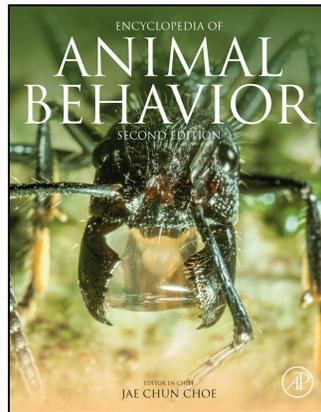


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Electric Signals

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Abstract

Weakly electric fishes generate low-amplitude electric signals to navigate and to communicate. These capacities have required the coevolution of electric organs for signal production and sensory pathways in the brain for signal detection. Electric signals exhibit a wide range of diversity across the hundreds of species of weakly electric fishes. Some species generate pulse-type signals, in which each electric pulse is followed by a variable period of silence. Other species generate wave-type signals, in which each pulse is followed immediately by the next pulse such that the signal is quasi-sinusoidal. Electric signal waveform often contains identifying information about the sender, and rapid, transient temporal or spectral modulation conveys information about behavioral state. Since the discovery of the weak electric sense almost 70 years ago, scientists have learned a remarkable amount about electric signal generation, detection, and contribution to natural behaviors. Here we highlight these topics, with extra emphasis on mechanisms of signal production, neural coding, and evolutionary ecology.

Keywords

Bioelectricity; Bioenergetics; Brain evolution; Electric organ; Electrocommunication; Electrogenesis; Electroreception; Electrosensation; Evolutionary ecology; Jamming avoidance response; Neural coding

Introduction

The ability of some fish to produce electric shocks has been recognized since at least ancient Egypt. These strongly electric fish, such as electric eels, electric catfish, and electric rays, use high-amplitude electric pulses to stun prey or to protect themselves from predators. In *On the Origin of Species*, strongly electric fish presented a problem for Charles Darwin: "The electric organs of fishes offer another case of special difficulty... it is impossible to conceive by what steps these wondrous organs have been produced" (Darwin, 1859). That is, his nascent evolutionary theory would suggest that the evolution of strong electrogenesis, or the ability to generate electricity, should have been preceded by weak electrogenesis, but Darwin had difficulty imagining what use weak electric signals would be. At the time, no fish capable of producing weak electric signals was known. It wasn't until the 1950s that the function of weak electrogenesis was discovered by Hans Lissmann.

Lissmann observed that the African fish *Gymnarchus niloticus* could avoid obstacles while swimming backwards. He placed a pair of electrodes, or electrically conductive wires, in the fish's tank and detected the fish emitting continuous electric signals. The signals from *G. niloticus* were several orders of magnitude weaker than those produced by strongly electric fish, placing them well outside the amplitude range that could stun other animals. For what other purpose could these fish be using electricity? To test whether fish could detect these weak signals, he played the animal's own signals through electrodes in its tank, and found that the fish would locate and attack the electrode (Lissmann, 1951). He also showed that these fish could distinguish between objects with different electric conductivity, even in darkness. Thanks to the observations of Lissmann and many scientists that followed, we now know that weakly electric fish use electric signals for two main purposes: navigation and communication.

Weakly electric fish have specialized sensory receptors in their skin to detect electric signals. Fish detect distortions in their own electric fields caused by nearby objects and use this information to electrolocate, or navigate. Weakly electric fish also detect the electric signals produced by other fish, and actively engage in electric communication with one another. Many weakly electric fish are nocturnal and live in places with lots of underwater vegetation, which are conditions that may make electric signals more reliable than visual or acoustic signals. The best studied groups of electric fishes, the Gymnotiformes of South America and the Mormyroidea of Africa, evolved electrogenesis independently. In contrast to the hundreds of volts amplitudes of strongly electric fish, weakly electric fish generate signals in the range of tens of mV to several volts.

The signals of weakly electric fish can be divided into pulse-type and wave-type categories based on waveform. Pulse-type fish generate signals with waveforms that are brief relative to the time intervals between them, such that there is a variable period of "silence" between each pulse (Fig. 1). Wave-type fish generate pulses whose interpulse intervals roughly match the pulse duration, such that the signal appears to be continuous or quasi-sinusoidal (Fig. 2). The majority of African species and almost half of South American species produce pulse-type waveforms. The remaining species generate wave-type waveforms.

In contrast to electrogenesis, electroreception, or the ability to detect electric fields, is an ancestral vertebrate trait lost by most vertebrate groups (Zupanc and Bullock, 2005). Almost all electrogenic animals are also electroreceptive (the stargazer is the only known exception), but relatively few electroreceptive animals are also electrogenic. For example, animals such as rays, sharks, salamanders, and platypuses can detect the very weak bioelectric fields generated by all organisms in water. However, these animals cannot produce their own electric fields for navigation, communication, self-defense, or predation.

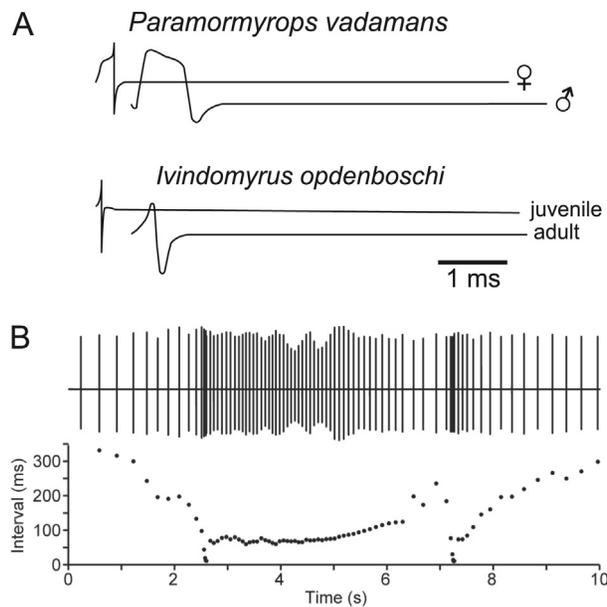


Fig. 1 Communication with pulse-type electric organ discharges (EODs) consists of the EOD waveform and pattern of interpulse intervals (IPIs). (A) The EOD waveform contains identifying information such as species, sex, and maturity. Modified from Zakon, H.H., Smith, G.T., 2009. Weakly electric fish: Behavior, neurobiology, and neuroendocrinology. In: Pfaff, D.W., Arnold, A.P., Fahrbach, S.E., Etgen, A.M., Rubin, R.T. (Eds.), *Hormones, Brain and Behavior*. London: Academic Press, pp. 611–638. Available at: <https://doi.org/10.1016/B978-012532104-4/50026-3>. (B) The pattern of IPIs conveys behavioral state. Top, 10 s of a continuous electrical recording from a single pulse-type fish. Each EOD appears as a tick mark due to the long timescale, and the amplitude changes as the fish moves relative to the recording electrode. Bottom, a plot of IPI vs. time for the continuous recording. Pulse-type fish rapidly modulate their IPIs from ~ 10 ms up to several seconds. From Baker, C.A., Kohashi, T., Lyons-Warren, A.M., Ma, X., Carlson, B.A., 2013. Multiplexed temporal coding of electric communication signals in mormyrid fishes. *J. Exp. Biol.* 216, 2365–2379. Available at: <https://doi.org/10.1242/jeb.082289>.

Electrolocation

Electrolocation, or the detection of electric fields to locate objects, can be either passive or active. During passive electrolocation, animals detect weak, low-frequency electric fields for prey or predator detection or for navigation (Zupanc and Bullock, 2005). For instance, sharks and rays can find prey animals buried in sand. All animals generate weak, low-frequency alternating current (AC) or modulated direct current (DC) electric fields ranging in intensity from about $10 \mu\text{V}$ up to a few mV, with intensity decreasing with distance. Although the source of these fields is not well understood, one hypothesized cause is ion flow across cell membranes, particularly in the head region. The ability to detect these weak electric fields is due to specialized cutaneous sensory receptors that are extremely sensitive to low-frequency electric signals. Electric potentials arising from muscle contractions are typically in a frequency range (>20 Hz) outside the sensitivity of these receptors. Additional sources of low-frequency or static electric fields include water currents, temperature gradients, and ion absorption at water boundaries (Wilkins and Hofmann, 2005).

During active electrolocation, animals produce their own electric signals, called electric organ discharges (EODs), and detect distortions of the resulting electric fields caused by objects with conductivity that differs from the surrounding water. This kind of electrolocation is considered active because it relies on fish producing their own electricity. Purely resistive objects, such as rocks or dead wood, cause changes in electric field lines that result in local increases or decreases in current density across the skin, depending on the resistance of the object relative to the surrounding water. Living objects, such as plants and animals, also have electrical capacitance, and this causes local distortions in the EOD waveform. Fish are remarkably sensitive to the size, shape, and distance of objects and can use their electric sense to navigate and recognize objects (von der Emde, 2013). Active electrolocation can be used to detect objects up to a few centimeters from the fish (Zupanc and Bullock, 2005). Active and passive electrolocation rely on anatomically and physiologically distinct sensory receptors.

Jamming avoidance response. When two wave-type fish are near each other, their EOD waveforms interfere. When the EOD frequencies are within ~ 10 Hz of one another, the resulting interactions impair electrolocation. To avoid this “jamming” effect, fish perform the so-called jamming avoidance response (JAR). The fish with the higher frequency shifts its frequency even higher, and the fish with the lower frequency shifts its frequency even lower (Heiligenberg, 1991). The net effect is to maintain a frequency difference of at least 20 Hz, which does not impair electrolocation.

Electric Communication

In addition to active electrolocation, weakly electric fish use their electric signals to communicate with conspecifics. Because signal amplitude decreases with distance, the range of electrocommunication signals is <1 m (Pappas and Dunlap, 2011). Pulse- and wave-type fish use distinct strategies to communicate.

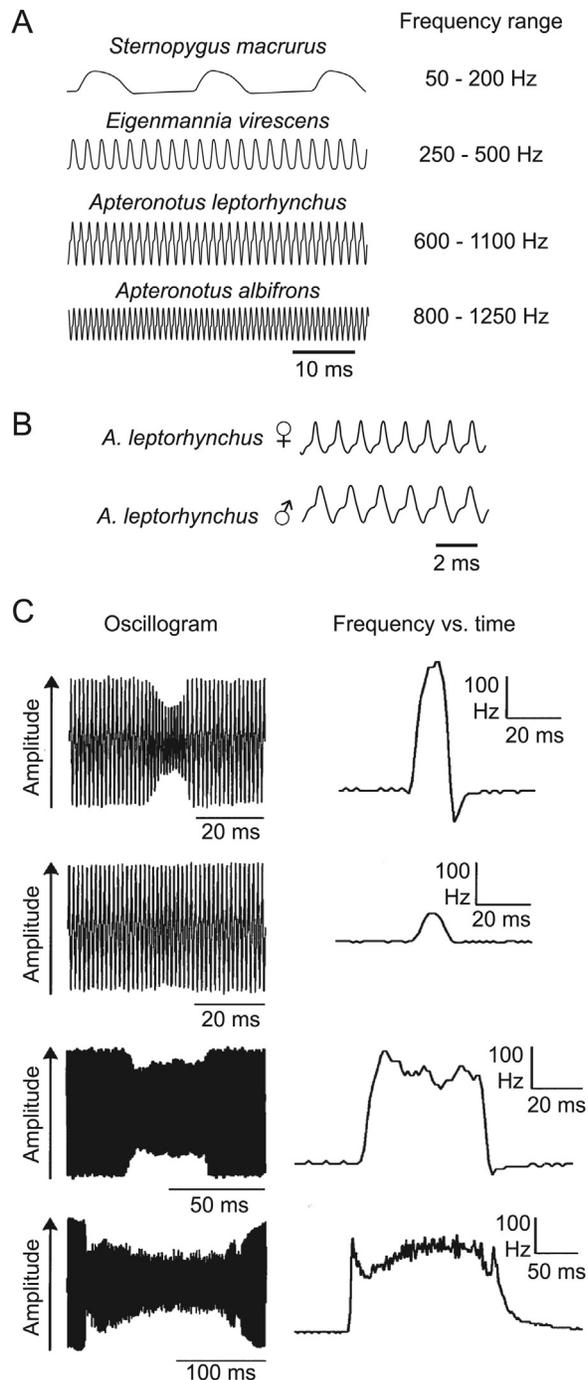


Fig. 2 Communication with wave-type EODs consists of the EOD frequency, waveform, and amplitude. (A–B) EOD frequency and waveform contain information about species and sex. From Smith, G.T., 1999. Ionic currents that contribute to a sexually dimorphic communication signal in weakly electric fish. *J. Comp. Physiol. A Sens., Neural, Behav. Physiol.* 185, 379–387. Available at: <https://doi.org/10.1007/s003590050398>. (C) Wave-type fish transiently modulate their EOD frequency and amplitude in a variety of social contexts. Four so-called “chirps” that differ in the degree and duration of frequency increases recorded from *Aptereronotus leptorhynchus* are shown. From Zupanc, G.K.H., 2002. From oscillators to modulators: Behavioral and neural control of modulations of the electric organ discharge in the gymnotiform fish, *Aptereronotus leptorhynchus*. *J. Physiol.* 96, 459–472. Available at: [https://doi.org/10.1016/S0928-4257\(03\)00002-0](https://doi.org/10.1016/S0928-4257(03)00002-0).

Communication with pulse-type electric signals. During electric communication, two components of pulse-type EODs carry information: the waveform and the intervals between successive EODs. Pulse-type EODs exhibit remarkable diversity in waveform across species, such that waveform may often be used identify species. Further, EOD waveforms within species can also vary with age, sex, and dominance status (Fig. 1(A); Carlson, 2002). Within an individual, however, waveform tends to be highly stereotyped across

time. The ability to detect and use the information within the EOD waveform varies across species (Carlson *et al.*, 2011). For instance, some species can recognize individuals on the basis of EOD alone (McGregor and Westby, 1992). In other species, EOD waveform is nearly invariant across individuals, such that waveform analysis would not reveal any additional information about the sender.

The pattern of intervals between successive EODs, or interpulse intervals (IPIs), conveys information about behavioral state (Fig. 1(B)). Across pulse-type species, a rich repertoire of IPI patterns has been associated with a variety of behavioral conditions (Carlson, 2002). Many species form dominance hierarchies and specific IPI patterns have been associated with dominance and submission. For instance, after a territorial dispute the dominant fish may emit bursts of EODs called scallops, whereas the submissive fish may cease signaling for up to several seconds. During aggressive encounters, fish may position themselves with their own electric organ (in the tail) next to the other fish's head, where the density of electroreceptors is highest, such that the two fish are aligned "anti-parallel" to one another. The fish then rapidly increase their electric discharge rates. Fish can also produce echo responses, in which a fish emits its own EOD with a defined time delay relative to another fish's EODs, and preferred latency avoidance responses, in which a fish avoids certain relative time delays.

Communication with wave-type electric signals. The frequency and waveform of wave-type EODs are often species- and/or sex-specific (Fig. 2(A–B)). In some species, EOD frequency also carries information about dominance status. Behavioral experiments suggest that wave-type species are sensitive to both EOD frequency and waveform (Zupanc and Bullock, 2005). Wave-type fish can rapidly and transiently modulate the amplitude and/or frequency of their EODs during social interactions. One type of rapid modulation is called a chirp (Fig. 2(C)). Chirps have been associated with territorial advertisement, aggression, and courtship, with the degree and/or duration of modulation varying across behavioral context (Zupanc and Bullock, 2005). During aggressive encounters, two males often chirp back and forth at a regular rate. Females are less likely than males to produce chirps during aggressive interactions; instead, they tend to produce long (up to a few minutes) increases in EOD frequency called rises. When two females are interacting, the female with the higher EOD frequency typically performs rises. Since higher frequencies are associated with dominance, rises in these contexts may play a role in establishing dominance hierarchies. Females also produce rises with males, but these signals are thought to be submissive or involved in courtship.

Electric Signal Production

Electric signal production is controlled hierarchically. EOD waveform is determined by the properties of excitable cells in the electric organ, termed electrocytes. EOD timing is controlled in a 1:1 manner by central command neurons. Modulations in the timing or frequency of EOD production are controlled by descending inputs to the command neurons. This organization makes electric signaling a powerful system for determining the neural basis of signal features at several levels of analysis, from genes to molecules to cells to circuits.

Central control of electric signal timing. Each EOD is initiated by synchronous spiking in a network of electrically coupled command neurons in the medulla (Dye and Meyer, 1986). In the South American gymnotiforms and the wave-type African fish *Gymnarchus niloticus*, these neurons are referred to as pacemaker neurons because they have cell-intrinsic mechanisms that lead to highly precise rhythmic firing at the fish's EOD frequency. In the pulse-type mormyrids, which generate EODs with much more variable timing, there is no evidence that these neurons are intrinsically rhythmic. Instead, their firing is determined by descending inputs. In both cases, however, spiking among these neurons directly drives EOD production in a 1:1 fashion by exciting adjacent relay neurons, which send the command signal down the spinal cord to activate electromotor neurons that then excite the electrocytes within the electric organ (Fig. 3). The use of separate command and relay neurons in both systems likely reflects functional convergence (Caputi *et al.*, 2005). The relay neurons are relatively large with correspondingly thick axons, which likely increases the effectiveness of electromotor neuron stimulation. These thick axons also increase action potential conduction velocity, and thereby minimize conduction delays down the spinal cord to maximize the synchrony of electromotor neuron stimulation. However, having such large somas means that the relay neurons have low input resistance, such that large amounts of synaptic current are needed to modify their spiking behavior. Placing smaller command neurons one level upstream circumvents this cost, allowing descending inputs to more effectively modulate EOD output. Synchronous output from the command neurons then provides sufficient current to excite the relay neurons.

The output of command neurons, and therefore the timing of EOD production, is influenced by multiple descending inputs to the medullary command neurons (Fig. 3). In both gymnotiforms and mormyrids, portions of the dorsal thalamus have been incorporated into the electromotor system, giving rise to a column of cells that extends from the dorsal thalamus in a caudal and ventrolateral direction towards the mesencephalon (Caputi *et al.*, 2005). In both groups, there are morphological and physiological differences between cells at the dorsomedial and ventrolateral ends of this column, and these exert different effects on the output of command neurons, with the dorsomedial population driving smooth increases in EOD rate and the ventrolateral population driving abrupt, transient increases in EOD rate. In both groups of fishes, the command neurons also receive input from a third, smaller group of neurons within the mesencephalon. These multiple inputs to the command neurons, acting separately or in concert, establish the electric signal repertoire by inducing the various types of frequency modulations used by wave-type fish and IPI patterns used by pulse-type mormyrids (Caputi *et al.*, 2005).

Peripheral control of electric signal waveform. In mormyrids, the electric organ is located in the caudal peduncle, at the base of the tail. It consists of 4 columns of electrocytes, a dorsal and a ventral column on each side. The electrocytes are homogenous in their

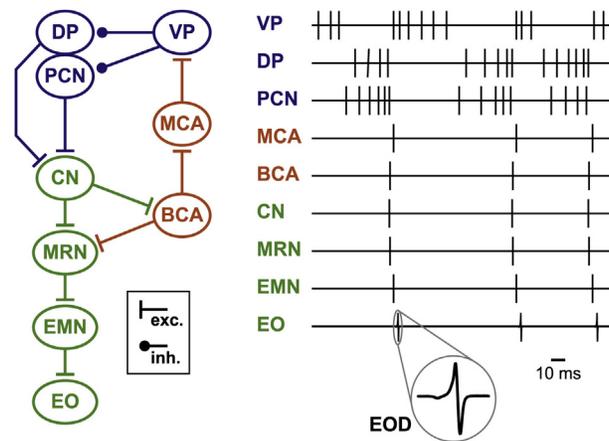


Fig. 3 Central control of EOD production in mormyrids. The command pathway is shown in green, the pre-command pathway is shown in blue, and the corollary discharge pathway is shown in orange. Each EOD is initiated by synchronous spiking among neurons in the medullary command nucleus (CN). This command is relayed to neurons in the medullary relay nucleus (MRN), both directly and indirectly via the bulbar command-associated nucleus (BCA). BCA gives rise to a corollary discharge pathway that allows electrosensory circuits to distinguish self-generated from external EODs, and that also feeds back into the pre-command pathway. The MRN axons project down the spinal cord to excite spinal electromotor neurons (EMN), which innervate electrocytes within the electric organ (EO) that produce the EOD. The CN neurons receive descending input from multiple precommand centers, including (but not limited to) the dorsal posterior nucleus (DP) and precommand nucleus (PCN). Neurons in DP and PCN receive inhibition from the ventroposterior nucleus (VP), which receives excitatory input from the mesencephalic command-associated nucleus of the corollary discharge pathway. This recurrent, command-derived inhibition serves to silence descending input to the command nucleus immediately following each EOD. DP, PCN, and VP neurons receive inputs from several different regions of the brain, which can mediate increases or decreases in descending excitatory input to CN to drive increases or decreases in EOD rate.

morphology and physiology. Thus, the electrical potential recorded from a single electrocyte is effectively a miniature version of the EOD (Bennett, 1971). When all the electrocytes are excited synchronously by spinal electromotor neurons, the electrical potentials generated by each electrocyte summate to produce the EOD.

Mormyrid electrocytes are large, thin, multinucleated, disc-shaped cells (Bass, 1986). A series of small stalkettes arise from each electrocyte, and these fuse to form a single large stalk that receives innervation from the axon of a spinal electromotor neuron. There is remarkable diversity in stalk morphology across species (Fig. 4). The stalk may arise from the posterior or anterior face of the electrocyte. Further, the stalk may reverse course and penetrate the electrocyte membrane so that it is innervated on the opposite side of the electrocyte from which it arises. In some species, this happens twice, resulting in a doubly penetrating electrocyte that is innervated from the same side from which it arises. Finally, some species have mixed electrocytes in which some stalkettes penetrate the membrane and others do not. There is a direct relationship between this morphological variation and the diversity of EOD waveforms across species (Fig. 4).

The electric organs of gymnotiforms are quite different from those of mormyrids (Bass, 1986; Bennett, 1971; Caputi *et al.*, 2005). They extend almost the entire length of the body. The electrocytes of wave-type gymnotiforms are long, tubular cells that extend along the longitudinal axis. Only the posterior face of these electrocytes is electrically excitable, and this face receives direct innervation from spinal electromotor neurons. The non-innervated anterior face generates a head-negative DC current. Thus, an action potential in the posterior face results in a head-positive, monophasic EOD waveform superimposed on a head-negative baseline. The size and density of electrocytes varies along the length of the electric organ, leading to variation in the local EOD amplitude along the length of the body. In one family, the Apterontidae, electrocytes are lacking entirely, and the electric organ is instead composed of the modified axons of spinal electromotor neurons, which form a nerve-like bundle that first heads in an anterior direction, and then reverses course to head in a posterior direction. Action potentials propagating down these axons therefore first generate a head-positive phase followed by a head-negative phase, giving rise to a biphasic EOD waveform.

In pulse-type gymnotiforms, the electric organ also extends nearly the entire length of the trunk. The electrocytes are flattened, cylindrical cells that exhibit remarkable diversity (Caputi *et al.*, 2005). Both the anterior and posterior faces can be electrically excitable, and in some species, the electrocytes can be innervated on both their anterior and posterior side. In some species, stalk-like processes extend from the electric organ and receive innervation, whereas in others such structures are lacking. Further, in some species there is heterogeneity in these features throughout the extent of the electric organ, as well as asynchronous activation of different electrocyte populations, leading to a complex EOD waveform that varies extensively along the length of the animal.

Hormonal regulation of electric signals. Sex differences in EOD waveform are due to the actions of gonadal steroid hormones acting directly on the electrocytes (Bass, 1986; Markham, 2013). These hormones may also be responsible for dominance-related differences in EOD waveform (Carlson *et al.*, 2000). In mormyrids, androgen hormones act on the anterior face of electrocytes, increasing both its thickness and the number of surface invaginations (Bass, 1986). This is associated with an increase in electrocyte action potential duration and therefore EOD duration, presumably due to an increase in membrane capacitance (Bass and Volman, 1987). In gymnotiforms, both androgens and estrogens act on electrocytes to alter the kinetics of voltage-gated sodium and

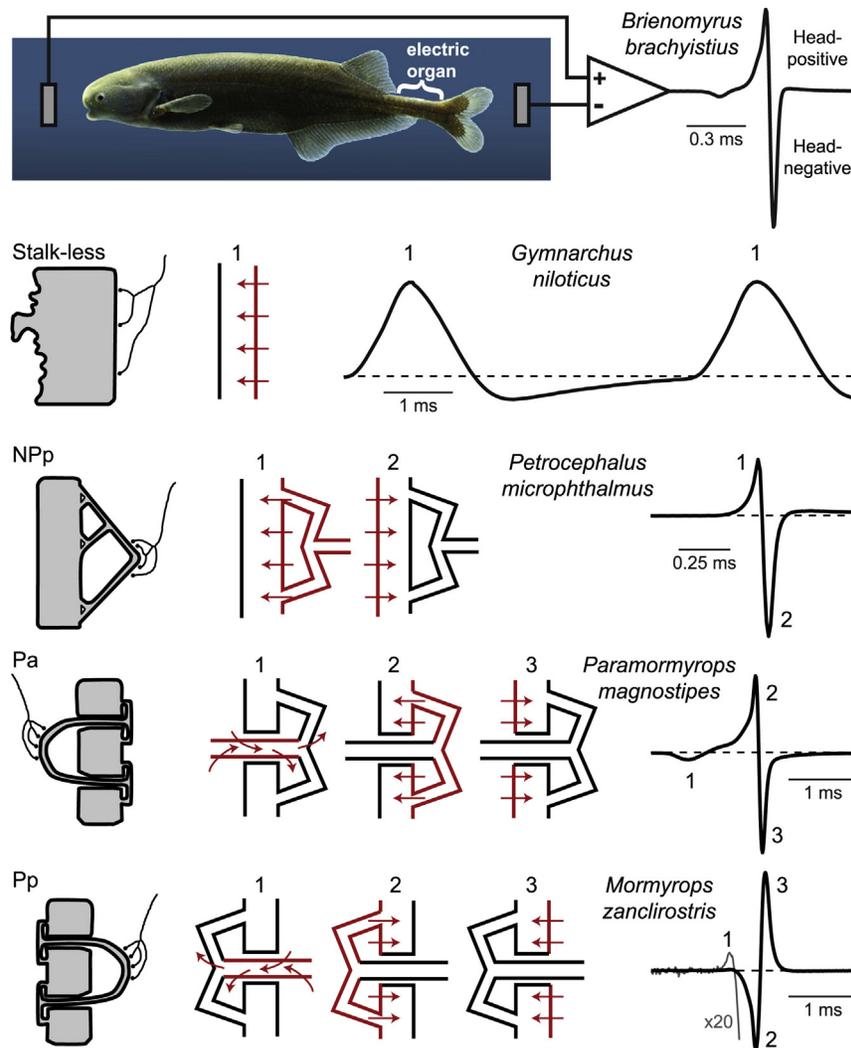


Fig. 4 EODs are generated by excitable cells in the electric organ called electrocytes. By convention, EODs are recorded with a recording electrode at the head and a reference electrode at the tail so that positive voltages represent head-positive components, and negative voltages represent head-negative components. Species diversity in EOD waveform among mormyroids is related to electrocyte morphology. Stalk-less electrocytes are found in the wave-type *Gymnarchus niloticus*, sister taxon to the mormyrids. They are innervated on their posterior membrane, which is electrically excitable. Inward current across the posterior membrane leads to current flow towards the head, resulting in a monophasic, head-positive EOD superimposed on a head-negative baseline. In the stalked electrocytes of mormyrids, both the anterior and posterior membranes are electrically excitable. Electrocytes with non-penetrating stalks that are innervated on the posterior side (NPP) produce biphasic EODs. Action potentials originating in the stalk propagate to excite the posterior membrane, leading to current flow towards the head and an initial head-positive phase. This current subsequently excites the anterior membrane, leading to current flow towards the tail and a second head-negative phase. Penetrating stalks generate a triphasic EOD by adding a small, early phase before the two main phases. For penetrating stalks that are innervated on the anterior side (Pa), the action potential propagating down the stalk results in an early head-negative phase, followed by excitation of the posterior membrane of the electrocyte and a head-positive phase, followed by excitation of the anterior membrane and a head-negative phase. For penetrating stalks that are innervated on the posterior side (Pp), the polarity is reversed, with a small head-positive phase, followed by a head-negative phase, and then a head-positive phase.

potassium channels, leading to a masculinization or feminization of EOD waveform, respectively (Markham, 2013; Stoddard *et al.*, 2006). In wave-type species, these gonadal steroid hormones also act centrally to induce changes in EOD frequency so that a quasi-sinusoidal EOD waveform is maintained. The electrocytes of gymnotiforms are also regulated by peptide hormones, which drive rapid circadian and socially induced changes in EOD amplitude and waveform (Markham, 2013). These rapid peptidergic effects are themselves regulated by the longer term actions of steroid hormones on electrocytes.

Evolutionary developmental mechanisms of electric signal diversity. Electric organs have evolved at least six times independently, in mormyroids, gymnotiforms, siluriforms, torpedinoids, rajoids, and uranoscopids (Bass, 1986). Except for the neurogenic organs of the Apterontidae, all other electric organs are myogenic, meaning they are derived developmentally either from skeletal muscle tissue or directly from mesodermal precursor cells. The electric organs of mormyroids are derived from skeletal muscle tissue (Bass, 1986). The transition from muscle to electric organ involves several phenotypic changes, including the loss of contractile ability.

Mormyrids first develop a functional larval electric organ, and then later develop a separate adult electric organ. Both organs are controlled by the medullary command nucleus, but are innervated by separate populations of spinal electromotor neurons (Bass, 1986). The larval electric organ eventually degenerates, but there is a period of time during which mormyrids generate both larval and adult EODs (Bass, 1986). *Gymnarchus niloticus*, the sister taxon to the mormyrids, maintains a single electric organ throughout life that closely resembles the larval electric organ of mormyrids. Thus, it's likely that the adult electric organ of mormyrids is derived evolutionarily from the larval electric organ, and that wave-type EODs evolved first in mormyrids followed by the evolution of pulse-type EODs (Hopkins, 1999).

The electrocytes of *Gymnarchus* and the larval electrocytes of mormyrids lack a stalk system (Fig. 4), suggesting that the stalks found in adult mormyrid electrocytes are a derived trait (Hopkins, 1999). There are two subfamilies within the mormyrids, the Petrocephalinae and Mormyriinae. All petrocephaline species have stalks that are innervated on the posterior side and that do not penetrate the electrocyte. Stalk anatomy is far more diverse in the mormyriines, and in the few species with penetrating stalks that have been studied, the electrocytes pass through an early developmental stage in which they lack penetrations. Thus, it appears that stalk penetrations are a derived trait of the mormyriines, and this is associated with far greater EOD waveform diversity compared to the petrocephalines (Sullivan *et al.*, 2000).

The myogenic electric organs of pulse- and wave-type gymnotiforms appear to follow distinct developmental trajectories (Kirschbaum and Schwassmann, 2008). Like mormyrids, wave-type species develop distinct larval and adult electric organs, and it appears that both arise from skeletal muscle. Interestingly, the Apterontidae, which have a neurogenic electric organ as adults, possess a myogenic larval electric organ that resembles those of other wave-type species. This suggests that myogenic electric organs are the ancestral state, and that neurogenic electric organs are derived. Most likely, a neurogenic electric organ is an adaptation for generating high EOD frequencies in apteronotids (well over 1000 Hz in some species). Pulse-type species, however, lack distinct larval and adult electric organs, and their electrocytes appear to differentiate directly from mesodermal precursor cells without a skeletal muscle intermediate. The developmental patterns of electric organs in wave- vs. pulse-type gymnotiforms have led to the suggestion that wave-type EODs are the ancestral state and that pulse-type EODs are derived, though the phylogenetic evidence for this is mixed (Kirschbaum and Schwassmann, 2008).

Molecular studies have revealed a remarkable example of convergent evolution in the generation of electric signal diversity (Arnegard *et al.*, 2010b). In both gymnotiforms and mormyrids, a particular voltage-gated sodium channel gene is expressed only in electric organ, while its paralog is expressed only in skeletal muscle. In non-electrogenic teleost fish, both paralogs are found in skeletal muscle. The compartmentalization of these genes into electric organ and muscle in weakly electric fishes allowed selection to drive electric signal diversity without affecting muscle function. Indeed, the paralog expressed in electric organ has experienced strong positive selection in both lineages, with substitutions occurring in regions that determine the kinetics of voltage-gated sodium channels. Such evolutionary changes likely alter the action potential waveforms of electrocytes, and therefore the EOD waveform.

Electric Communication Signal Detection and Central Analysis

The ease with which electric signals can be recorded, manipulated, and played back to fish has facilitated the study of how electro-sensory systems respond to and encode signal parameters such as amplitude, timing, and waveform.

Electroreception. Specialized sensory receptors in the skin, called electroreceptors, detect nearby electric fields. Ampullary electroreceptors detect weak DC and low-frequency (<0.1–50 Hz) AC sources for passive electrolocation (Bodznick and Montgomery, 2005). The electroreceptive abilities of non-electrogenic animals such as sharks, skates, rays, lampreys, paddlefish, salamanders, caecilians, and platypuses are due to ampullary electroreceptors.

In addition to ampullary electroreceptors, weakly electric fish have evolved tuberous electroreceptors specifically for detecting EODs. Tuberous electroreceptors are often maximally sensitive to stimulus frequencies near their own species-specific signals (tens of Hz to 1 kHz) (Kawasaki, 2005). In this way, the receptors essentially “tune into” species-specific frequency channels while limiting detection of heterospecific signals. Tuberous electroreceptors can be divided into two groups based on their responses to electric stimuli. Time-coding receptors generate a single action potential, or spike, for each cycle of a wave-type EOD or for each pulse of a pulse-type EOD (Fig. 5(A–B)). In contrast, amplitude-coding receptors may not spike on each EOD cycle or pulse, but instead increase or decrease their firing rate with an increase or decrease, respectively, in EOD amplitude (Fig. 5(A); Kawasaki, 2005). Timing cues in EODs convey information about waveform, whereas amplitude cues convey information about signaler size and distance. Amplitude- and time-coding electroreceptors innervate distinct neural pathways for the parallel processing of these two stimulus features.

In pulse-type mormyrids, the time-coding receptors mediate a pathway devoted to processing communication signals, whereas the amplitude-coding receptors mediate a pathway devoted to processing electrolocation signals. In the following discussion of sensory coding mechanisms, we focus first on the mormyrid time-coding pathway before briefly addressing gymnotiform communication signal processing.

Mormyrid time-coding tuberous receptors can take one of two anatomical and physiological forms that are associated with electro-sensory perceptual capabilities (Carlson *et al.*, 2011). Species that are sensitive to subtle variation in EOD waveform have tuberous receptors that are broadly distributed across the body with an increased density on the head. These receptors generate all-or-none spikes. In species that cannot detect EOD waveform variation, the receptors are grouped into three tight clusters on

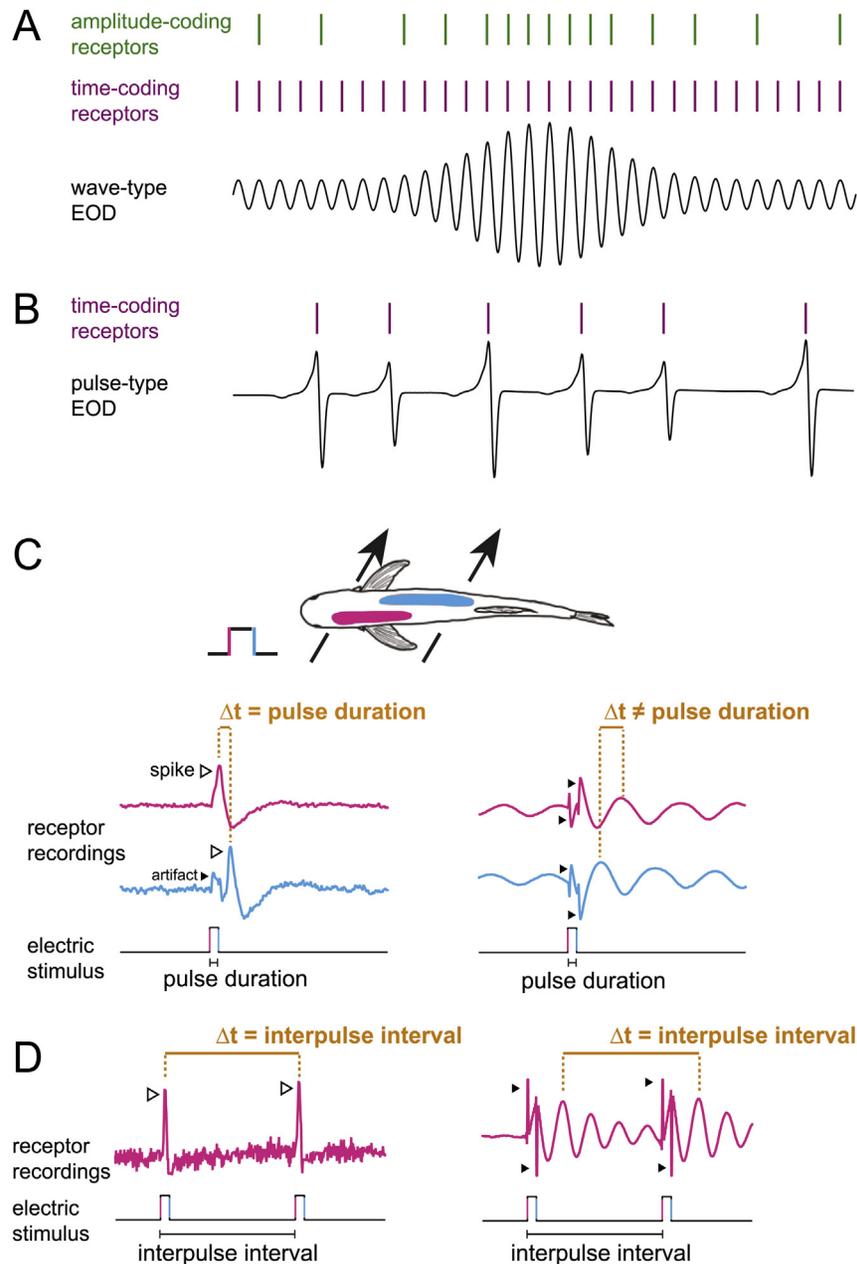


Fig. 5 Encoding of electric communication signals by tuberous electroreceptors. (A) In wave-type fish, amplitude-coding electroreceptors fire more spikes (represented by tick marks) when the EOD amplitude increases. Time-coding electroreceptors fire a single spike on each cycle of the EOD. Wave-type fish use the responses of both time-coding and amplitude-coding receptors to analyze communication signals. (B) In contrast to wave-type fish, pulse-type fish rely solely on the responses of time-coding receptors to analyze communication signals. Similar to the time-coding receptors in wave-type fish, those in pulse-type fish fire a single spike per EOD. (C) Top, due to the anatomy of electroreceptors in the fish's skin, tuberous receptors on opposite sides of the body will respond to opposite edges of an electric stimulus. A square electric pulse occurring on the fish's left side causes receptors on its left side to respond to pulse onset (magenta) and receptors on its right side to respond to pulse offset (blue). Bottom left, in mormyrid species with spiking receptors, comparison of the times of spikes from receptors on opposite sides of the body provides a read-out of pulse duration. Bottom right, instead of firing spikes, oscillating receptors respond to an electric pulse with a phase reset, with receptors on opposite sides of the body resetting to opposite phases. Comparison of the times of oscillatory peaks in receptors on opposite sides of the body reflects oscillatory period, not electric pulse duration. Open arrowheads indicate spikes and solid arrowheads indicate the stimulus artifact, or deflections in the recordings due to the stimulus. (D) Comparison of the spike times (left) or oscillatory peak times (right) within a receptor (here, the receptors responding to pulse onset) reflects the interpulse intervals in communication signals. Extracellular receptor recordings were modified from Baker, C.A., Huck, K.R., Carlson, B.A., 2015. Peripheral sensory coding through oscillatory synchrony in weakly electric fish. *eLife* 4, e08163. Available at: <https://doi.org/10.7554/eLife.08163>.

either side of the head, and these receptors generate continuous oscillations. With few exceptions, the vast majority of species in the subfamily Mormyriinae have spiking receptors whereas those in the subfamily Petrocephalinae have oscillating receptors. All tuberous electroreceptors are activated by inward current flow, which depolarizes the sensory cells at the receptor base. Sufficiently large depolarization evokes a single spike per EOD in the sensory cells of spiking receptors. In contrast, depolarization causes increased oscillation amplitude and a phase reset in the sensory cells of oscillating receptors (Baker *et al.*, 2015).

Spiking and oscillating receptors encode electric pulses in fundamentally different ways. Because spiking receptors respond to inward current, receptors on one side of the body will spike to pulse onset while receptors on the other side of the body will spike to pulse offset. Comparison of the spike times from receptors on opposite sides of the body will thus provide a read-out of pulse duration (Fig. 5(C); Hopkins and Bass, 1981). Oscillating receptors respond to inward current by resetting their oscillations to a peak, and to outward current by resetting to a trough. This means that oscillating receptors on one side of the body will reset to a peak and receptors on the opposite side will reset to a trough. Comparison of the times of oscillatory peaks in receptors on opposite sides of the body does not accurately reflect electric pulse duration within the natural range of EOD durations (Fig. 5(C); Baker *et al.*, 2015). Thus spiking receptors encode information about EOD waveform to be analyzed by downstream circuits in the brain, whereas oscillating receptors do not. In contrast to the differences in waveform encoding, both spiking and oscillating receptors encode the IPIs between EODs that convey information about behavioral state (Fig. 5(D); Baker *et al.*, 2015). Both receptor types also provide information about sender location, based on the spatial pattern of responses among receptors across the fish's body.

Central analysis of pulse-type communication signals. Because EODs are used for both electrolocation, in which a fish must detect distortions in its own electric signals, and communication, in which a fish must detect electric signals coming from other individuals, the electrosensory system needs a way to distinguish external signals from self-generated signals. Activity from the time-coding electroreceptors is relayed to the nucleus of the electrosensory lateral line lobe (nELL) in the hindbrain. Each time the fish's motor system generates an EOD, a copy of this command called a corollary discharge is sent to the nELL (Bell and Grant, 1989; Vélez and Carlson, 2016). The corollary discharge results in inhibition that cancels out receptor responses to the fish's own EODs. Thus nELL output reflects activity arising solely from the communication signals of other fish.

The output of the nELL is sent to the exterolateral nucleus (EL) of the midbrain. Species that can detect EOD waveform variation using spiking receptors have an EL that is subdivided into anterior (ELa) and posterior (ELp) regions, whereas species with oscillating receptors have a smaller, undifferentiated EL (Fig. 6(A); Carlson *et al.*, 2011). The circuitry within ELa analyzes the timing differences between the spikes of receptors on opposite sides of the body. ELa contains two cell types, large inhibitory cells and small excitatory cells, with the large cells inhibiting the small cells. Output from the nELL goes directly to the large cells but takes a more circuitous route to the small cells (Fig. 6(A)). The longer path to the small cells means that nELL input will be delayed by a duration dependent on the length of the projection. Small cells thus integrate fixed-latency inhibition from large cells and variably delayed excitation from nELL. When inhibition and excitation arrive simultaneously, the two inputs cancel each other and the small cell does not spike. However, if excitation arrives before or after inhibition, the small cell will spike (Fig. 6(B)). By using this delay-line anti-coincidence detection mechanism, the electrosensory system establishes an array of cells that respond to different time delays. If excitation and inhibition arise from receptors on opposite sides of the fish's body, ELa circuitry can effectively measure electric pulse duration.

The undifferentiated EL of species that cannot detect EOD waveform variation also contains excitatory small cells and inhibitory large cells but lacks the delay lines from nELL (Fig. 6(A)) (Vélez *et al.*, 2017). Thus the absence of peripheral encoding of waveform timing cues by oscillating receptors is accompanied by the absence of central circuitry for waveform analysis.

The small cells of ELa send their only outputs to ELp, which contains both excitatory and inhibitory multipolar neurons (Fig. 6(A)). ELp neurons are selective for particular IPIs with some cells responding most strongly to short IPIs, and others responding most strongly to long or intermediate IPIs (Fig. 6(C); Carlson, 2009). The combination of EOD waveform sensitivity in ELa and IPI sensitivity in ELp means that ELp output reflects both EOD waveform and IPI.

In species with an undifferentiated EL, small cells in the anterior region project to IPI-selective multipolar cells in the posterior region (Fig. 6(A–D); Vélez *et al.*, 2017). Since these species lack the ELa circuitry for waveform analysis, the output of EL reflects only IPI. Therefore the main difference in EL circuitry between species sensitive and insensitive to EOD waveform appears to be the elaboration of delay lines in ELa for waveform analysis. Electrosensory processing after EL and ELa/ELp remains poorly understood.

Central analysis of wave-type communication signals. In contrast to mormyrid pulse-type fish, which rely solely on time-coding electroreceptors to detect communication signals, gymnotiform wave-type fish use both time- and amplitude-coding receptors. Amplitude-coding electroreceptors project to pyramidal cells in the electrosensory lateral line lobe (ELL) (Clarke *et al.*, 2015). Here, some neurons (ON-cells) respond to increases in spike rate (ie, increase in EOD amplitude), and others (OFF-cells) respond to decreases in spike rate (ie, decrease in EOD amplitude). Time-coding electroreceptors relay their activity to spherical cells in the ELL. Spherical cells preserve the timing information relayed by the time-coding receptors by firing one spike for each electroreceptor spike. In contrast to pulse-type fish, which use corollary discharge to cancel out activity evoked by the fish's own EODs, wave-type fish use the pattern of activity in electroreceptors distributed across the fish's body to distinguish external from self-generated signals. For instance, self-generated signals will result in a signal that is uniform across the fish's body, whereas external signals will result in an asymmetric signal based on the relative position of the two fish. ELL output is sent to the midbrain torus semicircularis (TS), where information from amplitude- and timing-coding receptors converges. TS neurons are sensitive to amplitude or time modulations, or to a combination of amplitude and time modulations (Kawasaki, 2005).

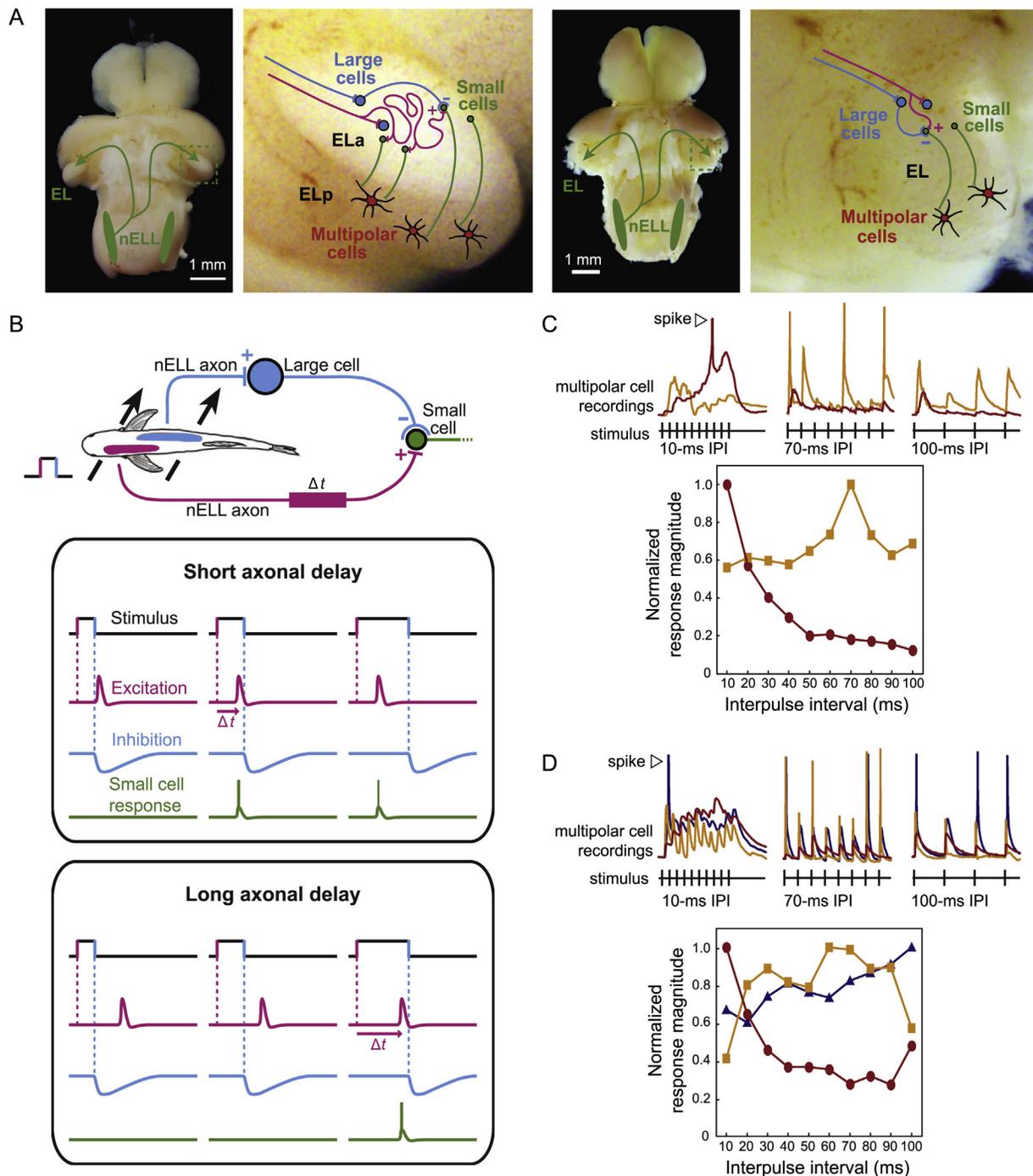


Fig. 6 EOD waveform and IPI analysis by central circuits. (A) Activity from time-coding electroreceptors is relayed to the nucleus of the electro-sensory lateral line lobe (nELL), which in turn projects to the exterolateral nucleus (EL) of the midbrain. Left, in species that can detect EOD waveform variation, the EL is enlarged and subdivided into anterior (ELa) and posterior (ELp) regions. nELL axons terminate onto large inhibitory cells (blue) and small excitatory cells (green), with the large cells in turn inhibiting the small cells. nELL axons project directly to large cells but follow a long, winding path called a delay line to small cells. Small cells then send their only outputs to multipolar cells in ELp. The circuit diagram is superimposed onto an enlargement of the region indicated by the dotted box. Right, EL anatomy in species that cannot detect EOD waveform variation is similar to that of species that can detect variation, but lacks the delay lines from nELL to the small cells. From Vélez, A., Kohashi, T., Lu, A., Carlson, B.A., 2017. The cellular and circuit basis for evolutionary change in sensory perception in mormyrid fishes. *Sci. Rep.* 7, 1–18. Available at: <https://doi.org/s41598-017-03951/s41598-017-03951-y>. (B) A delay-line anticoincidence detection mechanism in ELa small cells establishes sensitivity to EOD waveform variation. Small cells in ELa receive excitation (“+”) and inhibition (“-”) arising from receptors on opposite sides of the body. The inhibition arrives with a fixed time delay relative to the stimulus, whereas excitation arrives with a variable delay (Δt) proportional to the length of the delay line from nELL. The small cell will only respond when excitation and inhibition arrive non-coincidentally. Different small cells receive excitation that is delayed by different durations, resulting in a population of small cells that responds to a diverse range of stimulus durations. From Baker, C.A., Kohashi, T., Lyons-Warren, A.M., Ma, X., Carlson, B.A., 2013. Multiplexed temporal coding of electric communication signals in mormyrid fishes. *J. Exp. Biol.* 216, 2365–2379. Available at: <https://doi.org/10.1242/jeb.082289>. (C) Multipolar cells are sensitive to IPI. Top, *in vitro* intracellular recordings from two ELp multipolar cells during stimulation with three different IPIs. Bottom, plots of response magnitude vs. stimulus IPI reveal diverse IPI preferences across the two cells shown. (D) Same as (C) for multipolar cells in EL. Modified from Vélez, A., Kohashi, T., Lu, A., Carlson, B.A., 2017. The cellular and circuit basis for evolutionary change in sensory perception in mormyrid fishes. *Sci. Rep.* 7, 1–18. Available at: <https://doi.org/10.1038/s41598-017-03951-y>.

Neural basis of jamming avoidance response. The interference pattern between two wave-type EODs is called a beat and has a frequency equal to the difference between the two EODs. The beat amplitude and phase contain information about whether the neighboring fish's EOD is of higher or lower frequency. Fish rely solely on sensory information to perform the JAR, instead of taking into account their own pacemaker nucleus as a reference. The JAR has the notable distinction of being the only vertebrate behavior for which the entire neural circuitry, from sensory input to motor output, is known (Heiligenberg, 1991).

Neurons in the TS that receive input from both the amplitude-coding and time-coding pathways compute the sign of the EOD frequency difference. Some neurons respond when the frequency difference is positive, and other neurons respond when the difference is negative. TS neurons project to the nucleus electrosensorius (nE) in the diencephalon. Neurons in the dorsal nE respond to negative frequency differences and elicit an increase in EOD frequency via the diencephalic prepacemaker nucleus (PPn), which in turn excites the pacemaker nucleus (Metzner, 1993). Neurons in the ventral nE respond to positive frequency differences and inhibit the sublemniscal prepacemaker nucleus (SPPn) of the mesencephalon. The resulting reduction of tonic SPPn activity reduces the input to the pacemaker nucleus, thereby lowering EOD frequency (Metzner, 1993).

Evolutionary Ecology of Electric Signaling

Both the gymnotiforms and mormyroids are phylogenetically and phenotypically diverse. They inhabit a wide range of freshwater habitats, including rivers, lakes, streams, creeks, waterfalls, and swamps. Several factors appear to have played a role in the remarkable diversification of these fishes.

Evolutionary innovations. The evolution of electric organs and tuberous electroreceptors provides a clear example of evolutionary novelty (Carlson and Arnegard, 2011). Further, this novel phenotype can be considered a key innovation in that it allowed these fishes to exploit new ecological niches, and this was associated with high levels of species diversification and phenotypic divergence (Lavoué et al., 2012). Additional specializations within these fishes may also be driving diversification. Within the mormyrine subfamily of mormyrids, for example, the evolution of both EOD waveform sensitivity on the sensory side and greater lability in electrocyte stalk development on the motor side was associated with dramatic increases in the rates of EOD evolution and species diversification (Carlson et al., 2011).

Sexual selection. Several observations suggest that sexual selection has been a key driver of diversification in electric fishes. EODs play an important role in mate choice, and in many species there are large sex and dominance-related EOD differences during the breeding season (Carlson, 2002). In the *Paramormyrops* species flock of mormyrids, EODs have diverged more rapidly between species than body shape, body size, and trophic ecology, suggesting that sexual selection has been a primary driver of diversification in this genus (Arnegard et al., 2010a). The relationship between diversification rates and neural innovations related to electric communication within the Mormyridae is consistent with sexual selection acting on electric signals leading to increased diversification (Carlson et al., 2011).

Ecological adaptation. In the *Campylomormyrus* species flock of mormyrids, EOD divergence is associated with divergence in snout morphology. Both features may be related to specializing on different size classes of larval insect prey, as the frequency characteristics of different EODs may affect the detection of differently sized prey, and snout morphology may affect the accessibility of different prey items (Feulner et al., 2008). Under this scenario, EOD divergence reflects trophic niche segregation, with mate choice based on the EOD reinforcing divergence that arose initially through ecological adaptation (Feulner et al., 2009).

Bioenergetics of electric signaling. EOD production is metabolically costly. Theoretical and empirical studies of several gymnotiform species suggest that EOD generation may be responsible for as much as 30% of an animal's overall metabolic activity (Salazar et al., 2013). The electric fields resulting from an EOD approximate a dipole electric source in which field strength decreases with the inverse cube of distance (Hopkins, 1986). Doubling the active space of signaling would therefore require an 8-fold increase in signal amplitude at the source. This, combined with the high metabolic cost of signaling, effectively limits the active space of electric communication. Interestingly, there is some evidence from gymnotiforms that the anatomical organization of electrocytes within the electric organ is adapted to the conductivity of the water they inhabit, and this may be a form of impedance matching to the environment: adding electrocytes in series or in parallel along the length of the electric organ results in greater electric power output in low vs. high conductivity water, respectively (Hopkins, 1999).

The metabolic cost of electric signaling also increases with increasing EOD rate, and there is evidence of a trade-off between EOD frequency and amplitude across species (Salazar et al., 2013). Gymnotiform species with the highest EOD frequencies tend to live in fast-flowing, well-oxygenated water, and they have little to no tolerance for hypoxia (Crampton, 1998a,b). These high EOD rates establish a higher environmental sampling rate, which may be advantageous in a fast-moving habitat. However, they also demand more energy, which limits these fish to such habitats and may also come at the expense of a reduction in EOD amplitude. By contrast, species with lower frequencies are able to live in slow-moving, poorly oxygenated water and generate EODs with larger amplitudes.

Electrosensory predation. Although electric signaling provides a relatively private channel for communication, there are electroreceptive predators of both gymnotiforms and mormyroids, and several lines of evidence suggest that predation pressure may have been a driving force in the diversification of electric signals (Stoddard, 2002). In particular, an increase in the complexity of EOD waveforms renders them less detectable by highly sensitive ampullary electroreceptors, and this may drive increases or decreases in

EOD waveform complexity in areas with high vs. low predation pressure, respectively. In addition, sex differences in the EOD waveform of pulse-type fishes typically involve an elongation of the male EOD, making them more detectable by ampullary receptors (Hanika and Kramer, 2000, 1999). This may have played a role in the evolution of such sex differences, with sexual selection driving honest signaling.

See also: Neurons and Senses: Active Electroreception: Vertebrates; Electroreception in Vertebrates and Invertebrates.

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