Electric fish signals

Element 114 Reaching the island of stability

Carbon cycle A tale of two modes

Plant biology Genetics of the ‘green revolution’
Predation enhances complexity in the evolution of electric fish signals

Philip K. Stoddard
Department of Biological Science, Florida International University, Miami, Florida 33199, USA

Theories of sexual selection assume that predation is a restrictive, simplifying force in the evolution of animal display characters and many empirical studies have shown that predation opposes excessive elaboration of sexually selected traits. In an unexpected turnaround, I show here that predation pressure on neotropical, weakly electric fish (order Gymnotiformes) seems to have selected for greater signal complexity, by favouring characters that have enabled further signal elaboration by sexual selection. Most gymnotiform fish demonstrate adaptations that lower detectability of their electrolocation/communication signals by key predators. A second wave phase added to the ancestral monophasic signal shifts the emitted spectrum above the most sensitive frequencies of electroreceptive predators. By using playback trials with the predatory electric eel (Electrophorus electricus), I show that these biphasic signals are less detectable than the primitive monophasic signals. But sexually mature males of many species in the family Hypopomidae extend the duration of the second phase of their electric signal pulses and further amplify this sexual dimorphism nightly during the peak hours of reproduction. Thus a signal element that evolved for crypsis has itself been modified by sexual selection.

Weakly electric fish generate multipurpose electric signals for electrolocation and communication. Anatomical, physiological and developmental evidence together indicate that the ancestral waveform of the electric organ discharge (EOD) was an intermittent monophasic pulse. This primitive discharge type is rare in extant gymnotiform fish, having been replaced largely by continuous wave trains (in three families) or multiphasic pulsed waveforms (in three families) (Fig. 1). To address the forces that mould signal complexity, I focus here on the diverse EOD waveforms of pulse-discharging fish. I consider electrolocation, sexual selection and avoidance of predation as possible factors that could favour the switch from a monophasic to a multiphasic EOD. In fact, electrolocation can favour increased complexity of the EOD, and may well have done so in those species with accessory electric organs and enhanced waveform complexity at the head instead of the tail. But in the biphasic Brachyhypopomus species, local biphasy occurs at the tail but not at the head (Fig. 2) where electroreceptive exploratory behaviour occurs (P.K.S., unpublished data) and where electroreceptors are most dense. Therefore, among the Brachyhypopomus species with biphasic waveforms, the simplest example of signal enhancement, electrolocation could not have been involved with the transition from monophasy to biphasy in the main electric organ. Most Brachyhypopomus species display sexual dimorphism in the second phase of their biphasic pulse EODs, particularly at the tail (Fig. 2). But, before modification for sex recognition and mate attraction, the second phase would have existed probably in some sexually monomorphic form. Furthermore, in other gymnotiform families—such as Gymnotidae, Rhamphichthyidae and Apterontidae—this additional phase is present but not sexually dimorphic. Sexual selection thus does support the ancestral conversions from monophasy to biphasy.

Key predators of weakly electric gymnotiforms are pimelodid catfishes and the electric eel. Both the Gymnotiformes and their sister order Siluriformes (catfish) possess ampullary electroreceptors with extreme sensitivity to low frequencies. The ampullary system is specialized for detecting weak electric fields of prey. Gymnotiforms, but not catfish, evolved a second parallel electroreceptive pathway, the tuberous electroreceptor system, two
orders of magnitude less sensitive than the ampullary system, but
tuned to the higher frequencies of the EOD5–8. Tuberous electroreceptors sense the autogenous EOD during active electrolocation
of nearby objects such as prey, predators, mates and hiding places.
EODs and tuberous electroreceptors appear as matched co-adaptations
that allow electrolocation above the frequency range of the predator’s sensitive ampullary electroreceptors. What adaptations
shifted the EOD spectrum upwards?

The ancestral monophasic EOD pulse5 resembles a single-period cosine wave which has a low frequency spectral peak close to 0 Hz
(Fig. 3b), just where electroreceptive predators are maximally sensitive. Fig. 3 shows that the addition of a negative-going second phase shifts spectral energy upwards, above the best frequency
of the ampullary electroreceptors. The transition from monophasic to multiphasic EODs evolved at least twice among pulse families and a third time in a wave family Apterontidae
(Fig. 1). The wave fish Sternopygidae, Eigenmanniidae and Apterontidae generate EOD trains with even duty cycles (Fig. 1),
resulting in a further narrowing of the spectrum19,20.

Can the shift from monophase to multiphase reduce detection by
electroreceptive predators? To address this question I obtained a large electric eel and trained it with food to approach electrodes
playing a variety of electric playback signals (see Methods). In a
randomized series of trials, the eel was presented, at natural
intensities, with either the biphasic EODs of female Brachyhypopomus pinnicaudatus or the same waveforms rendered
monophasic by digital deletion of the second phase (Fig. 3c, d). The
electric eel was half as likely to approach the playback of the biphasic
EOD as the monophasic half-EOD even though peak-to-peak amplitudes of the biphasic stimuli were twice as great (approach
to biphasic EOD in 6/21 trials compared with approach to monophasic EOD in 12/18 trials; Fisher’s exact test, \( P = 0.01 \)).

I recorded EODs of three gymnotiform species that emit pulsed

---

**Figure 3** Biphasic EOD pulses have less energy at low frequencies than their monophasic counterparts. a, The ancestral monophasic EOD is modelled as a single-period inverted cosine wave (solid line). Addition of a second cosine wave, offset in time, produces a biphasic pulse (dashed line) that b, raises the frequency of the spectral peak and depresses spectral amplitudes below 600 Hz. Ampullary electroreceptors of electroreceptive predators are maximally sensitive around 8 Hz (Siluriformes) or 30 Hz (Gymnotiformes), and so the shift to biphasy should reduce detection by predators. c, Waveforms and d, power spectra of EODs used as playback stimuli with the electric eel; the biphasic pulse from a female Brachyhypopomus pinnicaudatus (dashed line) and the first phase only of the same EOD (solid line). In playback trials, the electric eel detected playback of the biphasic EOD less than half as often as when the first phase was delivered alone.

---

**Figure 4** Monophasic EODs of three species compared with each other and with biphasic EODs of congeners. a, Power spectra and EOD waveforms of three gymnotiform species with monophasic EOD pulses. The EODs and power spectra of all three monophasic species are extremely similar compared with the those of biphasic EODs (Fig. 3). The monophasic Brachyhypopomus is proposed to have lost the second phase of its EOD as an adaptation to resemble the dangerous electric eel Electrophorus. b, Phylogeny1, photographs and EOD waveforms of mature females of four closely related sympatric Brachyhypopomus species. All earlier branches in the superfamily show biphasic EODs, thus monophasy in this genus is a derived loss of the second phase. The EOD of monophasic Brachyhypopomus sp. 1 is significantly greater in amplitude than similarly sized members of its sister species, another feature that resembles the EOD of the electric eel.
EOD records of its three closest relatives\(^3\) (Fig. 4b). The EOD of the monophasic \textit{Brachyhypopomus} species is similar to that of the electric eel in waveform, duration and spectrum\(^4\) (Fig. 4a). The resting discharge rate was low (8–13 Hz), resembling an alert electric eel in both rate and variability.\(^5\) Calibrated daytime EOD amplitudes were 1.5–1.8 mV cm\(^{-1}\) at 10 cm, which is between five and ten times greater than specimens of its sister species \textit{Brachyhypopomus} sp. 2 (Fig. 4b). Thus the monophonic \textit{Brachyhypopomus} species appears to have lost the second phase of its EOD and boosted EOD amplitude, consistent with Hagedorn's proposal that this fish is a batesian electric mimic of the sympathetic electric eel. Further confirmation of the hypothesis could come only from experiments showing mutual avoidance of electric eels and monophonic \textit{Brachyhypopomus} by an electroreceptive predator.

In summary, predation avoidance is the strongest candidate as the driving force for the initial evolution of EOD complexity, in particular, the transition from primitive monophony to biphony. This conclusion is supported by three lines of evidence: (1) spectral comparison of monophasic and biphasic EODs; (2) demonstration that biphasic pulses are less detectable by a known electroreceptive predator; and (3) examples of specific adaptations (high voltage, geographic isolation and mimicry) that protect species with monophasic EODs. Sexual dimorphism in the second EOD phase of \textit{Brachyhypopomus} spp. (Fig. 2) seems to be the secondary modification of an adaptation for signal crypsis. Evolutionary escape from predation has been cited as a key factor promoting adaptive radiation.\(^2\) Thus spectral shifting may have contributed to the success of this order in tropical South America. A key question is whether this multi-phase evolution has happened in any gymnotiforms outside the geographic range of their electroreceptive predators. Several extant multi-phase gymnotiform taxa extend beyond the range of large electroreceptive predators.\(^2\) (O. Macadar, personal communication), but their centres of distribution lie in the predator-rich continental tropics and none could be argued to represent an independent origin of multiphasy.

A parallel story may emerge from Africa, where mormyrid electric fish have undergone extensive radiation and an electroreceptive predator, the catfish \textit{Clarias}, serves as their major predator.\(^2,2\) Nor are electric fish entirely unique in having protective signal adaptations exploited by sexual selection. Ctenuchid moths evoked acoustic signals to alert predatory bats of their toxicity, and these signals have likewise been co-opted for mate attraction.\(^2,2\)

**Methods**

An electric eel 1 m long was trained to receive food (goldfish) when it approached any playback of an electric field in its round aquarium (120 cm diameter, 60 cm deep). We played electric stimuli from a DC-coupled 5-cm carbon dipole at calibrated intensities equivalent to natural EODs.\(^7\) DC offset at 10 cm from the dipole centre was less than 0.05 \(\mu\)V cm\(^{-1}\). Training stimuli included a wide variety of monophasic and biphasic digitized EODs. Experimental stimuli included the biphasic EOD of a female \textit{Brachyhypopomus pinnicaudatus} and the same EOD with the second phase digitally removed (Fig. 3c, d). Trials were sequenced randomly. Playbacks of 1 min duration began while the eel rested on the tank bottom, at a distance of more than 60 cm from the electrode. A "blind" assistant rewarded all electrotactic approaches with food. A `blind' assistant rewarded all electrotactic approaches with food. A 'blind' assistant rewarded all electrotactic approaches with food.

---

\(^1\) Darwin, C. The Descent of Man, and Selection in Relation to Sex (Murray, London, 1871).


---

\(^\text{Present address: Rice Transformation Laboratory, Centre for Plant Molecular Biology, Tamil Nadu Agricultural University, Coimbatore 641 043, India.}\)