

REVIEW

CENTENARY ARTICLE



Living life with an electric touch

Angel Ariel Caputi*

ABSTRACT

The electric organ discharges (EODs) produced by weakly electric fish have long been a source of scientific intrigue and inspiration. The study of these species has contributed to our understanding of the organization of fixed action patterns, as well as enriching general imaging theory by unveiling the dual impact of an agent's actions on the environment and its own sensory system during the imaging process. This Centenary Review firstly compares how weakly electric fish generate species- and sex-specific stereotyped electric fields by considering: (1) peripheral mechanisms, including the geometry, channel repertoire and innervation of the electrogenic units; (2) the organization of the electric organs (EOs); and (3) neural coordination mechanisms. Secondly, the Review discusses the threefold function of the fish-centered electric fields: (1) to generate electric signals that encode the material, geometry and distance of nearby objects, serving as a short-range sensory modality or 'electric touch'; (2) to mark emitter identity and location; and (3) to convey social messages encoded in stereotypical modulations of the electric field that might be considered as species-specific communication symbols. Finally, this Review considers a range of potential research directions that are likely to be productive in the future.

KEY WORDS: Electric organs, Electric organ discharge, Electrocyte, Delay lines, Re-afference, Ex-afference, Active sensory system, Electric image, Electric color, Mexican hat filter, Gymnotiformes, Mormyroidea

Introduction

That some species of fish can produce electric fields (see Glossary) has long been known; for example, the strong electric organ discharges (EODs) of Nile catfish and Mediterranean torpedoes were known in ancient Egypt and classical Greece, respectively (Wu, 1984; Moller, 1995). Later, European colonization of America allowed old-world scientists to discover electric eels, whose modular electric organ (EO) structure inspired the first electric battery (Volta, 1800). At that time, it was already known that electric eels were able to detect a short circuit between a pair of wires inside their tank (Walsh, 1773). The weak EODs of the broadly distributed family Rajidae (Elasmobranchii), the superfamily Mormyroidea (Teleostei) from Africa and the order Gymnotiformes (Teleostei) from America (Fig. 1) puzzled Darwin, who wrote: 'The electric organs of fishes offer another case of special difficulty; for it is impossible to conceive by what steps these wondrous organs have been produced. But this is not surprising, for we do not even know of what use they are' (Darwin, 1872). A possible communicative function was subsequently conjectured by Franz (1912, cited by Moller, 1995): '[a] question for future research would be to consider

whether perhaps the mormyrids themselves appreciate the electric shocks of members of their species...'.

The subsequent development of electrophysiological techniques revealed that EODs result from the activity of specialized electrogenic units called 'electrocytes' (Albe Fessard and Buser, 1950; Keynes and Martins Ferreira, 1953; Bennett and Grundfest, 1959, 1961a,b; Bennett et al., 1961; Chagas and Paes de Carvalho, 1961). The EODs of several hundred species belonging to Gymnotiformes, Mormyroidea and Rajidae are species specific and consist of either continuous waves or series of discrete stereotyped pulses (Movie 1). Wave and pulse species are found in both Gymnotiformes (Coates et al., 1954) and Mormyroidea (Lissmann, 1951), indicating that these strategies evolved convergently in America and Africa.

Concomitantly, Hans Lissmann (1951) observed that *Gymnarchus niloticus* (the sole African wave species) was able to dodge obstacles while swimming in reverse (Movie 1), and proposed that weakly electric fish use their electric field as a carrier of sensory signals. This proposal was followed by a collection of inspiring articles in Journal of Experimental Biology (JEB). Together, these articles show that the signals resulting from the polarization of objects by self-generated electric fields inform a fish about object characteristics and location, and that the electric fields may also serve as communication signals (Lissmann, 1958; Lissmann and Machin, 1958; Machin and Lissmann, 1960). As a corollary, the significance of these signals for mate selection and for evolution was recognized – insight supported by the discovery of electroreceptor organs specifically tuned to the species-specific time course of the electric field (Wright, 1958; Fessard and Szabo, 1961; Bullock et al., 1961; Murray, 1962).

In the spirit of the JEB centenary, this Review re-visits old concepts in the search for new ideas for future research on EODs and their functions. This article is not intended to be a comprehensive review, but instead presents a fresh view of the mechanisms of electrogenesis and the electrosensory function of EODs in weakly electric fishes, while aiming to identify and prioritize unsolved questions and to stimulate the progress of this young but productive field.

EODs are fixed action patterns

Complex behaviors result from the combination of stereotyped actions organized by relatively simple neural circuits. These modular acts, so-called 'fixed motor patterns', are 'ready-made "motor tapes" as it were, that when switched on produce well-defined and coordinated movements: the escape response, walking, swallowing, the pre-wired aspects of bird songs...' (Llinás, 2002). Extending this concept, it was proposed that EODs are fixed action patterns in which the output is electrical rather than mechanical (Rodríguez-Cattáneo et al., 2008).

In motor systems, relatively large forces result from the sum of weak forces generated by muscle fiber contraction. The elasticity and viscosity of passive muscle elements allow them to integrate and filter the forces generated and apply them to the skeleton (Hoffer et al., 1992), resulting in a mechanical output that is a balance between force and displacement determined by the load

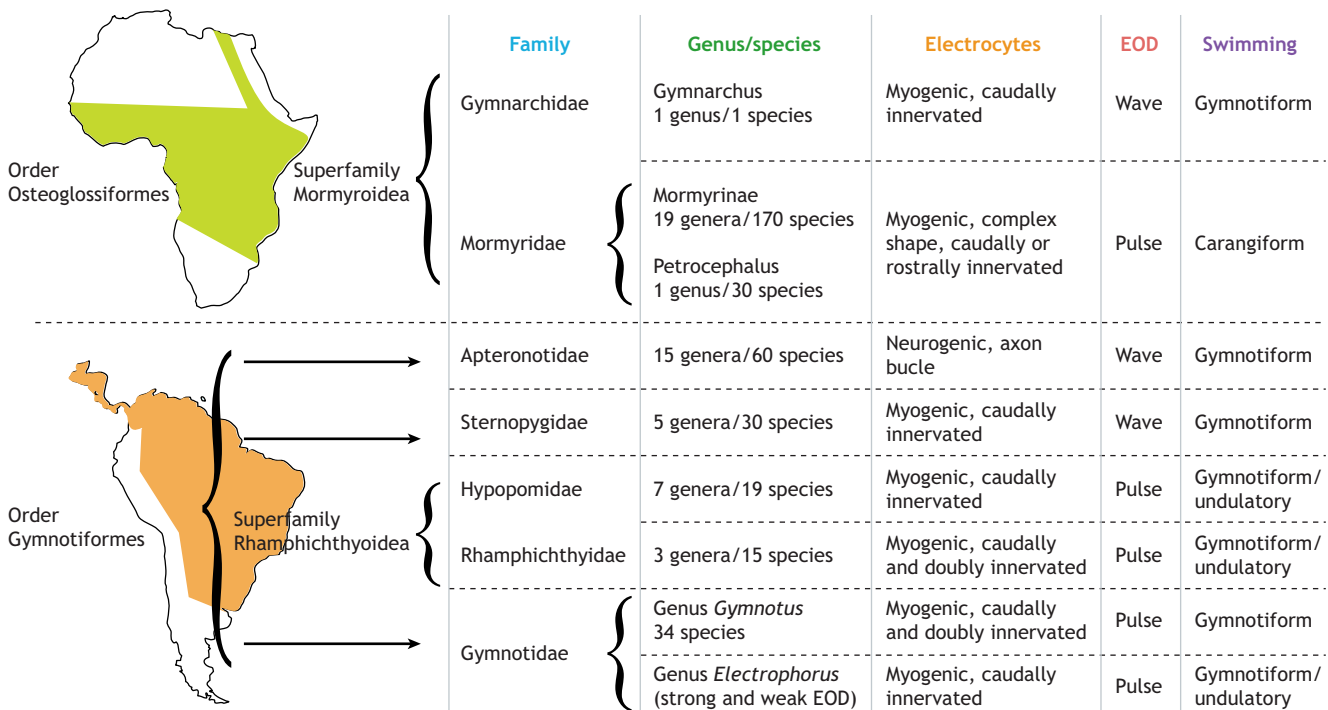


Fig. 1. The diversity of electric organs and electric organ discharges in weakly electric teleostei. The use of the electric organ discharge (EOD) for information purposes evolved separately and convergently in fresh water teleostei in Africa and America and in widely distributed Elasmobranchii (Rajidae) inhabiting both fresh and salty water. The figure compares the present families of weakly electric teleostei belonging to the orders Osteoglossiformes (superfamily Mormyroidea) and Gymnotiformes observed in the indicated regions of Africa (top) and America (bottom), respectively. The number of genera and species in each order, the electrocyte types, the type of EOD and the locomotion strategy are shown.

moved (Hoffer et al., 1989). Similarly, in electromotor systems, thousands of identically oriented electrocytes stacked in a connective tissue sleeve form an EO. Each electrocyte contributes a small fraction of the total current that is conducted along the EO. In the absence of an external conductive medium (such as tank water), the potential of the electrogenic system to generate external currents is represented by the electromotive force, which corresponds to the drop in voltage caused by the circulation of the electrocyte-generated current along the fish's body in the opposite direction to the flow of current inside the EO (Cox and Coates, 1938; Bell et al., 1976; Caputi et al., 1989, 1993; Caputi and Budelli, 1995). This is analogous to the isometric contraction of a muscle group, which reflects the potential to produce movement.

When water offers an external path, a fraction of the EO-generated current leaks through the skin: the source becomes distributed and can be modeled as an array of electromotive forces and electric impedance pairs (see Glossary; Caputi and Budelli, 1995). Swimming in a heterogeneous conductive medium produces a self-stimulating close field, resulting from the trade-off between the changing distribution of impedance of the surrounding medium and the fixed distribution of impedance of the fish's body (Caputi et al., 1998a,b, 2002; Caputi and Budelli, 2006). Beyond a few body lengths, the shape of the field approximates that of a dipole (see Glossary) with a species-specific time course (Aguilera et al., 2001). Changes in the time course and spatial distribution of these electric fields are specifically detected by a mosaic of cutaneous electrosensory receptor organs distributed over the body. This produces a species-specific information channel – with high signal-to-noise ratio – that is tuned for receiving and processing the electric images (see Glossary) carried by self-generated fields and those of conspecifics.

Just as bones and joints are essential for transmitting muscle actions, so the conductivity of the body links the EO output with the water, and the control of the fish's body movements is used to shape the self- and allo-generated fields (Fig. 2). Thus, the body of the moving fish can be considered as a self-controlled filtering device used to: (1) orient the field in order to polarize objects at the same time as orienting the electrosensory receptors to receive a self-generated 'electric image' of the nearby environment, and (2) elicit and receive allo-generated images. Consequently, one can decompose the electromotor act into two inextricable stages: (1) electrogenesis, defined as the action of transforming the fish's body into an electric source generating a stereotyped electromotive force pattern, and (2) imaging, which is the circumstantial result of the action depending on the impedance of the surroundings.

Electrogenesis

Electrogenesis by weakly electric fish involves precise coordination of a range of spatio-temporal processes at multiple levels of organization, from the sub-cellular level within the electrocytes to the whole-organism level, where the activities of multiple electrocytes are added. The electrocytes often show different excitable properties in the same species, and the electric fields produced are of different shapes and sizes. The currents generated by the electrocytes flow along the EO and close the circuit through the rest of fish's tissues and water. Thus, each deflection (see Glossary) of the EOD and the associated electric field results from the sum of currents generated at similarly oriented patches of membrane (Bennett and Grundfest, 1959). Some EOD deflections originate in the synaptic activation of a patch of membrane. Other deflections result from the propagation of a synaptically evoked action potential along the membrane until it reaches the opposite side of the

Glossary

Action current

In electrocytes, action potentials cause asymmetric depolarization of the membrane, which causes a flow of action currents. Their summation produces the electric organ discharge (EOD).

Apposition and superposition images

In apposition images, the juxtaposed points of the object are represented as juxtaposed in the image, creating a point-to-point map maintaining topographic adjacency. By contrast, in superposition images, every single point of the object of interest is represented by many points of the image and the representation of juxtaposed points partially overlaps.

Deflection

A change in sign or an abrupt change in slope of the time course of a signal.

Delay line

A mechanism for synchronizing the timing of events that are triggered by the same stimulus but have different processing times.

Dipole and multipole

Models used to represent electric sources. A dipole is represented by a single vector having magnitude and direction; a multipole is represented by various vectors in different orientations.

Electric field

A vector entity representing the strength and direction of the force exerted by an electric source on a unit of charge. Locally, in water it is the product of current density and water conductivity, and decays with distance to the source approximately following a power law depending on the presence of objects and borders.

Electric image

A physical stimulus pattern consisting of the electric field perpendicular to a given surface where an array of electric sensors is displayed. In the case of a fish, this surface is the skin. Self-generated electric images are those carried by the electric field generated by the receiver, whereas allo-generated images are those carried by the electric fields generated by other animals.

Electric impedance

A measure of the intrinsic electric properties of a piece of matter. It is represented by a scalar, vector or tensor magnitude that quantifies the opposition of matter to time-varying electric current. A piece of matter that has the ability to accumulate charge has capacitive impedance. A piece of matter that opposes the flow of current without accumulating charge has resistive impedance. Most objects have both resistive and capacitive components and therefore impedance is often represented by complex numbers.

Electrosensory fovea (fovea)

A mobile region of the sensory mosaic in which the density and variety of the receptor units and central representation in the nervous system are the largest; foveation arises from the ability of the animal to control the region of the image that is spatially sampled.

End plate potential

A change in transmembrane potential of an excitable syncytium in response to a chemical synaptic stimulus.

Ephaptic coupling

An electric field generated by one or more cells stimulates one or more neighboring cells.

Jeffress' circuit

A neurocomputational model that explains how a neural system can register and analyze small differences in the arrival time of signals at two points of a sensory mosaic. This allows an animal to estimate the direction of the source generating the signal.

Nodes of Ranvier

Some neuron axons are wrapped by glial cells which form 'tubes'. Between these tubes are microscopic gaps – the nodes of Ranvier. Usually, the density of voltage-gated channels is largest at these sites, supporting the 'saltatory' conduction of action potentials from node to node.

Permittivity

A measure of the ability of an object to store charge or develop a non-homogeneous distribution of charge under an electric field. A material with high permittivity polarizes more in response to an applied electric field than a material with low permittivity, thereby storing more energy in the material.

Size principle

Henneman's size principle is the basis for size-ordered activation of motor units during movement. Smaller neurons are recruited first, then the intermediate and finally the largest neurons. This is because, in general, larger motoneurons require a larger amount of membrane charge to reach the firing threshold.

Topologically spherical/non-spherical

A shape is topologically spherical if it has a closed surface that, when it is inflated, becomes a sphere. By contrast, shapes that are not topologically spherical have closed complex surfaces, e.g. a doughnut (or toroid).

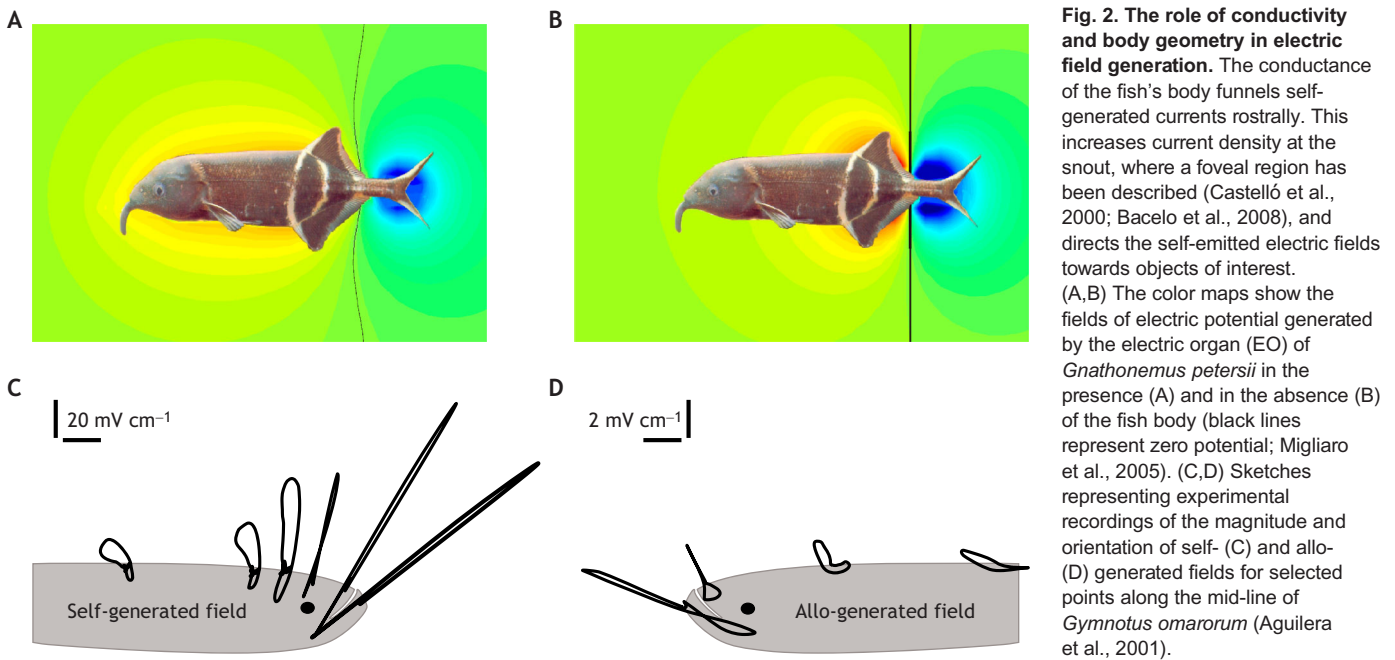
electrocyte. Finally, in most species, the local sum of the 'action currents' (see Glossary) generated at the caudal faces of small and densely packed neighboring electrocytes of the tail region stimulates the rostral membrane faces of the same and adjacent electrocytes (referred to as ephaptic coupling, see Glossary; Bell et al., 1976; Fig. 3A).

EOs are precise arrays of electrocytes

The EOs of the different electrogenic fish families are analogous structures serving a common function. EOs appeared several times in evolution and consequently show differences in their lineage, organization, location, innervation pattern and control mechanisms, reflecting their different developmental origins. Nonetheless, they show commonalities that exemplify how evolution converges on similar solutions to solve common problems. For example, in pulse Mormyroidea and Rajidae, the EOs are short and localized at the tail

region, whereas in the single species of wave Mormyroidea (*Gymnarchus niloticus*) and Gymnotiformes, the EOs extend across most of the length of the body. The EOs of Apterontidae consist of a complex plexus composed of modified axons of spinal electromotor neurons (Waxman et al., 1972) and exhibit neurogenic electrocytes (i.e. electrocytes that are derived from neural tissue) at the terminal portion of such axons. The EOs of the rest of the weakly electric fishes consist of connective tissue sleeves inside which syncytial excitable units of mesodermic or muscular lineage (myogenic electrocytes) are connected in series by a gelatinous connective tissue (Szabo, 1961; Trujillo-Cenóz and Echagüe, 1989; Gallant, 2019).

All electrocytes, whether neurogenic or myogenic, possess extensive excitable membranes, species-specific non-linear voltage-dependent channel repertoires and specifically located activation sites. Thus, while the contribution of each electrocyte to the EOD



depends on its shape, size, channel repertoire and activation mechanisms, the nature of the whole EOD depends on the diversity of electrocyte types, their distribution along the EO and the neural coordination mechanisms exhibited by each species (Box 1).

The repertoire and distribution of voltage channels in the electrocytes of different species are described more extensively elsewhere (Bennett, 1971; Sierra et al., 2005, 2007; Markham, 2013, 2019). Genome and transcriptome studies promise to rapidly enhance our knowledge of the genetic and evolutionary basis of electrocyte membrane properties (Zakon et al., 2006; Zakon, 2012; Gallant et al., 2014; Gallant, 2019). For example, one striking relevant discovery is the neofunctionalization of a voltage-gated Na^+ channel gene (Zakon, 2012). In separate fish lineages, a duplicate originating from a muscle-type Na^+ channel has been co-opted twice by novel myogenic EOs and once by a neurogenic EO (Zakon et al., 2006; Arnegard et al., 2010). In addition, advances in our understanding of the genetics of K^+ channels and the regulation of the co-variation of the Na^+ and K^+ electrocyte channel dynamics are contributing to our understanding of the shape and duration of electrocyte action potentials (McAnelly and Zakon, 2000; Swapna et al., 2018).

In pulse Mormyridae and the wave Gymnotiformes of the family Apterontotidae, electrocyte shape is a major factor determining their contribution to the EOD. The short EO of Mormyridae consists of convoluted, topologically non-spherical (see Glossary) electrocytes that are tightly stacked and identically oriented. The propagation of the activation along the complex membrane structure determines the characteristics of the species-specific EOD (Alves-Gomes and Hopkins, 1997; Hopkins, 1999; Sullivan et al., 2000; Gallant, 2019) (Box 1, panels A and B). Apterontotidae electrocytes (Box 1, panel C) consist of specializations of the terminal axon in which two 100 μm diameter swellings are separated by a thin 'hairpin' turn. Nodes of Ranvier (see Glossary) at the end of each swelling are less excitable (Box 1, panel C, top, green bands), resulting in decremental conduction of the action potential. The currents leaving through these passive nodes (Box 1, panel C, red and blue arrows) generate the head-positive and -negative deflections of the EOD waveform shown below (Box 1, panel C, red and blue waves; Bennett, 1971; Waxman et al., 1972).

In the remaining species, electrocytes are topologically spherical (see Glossary) and the location and timing of their activation by their synaptic contacts determine the time course of their contribution to the EOD. In wave species (including Sternopygidae, which are Gymnotiformes), *Gymnarchus niloticus*, some species of Gymnotidae (*Gymnotus cylindricus*, *Gymnotus obscurus*) and most Hypopomidae, electrocytes are innervated on their caudal face only (Bennett, 1971). The ways in which the rostral faces of singly innervated electrocytes are recruited is species dependent and diverse. The probability and timing of rostral face recruitment depends on membrane excitability (Bennett, 1971; Markham, 2013, 2019) and also on the excitatory effects of ephaptic currents generated by neighboring electrocytes (i.e. EO autoexcitability; Bell et al., 1976; Caputi et al., 1998b; Rodríguez-Cattáneo and Caputi, 2009; Rodríguez-Cattáneo et al., 2013).

During the process of EO auto-excitability, action currents synchronously elicited at the caudal electrocyte face are 'leakily' funneled along the EO and close the circuit through the surrounding tissue. A fraction of the action currents generated by each electrocyte are conducted along the EO. The conduction distance increases with the ratio between the sleeve and tissue resistance (i.e. the space constant of the sleeve; Fig. 3A). The sum of currents from neighboring electrocytes elicits a phase-locked activation of the opposite, non-innervated faces (Albe-Fessard and Buser, 1950). Thus, EO autoexcitability increases with electrocyte density. In some species, auto-excitability at the tail region is large enough to cause repeated activation of the rostral and caudal faces, thus generating multiple waves of activity (Rodríguez-Cattáneo et al., 2013; Waddell et al., 2016). Seasonal increases in water conductivity offer a parallel path for closing the circuit of ephaptic currents. Moreover, seasonal and sex-dependent modulation of electrocyte excitability facilitates the recruitment of rostral electrocyte faces in many pulse species of Gymnotiformes (Fig. 3B,C).

In most Gymnotidae and in Rhamphychtidae, electrocytes can be innervated on the rostral face, at the caudal face or on both faces. The coordinated activation of the synaptic activities of electrocytes with different innervation patterns allows them to contribute to the whole EOD with a variety of waveforms. Additionally, in these species,

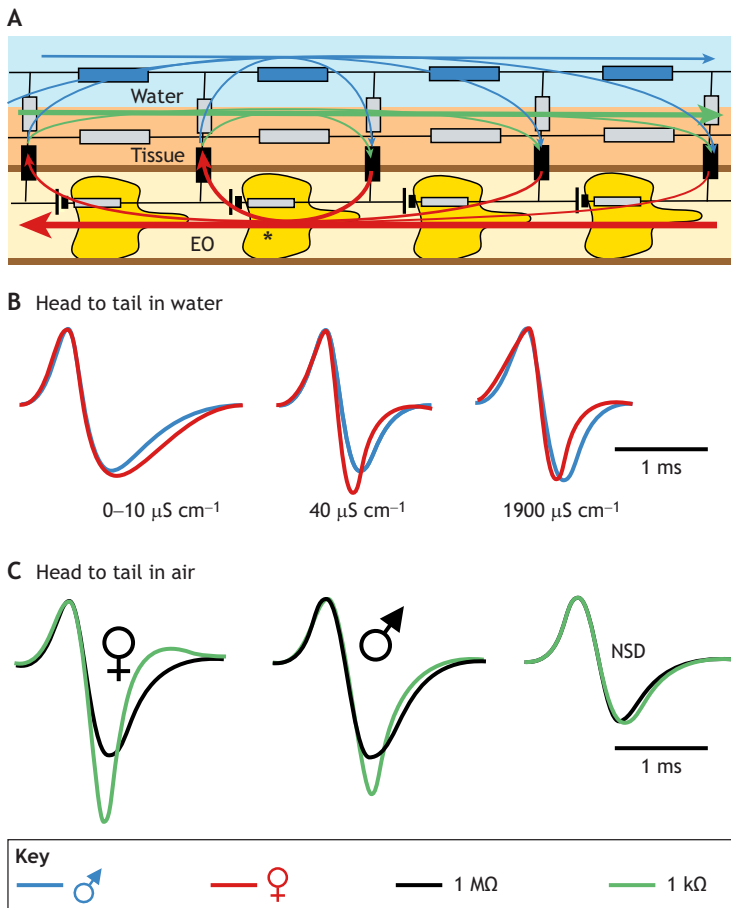


Fig. 3. Auto-excitability and its role in sex identification. In the genus *Brachyhyopomus*, seasonal modulation of electrocyte membrane excitability (Hagedorn and Carr, 1985) and the cooperative action of electrocytes (Caputi et al., 1998b) contribute to sex-dependent variation in the head-negative component of the EOD. (A) The diagram represents: (1) the flow of action currents (thin red arrows represent those generated by the electrocyte marked with an asterisk) generated at the innervated face of the electrocytes (yellow), (2) their summation with those generated by neighboring electrocytes (ephaptic currents; the thick red arrow represents the local sum of currents from many electrocytes along the EO) and (3) how these currents leak through the EO conductive sleeve (thick brown lines) and partially close the circuit (green and blue arrows). The sum of action currents generated by many electrocytes along the body tissue and water (orange and light blue shading) are represented by the long green and blue arrows, respectively. (B) Traces compare the effects of conductivity on the time course of the head-to-tail electric field of male (blue) and female (red) fish. (C) Traces show that increased ephaptic currents cause an increase in the head negative component when the head and tail of a fish otherwise maintained in the air are connected through a low value resistor (1 kW, green) in comparison to the head negative component observed when the value of such a resistor was high (1 MW, black). This only occurs in sexually differentiated fish (female and male, versus non-sexually differentiated, NSD), confirming the sexually dependent change in membrane excitability (Caputi, 1999).

different patterns of electrocyte innervation occur at different regions of the EO; their coordinated activity gives rise to very complex EODs (Caputi, 1999; Rodríguez-Cattáneo et al., 2013; Waddell et al., 2016).

Finally it should be mentioned that some Hypopomidae species – for example, *Steatogenis elecgas* (Hypopomidae; Bennett, 1971) – show a second EO at the head region. Furthermore, a whole clade of small-sized *Gymnotus*, including *G. javary* and *G. coropinae*, show a head-specific expansion of the EO (Castelló et al., 2009; Rodríguez-Cattáneo et al., 2013).

Species-specific coordination of the EOD time course

In almost all species of weakly electric fish, inputs of the spinal electromotor neurons controlling the EO originate from a command nucleus, the output of which is followed one-to-one by the EOD. The command nucleus stimulates a medullary relay nucleus whose axons project to spinal electromotor neurons, which in turn activate the electrocytes (Bennett, 1971; Dye and Meyer, 1986; Bass, 1986; Caputi et al., 2005; Caputi, 2011).

Mormyridae and Rajidae emit electric pulses at irregular intervals that depend on the integration of descending signals from the command nuclei (Bennett et al., 1967; Grant et al., 1999). These species have a compact EO composed of very similar electrocytes located at a similar conduction distance from the command nucleus; this facilitates the synchronous activation of all the electrocytes.

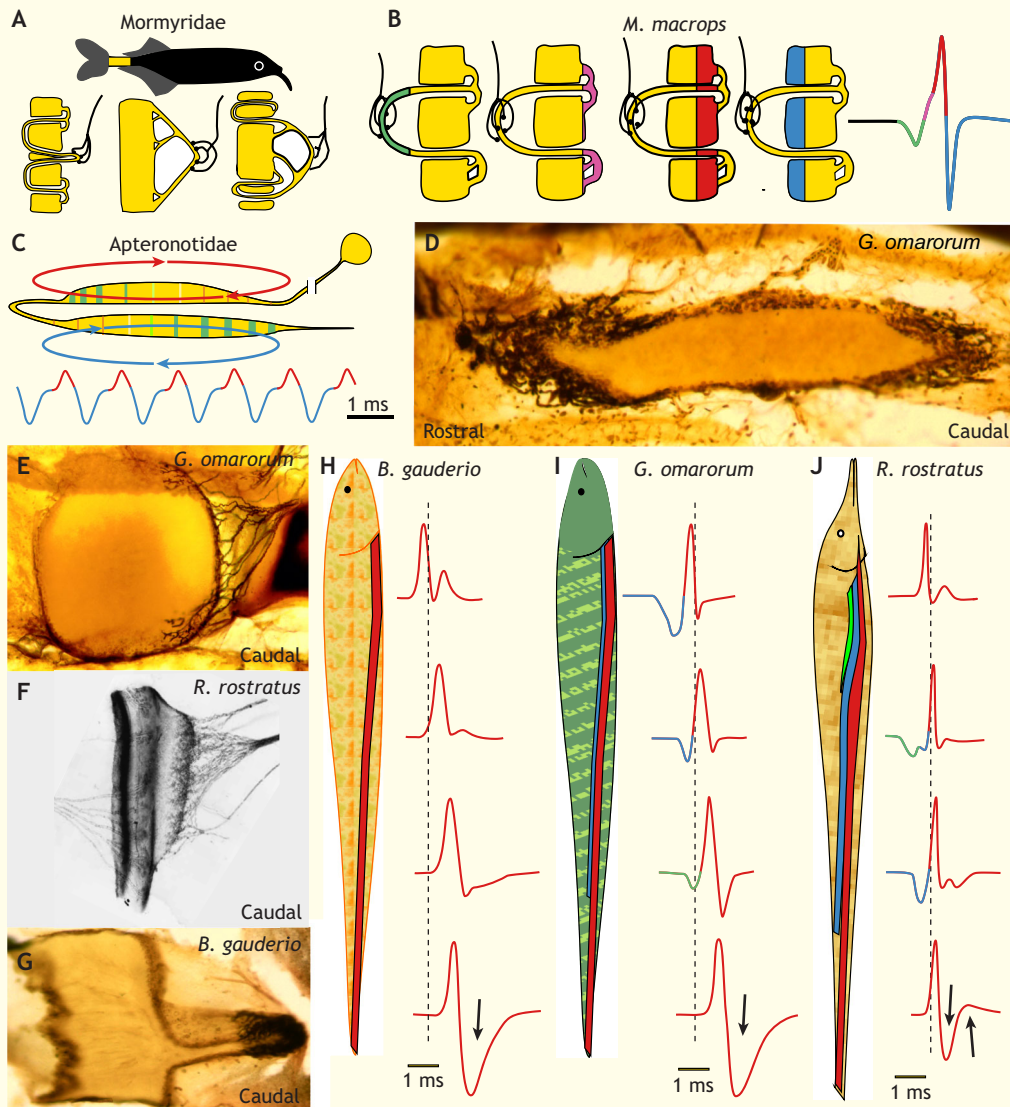
In Apterontidae, small rhythm-setting and large relay neurons are intermingled within the premotor command nucleus (Elekes and Szabo, 1985; Moortgat et al., 2000). In apterontids, all neurons of the electromotor system are also able to spontaneously fire action

potentials at a regular frequency (i.e. they display pacemaker properties). Bulbar command neurons fire at the highest frequency – driving the EOD above 2000 Hz in some species – which is the highest frequency of neural firing observed in nature. Relay neurons send thick, fast-conducting fibers that phase lock the intrinsic rhythmic firing of electromotor neurons, whose axonal terminal specializations function as electrocytes (Bennett, 1971; Smith, 2013). The successive activation of the arms of the hairpin-shaped electrocytes (Box 1, panel C) determines the biphasic discharge whose duration matches the firing interval of the command pacemaker nucleus (Waxman et al., 1972).

In the remaining species, including the families Gymnarchidae, Sternopygidae and all pulse Gymnotiformes, the EOs stretch over 90% of the length of the body; consequently, the distance from the electrocytes to the pacemaker nucleus increases along the body. To produce a stereotyped EOD output waveform, the coordinated activity of about a thousand similarly oriented electrocytes in these species is required. However, the electrocytes are located at varying distances (up to 30 cm) from the pacemaker. The mechanism by which coordination is achieved has been studied in *Gymnotus omarorum* and *Brachyhyopomus gauderio*. Synchrony results from the combination of three ‘delay-line’ mechanisms (see Glossary): (1) differential conduction velocities increase the conduction time of the shorter fibers of the bulbo-spinal tract (Lorenzo et al., 1990, 1993); (2) the farthest electromotor neurons are activated with shorter latency by the convergence of more synchronized inputs (Caputi and Trujillo-Cenóz, 1994; Caputi and Aguilera, 1996); and (3) differential conduction lengths increase the conduction time of electromotor neuron axons projecting to more rostral electrocytes (Bennett, 1971;

Box 1. Diversity of electrogenic mechanisms

Electrocytes of different species have different shapes and may be innervated either at a single face or on opposite faces. For example, pulse mormyrid species have a short electric organ (EO) (A) and electrocytes with very complex shapes (shown as schematic sagittal sections). The progress of an action potential along the network of stalks connecting different regions of the electrocyte generates longitudinal currents of different intensity and direction that are reflected in the head-to-tail deflections of the electric organ discharge (EOD) (shown in B for *Myomyrus macrops*; colors indicate the correspondence between active regions and EOD deflections; modified from Sullivan et al., 2000). (C) Aptereronotidae show specializations of the terminal axon forming a ‘hairpin’-shaped electrocyte. The two arms of this structure generate the head-positive (red arrows) and head-negative (blue arrows) currents and the corresponding deflections of the EOD waveform. (D–G) Gymnarchidae and the remaining species of Gymnotiformes have spherical myogenic electrocytes: the time course of their contribution depends on the innervation sites and the distribution of the channel repertoire. All Gymnotiformes have a long EO. In the tail region, electrocytes are small and only caudally innervated, as shown here for *Gymnotus omarorum* (E) and *Brachyhyppopomus gauderio* (G). In the rest of the body, the innervation pattern varies according to species. Gymnotidae and Rhamphychthyidae have doubly innervated electrocytes (D,F). *Rhamphychthys* also has only rostrally innervated electrocytes in the abdominal region. H–J correlate the distribution of different electrocyte types along the EO with the contribution of their differently innervated faces to the time course of EODs generated in different body regions (red, blue and green bands and traces correspond to caudally, doubly and rostrally innervated electrocytes). Note that in all three species, the last negative component (downward arrows) – and, in *R. rostratus*, the second positive rebound (upward arrow) – are generated by EO auto-excitability (D–J modified from Caputi, 1999, and Crampton et al., 2013).



Trujillo-Cenóz et al., 1984; Caputi and Trujillo-Cenóz, 1994). This results in a traveling wave sweeping the body at 400 m s^{-1} (Caputi, 1999). Despite this speed, the delay between the activities of equally innervated faces of the electrocytes at the abdominal and caudal portions of the EO is a large fraction of the duration of an action potential. This delay increases the complexity of the electric field in

pulse Gymnotiformes (Box 1, panels H–J) and in some wave emitters belonging to Sternopygidae and Gymnarchidae, where a phase opposition between the EOD components generated at the more rostral and more caudal regions of the fish’s body may be observed.

In addition, in most species of Rhamphychthyidae and Gymnotidae, the EOs are composed of various types of

electrocytes (Box 1, panels D–F), differing in their innervation pattern, size and membrane properties. In these species, electrocytes of different innervation types (which consequently contribute to the EOD with currents of different time courses) are contained in different tubes in the same body region. Each electrocyte contributes to the EOD with either a monophasic discharge, corresponding to the activation of a single face, or a multiphasic discharge, corresponding to the sequential activation of differently oriented electrocyte regions. Moreover, the activity of different electrocytes is driven by cholinergic synapses that may evoke either smooth and long end plate potentials (see Glossary; Lorenzo et al., 1988; Sierra, 2007) or sharp and brief action potentials, according to their size and channel repertoires (Bennett and Grundfest, 1959; Macadar et al., 1989). In these electrocytes, current direction alternates between caudal to rostral and vice versa owing to a precise sequence of activation of caudally and rostrally oriented faces. This is achieved by two mechanisms, depending on whether the electrocyte is doubly (Box 1, panels D and F) or singly innervated (Box 1, panels E and G; Trujillo-Cenóz and Echagüe, 1989; Macadar et al., 1989; Caputi et al., 1989).

Singly innervated electrocytes contribute to the EOD with a mono- or bi-phasic discharge, the latter of which is achieved by EO auto-excitability (Albe-Fessard and Buser, 1950; Bell et al., 1976; Caputi et al., 1998b; Rodríguez-Cattáneo and Caputi, 2009) (Fig. 3A). The probability of recruitment and synchronization of neighboring electrocytes by these ephaptic mechanisms increases with the space constant of the connective sleeve and also with the progressive decrease in electrocyte size and inter-electrocyte distance from abdominal to tail regions. This explains the increase along the EO of the final EOD wave observed in all pulse Gymnotiformes (Caputi et al., 1989, 1994, 1998a,b) (Box 1, panels H–J).

Doubly innervated electrocytes in Gymnotidae (Box 1, panel D) and Rhamphichthyidae (Box 1, panel F) contribute tri- and tetra-phasic discharges, resulting from the combination of a precise sequence of synaptic activation. In these electrocytes, the synchronized synaptic input to identically oriented faces causes the initial EOD deflection. This is followed by a phase-locked synaptic activation of opposite faces and finally by the successive activation of opposite faces in a ‘reverberating’ way, implemented by EO auto-excitability.

In pulse Gymnotiformes, different regions of the EO contribute with waveforms of different time course to the whole EOD. In *Brachyhyopomus gauderio*, the different regional contributions mainly depend on electrocyte size and density and their coordination mechanisms. The red band in Box 1, panel H, represents the location of the caudally singly innervated electrocytes shown in Box 1, panel G, which are present all along the EO. In *Gymnotus omarorum* and *Rhamphychtis rostratum*, there are both doubly innervated electrocytes (Box 1, panels D and F; blue bands in panels I and J) and singly innervated electrocytes (caudally innervated electrocytes are located along the red band in Box 1, panels I and J; rostrally innervated electrocytes are located along the green band in panel J), which are specifically located at different regions of the EO and contribute with different waveforms to the whole EOD (Caputi et al., 1989, 1994, 1998a,b). The present hypothesis regarding control of the EOD time course in *Gymnotus omarorum* is depicted in Box 2.

What are weak EODs for?

EODs of weakly electric fish are key for three functions. In Mormyroidea and Gymnotiformes, (1) they carry signals informing the fish about nearby objects, (2) they are signs recognized by other fish and (3) they are symbols of a communication system. Each of

these functions is discussed in more detail below. In Rajidae, EODs are emitted rarely in the absence of stimuli generated by other fish (Kramer, 1996). In these species, it is thought that the main role of EODs is to convey sexual calls (Sisneros and Tricas, 2002).

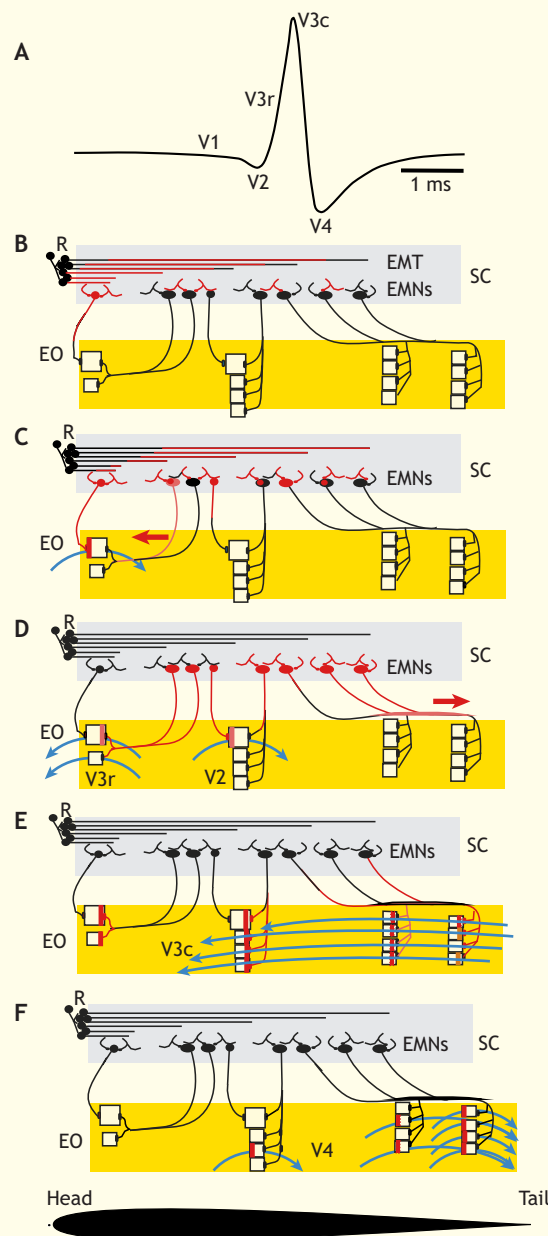
The EOD mediates ‘electric touch’

Analogous to light in vision, the EOD-associated field is the signal carrier that stimulates the electroreceptive mosaic of electric fish. However, unlike the visual sense, a self-generated pattern of transcutaneous current density is generated independently of the presence of any object (see discussion on different active systems in Box 3). When objects are present, the self-generated field causes a charge redistribution in the objects according to the difference in permittivity (see Glossary) between the object and the water (Lissmann and Machin, 1958; Caputi and Budelli, 2006; Nelson and MacIver, 2006; Benda, 2020). Polarized objects behave as virtual electric sources, so-called ‘stamps of the objects in the electric field’, just as the sun-illuminated moon behaves as a luminous object (Caputi and Budelli, 2006). For simple objects relatively far from the body, such a virtual source can be represented by two components: the local polarizing field and the object’s ‘imprimence’ (Lissmann and Machin, 1958). The EOD field provides an ego-centered perceptual coordinate system that moves with the fish, relaying upon the moving body the information about the object’s distance, altitude and azimuth. The imprimence is a summary of the object’s characteristics, including its material (i.e. impedance relative to the water, which causes changes in the stimulus time course) and geometry (i.e. size and shape; Rasnow, 1994, 1996; Pereira and Caputi, 2010; Boulrier, 2013; Ammari et al., 2013). All this information is integrated in the object’s ‘stamp’. According to this concept, the field that stimulates the skin (the ‘re-afferent signal’) can be considered as the sum of two fields: the first directly generated by the fish EOD that exists in the absence of the object, and the second indirectly generated by the fish EOD, virtually generated by the object stamp (the ‘ex-afferent signal’; von Holst and Mittelstaedt, 1969; Fig. 4). The electrosensory system of Mormyroidea and Gymnotiformes is organized to extract the ex-afferent information that represents the object and is contained in the re-afferent image projected on the skin. The geometry and location of the object appear to be encoded by the spatial pattern of the image (Rasnow, 1996; Caputi et al., 1998a,b; Budelli and Caputi, 2000) (Fig. 4), whereas the object’s material appears to be encoded in the time course of local stimuli (Fig. 4 and Box 4).

To understand how electric fish evaluate an object’s geometry and location, one must take into account that unlike the apposition images (see Glossary) formed in the vertebrate retina, the electrosensory mosaic receives superposition images (see Glossary). Signals originating from every point in space project with different weights onto different points on the skin and, consequently, each electroreceptor is stimulated by the weighted sum of the signals generated at different points in the surrounding space (Caputi and Budelli, 2006; Pereira and Caputi, 2010) (Fig. 4). These relative weights show large variations when the objects are close by, causing the largest increments in electric images at the region of the skin closest to the object. In addition, objects of different shapes and size located at about the same site relative to the fish’s body generate images of different profiles. In this case, the stamp-generated field resembles the field of a multipole in which components project with different weight onto different regions of the skin. By contrast, when the fields of objects that are far away reach the skin, they resemble that of a single dipole: distant objects have similar image profiles varying by their location. Consequently,

Box 2. From a single impulse to a fixed action pattern

(A) The EOD of *Gymnotus omarorum* is complex and has four main components (V1–V4), which have different origins along the EO. (B) Action potentials originate at the relay nucleus (R) somatas and run along axons of different diameter and length, forming an electromotor tract (EMT). Action potentials travel along the spinal cord (gray, SC) at different velocities (active regions in red). Because the shorter fibers are slower, the mean speed of the fiber population increases along the spinal cord, reducing the difference in timing at which signals reach the electromotor neurons (EMNs). (C) The first activated EMN pool projects onto the rostral face of the abdominal electrocytes (white boxes) where the EMNs provoke end plate potentials at about 2 ms after the relay, causing a long-lasting head-negative component (V1). Simultaneously, the volley reaches the central portion of the cord, where it recruits large EMNs giving origin to a recurrent nerve running from the caudal to rostral direction (red arrow points towards the head) that, after adding an extra delay, (D) elicits action potentials at the caudal face of abdominal electrocytes, producing a sharp positive peak in the EOD (V3r) at about 3.5 ms. At the central region of the body, the rostral and caudal faces are innervated by the axons of two EMN pools with small and large somatas, respectively. Small EMNs projecting onto the rostral faces are recruited first, according to the ‘size principle’ (see Glossary; Henneman, 1957); they activate the rostral faces of the electrocytes of the superior tube, causing an early sharp head-negative component (V2) at the same time as V3r. Large EMNs lying on the centro-caudal quarter of the cord project onto the caudal regions of the central electrocytes and – through a thick antecurrent nerve (thick red line) – onto the caudal EO, where a large number of caudally innervated electrocytes are densely stacked (arrow points towards the tail) (arrow points towards the tail). (E,F) At about 4.1 ms after the activation of the relay nucleus, this projection creates a biphasic head-positive/negative response at the tail (V3c–V4). The rostro-caudal reduction in electrocyte size and inter-electrocyte distance progressively improves the efficacy of auto-excitability, causing an exponential growth of the late negative component generated at rostral faces (V4, see Box 1, panels H–J, arrows) – their contribution is minimal at the large separated abdominal electrocytes and maximal at the small caudal electrocytes. Figure modified from Caputi (1999).



Box 3. What type of active sense is electroreception?

The term 're-afference' (von Holst and Mittlesteadt, 1969) was coined to note that most sensory images contain information generated by both animal actions and external sources. Information from external objects is termed 'ex-afference'. The expression 'active sense' was introduced to denominate one form of re-afference in which the animal takes an active role in perception through the self-generation of the sensory signal carrier (for example, in echolocation and active electroreception). However, this is not the only way in which animals generate re-afference (Caputi, 2004). Animals may also alter sensory images by changing the position of their sensory mosaic relative to the object of interest, by filtering incoming signals using pre-receptor mechanisms (e.g. orienting the ears, the eyes or the olfactory/electroreceptive antennae) or by altering the responsiveness of the receptors (e.g. some sensory receptor organs as hair cells in the cochlea and lateral line, and the tension of muscle spindles are under efferent control, changing their gain). To discriminate between active-sensing forms, the prefixes 'homeo-' and 'allo-' were introduced (Zweifel and Hartmann, 2020). In allo-active senses, the receiver acts on the afferences using a type of energy that differs from that of the carrier (for example, mechanical versus light, as in vision). In homeo-active senses, the receiver acts on the afferences and on the environment using the same type of energy (for example, in touch, mechanical energy is used as a carrier to apply the necessary pressure to stimulate the receptors and also to change the point of view when the hand adapts to the object and moves the fingers to evaluate shape). Active electroreception shows that homeo- and allo-active concepts are not mutually exclusive. Object polarization is carried out combining different energy types because the electromotor and skeletomotor systems act separately but synergistically to generate an ego-centered 'electrosensory bubble' that is oriented to optimize the polarization of nearby objects. On the sensory side, the time course of the self-generated polarizing field optimally matches electroreceptor responsiveness (Hopkins, 1976; Caputi and Aguilera, 2019), creating a semi-private channel with a high signal-to-noise ratio while an 'electrosensory fovea' positioned by the skeletomotor system is used for tracking and exploring objects.

the stimulus image of distant objects is of low intensity, broad and of low contrast (Rasnow, 1996; Sicardi et al., 2000). Object discrimination from the background vanishes at a distance of about

one-half of the fish length, but the limits of the 'sensory bubble' moving with the fish are not clear: this can be compared to a human seeing through the fog (Pereira et al., 2012). Furthermore, images of more than one object soon become fused, reaching the limit of 'electric acuity' at about one-half of the distance corresponding to the object's detection threshold (Pereira et al., 2012).

Because the net current through the skin is null (Lagrange, 1773), electrosensory images consist of regions of skin where the current density increases at the expense of other regions, where it decreases (Caputi et al., 1998a; Pereira and Caputi, 2010). Signal projection weights depend on the ratio between the distance to the object and the curvature radius of the skin. When this ratio is small, the images of nearby objects represented here have a center-surround 'Mexican hat' profile (i.e. with a broad, low brim and a high central peak; Fig. 4). This profile indicates the presence of a filter commonly used for border detection in image processing (Marr and Hildreth, 1980). Most animals implement this filter at the neural level using a mechanism called lateral inhibition, but in electric fish, this filtering occurs twice – firstly at the physical image-generation stage (i.e. a pre-receptor mechanism) and secondly in the early sensory centers.

On the side of the fish, the Mexican hat filtering profile is observed. However, in front of the fish, large objects globally alter the flow of currents, causing a bell-shaped increment (those more conductive than water increase current flow and those less conductive decrease it), the spatial profile of which does not depend on the shape of the object but on the shape of the snout (Fig. 4). In contrast, small objects close to the skin generate a Mexican hat profile. In this case, there is also a reciprocal polarization between the fish's body and the object. This causes a juxta-cutaneous fringe of 'hypersensitivity' that allows the fish to evaluate the 'electric texture' of object surfaces (Caputi et al., 2011, 2013). This, and the increase in current density at the perial region due to body funneling, increases the contrast of objects at the region where electroreceptor organs have the highest density and functional variety (this is the so-called 'electrosensory fovea'; see Glossary; Castelló et al., 2000; Bacelo et al., 2008). Placing this fovea at the large curvature regions appears to be an optimal design for evaluating whether an object will fit into the mouth (Movie 2).

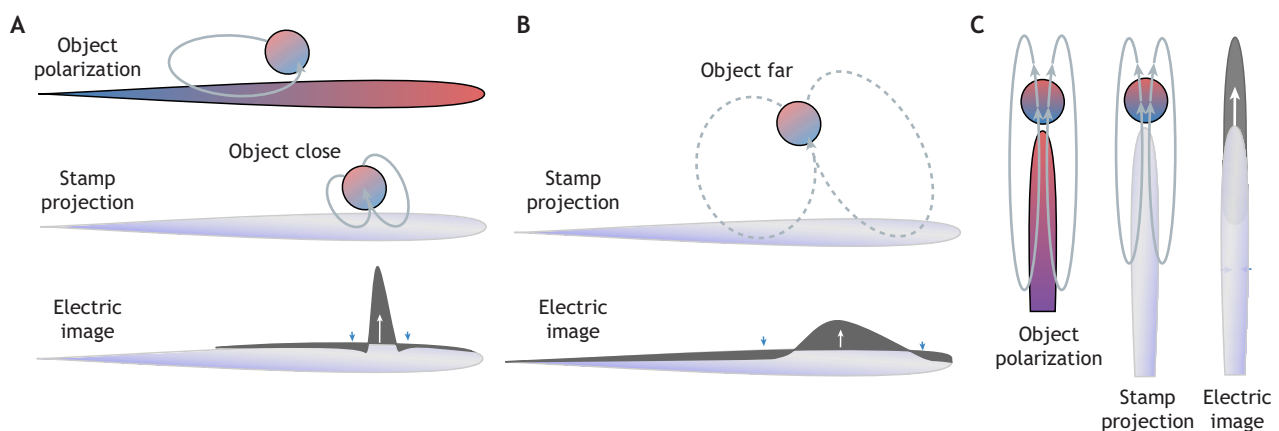
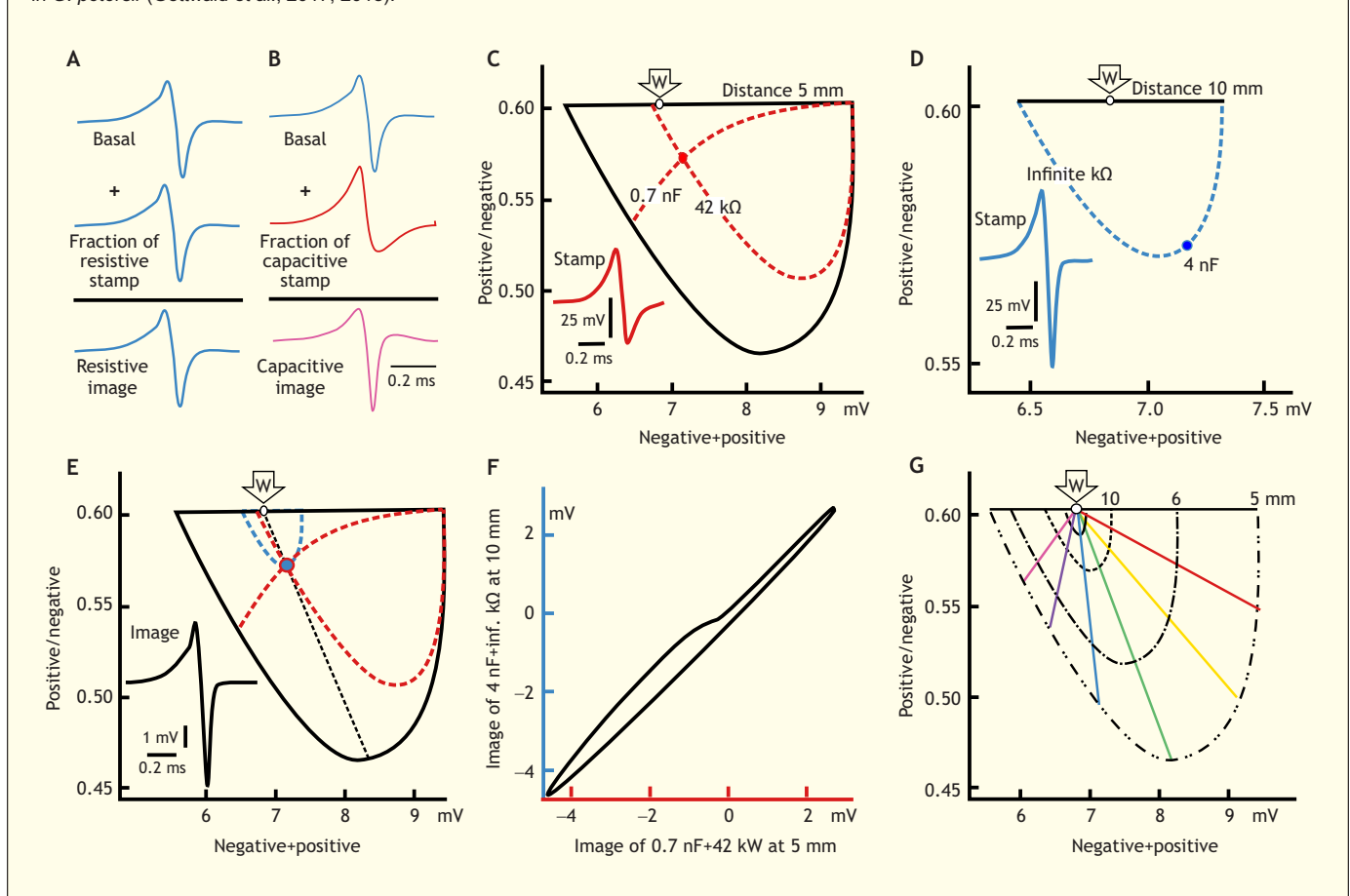


Fig. 4. Image formation and the peripheral Mexican hat filter. Objects are polarized by the electric fields generated by the fish (red and blue regions within the object). As a result of polarization, objects behave as virtual sources, projecting their images onto the fish's body (gray arrows). This causes electric images consisting of patterns of local changes in transcutaneous current (represented in the sketches by the gray shading). Objects that are more conductive than water facilitate the current flow and increase the current on the region of the skin closest to their surface (white arrows in all panels). This increase is equal to the total current decrease across the rest of the skin (blue arrows in all panels). (A) As a result of this process, on the side of the fish, the current stimulating the skin follows a 'Mexican hat' profile with a narrow, high-current 'top' surrounded by a wide, shallow 'brim'. (B) Increasing the distance to the object causes a reduction in polarization and a further reduction in the current reaching the fish and also increases the width of the 'top'. (C) In front of the fish, the presence of large objects only increases the rostral flow of current and the surround effect is negligible. Objects less conductive than water cause the opposite effect (not represented here).

Box 4. Electric color

In vision, color results from the evaluation of different wavelength ranges by different receptor types. *Gnathonemus petersii* has two electroreceptor types, one that responds only to the stimulus amplitude and the other that responds only to its time course (Bell, 1990; von der Emde and Bleckmann, 1992, 1997). Theoretical analysis of the imaging process suggested that *G. petersii* is able to evaluate the 'electric color' of objects (Budelli and Caputi, 2000). When the object has capacitive components, the time course of the stimulus image (i.e. the re-afference), consisting of the sum of a field proportional to the stamp projected on the skin (i.e. the ex-afference) and the basal field, depends heavily on object impedance (A,B; von der Emde, 1990). Considering a space in which the ratio of the positive and negative peaks of the stimulus are plotted against their sum (C–E, where horizontal lines correspond to pure resistive objects and U-shaped lines to pure capacitive objects), Budelli and Caputi (2000) proposed that the slope of the line passing through the points corresponding to the object (red in C, blue in D) and a point corresponding to the absence of objects, marked by the arrow labeled W (water alone) is an impedance-related, distance-invariant parameter similar to color. In C and E, the red dashed lines correspond to all objects having either the same capacitance (0.7 nF) or the same resistance (43 k Ω), and their intersection (red points) corresponds to the object. The blue points in D and E correspond to a pure capacitive object (4 nF). As object distance increases from 5 mm (C) to 10 mm (D), the same point (blue encircled by red point in E) in the space corresponds to different objects (compare red and blue lines in E). When the same object changes position, the representative point moves along the dotted line (the object's 'color line'). Although time courses of the stamps differ (insets in C–E), the stimulus on the skin is similar (F). According to this view, all objects represented by the same line are practically indistinguishable by the fish, so they have the same 'electric color' (G). This was confirmed behaviorally in *G. petersii* (Gottwald et al., 2017, 2018).



Object impedance is encoded as changes in the time course of the local stimuli over the skin. In vision or audition, the frequencies of the stimulating spectra are combined in a precise way, giving origin to the idea of object 'qualia'. For example, the same color or chord can be generated by the combination of different frequencies in a family of well-defined proportions, and the set of stimuli generating the same qualitative sensation can be considered equivalent. This provides the animal with the ability to qualitatively classify objects according to their color or the sounds according to their timbre. In *Gnathonemus petersii* and *Gymnotus omarorum*, families of time courses of a local stimulus serve to encode object impedance, providing these fish with a sort of 'electric color' (Budelli and Caputi, 2000). As explained in Box 4, the stimulus space of these pulse fishes can be partitioned into families of

stimuli defined as those having the same relationship between the peak-to-peak amplitude and the ratio of the deflections (von der Emde and Ronacher, 1994; Aguilera and Caputi, 2003; Gottwald et al., 2017, 2018). As in other senses, encoding of qualitative aspects is based on the presence of two types of electroreceptors with differential sensitivity to changes in amplitude and waveform at the foveal and perifoveal regions (von der Emde and Bleckmann, 1992, 1997; Rodríguez-Cattáneo et al., 2017; Caputi and Aguilera, 2019). Interestingly, qualia discrimination is not only used for evaluation of object impedance. The electric color of the images generated by the EOD of other fish is also used to discriminate conspecifics from allo-specifics and male from female conspecifics (Hopkins and Bass, 1981; Waddell and Caputi, 2020) (Movie 3).

Finally, there is an important dynamic aspect to address (see also [Box 3](#)). In most species of weakly electric fish, the EO is not present in the head region; consequently, current leaves the snout and spreads out in a cone within which the time course of the polarizing field is relatively constant, and its amplitude and orientation are site specific (Caputi and Aguilera, 2020). The fish can orient this ‘foveal field’ towards objects of interest, using the snout to direct a ‘polarizing current beam’, simultaneously orienting the fovea to optimize reception of the electric image (Caputi and Aguilera, 2020) ([Fig. 2](#)). The fish can then orient its head (and, in *Gnathonemus petersii*, a chin appendage; Bacelo et al., 2008; Amey-Özel et al., 2015) towards objects of interest. This enhances image resolution by both increasing the object’s stamp and allowing the fish to receive the stamp-generated field at the most dense and qualitatively rich area of the sensory mosaic (Caputi et al., 2013; Caputi and Aguilera, 2020). Foveal movement, exploring an object’s surface (Toerring and Moller, 1984; Nelson and MacIver, 1999) ([Movie 2](#)), combined with sensory adaptation mechanisms enhancing transient changes in the re-afferent signals (Bell et al., 1993, 1997; Caputi et al., 2023), improve the evaluation of electric texture, just as fingertip stroking movements do when humans evaluate tactile texture (Caputi et al., 2013; Rodríguez-Cattáneo et al., 2020) ([Movie 2](#)). Consequently, within the ‘electrosensory bubble’ there are two electrosensory receptive fields: one a peripheral, omnidirectional field (Snyder et al., 2007) adapted for object detection and the other a foveal field adapted for close object examination (Caputi and Aguilera, 2020).

EODs as signs of species, sex and location

A sign is an event whose occurrence indicates the probable occurrence of something else. Just as a bark is a sign of a dog’s presence and location, an allo-generated EOD waveform is a sign of the presence, identity and location of a nearby sympatric individual. However, just as a barking dog may interfere with signal perception when one is listening to music, a fish close by may interfere with active electrolocation. This trade-off between signature and interference is solved in different ways by different taxa.

Pulse Mormyridae distinguish allo-generated stimuli from self-generated input through the use of an EOD command-driven inhibitory corollary discharge that separates these stimuli to distinct processing pathways. There is a dedicated sensory path for receiving allo-generated signals (Bell and Grant, 1989); in this pathway, the corollary discharge blocks self-generated sensory inputs in the first processing relay in the brain, eliminating self-interference (Bell and Grant, 1989). By contrast, in the dedicated sensory path for active electroreception, the corollary discharge gates the signals, letting in those generated by the self-generated EOD (Bell, 1989). Pulse Gymnotiformes, which produce electric signals in a regular rhythm, show fast and transient increases in EOD frequency when the EOD of another fish precedes or coincides with the self-generated EOD, thus reducing the probability of future coincidence (Westby, 1975).

Both Mormyroidea and Gymnotiformes have evolved a fast electrosensory path that responds with a single spike to allo-generated EODs (Hopkins, 1986; Castelló et al., 2008; Carlson, 2019). The difference in latency between primary afferent spikes generated on different sides of the fish informs the fish of the orientation of the field emitted by a conspecific. These signals are analyzed in both cases by a Jeffress’ circuit (see Glossary), similar to that observed in the auditory systems of birds and mammals (Carr, 1993). Consistent with this ability to detect field orientation, these fish have an electrostatic reaction – they align their body with the field orientation, swimming along the field lines (Schluger and

Hopkins, 1987; Shieh et al., 1996; Hopkins, 2005; Waddell and Caputi, 2020) ([Movie 3](#)). This side-to-side orientation of the body to the stimulus is perhaps analogous to the way in which humans orient their head toward an interlocutor during verbal communication. Experiments using constant field stimulation indicate that the side-to-side gradients caused by the disparity of the fish’s body and field angle, and the gradient of the time derivative of the stimulus at the head region (which is a cue for identity and approaching side) are sufficient to evoke the electrostatic response in pulse Gymnotiformes (Waddell and Caputi, 2021), although several other models have been proposed (Schluger and Hopkins, 1987; Hopkins, 2005) and have been tested in artificial devices (Boyer et al., 2013).

In pulse teleostei, species- and sex-specific EOD time courses let other fish know the identity of the emitter. Playback of synthetic EOD series using either random sequences or phase-locked stimuli showed the importance of EOD time course rather than the power spectral density or the timing pattern to cue species and sex recognition of a distant emitter (Hopkins and Bass, 1981; Bass and Hopkins, 1983; Waddell and Caputi, 2020). In addition, when pulse gymnotiforms are exposed simultaneously to two playback time courses, they are attracted to the source better representing the same species and the opposite sex (Waddell and Caputi, 2020, 2021).

In the case of wave fish, amplitude modulations of the EOD have a beat frequency equal to the difference between the two EOD frequencies. When fish move relative to one another, or there is more than one fish, one can observe slow and less predictable ‘envelopes’ consisting of variation in the degree of amplitude modulation (Stamper et al., 2019; Benda, 2020). Central processing of EOD beats allow *Eigenmannia* (a gymnotiform; [Movie 1](#)) and *Gymnarchus* to avoid interference from conspecifics. These species have evolved a similar mechanism for jamming avoidance: they evaluate both the amplitude and phase of the temporospatial pattern of interference to identify whether their own EOD has greater or lesser frequency than the interfering signal (Watanabe and Takeda, 1963; Bullock et al., 1972; Heiligenberg, 1991; Kawasaki, 1993). This elicits jamming avoidance and socially evoked responses that consist of shifting their own EOD frequency either up or down, which increases the beat frequency sufficiently to reduce the interference pattern. Although much is known regarding the central processing of envelopes in Apterontidae (Metzen and Chacron, 2014, 2019), understanding the neuroethological meaning of these signals is a future challenge.

EODs as symbols of electrocommunication languages

Communication involves congruent changes in the behavior of two or more individuals coordinated by messages ciphered in a common code. EOD timing patterns and self-deformation of the species-specific EOD time courses appear to be symbols of a code that is currently only partially understood. Evidence for this are the ‘rasps’ and ‘chirps’ expressed by both Mormyridae and Gymnotiformes. These signals involve explosive and brief increases in EOD repetition rate, and often occur during courtship or aggressive encounters – they are discussed in more detail below.

More than 10 stereotyped timing patterns have been identified during courtship, foraging and aggressive interactions in mormyrids (Hopkins, 1988; Carlson, 2002; Arnegard and Carlson, 2005; Gebhardt et al., 2012; Carlson and Gallant, 2013; Worm et al., 2021). Amongst these, rasps are bursts of a few pulses separated by longer intervals. During courtship, male rasps are followed by a female response and vice versa (Hopkins, 1981). This ‘rasp matching’ suggests that a dialog is occurring between males and females (Wong and Hopkins, 2007). In pulse Gymnotiformes, chirps consist of rapid increases in the pacemaker activity that often

overwhelm the EOD coordination mechanisms, causing a reduction in amplitude and major changes in the time course of the field. Chirps appear to be the symbols that make up sex communication messages in *Brachyhypopomus* and social ranking signals in *Gymnotus* (Silva et al., 2007; Silva, 2002, 2019).

In wave fish, chirps consist of fast accelerations of the EOD. Chirps emitted under different circumstances vary in the onset, degree and duration of the frequency modulation. They are frequently ‘answered’ with other chirps during aggressive and sexual encounters, indicating that they are symbols of a communication code (Smith, 2013; Zupanc et al., 2006; Gama-Salgado and Zupanc, 2011). Chirps provoke fast changes in the amplitude and phase modulations of EODs that are well discriminated at the level of electroreceptors and in the central electrosensory lobe (Benda et al., 2005; Hupé et al., 2008), and there is indirect evidence that self- and allo-generated chirps are segregated by corollary discharge mechanisms at the preglomerular complex, which is the sole brainstem gate to the forebrain (Wallach et al., 2022). Wave fish also produce elaborate ‘electric serenades’ during courtship. In the presence of females, *Sternopygus* males display frequency increases and decreases that range from 50 to 150 Hz, and female *Eigenmannia* produce elaborate ‘warbling’ during courtship and spawning (Hopkins, 1988).

Future directions

Although the rapid rate of knowledge acquisition in this field makes it hard to predict the most fruitful research directions, here I suggest some areas that are likely to be particularly productive. Firstly, further research into the membrane channels expressed in electrocytes is likely to be beneficial. The astonishing neural firing properties of Apterontidae are conferred by a particular type of voltage-gated Na⁺ channel (Thompson et al., 2018); the acetylcholine receptor has also been widely studied in electrocytes (Keesey, 2005). Elucidating further details of the function of ionotropic and metabotropic membrane channels expressed in electromotor neurons and electrocytes would greatly contribute both to our understanding of the functional evolutionary adaptations of electric fish and to our knowledge of neuronal intrinsic and synaptic properties in general.

Weakly electric fish also offer a good opportunity to investigate the genetics and development of EODs. The species-specific EODs of mormyrids offer an opportunity to explore how functionally significant electrocyte membrane shapes are genetically encoded and developmentally expressed. In addition, although the EOD of the larvae of all pulse Gymnotiformes are monophasic (Pereira et al., 2007), some electrocytes of adult *Gymnotus* and *Rhamphichthys* are doubly innervated. What are the developmental processes underlying electromotor neuron differentiation and their target affinity?

Investigations focused on the evolution of EOs are also likely to be productive. For example, what evolutionary forces led to the appearance of supplementary EOs as seen in the genus *Steatogenys* and head extension of the EOs as seen in *Gymnotus coropinae*, *Gymnotus javary* and other members of the same clade? Where are the electromotor neurons that innervate these EOs, and what are their functions? Furthermore, the distinction between myogenic and neurogenic EOs is an interesting one. There are actually two known species of weakly electric fish that exhibit mixed neurogenic and myogenic components in their EODs: the activity of the posterior electromotor nerve innervating the tail region of *Gymnotus carapo* and *Gymnotus sylvius* has enough strength to contribute to the electric field (Rodríguez-Cattáneo et al., 2013). Are there other similar examples?

It is known that EO auto-excitability is plastic: habitat variables, including temperature and changes in conductivity, cause

acclimatory changes in EO auto-excitability (Kramer and Kuhn, 1993; Moller, 1995; Caputi et al., 1998b). The role of electrocyte membrane excitability in plasticity is well documented (Markham et al., 2009; Markham and Stoddard, 2013; Markham, 2019). It is also known that both major groups of weakly electric fishes express a number of genes – including two collagen genes, a glycosyltransferase and dystrophin (Gallant et al., 2014; Gallant, 2019) – that are likely to determine the space constant of the connective sheath and the magnitude of the longitudinal ephaptic current supporting EO autoexcitation. Is the expression of these genes modulated seasonally?

There are also many questions surrounding the sensory roles of EODs, and comparisons made across the different groups of weakly electric fish are likely to be informative. For example, the patterns of the time course of the received signals are of relatively low spatial complexity in Mormyridae, intermediate complexity in *Gymnarchus* and wave Gymnotiformes, and high complexity in pulse Gymnotiformes. What are the sensory consequences of these different degrees of complexity? Is it possible to electrolocate precisely by evaluating the patterns of the stimulus time course? What is the communication role of the complex fields generated by pulse fish close to the skin? The hypothesis of electric color is an intriguing one – in order to confirm this idea, it would be necessary to identify electric color-sensitive neurons in higher centers. Are there specific neurons that are involved in identifying conspecifics’ color? Another question regarding the sensory aspects of the EOD relates to circadian changes: it is known that pulse Gymnotiformes show different emission patterns across the circadian cycle, including changes in the electric field amplitude (*Brachyhypopomus gauderio*: Franchina and Stoddard, 1998; Stoddard et al., 2006; Silva et al., 2007; Migliaro, 2018; Migliaro et al., 2018; Vazquez et al., 2023) and pattern of repetition (*Gymnotus* spp.: Forlim and Pinto, 2014; Camargo et al., 2023), even in isolated fish. What are the sensory roles of these changes?

Finally, one of the most intriguing aspects of EO function is its possible role in communication. A language is a structured system of communication that consists of grammar and vocabulary. I have previously argued that the alternation between chirps, rasps and other typical EOD patterns during interactions between weakly electric fish suggests that these features could be part of a vocabulary. Exploring whether there are systematic alternations in these patterns during fish communication may unveil whether there are specific rules suggesting a sort of grammar.

Conclusions

Seven decades after Lissmann’s discovery of the functional role of the EOD and its importance in evolution, research on an effector system that humans do not have – and on a sensory system that does not evoke human-intuitive sensations – has greatly contributed to the understanding of the function and evolution of sensory–motor loops. First, electrogenesis is now well understood from the cellular to the whole-organism level. This understanding has led to the discovery of new variants of voltage-gated channels supporting astonishing electrophysiological properties and has revealed generalizable concepts, such as the combination of delay lines for achieving synchronous and coordinated activities. Second, the study of electric fish has helped us to understand the imaging process in active systems, thanks to the clear separation between the energy types of the signal carrier (the electric field generated by the electromotor system) and those involved in positioning the carrier source, the electrosensory mosaic and prereceptor conditioning the signals (animal movements controlled by the skeleto-motor system).

Knowledge gained from studying these fish has also contributed to general imaging theory, by improving our understanding of generalizable concepts such as an object's stamp and imprudence. Furthermore, the more than 500 known species of weakly electric fish show both different solutions to the same neurobiological problems (for example, whereas mormyrids use electrocyte geometry to produce complex waveforms, gymnotiforms use multiple innervation and diversity of electrocytes) and the use of similar mechanisms to solve different problems (for example, to evaluate the time course of the stimulus to actively evaluate the object impedance and to recognize a conspecific). Unveiling how variation in the organization and time course of the EODs contributes to different strategies for species survival, as well as understanding the genetic encoding and phenotypic expression of the EOD, is a major challenge that might shed light on general evolutionary mechanisms.

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Competing interests

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