

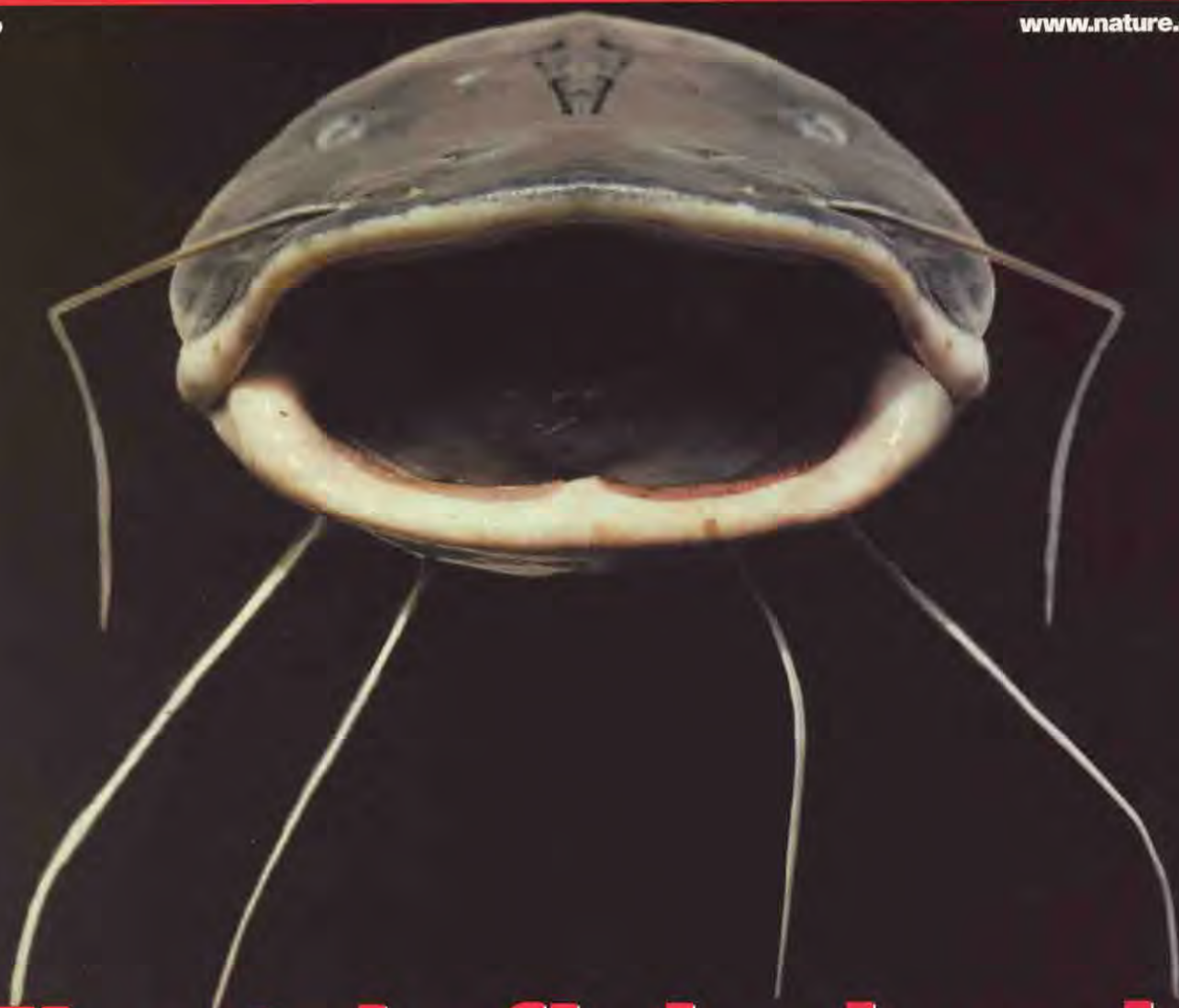
15 July 1999

International weekly journal of science

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Electric fish signals

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Acknowledgements. We thank T. Lunell (AEA Tech. plc) for providing the video of the oil slick and the environmental data for the CASI images. We also thank the Environment Agency for supplying the CASI images, and V. Byfield for calibrating them; and A. Hall for help in collecting the sonar data. The observations in the North Sea were funded by an EEC/MAST contract. W.A.M.N.S. is supported by NERC.

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Predation enhances complexity in the evolution of electric fish signals

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Theories of sexual selection assume that predation is a restrictive, simplifying force in the evolution of animal display characters¹ and many empirical studies have shown that predation opposes excessive elaboration of sexually selected traits². 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 pulses³ and further amplify this sexual dimorphism nightly during the peak hours of reproduction⁴. Thus a signal

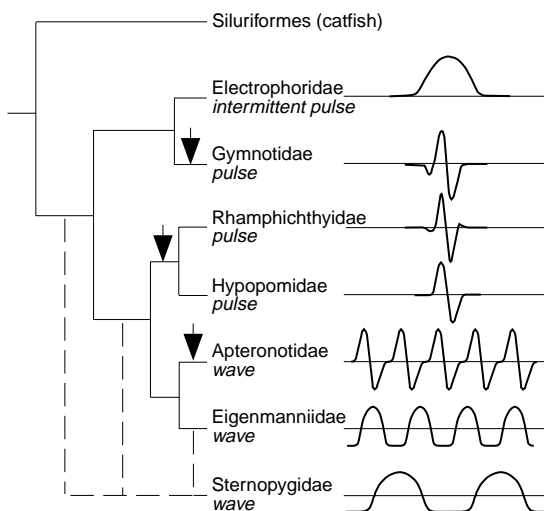


Figure 1 Molecular-morphological consensus phylogeny of the gymnotiform families^{22,30} is plotted along with schematic electric organ discharge (EOD) waveforms of representative species. Arrows depict postulated transitions from simple monophasic to multiphasic EOD waveforms. Dashed lines represent equally supported alternate phylogenies. Aptereronotidae possess independently derived electric organs, thus the biphasic EOD is derived in this family.

element that evolved for crypsis has itself been modified by sexual selection.

Weakly electric fish generate multipurpose electric signals for electrolocation and communication^{5,6}. Anatomical, physiological and developmental evidence together indicate that the ancestral waveform of the electric organ discharge (EOD) was an intermittent monophasic pulse^{5,7–9}. 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 tail⁹. But in the biphasic *Brachyhypopomus* species, local biphasy occurs at the tail but not at the head (Fig. 2) where electrosensory exploratory behaviour occurs (P.K.S., unpublished data) and where electroreceptors are most dense¹⁰. 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)^{11–13}. But, before modification for sex recognition and mate attraction^{13,14}, the second phase would have existed probably in some sexually monomorphic form. Furthermore, in other gymnotiform families—such as Gymnotidae, Rhamphichthyidae and Aptereronotidae—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^{12,15}. Both the Gymnotiformes and their sister order Siluriformes (catfish) possess ampullary electroreceptors with extreme sensitivity to low frequencies^{16–18}. The ampullary system is specialized for detecting weak electric fields of prey (passive electrolocation) but is tuned below the spectrum of most gymnotiform EODs. The best frequencies for gymnotiform and catfish ampullary receptors are about 30 Hz and 8 Hz (refs 16, 18) respectively, whereas the spectral peaks of gymnotiform EODs are generally much higher, in the range of 50–3,000 Hz (ref. 19). Gymnotiforms, but not catfish, evolved a second parallel electroreceptive pathway, the tuberos electroreceptor system, two

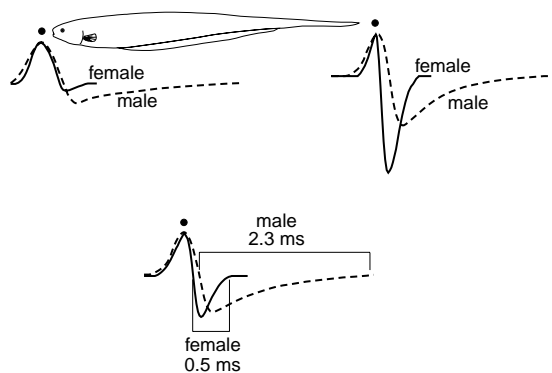


Figure 2 Local and remote EODs of male and female *Brachyhypopomus pinnicaudatus*. EOD waveforms were recorded at locations indicated by the dots. Amplitudes are rescaled here to normalize peaks of the first EOD phase. Note that the EODs are sexually dimorphic, with the male's second phase extended in duration, and that the EOD local to the head is nearly monophasic, particularly in the female.

orders of magnitude less sensitive than the ampullary system, but tuned to the higher frequencies of the EOD^{6,20}. Tuberos electroreceptors sense the autogenous EOD during active electrolocation of nearby objects such as prey, predators, mates and hiding places. EODs and tuberos 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 Apteronotidae (Fig. 1). The wave fish Sternopygidae, Eigenmanniidae and Apteronotidae generate EOD trains with even duty cycles (Fig. 1), resulting in a further narrowing of the spectrum^{19,20}.

Can the shift from monophasy to multiphasy 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

monophasic EODs (Fig. 4a). Each has a unique circumstance that reduces its vulnerability to electroreceptive predators. The first species, the electric eel, is itself an electroreceptive predator and produces a low-voltage, monophasic EOD for electrolocation but can also produce high-voltage discharges (to 600 V) for defence and prey capture²¹. Current phylogenies place the electric eel at or near the root of the order Gymnotiformes, with monophasy primitive, but well defended in all respects²². The second species with a simple monophasic EOD is *Gymnotus cylindricus*, common to streams of middle America. The *G. cylindricus* species group, the northernmost gymnotiform, inhabits a geographic refuge devoid of the two key electroreceptive predator groups, the electric eel and large pimelodid catfishes²³. The third species with a monophasic EOD is a small, defenceless *Brachyhypopomus* from Amazonia, a region rich in electroreceptive predators. A well-resolved phylogeny shows that this monophasic species is derived from a biphasic ancestor³. This species has the largest electric organ in its genus³. Field workers frequently mistake its EOD for that of the sympatric electric eel (J. Alves-Gomes, personal communication). On the basis of her field studies of fish in northern Peru, M. Hagedorn (personal communication) proposed that the monophasic *Brachyhypopomus* is a batesian mimic of the electric eel.

I took calibrated EOD recordings of three specimens of the monophasic *Brachyhypopomus* and compared them with calibrated

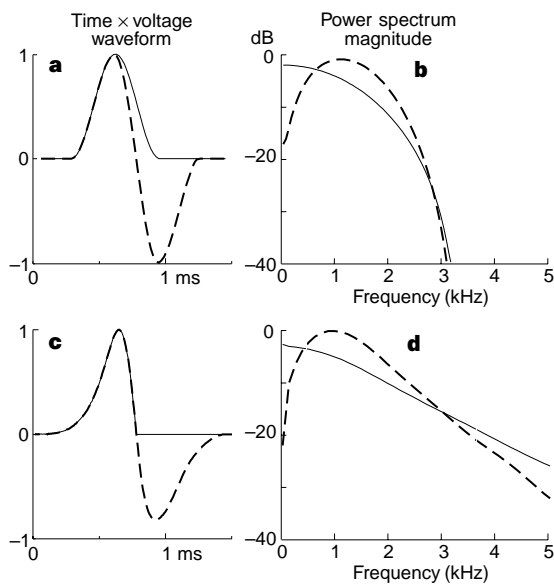


Figure 3 Biphasic EOD pulses have less energy at low frequencies than their monophasic counterparts. **a**, The ancestral monophasic EOD is modelled as a single-period inverted cosine wave (solid line). Addition of a second cosine wave, offset in time, produces a biphasic pulse (dashed line) that **b**, 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.

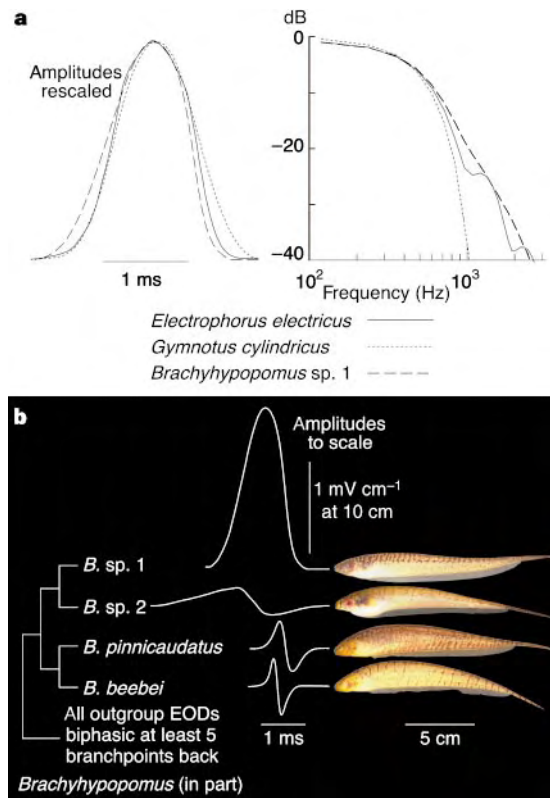


Figure 4 Monophasic EODs of three species compared with each other and with biphasic EODs of congeners. **a**, Power spectra and EOD waveforms of three gymnotiform species with monophasic EOD pulses. The EODs and power spectra of all three monophasic species are extremely similar compared with those 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**, Phylogeny³, 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 relatives³ (Fig. 4b). The EOD of the monophasic *Brachyhypopomus* species is similar to that of the electric eel in waveform, duration and spectrum²⁴ (Fig. 4a). The resting discharge rate was low (8–13 Hz), resembling an alert electric eel in both rate and variability²⁴. 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 species³ *Brachyhypopomus* sp. 2 (Fig. 4b). Thus the monophasic *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 sympatric electric eel. Further confirmation of the hypothesis could come only from experiments showing mutual avoidance of electric eels and monophasic *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 monophasy to biphasy. 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 *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 radiation²⁵. Thus spectral shifting may have contributed to the success of this order in tropical South America. A key question is whether signal multiphasy evolved in any gymnotiforms outside the geographic range of their electroreceptive predators. Several extant multiphasic gymnotiform taxa extend beyond the range of large electroreceptive predators²³ (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 *Clarias*, serves as their major predator^{26,27}. Nor are electric fish entirely unique in having protective signal adaptations exploited by sexual selection. Ctenuchid moths evolved acoustic signals to alert predatory bats of their toxicity, and these signals have likewise been co-opted for mate attraction^{28,29}. □

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 EODs⁴. DC offset at 10 cm from the dipole centre was less than 0.05 μV cm⁻¹. Training stimuli included a wide variety of monophasic and biphasic digitized EODs. Experimental stimuli included the biphasic EOD of a female *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. In the first set of trials, playback rate simulated a repeated social signal, 0.5 s at 50 Hz alternated with 0.5 s at 200 Hz. In a second set of trials playing the truncated stimulus only, rate modulation had no effect on frequency of approach (19/21 trials with rate modulation compared with 19/20 trials at 50 Hz). I measured EOD amplitudes (Fig. 4b) by methods published previously⁴.

Received 30 March; accepted 19 May 1999.

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Acknowledgements. M. Olman trained and tested the electric eel, which was provided by H. Zakon. T. Lopez donated its food. F. Torres provided me with live gymnotiforms from Peru, photographed by G. Valcarce. The Organization for Tropical Studies supported field collections with B. Rasnow. J. Alves-Gomes, W. Crampton, W. Heiligenberg, C. Hopkins, J. Sullivan, D. Taphorn and particularly M. Hagedorn contributed helpful insights. T. Collins, K. Condon, G. Read, M. Ryan and J. Trexler improved the manuscript. Support came from the NIH. Experiments complied with NIH 'Principles of Animal Care' No. 86-23, rev. 1985.

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'Green revolution' genes encode mutant gibberellin response modulators

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World wheat grain yields increased substantially in the 1960s and 1970s because farmers rapidly adopted the new varieties and cultivation methods of the so-called 'green revolution'^{1–4}. The new varieties are shorter, increase grain yield at the expense of straw biomass, and are more resistant to damage by wind and

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