6] A.H. Bass, Electric organs revisited, in: T.H. Bullock, W. Heiligenberg (Eds.), Electroreception, Wiley, New York, 1986, pp. 13–70.

[7] J. Bastian, Frequency response characteristics of electroreceptors in weakly electric fish (Gymnotoidei) with a pulse discharge, J. Comp. Physiol 112 (1976) 165–190.

[8] M.L.V. Bennett, Modes of operation of electric organs, Ann. N.Y. Acad. Sci. 94 (1961) 458–509.

[9] M.L.V. Bennett, Electric organs, in: W.S. Hoar, D.J. Randall (Eds.), Fish Physiology, Academic Press, London, 1971, pp. 347–491.

[10] E.A. Brenowitz, Environmental influences on acoustic and electric animal communication, Brain Behav. Evol 28 (1986) 32–42.

[11] A. Caputi, O. Macadar, O. Trujillo-Cenóz, Waveform generation in *Rhamphichthys rostratus* (L.) (Teleostei, Gymnotiformes). The electric organ and its spatiotemporal activation pattern, J. Comp. Physiol. A 174 (1994) 633–642.

[12] A.A. Caputi, The electric organ discharge of pulse gymnotiforms: the transformation of a simple impulse into a complex spatiotemporal electromotor pattern, J. Exp. Biol. 202 (1999) 1229–1241.

[13] A.A. Caputi, O. Macadar, O. Trujillo-Cenóz, Waveform generation of the electric organ discharge in *Gymnotus carapo*. III. Analysis of the fish body as an electric source, J. Comp. Physiol. A (1989) 361–370.

[14] A.A. Caputi, A.C. Silva, O. Macadar, The electric organ discharge of *Brachyhypopomus pinnicaudatus*: The effects of environmental variables on the waveform generation, Brain Behav. Evol 52 (1998) 148–158.

[15] W.G.R. Crampton. The Electric Fish of the Upper Amazon: Ecology and Signal Diversity. PhD thesis, Oxford, 1996.

[16] P.R. Ehrlich, P.H. Raven, Butterflies and plants: a study in coevolution, Evolution 18 (1964) 586–608.

[17] J.A. Endler, Signals, signal evolution, and the direction of evolution, Am. Nat. 139 (1992) S125–S153.

[18] M.B. Ferrari, H.H. Zakon, Conductances contributing to the action potential of *Sternopygus* electrocytes, J. Comp. Physiol. A 173 (1993) 281–292.

[19] S.V. Fink, W.L. Fink, Interrelationships of the osteriophysan fishes (Teleostei), Zool. J. Linn. Soc. 72 (1981) 297–353.

[20] C.R. Franchina, Ontogeny of the electric organ and the electric organ discharge in the weakly electric fish *Brachyhypopomus pinnicaudatus* (Teleostei, Gymnotiformes), J. Comp. Physiol. A 181 (1997) 111–119.

[21] C.R. Franchina, V.L. Salazar, C.H. Volmar, P.K. Stoddard, Plasticity of the electric organ discharge waveform of male *Brachyhypopomus pinnicaudatus*. II. Social effects, J. Comp. Physiol. A 187 (2001) 45–52.

[22] C.R. Franchina, P.K. Stoddard, Plasticity of the electric organ discharge waveform of the electric fish *Brachyhypopomus pinnicaudatus*: I. Quantification of day-night changes, J. Comp. Physiol. A 183 (1998) 759–768.

[23] H.C. Gerhardt, M.L. Dyson, S.D. Tanner, Dynamic properties of the advertisement calls of gray treefrogs: patterns of variability and female choice, Behav. Ecol 7 (1996) 7–18.

[24] M. Hagedorn, The electric fish *Hypopomus occidentalis* can rapidly modulate the amplitude and duration of its electric organ discharges, Anim. Behav 49 (1995) 1409–1413.

[25] M. Hagedorn, C.E. Carr, Single electrocytes produce a sexually dimorphic signal in South American electric fish, *Hypopomus occidentalis*, (Gymnotiformes, Hypopomidae), J. Comp. Physiol 156 (1985) 522–523.

[26] M. Hagedorn, M. Womble, T.E. Finger, Synodontid catfish: a new group of weakly electric fish, Behavior and anatomy, Brain Behav. Evol 35 (1990) 268–277.

[27] S. Hanika, B. Kramer, Electrosensory prey detection in the African sharptooth catfish, *Clarias gariepinus* (Clariidae), of a weakly electric mormyrid fish, the bulldog (*Marcusenius macrolepidotus*), Behavioral Ecology & Sociobiology 48 (2000) 218–228.

[28] W. Heiligenberg, R.A. Altes, Phase sensitivity in electroreception, Science 199 (1978) 1001–1004.

[29] C.D. Hopkins, Stimulus filtering and electroreception: tuberous electroreceptors in three species of gymnotiform fish, J. Comp. Physiol 111 (1976) 171–208.

[30] C.D. Hopkins, Neuroethology of electric communication, Annu. Rev. Neurosci. 11 (1988) 497–535.

[31] C.D. Hopkins, Signal evolution in electric communication, in: M.D. Hauser, M. Konishi (Eds.), Design of Animal Communication, MIT Press, Cambridge, 1999, pp. 461–491.

[32] C.D. Hopkins, A.H. Bass, Temporal coding of species recognition signals in an electric fish, Science 212 (1981) 85–87.

[33] C.D. Hopkins, N.C. Comfort, J. Bastian, A.H. Bass, Functional analysis of sexual dimorphism in an electric fish, *Hypopomus pinnicaudatus*, order Gymnotiformes, Brain Behav. Evol 35 (1990) 350–367.

[34] C.D. Hopkins, W. Heiligenberg, Evolutionary designs for electric signals and electroreceptors in gymnotoid fishes of Surinam, Behavioral Ecology & Sociobiology 3 (1978) 113–134.

[35] F. Kirschbaum, Reproduction and development in mormyriform and gymnotiform fishes, in: P. Moller (Ed.), Electric Fishes History and Behavior, Chapman & Hall, London, 1995, pp. 267–301.

[36] E.I. Knudsen, Spatial aspects of the electric fields generated by weakly electric fish, J. Comp. Physiol 99 (1975) 103–118.

[37] B. Kramer, A field study of African elephantfish (Mormyridae, Teleostei): Electric organ discharges in *Marcusenius macrolepidotus* (Peters, 1852) and *Petrocephalus catostoma* (Günther, 1866) as related to sex, J. African Zool 111 (1997) 313–341.

[38] M.J. Lannoo, S.J. Lannoo, Why do electric fishes swim backwards? An hypothesis based on Gymnotiform foraging behavior

interpreted through sensory constraints, Env. Biol. Fish 36 (1993) 157–165.

[39] J.G. Lundberg, C. Cox Fernandes, J.S. Albert, M. Garcia, *Magosternarchus*, a new genus with two new species of electric fishes (Gymnotiformes: Apteronotidae) from the Amazon River basin, South America, Copeia (1996) 657–670.

[40] G.S. Merron, Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis*, in the Okavango Delta, Botswana, J. Fish Biol. 43 (1993) 575–584.

[41] S. Reid, La biologia de los bagres rayados *Pseudoplatystoma fasciatum* y *P. tigrinum* en la cuenca del rio Apure–Venezuela, Rev. UNELLEZ Cien. Tec 1 (1983) 13–41.

[42] M.J. Ryan, S. Rand, Female responses to ancestral advertisement calls in Tungara frogs, Science 269 (1995) 390–392.

[43] C.A. Shumway, R.D. Zelick, Sex recognition and neuronal coding of electric organ discharge waveform in the pulse-type weakly electric fish, *Hypopomus occidentalis*, J. Comp. Physiol. A 163 (1988) 465–478.

[44] A. Silva, L. Quintana, M. Galeano, P. Errandonea, O. Macadar, Water temperature sensitivity of the EOD waveform in *Brachyhypopomus pinnicaudatus*, J. Comp. Physiol. A 185 (1999) 187–198.

[45] P.K. Stoddard, Predation enhances complexity in the evolution of electric fish signals, Nature 400 (1999) 254–256.

[46] P.K. Stoddard, Electric signals: predation, sex, and environmental constraints, in: P.J.B. Slater, J.S. Rosenblatt, C.T. Snowdon, T.J. Roper (Eds.), Advances in the Study of Behaviour, Academic Press, London, New York, 2002, pp. 201–242.

[47] P.K. Stoddard, B. Rasnow, C. Assad. Electric Organ Discharges of the Gymnotiform Fish *Brachyhypopomus* spp, presented at Nervous Systems and Behavior, Proc. 4th Intl. Congress of Neuroethology, Cambridge, England, 1995.

[48] P.K. Stoddard, B. Rasnow, C. Assad, Electric organ discharges of the gymnotiform fishes: III. *Brachyhypopomus*, J. Comp. Physiol. A 184 (1999) 609–630.

[49] J.P. Sullivan. A Phylogenetic Study of the Neotropical Hypopomid Electric Fishes (Gymnotiformes: Rhamphichthyoidea). PhD thesis, Duke University, 1997.

[50] J.P. Sullivan, S. Lavoue, C.D. Hopkins, Molecular systematics of the African electric fishes (Mormyroidea: teleostei) and a model for the evolution of their electric organs, J. Exp. Biol. 203 (2000) 665–683.

[51] T. Szabo, Anatomy of the specialized lateral line organs of electroreception, in: A. Fessard (Ed.), Handbook of Sensory Physiology, Springer-Verlag, Berlin, 1974, pp. 13–58.

[52] G.A. Unguez, H.H. Zakon, Phenotypic conversion of distinct muscle fiber populations to electrocytes in a weakly electric fish, J. Comp. Neurol. 399 (1998) 20–34.

[53] D. Watson, J. Bastian, Frequency response characteristics of electroreceptors in the weakly electric fish *Gymnotus carapo*, J. Comp. Physiol 134 (1979) 191–202.

[54] G.W.M. Westby, The ecology, discharge diversity and predatory behaviour of gymnotiforme electric fish in the coastal streams of French Guiana, Behav. Ecol. Sociobiol 22 (1988) 341–354.

[55] D.D. Yager, C.D. Hopkins, Directional characteristics of tuberous electroreceptors in the weakly electric fish, Hypopomus (Gymnotiformes), J. Comp. Physiol. A 173 (1993) 401–414.

[56] H.H. Zakon, The electroreceptive periphery, in: T.H. Bullock, W. Heiligenberg (Eds.), Electroreception, Wiley, New York, 1986, pp. 103–156.

[57] M. Zuk, G.R. Kolluru, Exploitation of sexual signals by predators and parasitoids, Quart. Rev. Biol. 73 (1998) 415–438.