



Electric fish as an object of fundamental research

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Abstract. The aim of this work is to show the role of research on electric fish and their role in fundamental problems' solvation. We are trying to involve additional specialists in our studies. *Methods.* We have developed a setup allowing simultaneous multielectrode registration and visualization of electric fields around fish, which is a novel tool in electric fish studies. *Results.* The article is a review. We tried to show the history of electric fish research and the peculiarities of the Russian school of electroecology.

Keywords: electric fish, electrodynamics, electrophysiology, electroethology, electroecology.

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Introduction

It is of great advantage to the student of any subject to read the original memoirs on that subject, for science is always most completely assimilated when it is in the nascent state.

James Clerk Maxwell [1]

Among the readers of the journal “Izvestiya VUZov: Applied Nonlinear Dynamics” there are many highly qualified specialists in the analysis of complex processes. The aim of this work, prepared by the staff of the Severtsov Institute of Ecology and Evolution, is to invite these specialists to apply their particular skills in our field of research – electroecology.

Electroecology, as a science, investigates the role and significance of various electrical events in the lives of animals. At the outset it should be noted that we are talking about

aquatic animals. Many of them have specialized electroreceptors allowing them to perceive surrounding electric fields. Among the many species of fish, those known as electric fish are capable of emitting electrical discharges, a phenomenon which is reflected in their species and generic names. Strongly electric fish – electric rays, eels, catfish and stargazers – generate powerful (hundreds of watts) electrical discharges for attack and defense [2]. Then there are fish, such as African mormyrids (Mormyridae family) and *Gymnarchus niloticus*, and South American gymnotids (gen. Gymnotiformes), which regularly or even continuously generate discharges with a power of unit-fractions of Watts for location and communication [3]. Yet other electric fish are capable of generating weaker discharges, often of an unstable form, but only in social interactions [4,5] and even in the most common fish, which are not classified as electric fish, such as common carp or zebrafish [6], various physiological processes, such as respiratory movements, are accompanied by changes in electrical potentials which are measured in a range of hundreds of microvolts. Considering that the threshold of electrosensitivity in some fishes can be much lower, for example, in the Amur catfish *Parasilurus asotus* about $0.05 \mu\text{V}/\text{cm}$ [7], fish can thereby perceive a wide variety of electrical events.

Any field of knowledge and any scientific problem demands an appropriate tool. In studies of visual or acoustic communication, we can rely to some extent on our natural cognitive abilities and sensory perception. However, even in these areas, new technical means can radically change the picture. For example, the use of ultrasound equipment has made it possible to detect echolocation in cetaceans and bats [8].

In electroecology, where natural perception of electrical signals is absent in humans, our need for technical assistance and physical models is even more acute. The gymnarch's faculty of electrolocation was discovered, by Hans Lissmann [9], only with the assistance of an oscilloscope. Further application of a similar technique made it possible to register electrical discharges from many other fish. Nevertheless, with such classical registration of electrical signals, the problem

of interpretation remained. In experiments involving more than one fish, it was difficult to determine the precise individual that generated a discharge. Moreover, often there were doubts as to the source of the electrical signals – was it really a fish, and not perhaps fluctuations of electrochemical potentials on the electrodes, or even some external sources? Therefore, to make progress in electroecology by solving the problems described above, a more sophisticated tool was necessary. To this end, we crafted a multielectrode matrix capable of recording electrical potentials [10], which were precisely synchronized with a video recording [11]. This allowed superimposing the electric fields generated by suitably sized fish on a video record of their activities, permitting the correlation between electrical events and observed behaviors (Fig. 1).

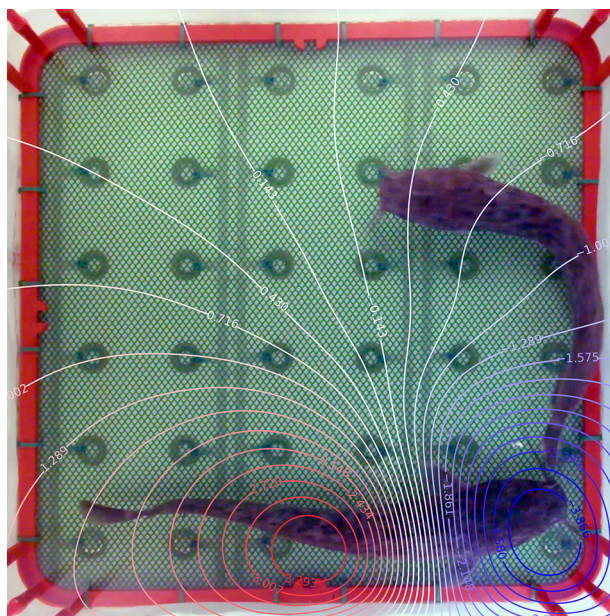


Fig 1. Electric field of the African Sharp-Tooth catfish (*Clarias gariepinus*) during the attack. The numbers on the equipotentials reflect the values of the electric potential (mV). The color reflects the polarity: during discharge, the catfish's head is electronegative

Our technique makes it possible to evaluate the values of electrical potentials, for example, on the body of a fish, which can be compared with the thresholds of

electrosensitivity or the thresholds for the manifestation of motor reactions. Moreover, it became possible to produce videos (press [link](#)) demonstrating electrical events in a real behavioral experiment.

Once the instrument is manufactured and the primary experimental data are obtained, the issue of processing and interpretation of that data comes to the fore. One of the chapters of Thomas Kuhn's famous book "The Structure of Scientific Revolutions" [12] is called "Normal Science as Puzzle Solving." The point is that researchers are particularly enthusiastic about solving puzzles, which allows them to demonstrate both their talent and skill. This is precisely such tasks that the described field of knowledge described herein, electroecology, provides in abundance. Currently, for example, nothing is known about the functional significance of weak electrical signals generated by catfish from the genus *Synodontis*. Moreover, there are many fish for which we were able to register electrical activity, despite the fact that these species were previously considered electrically inactive.

Often, the solution, and the very formulation of a scientific problem, is impossible without a sufficient amount of experimental data, just as Isaac Newton's celestial mechanics, and with it differential calculus, emerged from his interpretation of the long term astronomical observations of Tycho Brahe together with Johannes Kepler's subsequent analysis. Our tool is somewhat similar to Brahe's telescope, in that it provides information previously unavailable to the scientific community. Note that, as in the case of Newton's Principia, in electroecology, the final assembly of elements into a complete picture is likely to require completely different skills, tools and knowledge beyond those involved in the collection of primary data. Like Brahe, we are ready to share our primary data (electrical and video recordings) and the initial set of processing programs, together with our experience in studying electric fish, striving to expand the community of specialists interested in electroecological research and, perhaps, to produce our very own 'Newton'.

In inviting specialists to a novel field the onus is on us to describe what is interesting about it, what fundamental problems it addresses, and what scientific achievements it has, so far, the right to be proud of. In this regard, we will try to present several vivid episodes from the history of electric fish research, with due regard to the needs of non-specialist readers. Furthermore, we will reference notable researchers, the problems tackled, the objects of investigation, the methods and tools used, as well as the results obtained and conclusions drawn.

1. Foundations of electrodynamics: Fish as a source of galvanic current

At the turn of the XVIII–XIX centuries, electrical theory was divided into two separate, barely overlapping scientific fields – electrostatics and electrodynamics. This division in the XIX century resulted in the introduction of two different systems of physical units in which the same type of quantities had different dimensions. For example, the resistance in the electrodynamic system of units has a velocity dimension, and a resistance unit of 1 ohm corresponds to a speed of 10000 km/s [13].

Electrostatics in those days was focused on the interaction of charges and charged bodies. The forces of interaction could be measured with electroscopes or torsion scales, and the charge separation was carried out using a triboelectric electrostatic generator. Primitive capacitors, Leyden jars, were used to accumulate electric charge. Scientists argued about the nature of the force that repulses same-sign charges and the degree of equivalence between the forces of repulsion and attraction [14]. However, in general, it was a logical extension and generalization of the Newtonian theory of mechanics.

On the other hand, electrodynamics was based on the assumption that electricity is the flow of ether, although there were no instruments to measure these flows, no mathematical equations describing these flows, and no distinct hypotheses about the causes of this supposed movement of ether. The main object of research in early electrodynamics was electric fish, and after Galvani's discoveries, this was extended to other living beings and even individual organs. Michael Faraday's article "Notice of the character and direction of the electric force of the *Gymnotus*" begins with the words: "No matter how amazing the laws and phenomena of electricity are when they are revealed to us in inorganic or dead matter, their interest can hardly be compared with that inherent in the same force when it is connected with the nervous system and with life" [15].

After the invention of the Leiden jars, capable of accumulating and storing the electric charge generated by the triboelectric electrostatic generator, the practice of testing the physiological effect of their discharge on oneself came into tradition. The effect was strong and very similar to that caused by Surinamese gymnotes, later called electric eels (*Electrophorus*), and sea rays of the genus *Torpedo*, later called electric rays. This analogy allowed researchers to assume that the massive cellular structures that distinguish these fish from non-electrical ones, are electrical organs and that electricity is responsible for the observed physiological effects [2, 16]. This idea met with vigorous objections from supporters of the electrostatic theory. Since fish live in water, and water, especially saline sea water, conducts electric current, then, according to the electrostatic theory, electrical phenomena should be absent within electro-conducting media. Therefore, the electric fish cannot exist in theory.

John Walsh conducted a series of experiments with electric stingrays [16, 17]. Several (at least three) people holding hands were used as a means of registration. The participants at each end of the chain dipped their hand into a body of water containing a stingray, tried to provoke its electrical discharge and then shared their impressions. Control experiments were carried out using charged Leiden jars as a source of electricity instead of the stingray. During the experiments, the electrical circuit varied. If the circuit consisted of people and conductors, including metal wires and wet ropes, then the discharge was transmitted. If there was an insulator or a break in the circuit, then the discharge was not transmitted. It was found that the effects of the stingrays and Leyden jars were identical. However, during the discharges, the body of the stingray remained completely motionless, and the discharge itself was not accompanied by any crackling or glow characteristic of a spark breakdown. Many scientists found Walsh's arguments in favor of the electrical nature of stingray discharges convincing, and in 1773 Walsh was awarded the Copley Medal by the Royal Society for this work.

Nevertheless, fundamental questions remained, as posed by Henry Cavendish [18] in a work that begins with the words: "Although Mr. Walsh's evidence that the impact of *Torpedo* is caused by electricity is such that it leaves little room for doubt, for the time being it should be confessed that there are some circumstances that at first glance seem hardly consistent with such a hypothesis. I therefore propose to investigate whether these circumstances are really incompatible with such a view and to give an account of some attempts to imitate the actions of these animals with electricity".

In particular, Cavendish asked:

- Why does the current from the ray flow through the human body, if it is much easier for it to flow through water?
- Why are no sparks, glow, attraction and repulsion observed during the discharge of fish?
- Is it possible to construct a model of a stingray permitting us to feel analogous electric discharges in water?
- Whose discharge is stronger, a natural stingray or a Leyden jar charged from an electrostatic generator and connected to a stingray model?

The answer to the first question emphasized one of the most important differences between electrostatics and electrodynamics, which in the XIX-th century was often called ‘galvanism’, and later ‘electrodynamics of conducting media’. Indeed, in water, and any other conducting medium, current flows along all available paths. Even in circuits with relatively high resistance, some part of the total current flows from the ray through the water, human hands and bodies, and again through the water and to the ray. On the other hand, a spark or lightning in air passes along a certain path. Later, Richard Feynman extended Cavendish’s principle to the case of a single electron, replacing the resistances of possible paths with their probabilities [19].

Answering the last of the above questions, Cavendish emphasized that there are two different quantities: electrical voltage and the amount of electricity (charge) – the higher the voltage, the greater the spark gap and the brighter the spark, and if the voltage is too low, the spark is not observed at all. The magnitude of the physiological effect, on the contrary, is determined by the amount of electricity flowing through the human body rather than the voltage. Cavendish found that voltage and charge are connected through a quantity, which is still called ‘capacity’. A Leyden jar charged from an electrostatic generator has a high voltage, but a small charge, unlike the electric organs of the stingrays, which, according to Cavendish, are banks of capacitors of very large capacitance.

Cavendish proposed an experimental procedure for measuring capacitance using a reference capacitor. The measured capacitor was charged to a certain voltage, and then connected to the reference. After that, the reference capacitor was disconnected, discharged and reconnected to the measured one again. At each step, the voltage on the tested capacitor was measured using an electroscope. The process was continued until the voltage on the measured capacitor dropped by half. The measurement result was expressed in inches corresponding to the diameter of a metal ball of the same capacitance. The capacitance of one Leyden jar of those times was approximately 1–10 nF. The battery used in Cavendish’s experiments was composed of 49 Leyden jars connected in parallel, with a capacitance of about 500 nF (at a voltage of about 20 kV). If we use modern data on the voltage and current of electric stingrays (approx. 50 V and 30 A), then an equivalent capacitor would have to have a capacitance 4000 times larger in order to cause a similar physiological effect with the same charge. This determines the technical complexity of simulating a stingray’s discharge.

Cavendish made a ‘successful’ model of an electric ray from a layered stack of wet leather sandwiched between plates made of an alloy of lead and tin. This design was a new type of capacitor, which is now known as ‘electrolytic’ and which could have a capacitance of thousands of microfarads. The large capacitance of the electrolytic model of the stingray submerged in water extended the duration of the discharge of the battery of Leyden jars, connected to the model of the stingray submerged in water long enough for experimenters to feel the physiological effect. Maxwell wrote that this was one of only two occasions when Cavendish allowed outsiders into his laboratory [20].

In addition to electric fish, Luigi Galvani’s experimented with ordinary frogs, not with whole live frogs, but with their specially prepared hind legs, which played a very important role in the establishment of electrodynamics [21]. In the well-known disputes between Volta and Galvani, one of the fundamental points of disagreement was the degree of similarity of electricity in electric fish and in the frogs’ legs. Galvani believed that these phenomena differ only quantitatively, but not qualitatively, while Volta believed that electricity flows only in the electrical organs of fish, whereas some unknown nervous fluid flows in the nerves and muscles of frogs.

Historians of science attribute the genesis of Galvani's research to his wife, Lucia Galleazzi [22, 23], who was sitting in her husband's laboratory, twirling the handle of the electrostatic generator and admiring the flashing sparks. Meanwhile, Galvani's assistant was dissecting a frog, which twitched vigorously when in contact with the scalpel. An observant woman, she drew her husband's attention to the fact that convulsions coincided precisely with the sparks between the balls of the electrostatic generator. Two circumstances were surprising: 1. The electrostatic generator was not connected to the frog; 2. The work involved a prepared frog's leg only, that is, the effect was preserved even when the head was cut off. As Galvani wrote: "Then I lit up with incredible zeal and a passionate desire to explore this phenomenon and bring to light what was hidden in it" [21].

In further experiments by Galvani, he found that in order to obtain the effect, the nerve from the spinal cord to the muscle should be left intact, but exposed, and the researcher should touch the nerve with a scalpel at the moment when the spark flies. If the scalpel has a bone handle, then the experimenter should touch the scalpel rivets "opening the way to the electric fluid". If one just put a scalpel on a nerve, then the effect is not observed. However, if one attaches a piece of wire to the scalpel and directs it to the floor, and attaches another piece of wire to the nerve and directs it to the ceiling, the effect will appear. This arrangement results in a dipole antenna with a neuromuscular preparation as a receiver, which can be used as a registration device, called, after Carlo Matteucci, a 'galvanoscopic frog' [24]. Attempts to register the discovered galvanic effect with traditional devices, such as electrosopes, having the best sensitivity for that time, did not lead anywhere even when the galvanoscopic frogs were convulsing. This bionic current sensor was used for more than a hundred years.

In his next series of experiments, Galvani tried to register atmospheric electrical phenomena using galvanoscopic frogs. It should be noted that in that era, the employment of lightning rods was the only practical application of electricity, and the one which excited the interest of researchers in this field. In Galvani's experiments, prepared hind legs were suspended in the open air, wires from a lightning rod were attached, and intense convulsions were observed during a thunderstorm. With each bolt of lightning, the frogs' legs twitched.

One day, in clear weather with a light breeze, Galvani noticed that, touching the cast-iron railing of the balcony, the frog legs suspended on copper hooks twitched. Pressing a leg to the railing and observing its convulsions, Galvani decided to put a copper hook in contact with the nerve, a neuromuscular preparation in itself, with the cast iron contacting the muscle. Later he has shown that the connection of the nerve and muscle using an arc made of two different metals causes contraction. Initially, the name 'galvanic cell' was used for this combination of two different metals and prepared frog's leg. Subsequently, in Volta's experiments, the galvanic cells lost their neuromuscular component, but retained the electrolytic layer in its place.

In addition to the actual galvanic cell, Galvani discovered galvanic currents flowing in nerves and muscles, which radically expanded the understanding of the scale of electric phenomena in living matter. It turned out that electricity is not only involved in lightning, St. Elmo's lights, triboelectric effects and exotic fish, but it is, indeed, the basis of life. Galvani wrote: "As for voluntary movements, perhaps the soul, by means of its amazing power, can either in the brain, which is most likely, or outside of it, in the nerve that it has chosen for itself, generate, as it were, some kind of push, thanks to which a nerve-electric fluid immediately flows from the corresponding part of the muscle to that part of the nerve to which he was directed by this push" [21].

Galvani's discoveries made such a strong impression that for almost a hundred years electric current was called galvanic, electric current sources were called galvanic cells, and electric current meters were called galvanometers. The first physical interpretation of his results was given by Alessandro Volta. In 1794, Volta was also awarded the Copley Medal for "Reports explaining some of Professor Galvani's experiments". Volta's most significant result was the establishment of the fact that, in Galvani's experiments with the closure of a nerve and a muscle by an arc composed of two metals, the current source (the force that moves electricity) was neither a nerve nor a muscle, but the contact of two different metals. The experimental proofs given by Volta were clear and easily reproducible, for example, using a zinc-silver pair and an electroscope – and so the 'animal electricity' as described by Galvani, was interpreted by Volta as just another unsubstantiated hypothesis.

After receiving the Copley medal, Volta experimented over a long period with various pairs of metals, trying to create a current source comparable to the electrical organs of fish. However, the contact potentials are not sufficient for this purpose. Then, with reference to the anatomy of the electrical organs of fish, Volta introduced layers of paper soaked in acid between pairs of dissimilar metals. This is how the Voltaic pile came about, one of the revolutionary inventions of the past millennium, and the prototype of all modern battery cells and accumulators. In his letter to the Royal Society, Volta reported about his invention: "This device, more similar in essence, as I will show later, to the natural electric organ of an electric stingray or electric eel than with a Leyden jar and known electric batteries, I will call an artificial electric organ" [25].

Despite the obvious ability of the Voltaic pile to generate electric current, the source of power in the galvanic cell remained unclear for several decades. In 1838, Faraday wrote: "This issue is currently of extreme importance for the theory and for the development of electrical science. Opinions on this vary, but the most significant are two, of which the first finds the source of power in contact, and the second in chemical force. The dispute between them concerns the most basic principles of electrical action, because the opinions are so different that the two people who respectively accepted them are forced to further disagree on all points relating to the possible and profound nature of the agent, or the force on which the phenomenon of the galvanic cell depends" [26]. In the end, Faraday proved that the source of power in galvanic cells is the energy of chemical reactions occurring inside them, and not a simple contact of two metals.

The enthusiasm generated by Galvani's discoveries derived, first of all, from a desire to create fundamentally new methods of medical treatment, and even one to raise the dead. However, countless experiments since have not yielded any positive results. Volta's scepticism seemed increasingly convincing, as he argued that electricity only excites the nerve, and what happens next, for example, how nervous excitement causes muscle contraction, remains unknown. What is the life force, can it be investigated experimentally and what relationship has it with electricity? According to Faraday's hypothesis, the electric organs of eels and rays are converters of some vital force into electrical energy [15]. The question therefore arises: Is it possible to restore vitality by passing a current through the body of an electric eel in the opposite direction? This bold hypothesis was not confirmed, but experiments and ensuing discussions, brought an understanding of the source of the power of the Voltaic pile and an understanding of the nature of electromotive force as an energy flow, and not as a force of the interaction of the bodies.

The further development of classical electrodynamics did not rely on experiments with live electric fish. The discovery of magnetism, the interaction of electric and magnetic fields, the discovery of electromagnetic waves, together with multiple practical applications of electricity – all this was predominately based on mathematics, while biology and bionics ceased to serve as a source of new ideas.

2. The establishment of electrophysiology: Fish as a neuromuscular preparation

Despite Volta's convincing arguments in favor of the fact that the source of voltage is the contact of two different metals, and the arguments of Faraday, who determined that chemical reactions are the source of power in a Voltaic pile, an extremely important question remained open: Do any electrical processes occur in living organisms? Is the frog's leg a source of current, as Galvani believed, or is it a purely passive structure, with the electric current in living organisms flowing only in specially arranged electrical organs, as Volta believed? This nascent field of science, which comprises the study of electrical phenomena in living things, is today known as electrophysiology, and one of the brightest names in this field is Carlo Matteucci.

Carlo Matteucci, a graduate of the University of Bologna, was an apologist for Professor Galvani, and his ideas on animal electricity [27]. They could not have known each other, since Galvani passed away in 1798, and Matteucci was born in 1811. Matteucci received a broad education: mathematical, physical, and chemical, and soon began to publish scientific papers on chemical processes in voltaic piles, and on electromagnetic induction. He also published in the field of telegraphy. Later Matteucci became a well-known politician and even served as the Minister of Education of Italy. In 1844, at the age of 33, he was awarded the Copley Medal for "Studies of Animal Electricity" [28], and in 1870, a new medal was established in honor of Carlo Matteucci, and only awarded to physicists. The many recipients included Helmholtz, Fermi, and Pauli.

Matteucci entered into the dispute on animal electricity, benefiting from the same advantages that the physicist Volta had in relation to the anatomist Galvani: Namely, mastery of the theoretical concepts and the logic of argument when conducting disputes in a professional environment, together with an experimental ability including the creation of new devices and improvement of existing ones. He also enjoyed an extensive acquaintance within the physical scientific community. Nevertheless, he entered this dispute resolutely under the banner of Galvani. Just like Volta, Matteucci mastered the manufacture of 'galvanoscopic frogs' which he employed extensively in his research. Where necessary, Matteucci also used synthetic instruments, such as the galvanometer with a magnetic frame of the Nobili design, and the kymograph – this being the first mechanical data recorder.

Matteucci's memoirs were published in the Proceedings of the Royal Society, gathered under the general heading "Electrophysiological research". Like Galvani's treatise and Volta's letters on animal electricity, these memoirs give an evolutionary picture of his scientific search from the first bright successes through a period of painful misunderstanding to a long exhausting siege, and, finally, to the 'appearance of tissue' and 'straightening sigh' (Osip Mandelstam).

If Galvani was right, and the functioning of a living being is based on the flow of electrical fluids, then how exactly does this happen? What does the brain do? Is electricity generated from blood? How does the brain control organs and muscles? What do nerves do? What is common and what are the differences between electrical organs and ordinary muscles?

Matteucci's first successes were related to electric fish. In the 1830s, many people tried to get 'clean electricity' from *Torpedo* rays, that is, a spark. However, the task was technically difficult, since the amplitude of the discharge of the ray is only about 50 V, while an amplitude of kilovolt scale is necessary to get such a spark. Following Faraday, many experimenters tried with the use of inductors but failed. Matteucci's innovations were, first, to direct the entire current of the discharge to flow through the coil, restricting any bypasses through the water, and, second, to break the circuit immediately after the start of the discharge. Thus the discharge energy, converted into magnetic field energy, reverts into electrical form thereby inducing in the coil a

voltage sufficient for spark generation. The experiments were performed by his co-author Santi Linari, but the technique was proposed by Matteucci [29].

Later, Matteucci himself began experimenting with the electric organs of Torpedo rays. By the end of the 1830s, he had established that in the brain of a stingray there is but one part that controls electrical discharges – that being the bottom of the fourth ventricle, which Matteucci named the ‘electrical lobe’. Stimulation of this part of the brain by current, touch, or chemical action causes a discharge, whereas similar stimulation of any other part does not. Indeed, if you remove the entire brain, except for the electrical lobe and the nerves coming from it, the ability to generate discharges remains. Matteucci also traced and described the associated nerves and showed that if they were cut, the brain would lose its capacity to initiate discharges. At the same time, stimulation of nerves below the cut causes discharges, but only in that part of the organ where this nerve terminates. An electrical organ consists of many specialized cells, now known as ‘electrocytes’ and called ‘prisms’ by Matteucci. The electrocytes are connected in series, which are organized in rows running parallel to the axis of the organ. When connected in parallel, rows of electrocytes form a powerful battery. If you cut the nerves innervating different parts of an electrical organ, then the discharge power drops in proportion to the fraction of the organ affected. Nevertheless, the source of the electrocyte’s energy remained undiscovered.

Based on the results of his experiments with electric fish, Matteucci hypothesized an electrical nature for the nerve agent that transmits commands from the brain to the organ. Although it became apparent that blood flow is not involved in this process, as for the clarity of the experiments, the preparations were thoroughly cleaned of blood and other physiological fluids. Finally, Matteucci assumed the principle of uniformity of signals transmission in the nervous system, regardless of whether such transmissions go to electrical organs or to ordinary muscles. Matteucci returned to the investigation of electric fish more than once, but most of these later experiments were carried out on non–electric animals, such as frogs, pigeons and rabbits.

Volta and his supporters insisted that the cause of all the electrical phenomena observed in Galvani’s experiments were artifacts: Metal contacts, temperature gradients or inductive interferences. Thus, in experiments with animal electricity, it was very important to demonstrate the absence of any possible extraneous sources. In addition, it was important that the experiments could be reproduced by other researchers, and with minimal effort [30]. Thus, the use of dissected frogs both as current sources and as sensors of electrical events was not a mere whim, but was necessary to make the experiments clear and reproducible.

Thus, Matteucci’s experiment, proving that the source of electricity is the muscle, was very clever and convincing. Volta had repeatedly stressed that, in animals, all electrical phenomena are confined to the nerves, and that although the mechanism of muscle contraction was unknown, it was certainly initiated by the action of nerves. So, the first thing Matteucci did was to cut off the nerve including the area of contact between the nerve and the muscle, with only half of the frog’s hind leg remaining. Then he assembled a closed circuit including a Nobili galvanometer and not one, but several frog legs laid out in such a way that the cut of one leg met the intact surface of the muscle of the adjacent leg (Fig. 2).

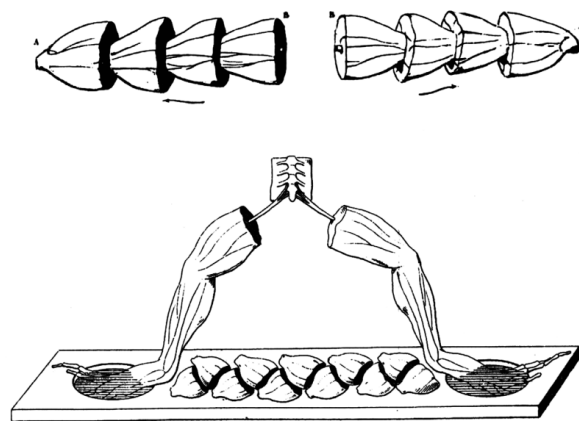


Fig 2. An illustration of Matteucci’s experiments from his 1845 work, showing how the halves of frog legs were connected to form sequential batteries [30]

Matteucci's hybrid apparatus thus involved a kind of 'frog-legged' Voltaic pile. To show that the cause of the discharge is not the galvanometer and its contacts, namely the muscles, a classic neuromuscular galvanometer was used as an indicator in his second series of experiments. Matteucci demonstrated that the magnitude of the recorded current has a linear relationship with the number of halves of frog legs, which finally proved that the muscles themselves are the source of electricity. Moreover, the battery assembled from frogs' legs was able to cause electrolytic decomposition of potassium iodide. The latter allowed him to determine the direction of the current flow, and the dissected surface turned out to be electronegative. Matteucci believed that the cause of the current is not the damage itself, but the fact that by touching the area of the cut with a galvanoscope, electrical contact is established between the surface of the muscle and its interior. No difference was found in electric potential between different areas of the damaged muscle, nor the intact ones.

The described current was labelled 'muscular' by Matteucci [30], whereas in modern scientific literature it is known as 'damage current'. The current which was originally discussed in the experiments of Galvani and Volta, flows simultaneously with muscle contractions but in the opposite direction to the muscular current. Matteucci calls the former current the 'proper current' [31]. But how do proper and muscular currents relate? Is there a muscular current in an intact frog? In order to experiment with the proper current, it was necessary to preserve the nerves, to avoid damage to the muscles and to lay out the battery in such a way that the nerve of one leg was in contact with the leg of the other (Fig. 3).

All experiments on the muscle current were repeated with the proper current and their complete similarity was confirmed. Yet, the question of where the 'animal' electricity comes from remained open. Matteucci considered three options. According to the first, the source is the ambient air. In experiments conducted in media of various gases, it was shown that in a hydrogen medium the current was greater, and in one of oxygen it was less. Nevertheless, the main conclusion was that the muscle current is determined by the muscle itself, and doesn't originate in the surrounding gas.

According to the second option, the current source was the contact of the heterogeneous inner surface of the muscle and its homogeneous shell. Indeed, the contact of any differing materials can cause a contact electric potential difference. To test this second hypothesis, Matteucci cut rings from the caecum of a bull about the same size as frog's thighs. He filled these rings with fibrin from whipped bovine blood and assembled a battery of twenty such cells, similar to those made from frog's legs (Fig. 2). No signs of current were detected from this battery. However, by alternating frog's legs and pieces of caecum with fibrin, Matteucci registered a current, but somewhat less than that from those legs without inserts of segments of intestine. Thus, it was established that contact electric potential difference is not responsible for muscle current.

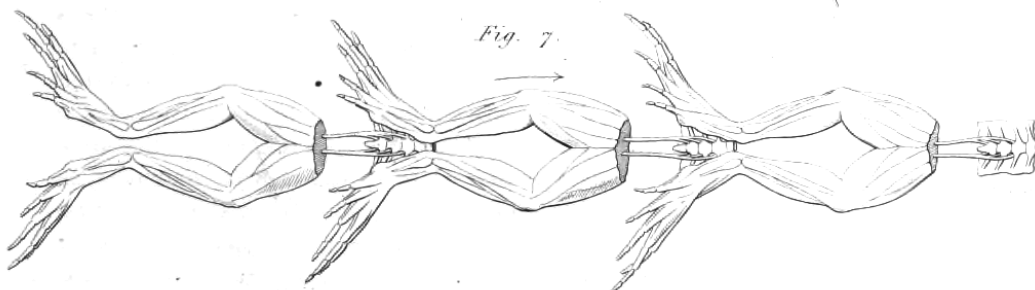


Fig 3. An illustration of Matteucci's experiments on induced contraction from his 1845 article [30], demonstrating how muscles and nerves from different frog legs were brought into contact

The third hypothesis, to which Matteucci gravitated from the very beginning, proposes that electricity arises as a result of the chemical interaction of blood with muscle fibers. The restoration of electricity in the muscles is related with the nutrition of the animal, and the muscle itself is somewhat similar to a galvanic cell. The muscle ends with a tendon, and the currents registered between the tendon slice and the muscle shell are the same as those between the muscle slice and its shell. Matteucci wrote: “We must never forget the analogy between the muscular electro-motor element and the Voltanian element: the zinc is represented by the discs of the muscular fibre, the acid liquid by the blood, the platinum by the sarcolemma” [31]. When powered, chemical reactions occur that charge the column, and when a muscle contracts, electricity is consumed for mechanical work.

In contemplation of the physiology of electric fish, the most interesting of Matteucci’s discoveries is the ‘induced contraction’ [24]. Galvani had already shown that the contraction is observed when the nerve is placed on damaged and undamaged areas of the muscle using a glass rod. Matteucci modified this experiment by demonstrating that the nerve of one galvanoscopic frog, placed above the muscle of another one, is able to induce muscle contraction of the first specimen in response to the excitation of contraction in the second one. The effect of induced contraction is also observed when the nerve of a galvanoscopic frog is brought into contact with the muscle of another animal. Today this phenomenon is called ‘secondary tetanus’ or ‘the Matteucci experience’.

Matteucci showed that if any liquid was dropped on the inducing muscle between the muscle and nerve leaving the induced muscle, then the effect persists. Moreover, the liquid can be even an insulating one: “Of the many liquids, there was not a single one that would prevent the induced contraction. Pure water, slightly acidified water, salt water, serum, blood, olive oil, diluted alcohol, alcohol solution of varnish (polish), rosin, light oil, turpentine – all these liquids were tested in the experiment and always induced reduction took place. I always dripped a few drops of fluid on the muscle, and then placed a nerve on it, placing it in the same fluid. Induced contraction was observed even if a thin layer of felt impregnated with these liquids was placed between the nerve and the muscle. The low electrical conductivity of some of the liquids used (oil, turpentine, polish, etc.) made me doubt that the induced contraction would not exist even despite the presence of an insert from an absolutely insulating body. I was convinced that through a layer, even a very thin one, of these fluids, neither muscle current nor true current propagate. Therefore, there is no doubt that if the induced contraction propagates through the layer of the mentioned bad conductors, this induced contraction cannot be associated with the current generated in the contracting muscle and passing from there into the nerve of the galvanoscopic frog” [24]. By publishing these results, Matteucci demonstrated a remarkable scientific honesty, since they directly contradicted his own prior conclusions on the electrical nature of the interaction of nerve and muscle.

Matteucci was trying to find another mechanism for transmitting excitation. For example, he tried to cause a muscle contraction by putting a nerve on a sounding string. However, all these experiments brought him back to his original electrical hypothesis – but how then does one explain the passage of current through insulating fluids?

In later experiments the inducing muscle was inactivated (by heating, for example) and was used as a passive conductor of a signal from an external almost discharged Leyden jar. Those influences which affect the muscles’ ability to contract had already been described by Matteucci [32]. And so, these signals caused contractions of the induced muscle, even in the presence of insulating liquids and even with thin mica plates between them. In the latter case, the effect was weakened, but did not entirely disappear. These results reanimated the electrical

hypothesis, and once again confirmed Matteucci's claim that in addition to physical current meters, galvanoscopic frogs should be used in electrophysiological experiments: "In fact, none of our electroscopic instruments are able to show us the existence of an electric discharge similar to that given by a very small jar, previously discharged three or four times in a row by a metal conductor. Only a galvanoscopic frog can indicate the existence of these discharges" [32]. The experiments demonstrated that the electricity in nerves is not a direct current, but resembles discharges of electric fish.

The impact of electric potentials from a muscle of one creature on the nerve of another one is qualitatively the same phenomenon as the strike of highly electric fish on their victims [33]. The only difference being that in the case of electric eels and rays, the potentials and currents of the discharge and distances of interaction are much greater. Considering fish with weak electrical organs: Can they cause induced contraction in other organisms? And, if not, how did electric fish appear in the process of evolution? This problem was considered by Charles Darwin to be one of particular difficulty, and is today regarded as one of Darwin's puzzles [34]. Before becoming an effective weapon, electrical organs had first to go through the initial stages of evolution, when they were primitive, small and low-powered. The Rajiformes stingrays, for example, were mentioned by Darwin as an example of the low-powered electric fishes.

The electrical organs of rajiform stingrays were first described by the Scottish researcher James Stark in 1844. Stark only described the morphology of the organs and did not conduct physiological studies. Nevertheless, he insisted that he had found an electric apparatus in these rays, referring to the fact that fishermen had experienced the characteristic sensations produced by weak electrical discharges [2]. Two years later, the French histologist Charles-Philippe Robin independently discovered and described these organs, located in the tail of *Raja*. In 1846, Johannes Peter Müller, an anatomist of repute, also became interested in Rajiformes. He found no noticeable electrical effects and sought advice from Matteucci, who had similar results and concluded that it was a non-electric fish. Nineteen years later, Robin repeated the studies of these rays and showed that the galvanoscopic frog twitches in cases when the nerve touched the body of the stingray or when the skin of the fish near the electric organ was damaged [35].

Meanwhile, the question of whether the discharges of Rajiformes cause induced contractions at a distance from the fish lacked a convincing answer. Much later, it was found that these rays have a specialized electrical sense that allows them to sense the discharges of their conspecifics, and which makes electrical communication possible [4].

If we judge the progress of a field of science by the awards of Copley medals, then after Matteucci, a century elapsed before the next serious breakthrough in the understanding of electrical processes in nerves and muscles. The medal was awarded in 1965 to Alan Hodgkin for his discovery of the mechanism of excitation and transmission of nerve impulses and his contribution in neurophysiology. In 1967, Bernard Katz was awarded the medal for the discovery of the mechanism of transmission of nerve impulses through the synapse, and, in 1973, Andrew Huxley for the study of the mechanisms of nerve impulse transmission and activation of muscle contraction. As for the role played by electric fish in the progress of electrophysiology after Matteucci, you can read "The Shocking History of Electric Fish", a wonderful book by Finger and Piccolino [2]. Thus, in the ongoing studies of the mechanisms of transmission of nerve impulses, and neuromuscular synapses, including those awarded the Nobel Prizes and Copley medals, electric rays and eels often served as the objects of research. The researchers were not interested in electric fish themselves, but only as convenient preparations, as, for example, a giant squid axon. Fortunately, and due to this circumstance, the physiology of the electrical organs of fish has been thoroughly described for all types of electric fish [36].

3. The discoveries of Hans Lissmann: Fish as a receiver-transmitter of weak electrical signals

A new era in the research of electric fish began with the discoveries of Hans Lissmann, an expert on animal locomotion. One day, a certain Dr. Morris presented him with an African fish, *Gymnarchus niloticus*, which exhibited an unusual way of swimming. The undulating movements of its long dorsal fin, permit the *Gymnarchus* to swim both forward and backward with equal ease – and curiously, when moving backwards it successfully avoids obstacles, a fact which aroused Lissmann’s keen interest.

Lissmann suggested that the mechanism of the orientation of *Gymnarchus* might be based on an electrical sense. Using an oscilloscope connected via an amplifier to electrodes lowered into the water, Lissmann detected a continuous quasi-sinusoidal signal with a fairly stable frequency of about 300 Hz and an amplitude of about 30 mV near the fish. Both the amplitude and phase of the recorded signal were observed to change with each turning movement of the *Gymnarchus*. This indicated that the signal came from the fish, and was not a mere artefact of registration. In February 1951, Nature published a short report by Lissmann “Continuous electrical signals from the tail of the *Gymnarchus niloticus* fish” [9]. The fish generated a continuous signal regardless of its speed and direction of movement. Observations have shown that the *Gymnarchus* reacts to distortions of its own field, caused by foreign objects such as copper wire or the walls of its tank, and also reacts to external alternating electric fields of similar frequency. If the *Gymnarchus* is artificially presented with its own signal then the fish appears to be able to detect its source and usually attacks it. In addition to the *Gymnarchus*, preliminary experiments were performed on its close relatives, the African mormyrids, as well as on South American gymnotids, one of whose representatives is an electric eel.

Seven years later, in 1958, Lissmann’s main paper “On the function and evolution of the electrical organs of fish” was published in the Journal of Experimental Biology [3]. It began with a reference to the aforementioned puzzle presented by Darwin: “The inadequacy of the functional and evolutionary theories of the electrical organs of fish has become clear for a long time.” The way out of this impasse was expressed by Lissmann as follows: “It seems important to consider electrical organs, not as interesting organs in themselves, but as part of the general organization of the fish, which plays a role in its interaction with the surrounding world” [3].

Lissmann’s main conclusions can be formulated as follows: Since the fish he described as ‘weakly electric’ are able to detect objects using their own electrical signals, they must have a specialized sensitivity to perceive very weak electric fields. Moreover, according to Lissmann, electrosensitivity should have evolved first and served as the main prerequisite for the subsequent development of specialized generation of signals. Therefore, electro-sensitive animals should noticeably outnumber those generating electrical signals. Specialized electrosensitivity requires fish to have specialized receptors in contact with corresponding brain parts. The skin of a weakly electric fish is arranged in a special way, consisting of a thick multi-layered epidermis with high electrical resistance, permeated with a dense network of channels going to sensory cells and filled with a electro-conducting substance. Thus, the surface of its body might be thought of as the ‘retina’ of an electric eye, which allows the weakly electric fish to construct cognitive images of surrounding electric fields.

Regarding the general organization of the electrosensory system of weakly electric fish, Lissmann’s conception both connected and explained such phenomena as the strange body shapes peculiar to electric fish, an unusual manner of swimming, a huge (for a fish) brain, and the prevalence of electric fish in muddy waters, where vision is almost useless. Like many of his ideas, Lissmann’s hypothesis on the connection of body shape and swimming style with

the requirements of electroreception has found and is still finding, many new confirmations. This is what explains the exotic appearance of many extant electro-sensitive animals today, for example, hammerhead sharks. The question “Why?”, central to Darwinian evolutionary theory and cunningly reformulated as “How does it arranged?”, was directly attacked by Lissmann, and satisfactorily answered. In this way it became much clearer as to why the electro-sensitive system is arranged as it is, and not otherwise.

The experimental study of the functions of the electric sense differs from similar work on non-electric animals in that human experimenters, obviously, cannot perceive electric fields and currents with their own senses – one can imagine it as a kind of blindness. For many experimental purposes, we can at least qualitatively rely on our eyes and ears and on the experience of our visual and auditory perception. Humans can, for example, see changes in mating coloration in salmon, just as we assume the salmon do, and we take it into account in our consideration of their behavior. Likewise we hear the capercaillie or the croaking of frogs and posit that they are not without importance to them, just as sound communication is important to us. In the case of electric fish, being ‘blind’ in this manner, we have to rely on devices and physical models rather than our eyes and ears.

Lissmann’s recording equipment was simple, and consisted of a dipole antenna composed of two electrodes, a battery-powered amplifier, headphones, a tape recorder, and an oscilloscope. With this setup, Lissmann registered the same regular electrical signals in African rivers that he had observed in the laboratory, and so demonstrated that fish actively use electrical signals in nature. The detected electrical signals differed in shape, frequency and rhythm, as one might expect from different fish species.

The purpose of the electro-sensitive and electro-generating systems of weakly electric fish was revealed by Lissmann in a series of ingenious behavioral experiments performed jointly with Ken Machin [37]. The experimental *Gymnarchus* were trained to distinguish objects, having identical shape and color, but different electrical conductivity. For this purpose, clay vessels containing conductive (metal) or dielectric (glass or paraffin) rods were used. A worm was placed next to one of two externally identical vessels, and if the *Gymnarchus* tried to grab a worm adjacent to a vessel with a glass or paraffin inside it was deterred (negative reinforcement). It turned out that the *Gymnarchus* easily distinguishes vessels by their contents and confidently takes the food that was intended by the experimenter for its consumption (Fig. 4).

Lissmann continued these experiments with banded knifefish (*Gymnotus carapo*), having successfully trained several fish to take food in the presence of a non-conductive disk and refuse it in the presence of an aluminum disk of the same size. These experiments were carried out with equal success both in the light and in the dark. Then the fish were prompted to distinguish an aluminum disc from a disc painted with aluminum paint, but still non-conductive. Lissmann varied the materials of the non-conductive discs, as well as the metals of the conductive ones. These changes did not dissuade the trained fish from confidently performing tasks, which thereby permitted the observer to infer that it was the electrical, and not the chemical properties of the materials which were the key determinants.

Since the metals used in these experiments could cause the flow of additional currents perceptible to the fish, several control experiments were conducted in their absence. Preliminary experiments showed that a fish reacts to the rapid movement of a magnet just outside the aquarium. Thus the fish were trained to take food when a magnet was fixed in close proximity to the aquarium, but behind an opaque screen, and to refuse it in the absence of a magnet. And vice versa – to take food in the absence of a magnet. In these experiments, Lissmann wasn’t trying to prove the direct magnetic sensitivity of fish, but rather, their ability to perceive magnetic

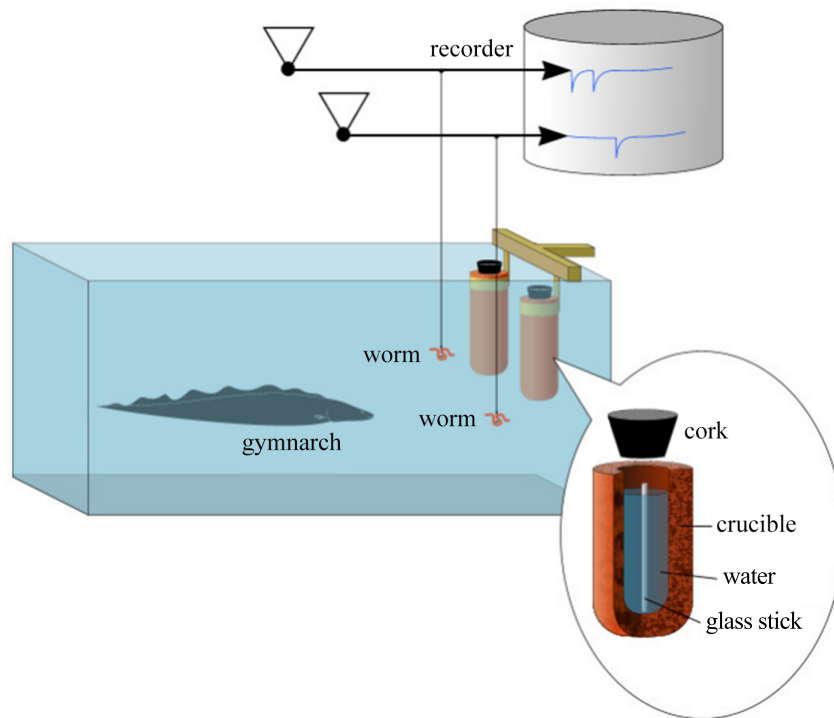


Fig 4. Illustration from the work of H. Lissmann and K. Machin, showing the ability of *G. niloticus* to distinguish between conductive and non-conductive objects [37, 38]

fields indirectly, using electric currents in water induced by a moving magnet, or by a stationary magnet in the case of a moving fish.

After describing the biological arguments in defence of the faculty of electrolocation in fishes, Lissmann formulated an appropriate physical model. In a homogeneous aquatic environment, a fish creates a nearly dipole electric field. Any object whose electrical conductivity differs from that of water will distort the original configuration of the field. It was assumed that the fish is able to feel this distortion. Such an approach to electrolocation differs qualitatively from modern radar technology, since electric fish do not register signals reflected from objects, but only perceive distortions in the surrounding electric field structure. Such a non-wave quasi-static model of electrolocation is not trivial despite its external simplicity and clarity.

Returning to 'Darwin's puzzle', that is, the history of the origin of electrical organs, Lissmann reprises some of the well-known difficulties of evolutionary theory: That the electrical organs in each group of electric fish arose independently. Embryology and innervation clearly indicate that electrical organs originated from muscles, but there is nothing special in fish muscles directing their transformation into electrical organs. Moreover, there is no particular group of muscles that was more predisposed to such transformation, since the organs originated from different groups of muscle, including those of the tail, trunk or even the eye. It turned out that consideration of the problem at the level of the electrical organs in extant species did not lead to a solution, rather, it was necessary to ascend to the level of the whole functional complex, of which these organs were but a part.

In assuming the existence of electroreception, Lissmann was obliged to indicate those necessary structures which act as electroreceptors. He was looking for electroreceptors among the afferent fibers which had been described histologically in weakly electric fish but were not

found in other aquatic animals. Members of the Mormyridae family have such special afferent fibers which form a dense network of channels in their skin. These channels are filled with an electro-conducting gel and the sensory cells are located at the bottom of the channel. Lissmann pointed out, that similar channel organs were described earlier in other fish [3].

In 1958, when the Lissmann's work was published, a dispute on the functions of similar sensory endings in stingrays (so-called, canal organs or 'Lorenzini ampullae') was already ongoing in the scientific literature. Lissmann pointed out that these organs are extremely sensitive to changes in pressure and temperature, up to 0.05 °C. He found, however, a number of contradictions in the temperature hypothesis:

1. Why was it necessary to hide sensitive temperature receptors deep in the body?
2. The innervation of these receptors are somatotopic, that is, the brain centers processing signals from areas proximate on the body surface are in their turn also brought together in close proximity in the brain. But, why do temperature receptors need this?

Before imposing that ampullary organs can be electroreceptors, Lissmann addressed a very significant problem: Many fish (for example, sturgeon and sharks) have ampullary organs, but are without specialized electrical organs. Lissmann suggests the solution to this problem: Electroreception is not a consequence of the ability to generate electric signals, but, on the contrary, its prerequisite. Electro-sensitivity, therefore, should have preceded the occurrence of electrical generation in evolution. So, there should be many more electro-sensitive animals than those capable of generation. In other words, the electro-generating animals might be thought of as a subset of the electro-sensitive ones. In particular, Lissmann and Machin demonstrated the presence of high electrical sensitivity in the African sharp-tooth catfish, and in the title of their publication, it was emphasized that these catfish are non-electric [39]. This very important and illustrative work, clearly revealed how shortcomings in the methods of registration and in the conduct of experiments can lead the researcher to incorrect conclusions as to the ability or inability of certain fish to generate discharges.

Lissmann's assumption about the widespread occurrence of electro-reception was brilliantly confirmed, as it has been subsequently described in a variety of animal groups, including cyclostomes, amphibians and even mammals. Moreover, it is now considered proven that ampullary electroreceptors were present in the very first vertebrates [40, 41].

The postulated emergence of electroreceptors, as an evolutionary process that preceded the emergence of electrical organs, demands that the theorist detail and describe the proposed electrical stimuli, which a non-electric or pre-electric fish could perceive. One can speculate that this might include muscle action potentials, ventilatory potentials or heart beat potentials from prey, predators, individuals of the same species and from the fish themselves. These speculations were convincingly confirmed in later experiments conducted by different researchers, including the founder of the Russian School of Electroecology, Vladimir R. Protasov [42].

Concluding his article, Lissmann used a term that subsequently gained currency in various reviews and popular articles – 'an electroreceptive retina': "Such a fish living in a special electric world receives a variety of information through sensory organs distributed over the entire surface of its body, which can be likened to an 'electroreceptive retina'" [3]. Thanks to Lissmann, we employ something similar to such a 'retina' in our method of visualizing the electric fields generated by fish [10, 11].

Prior to the publication of Lissmann and Machin's work [37], the electro-sensitivity of fish was underestimated by 5–6 orders of magnitude. Using the techniques of behavioral experiments, they showed that sensitivity thresholds can reach current densities of 20 pA/cm² or electric field strength of fractions of μV/cm. Taking into account the density of electro-receptors in the skin and the duration of electric discharges, these values correspond to the passage of thousands of ions through a single receptor [43].

4. Studies of the mechanisms of electrical generation and electroreception

Lissmann's claims that *Gymnarchus*, mormyrids and gymnotids have electroreception, and are capable of electrolocation and electrocommunication were confirmed by his behavioral experiments, as well as physical calculations performed by Machin [3,37]. Lissmann's arguments, as well as Machin's estimates, were very convincing. However, scientific society was interested in specific details, details that required additional research. Furthermore, Lissmann's lively publications attracted many specialists to the study of mormyrids and gymnotids, foremost among whom we would like to name M. Bennett, T. Szabo, T. Bullock, W. Heiligenberg and V. Protasov. Once again, we draw the attention of our readers that we do not pretend to observe the whole history of investigations of the mechanisms of electrogeneration and electroreception. Equally, we do not try to draw the current state in the field. We only spot some striking and/or curious episodes of fundamental research on electric fish that were (at our glance) significant for determining the direction of further development of science.

Bennett's review on electric organs [36] remains one of the most cited when it comes to the physiology of the electrical organs of fish. A powerful school of bioelectrogenesis research was formed in the 1950s [44], and Bennett applied the theoretical concepts, methods and approaches of this school to electric fish, describing their morphology, physiology, and the mechanisms of electric activity control. Summarizing the extensive literature devoted to the structure of electric organs and the mechanisms of electric signal generation, we describe hereunder its main provisions and conclusions.

Electrical organs evolved independently in different groups of fish. This is evidenced, for example, by the appearance of such organs in different parts of the body in different fish species. By the time of Lissmann's publications, electrical organs had already been discovered and described in species belonging to six different orders, and in all six cases those electric organs arose independently [36, 45]. In his review, Bennett described only strongly electric catfish (*Malapterurus*) among Siluriformes and only strongly electric stargazers (*Astroscopus*) among Trachiniformes. Later, the ability to generate electric signals was shown for many Siluriformes, but electro-generating structures have, to date, only been described for catfish of the genus *Synodontis* [46–48]. In addition to the strongly electric *Astroscopus*, weakly electric *Uranoscopus* were also found among the stargazers [4, 49, 50]. It should be noted that, amongst all those electric fish having anatomically distinct electric organs, only stargazers lack the faculty of electroreception. This fact is confusing and particularly relevant when discussing the possible functional purposes of electric organs [49–51].

Electrical organs consist of specialized cells, called 'electrocytes', whose number can range from hundreds to millions in weakly electric and strongly electric fish, respectively. These organs are of neuromuscular origin, and in the process of evolution, not only muscle fibers, being the precursors of electrocytes, but their associated neurons and synapses also underwent transformation. Moreover, in the representatives of the Apterontidae family, the muscular component was lost and the modified axons of motoneurons evolved into the electro-generating structure. Thus, the general principles of electro-generation in electrocytes are the same as in ordinary nerve and muscle cells [36]. The tissues surrounding the electrical organ have high resistance, forming an insulating shell that prevents the shunting of current through internal organs, thereby reducing potential self-harming effects [36].

In fish, the resting potential is about 60 mV [44]. With chemical or electrical excitation, the permeability of the membrane to sodium ions increases dramatically, which permits the entry of

an avalanche-like sodium current into the cell in the same way as it occurs in human neurons and muscles (action potential). The typical duration of this process is in the order of one millisecond.

The qualitative differences between electrocytes and muscle cells are: The absence of a contractile apparatus in the former. Besides that, in many electric fish, the electrocytes are flattened along the axis of the organ (along the current lines). There are also a number of morphological peculiarities at tissue level. As a rule, synaptic plates are significantly enlarged, and all electrocytes are innervated from only one side, rostral or caudal. In this case, only the membrane at the innervated side of electrocyte is electrically excitable. In mormyrids, the electrocytes have bilateral innervation, and membranes at both sides are electrically excitable. The excitation of the opposite side of the electrocyte occurs with a delay, which results in the generation of biphasic bipolar electric signals. The shape of such discharges is sensitive to differences in the length of the delay between the excitation of the rostral and caudal membranes.

The large area of synaptic contact and the pronounced asymmetry of innervation allows the rapid and simultaneous depolarization of many cells, which leads to a summation of local transmembrane currents and voltages. This does not happen with the contraction of ordinary muscles due to the out-of-sync nerve impulses and irregular innervation of muscle fibers. The higher the degree of synchronicity in the excitation of electrocytes, the closer the form of discharge of the whole organ is to that of a single electrocyte. The latter is, in turn, determined by the morphological features of the electrocyte itself and its innervating axon. The degree of morphological specialization of electric organs is such, that mature individuals of the same sex and species generate discharges of very similar shapes, which allows researchers to regard this characteristic as a taxonomic feature, and thereby another determinant of the species of a fish specimen [52–56].

Two types of rhythm were found in gymnotids:

1. pulsating, with the pauses between the distinct discharges, which, as a rule, exceed the duration of the discharges themselves;
2. wavelike, in which individual discharges merge into a continuous periodic signal whose frequency changed with behavior.

It should be noted that after several taxonomic revisions, all ‘wavelike’ and ‘pulsating’ gymnotid species were allocated to various families. All mormyrids are pulsating, save for *Gymnarchus*, which has a wavelike character of generation. If the shape of the discharge is determined by the morpho-physiological characteristics of electrical organs and does not change from discharge to discharge, then the rhythm of generation, as set by the central nervous system, may be regarded as a form of behaviour, especially in ‘pulsating’ fish.

Electrocytes are innervated by electromotoneurons located in the spinal cord. The number of electromotoneurons is, apparently, determined by the evolutionary origin of the related electrical organs, and not by their current structure [49]. For example, several million electrocytes in an electric catfish (*Malapterurus*) are innervated by only two electromotoneurons, whereas about five hundred electrocytes of the Peters’s elephantnose fish (*G. petersii*) are innervated by as much as two hundred electromotoneurons [57,58].

Electromotoneurons are, in their turn, innervated by relay neurons, which are innervated by pacemaker neurons located in the electromotor nuclei in the medulla oblongata. The pacemaker or command nucleus governs the rhythm of generation, and is regarded as the highest level in the control circuit of an electric organ [59]. Neurons of the relay nuclei switch the signals between the pacemaker and motor neurons, providing a correct synchronization of the excitation of the latter [36]. However, the synchronous excitation of all electromotoneurons by relay cells does not, by itself, provide synchronous excitation of all electrocytes, since the propagation time of

nerve impulses may exceed the duration of the discharge. The nerve impulse propagation time compensation is provided at the structural level of the axon: Fibers going to distal parts of an electric organ have a larger diameter and/or pass in a more direct route than fibers going to cells in proximal parts of that organ [36].

With the exception of stargazers, all known fish capable of generating discharges are also able to perceive electrical signals. In the early days of electroecology [3, 37], electro-sensitivity was evident in behavioural experiments involving the use of artificial electric signals to mimic prey. These methods were habitually employed in the 1960s, in behavioural studies of sharks and rays [41]. Electro-sensitivity thresholds, as determined in such experiments, were called 'behavioural', and, in sharks and rays, they were as small as about 5 nV/cm [60]. In freshwater electro-sensitive species, values of about 0.1–10 μ V/cm were found [61]. Ordinary freshwater fish can also react to electric fields, in their case with a strength of about 1 mV/cm or more, however, these reactions are usually involuntary and are not associated with the presence of specific electroreceptors [62].

Studies of the physiology of electroreceptors were initiated in the late 1960s by Thomas Szabo and Theodore Bullock, who assembled two separate groups of specialists, in Europe and the USA, respectively [63]. An active collaboration ensued. In the mid-1970s, Walter Heiligenberg began cooperation with Bullock. Heiligenberg was a student of the famous zoologist Konrad Lorenz, one of the founders of ethology, and quickly became one of the leaders in the neurophysiology of electric fish [64]. In 1986, under the editorship of Bullock and Heiligenberg, a collection of review articles was published on various aspects of electroreception [65] – this collection is still one of the best introductions to this field of science.

In relation to electroreceptors the concept of the 'electrosensitivity' requires clarification, first of all, of what kind of physical stimulus the receptor reacts to. This may be an electric potential difference on a sensory cell or between the pore and the basement membrane of the skin epithelium, or a current flowing through a receptor. Arguments have been made in favor of the view that electroreceptors are more 'voltmeters' than 'ammeters' [41].

The term 'electroreceptor' refers to an anatomical structure consisting of an epidermal capsule or ampulla located in an invagination of the basement membrane of the skin epithelium, and containing sensory cells. A channel connects the ampulla with the external environment through the pore. Electroreceptors are unevenly distributed throughout the body surface. The maximum density was found in the head area (up to 20–80 pcs/mm²), the minimum was found in the tail part of the body (1–2 pcs/mm²), and the receptors were absent close to the electric organ. Their total number may amount to tens of thousands in fish with a length of 20–30 cm [65]. Comparison of the receptors of different fish species revealed two types of them: Ampullary (ampullae of Lorenzini), and tuberous. Ampullary receptors have been found in all electrosensitive animals, and tuberous receptors have been described only in mormyrids and gymnotids, although their presence was also assumed for certain catfish [66].

Morphologically, ampullary and tuberous receptors differ in the relative ratio between the areas of the apical and basal membranes of sensory cells. In ampullary receptors, the area of the former is much smaller than the latter, while, in tuberous receptors, it is the opposite. In addition, in the capsule of tuberous receptors, the volume between sensory cells and the pore is filled with so-called 'plug cells'. Therefore, there is no direct galvanic contact between the sensory cells and the environment. Plug cells, together with tightly connected covering cells, form an equivalent sequential capacity [61], which is in line with the specialization of tuberous receptors to perceive high-frequency signals, although there is, as yet, no complete and detailed understanding of their physiology.

Low-frequency ampullary receptors are sensitive to signals in the range of 0.1–50 Hz, and high-frequency tuberous receptors to those in the range of 50–2000 Hz [65]. The difference in these ranges is of biological significance. Ampullary receptors are involved in passive electrolocation, in particular the detection of electric fields accompanying the breathing of prey, as well as orientation in a matrix of natural electromagnetic fields [41]. Meanwhile, it is thought that tuberous receptors are specialized for active electrolocation and communication, that is, for the perception of the fish-generated discharges.

There are two types of tuberous electroreceptors in mormyrids. Receptors of the first type respond to each discharge with a single spike, whereas the second type of receptor responds with multiple spikes, and their number reflect the amplitude of the stimulus. This physiological difference corresponds to two kinds of receptors, morphologically different, known as knollenorgans and mormyromasts, respectively [58]. It was shown that the phase and amplitude of the perceived signals are already separated at the basic levels of processing of electrosensory information. Knollenorgans are designed to register the precise moment of arrival of the stimulus' front (time-coding receptors). Mormyromasts also respond to the signal with a series of spikes encoding the amplitude of the signal (amplitude-coding receptors). Functionally, gymnotids also have two types of receptors: amplitude-coding and time-coding, but the morphological differences between them are not so prominent. Besides that, the amplitude-coding ones code it with the probability of generation of a single spike (the greater the amplitude – the greater the probability), rather than with the length of their train as in mormyrids (the greater the amplitude – the longer the train)! [61].

Walter Heiligenberg not only performed many behavioural, neuroanatomic and neurophysiological experiments with his own hands, including intracellular registration of responses from hundreds of neurons in different parts of the brain, but he was also very much a human unifier, gifted in involving other people in his work. His tragic death in a plane crash at the age of 56 has significantly impoverished this area of science. Unlike many specialists who limit themselves to the question: ‘What is its structure and how does it work?’, Heiligenberg, like Lissmann, always emphasized the question: ‘What is its purpose?’ Moreover, he considered the preliminary attribution of functions, albeit hypothetical, as a prerequisite for research. No longer confined to pure electrophysiology, solely focused on the analysis of signals within the central nervous system, Heiligenberg's research, extended to neuroethology, to include the behaviour of the fish under study.

Although Heiligenberg did not hide his strategic interests concerning the general principles of the functioning of the central nervous system, his main experimental efforts were aimed at a very specific problem: “How is the jamming avoidance response (JAR) is carried out in glass knifefish (*Eigenmannia virescens*)?” This phenomenon is the ability of ‘wave’ gymnotids to modulate their own signal frequency in response to the application of an external signal of similar frequency. Thus, the resulting frequency difference (D_f) prevents interference with the normal electrolocation of neighbouring fish.

Heiligenberg began his research with a series of behavioural experiments on different fish species in order to determine their electrolocation ability in the presence of an external artificial signal [67–70]. Already in the first of these works, he proved the relationship between JAR and the electrolocation of moving objects. He tried to determine the contribution of different parts of the body surface to the total reaction of the fish. He also raised the question of how the fish determines its own frequency. The problem is that gymnotids, unlike mormyrids, have no direct connection between the command center of the electro-generating system and the electrosensory

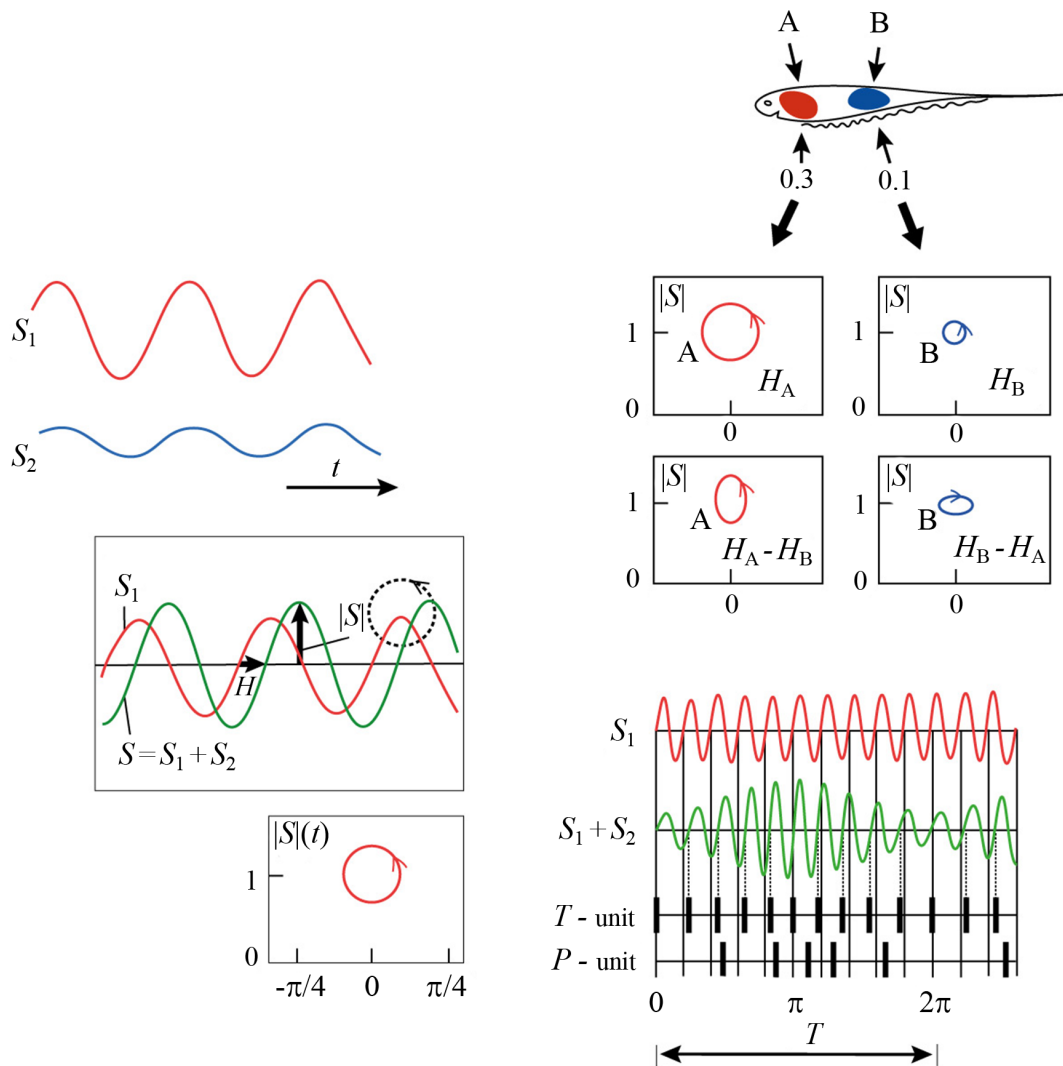


Fig 5. Determination of the sign of the difference of frequencies during the jamming avoidance reaction in *Eigenmannia virescens* [73]. Explanations in the text

lobe. That is, the parameters of their own signal can be restored only from the response of their own electroreceptors.

A long scientific discussion [71, 72] eventually led to a harmonious model [73]. Summation of two sinusoidal signals (fish signal S_1 with a frequency f_1 , and interference S_2 with a frequency f_2) results in $S = S_1 + S_2$. Its amplitude $|S|$ and phase H change sinusoidally with a period $T = 1/(f_1 - f_2) = 1/D_f$ (classical beat, Fig. 5). The phase H changes in time and nullifies in the maxima of the sum of the amplitudes ($|S_1| + |S_2|$) and the minima of their difference ($||S_1| - |S_2||$). Thus, on the plot reflecting the dependence of H on $|S|$, an ellipse or a circle will be obtained with the appropriate selection of axis scales. If $f_2 > f_1$, then the image point would move along this ellipse counter-clockwise, and clockwise if $f_2 < f_1$.

To calculate the absolute phase (H), one needs to know the true intrinsic signal S_1 , and, as there is no efferent copy of it in the brain of gymnotids, they cannot know the absolute value of the phase. Therefore, the fish compares the signals in two distant areas of the body surface – **A**

and **B** (Fig. 5). Let's say, in section **A**: $|S_2|/|S_1|=0.3$, and in section **B**: $|S_2|/|S_1|=0.1$. Then the radius of the circle displaying the dependence of $|S_A|$ on H_A is three times larger than the radius of the circle displaying the dependence of $|S_B|$ on H_B . If we now plot the dependence of $|S_A|$ and $|S_B|$ on the relative phases $(H_A - H_B)$ and $(H_B - H_A)$, respectively, then the circles would transform into ellipses, as only the horizontal dimensions transform. For region **A**, the maximum value $(H_A - H_B)$ would be $(2/3)H_A$, and for region **B**, the relative phase value $H_B - H_A = -2H_B$. Phase inversion in the second case leads to an inversion of the direction of movement of the image point. Thus, the sign of D_f and, accordingly, the direction of the frequency shift can be determined by the direction of the image point's rotation, while its magnitude can be determined according to the vertical span of the ellipse. Since there are at least two ellipses, having opposite directions of rotation, the sign of the frequency shift is determined by the larger one, that is, by the area of the body surface where the interference has greater amplitude. Similar reasoning can be repeated with respect to any other pair of body surface areas, and the total effect can be calculated by integration.

Let's address the meaning of the phase difference in the Heiligenberg's model. It is not related to delays in the propagation of an electrical signal in water caused by the magnetic interaction of currents in the source and spreading currents. In the case of freshwater weakly electric fish, taking into account the frequencies of their discharges, the distances of their interactions are much shorter than the skin depth in water. Accordingly, the discharge patterns can be considered as absolutely synchronous [74]. However, there is a significant difference between our multielectrode registration system [10, 11] and the perception system of fish. In our system, we register a complete discharge pattern on each electrode. If the sampling frequency is 50 kHz and the source frequency is 500 Hz, then for each channel we will register and store 100 points per the signal period. In fish, each receptor gives only one value for one period of wave-shaped signal or for one pulse. The receptors located closer to the source of the discharge (during communication) or to the object distorting the field (during electrolocation) would trigger first. The further the receptor is from the source, the later the response. The time course of the signal is transformed into a spatial image. This is somewhat similar to a stroboscopic oscilloscope [75], which permits the analysis of very fast processes.

According to Heiligenberg's conclusions, the separation of information into amplitude and phase takes place at the level of the electroreceptors. The phase difference is calculated in the sixth layer of the midbrain torus. The analysis of the direction of rotation is performed in the torus, tectum and electrosensory core. Heiligenberg notes that the structures controlling JAR are clearly redundant in this case, since the same could be 'done' without going beyond the medulla oblongata and midbrain, as is achieved in mormyrids by copying their own signal inside the brain. But, in all likelihood, the central processing mechanisms identified during the study of JAR are associated with more general functions and their redundancy, according to his reasoning, provides greater freedom for evolutionary development. This freedom, in particular, is due to the relative independence of processing activity from the modality of the stimulus. After the system of corresponding receptors separates the stimulus into orthogonal components, the latter are projected onto separate neural structures. Their components are composed of repeatedly replicated short chains of common neurons that can be formed according to relatively simple genetic instructions. An abundant network of connections, both within and between these structures, as well as a variety of senso-motor connections allow the evolutionary emergence of new behaviours simply by the formation of new or the weakening of old synaptic connections. Research on the processing of electro-sensory information in the brain of weakly electric fish and identifying the role of feedback in the electro-sensory lobes of the brain is actively continuing at the present time [76, 77].

5. The Russian School of Electroecology: The study of fish as living creatures in a real environment

The Russian National School of Electroecology was initiated by Vladimir R. Protasov in the late 1960s at the Institute of Evolutionary Morphology and Ecology of Animals (IEMEA) of the Academy of Sciences of USSR, now the Severtsov Institute of Ecology and Evolution of the RAS. Following Darwin and Lissmann, Protasov considered strongly electric fish as a mere artifact, albeit an exotic one, of the general evolutionary process and general biodiversity [42]. Meanwhile, the specialization of Western scientists, primarily Carl Hopkins, Bernd Kramer, and his students, in the study of mormyrids and gymnotids [52–54], lead to a narrowing of the term ‘weakly electric fish’ to include these two groups only. For a long time, it was thought that all catfish, other than electric catfish, were able to perceive electric signals, but unable to generate them [78]. Protasov, on the other hand, believed that many more electric fish, remained yet unrecognized, and that among living fish species transitional forms were to be found, between non-electric fish and strongly electric ones. Such transitional forms should, he speculated, generate relatively weak and irregular electrical signals of long duration.

Protasov’s team began work with a comparative study of the Black Sea stargazers of the genus *Uranoscopus* and weakly electric rays *Raja clavata* [4, 79–81]. The interest in stargazers stems from the strong electric activity found in their relatives – the strongly electric *Astroscopus* stargazers. Histological and morphological features of electrogenerating structures and electrophysiological mechanisms of signal generation were subsequently discovered in the Black Sea stargazer *Uranoscopus scaber*. Later, the ability to generate similar electrical discharges was shown for other species of the genus *Uranoscopus* native to the South China Sea [50].

Studies of weakly electric catfish began in 1990 with the work of American authors who registered the weak electrical discharges of *Synodontis* catfish. Their source being the protractor muscle, connecting the vertebral column and the swim bladder [46]. In the first Russian work on these fish, it was shown that, despite the obvious discrepancy between the frequency characteristics of ampullary electroreceptors and the duration of the discharges, *Synodontis* respond to the latter by changing the rhythm of their own generation [82]. Moreover, in the process of social interactions, the amplitude of the signals increased hundreds of times, and their shape and duration also changed, which is unusual for mormyrids and gymnotids [83].

Electrical discharges of African catfishes of the genus *Clarias* were recorded in the field [84]. The duration of discharges exceeded 25 ms, which corresponds to the perception range of ampullary electroreceptors [65]. As noted above, Lissmann and Machin demonstrated the high electrical sensitivity of *Clarias* but failed to discover its electrogeneration ability [39]. This failure was due to three peculiarities of *Clarias*’s discharges:

- 1) the discharges are generated only during active social interactions and never observed in lone individuals;
- 2) the discharges are long (tens or hundreds of milliseconds), which requires special equipment having lower cutoff frequencies of no more than a fraction of a hertz, which is not the case for standard audio amplifiers;
- 3) the discharges are infrequent, which requires a special standby mode for the equipment.

Clarias catfish, as an object of study, would seem to offer a promising opportunity for expanding our understanding of the evolutionary history of electric fish and the ecological role of electrical signals. Despite the low power of their discharges, these catfish can perceive the signals of their fellows, signals which are only generated during social interactions, including fights and mating. The latter fact clearly indicates their function as a medium of communication, although their meaning, for now, is somewhat obscure.

Clarias can generate a special ‘spawning’ train of electric pulses, which was not observed in other situations, and, moreover, this train is an obligatory element of the spawning ritual [85,86]. The spawning train of pulses is generated by the female, and the first pulse is observed approximately 100 ms before the first eggs are ejected. At the same time, the male presses its cheekbone to the female’s flank, immediately adjacent to the ovaries. The current hypothesis is that the female’s spawning train of discharges induces, in the male, involuntary muscular contractions resulting in the behaviour described above.

This assumption suggests a possible evolutionary path from the communication function of electrical signals in weakly electric fish to the weaponized function seen in strongly electric ones. Indeed, it can be speculated that when the increased power of the female spawning discharges first began to augment the effectiveness of male assistance in spawning, the power of these discharges thereby fell under positive natural selection pressure, and so, gained in strength. More powerful discharges would, in turn, gain new functions, selection pressure would increase, to eventually lead to a strongly-electric fish, even one having a huge electric organ filling almost the entire body.

The success of the Russian school in the registration and description of the electrical discharges of weakly electric fish was largely facilitated by developments in the field of registration equipment. As the discharges are mostly infrequent, the equipment had to work in a standby mode, which allowed recording of all electrical events [87]. Since the duration of the discharges is sometimes measured in seconds, the lower cutoff frequency should not exceed a hundredth of a hertz. Testing the ability of fish to generate electricity required the design and execution of behavioural experiments involving several test specimens, which were allowed a sufficient period of acclimation in conditions as close to natural as possible.

The successful discovery of electric discharges in clariid catfishes justified the necessary modifications in registration methodology. These improvements resulted in a significant expansion of the list of electrically-active fish, including representatives of other families of catfishes [88], and also polypteruses [89] and protopteruses [5]. Until now, it was generally accepted that freshwater electric fish inhabit only Africa and South America [78]. However, using a new technique, it became possible to register electric signals from two Asian catfish species: *Ompoc bimaculatus* [90] and *Parasilurus asotus* [91]. Researchers, including Darwin, had often asked: Why is it that only fish generate electric discharges and not, for example, aquatic amphibians? Tackling this question, we tested the giant Chinese salamander (*Andrias davidianus*), which finally allowed us to detect its electrical signals [92].

The development and use of multielectrode registration systems made it possible to analyze the distribution of an electric field in space [10]. Parallel recording of the electrical activity of multiple test fish and concurrent video recording of their behaviour in the experimental tank permitted identification of the particular fish which was the source of an observed electrical signal. External sources could also be determined [11].

It should be noted that the search for new electrically-active species turns out to be more difficult the less advanced their electrogeneration system is. On the other hand, it is precisely such intermediate cases that are most interesting when studying the processes of the evolution of these systems. Moreover, in order to understand how a particular system of organs develops and evolves, it is necessary to discover its functions. Without this, it is impossible to understand how natural selection worked in a particular case, and why development went one way and not another.

For humans, the discernibility of the functions of fish-generated electrical discharges decreases rapidly with the transition from highly specialized fish to less specialized ones. So, there

is no doubt that electric eels, stingrays and catfish use electricity for hunting and protection. In order to prove the abilities of specialized but weakly electric mormyrids and gymnotides in electrolocation and electrocommunication, additional studies were required, and as a result, the functions of their electrical activity were reliably established [3, 65]. But already in the case of *Synodontis*, although leading Western experts use the terms ‘electrocommunication’ and ‘electrolocation’, no reliable evidence of such functions for these fish was provided [48, 93]. Moreover, at present, only ampullary electroreceptors were found in catfishes. These receptors are adapted for the perception of electrical signals lasting more than 20 ms [39]. When a signal’s duration drops to units of milliseconds, the efficiency of perception also drops sharply. Thus, the duration of *Synodontis* discharges (units of milliseconds) does not fit the effective range of perception of their own electroreceptors. Such a case is not a unique. Recall that no electroreceptors were found in electrically active stargazers [49–51].

Amongst all these difficulties, the most significant one, in our opinion, is the problem of analyzing and interpreting the experimental data obtained. Fortunately, we are now in the possession of a powerful tool for recording and visualizing electrical events, one which enables comparison of the distribution of the electric field, in time and space, with a raster image of an experimental tank and audio recordings. However, these data require thoughtful and non-trivial analysis aimed at establishing a relationship between the events observed in the video and audio channels and those events that appear in the electrical channel.

We believe that other researchers, with a desire to participate and an ability to work analytically, will join in the analysis of data arrays garnered in behavioural experiments – even if they are only equipped with a computer. It is important that the original electrical and video recordings were made available in the public domain, and that a suitable media platform was provided. The recordings allow ichthyologists to see correlations between electrical events and fish behaviour, while electrical data allow programmers and data processing specialists to propose new methods of analysis, and also, hopefully, behavioural interpretations.

Conclusion

Faraday claimed that studying electricity in living matter is far more interesting than in inorganic or dead matter. Studies of living organisms are becoming more and more relevant, and not so much those addressing their morphology and physiology, but rather those dealing with their behaviour and ecology. Many diverse problems of nonlinear dynamics are concentrated here. In particular, one of the urgent fundamental and applied problems is the possibility of using aquatic animals as biosensors for assessing the state of the aquatic environment. Considering the growing variety and scale of new artificial materials polluting the environment, such as household chemicals, pharmacological substances, and nanomaterials, standard chemical analysis fails to provide continuous monitoring of the state of the aquatic environment. Therefore, preliminary biomonitoring, and detection of hazardous situations is required [94]. If we use living organisms as sensors, then formal algorithms for analyzing their behaviour and condition are needed, allowing us to distinguish between the normal and the abnormal behaviour.

Continuous noninvasive monitoring of the physiological state and behaviour of aquatic animals using multi-electrode matrix registration is being used more and more widely [6, 95]. As mentioned above, we have collected a large volume of primary data obtained during behavioural experiments using parallel video recording and multielectrode electrical recording. Happily, we are now ready to share this data with interested readers.

References

1. Maxwell JC. A Treatise on Electricity and Magnetism. Vol. 1. Oxford, UK: Clarendon Press; 1873. 425 p.
2. Finger S, Piccolino M. The Shocking History of Electric Fishes: From Ancient Epochs to the Birth of Modern Neurophysiology. Oxford: Oxford University Press; 2011. 496 p. DOI: 10.1093/acprof:oso/9780195366723.001.0001.
3. Lissmann HW. On the function and evolution of electric organs in fish. *Journal of Experimental Biology*. 1958;35(1):156–191. DOI: 10.1242/jeb.35.1.156.
4. Baron VD. Possible role of electroreception in the behavior of marine weakly electric rays *Raja clavata* (Rajidae). *Sensory Systems*. 1994;8(3–4):147–161 (in Russian).
5. Orlov AA, Golubtsov AS, Baron VD, Pavlov DS. Bioelectric fields of the African marbled lungfish *Protopterus aethiopicus* (Sarcopterygii: Protopteridae), African (*Heterotis niloticus*) and South American silver (*Osteoglossum bicirrhosum*) arowanas (Actinopterygii: Osteoglossidae): Primitive electrogenesis? *Journal of Ichthyology*. 2015;55(6):874–879. DOI: 10.1134/S0032945215060120.
6. Soh Z, Matsuno M, Yoshida M, Tsuji T. Real-time cameraless measurement system based on bioelectrical ventilatory signals to evaluate fear and anxiety. *Zebrafish*. 2018;15(2):133–144. DOI: 10.1089/zeb.2017.1491.
7. Asano M, Hanyu I. Sensitivity to electricity in the catfish, *Parasilurus asotus*. *Comparative Biochemistry and Physiology Part A: Physiology*. 1987;86(3):485–489. DOI: 10.1016/0300-9629(87)90530-5.
8. Griffin DR. *Listening in the Dark: The Acoustic Orientation of Bats and Men*. New Haven CT: Yale University Press; 1958. 413 p.
9. Lissmann HW. Continuous electrical signals from the tail of a fish, *Gymnarchus niloticus* Cuv. *Nature*. 1951;167(4240):201–202. DOI: 10.1038/167201a0.
10. Olshanskiy VM, Zlenko DV, Orlov AA, Kasumyan AO, Moller P, MacMahon E, Xue W. Multielectrode registration of episodic discharges generated by weakly electric fishes. *Izvestiya VUZ. Applied Nonlinear Dynamics*. 2022;30(2):239–252. DOI: 10.18500/0869-6632-2022-30-2-239-252.
11. Zlenko DV, Olshanskiy VM, Orlov AA, Kasumyan AO, MacMahon E, Wei X, Moller P. Visualization of electric fields and associated behavior in fish and other aquatic animals. *Behavior Research Methods*. 2023. DOI: 10.3758/s13428-023-02175-5.
12. Kuhn TS. *The Structure of Scientific Revolutions*. Chicago: University of Chicago Press; 1962. 264 p.
13. Maxwell JC. A Treatise On Electricity And Magnetism. Vol. 2. Oxford, UK: Clarendon Press; 1873. 444 p.
14. Rosenberger F. *Die geschichte der physik in grundzügen*. Bd. 3. Braunschweig: F. Vieweg und Sohn; 1890. 300 s. (in German).
15. Faraday M. On the character and direction of the electric force of the Gymnotus. In: *Experimental Researches in Electricity*. Vol. 2. London: Richard and John Edward Taylor; 1844.
16. Piccolino M. *The Taming of the Ray: Electric Fish Research in the Enlightenment from John Walsh to Alessandro Volta*. Firenze: Olschki; 2003. 221 p.
17. Walsh J. Of the electric property of the torpedo. In a letter from John Walsh, Esq; F. R. S. to Benjamin Franklin, Esq; LL. D., F. R. S., Ac. R. Par. Soc. Ext., &c. *Phil. Trans. R. Soc.* 1773;63:461–480. DOI: 10.1098/rstl.1773.0039.
18. Cavendish H. An account of some attempts to imitate the effects of the torpedo by electricity. *Phil. Trans. R. Soc.* 1776;66:196–225. DOI: 10.1098/rstl.1776.0013.

19. Feynman R. The Character of Physical Law. United States: BBC; 1965. 173 p.
20. Maxwell JC. The Electrical Researches of the Honourable Henry Cavendish. London: Frank Cass & Co.; 1879. 534 p. DOI: 10.1017/CBO9780511696480.
21. Galvani L. De Viribus Electricitatis in Motu Musculari Commentarius. Bononiae: Ex Typographia Instituti Scientiarum; 1791. 80 p. (in Latin). DOI: 10.7916/D8HB0NHQ.
22. Lebedinsky AB. The role of Galvani and Volta in the history of physiology. In: Galvani A, Volta A. Selected Works on Animal Electricity. Moscow, Leningrad: Biomedgiz; 1937. P. 7–63 (in Russian).
23. Piccolino M, Bresadola M. Shocking Frogs: Galvani, Volta, and the Electric Origins of Neuroscience. Oxford: Oxford University Press; 2013. 400 p. DOI: 10.1093/acprof:oso/9780199782161.001.0001.
24. Matteucci C. Electro-physiological researches – third memoir. On Induced contractions. Phil. Trans. R. Soc. 1845;135:303–317. DOI: 10.1098/rstl.1845.0013.
25. Volta A. On the Electricity Excited by the Mere Contact of Conducting Substances of Different Species. In a letter from Mr. Alexander Volta, F. R. S. Professor of Natural Philosophy in the University of Pavia, to the Rt. Hon. Sir Joseph Banks, Bart. K.B. P. R. S. Phil. Trans. R. Soc. 1800;90:403–431. DOI: 10.1098/rsp.1800.0016.
26. Faraday M. On the source of power in the voltaic pile. In: Experimental Researches in Electricity. Vol. 2. London: Richard and John Edward Taylor; 1844.
27. Piccolino M. Electric fishes research in the nineteenth century, following the steps of Carlo Matteucci and Giuseppe Moruzzi. Archives Italiennes de Biologie. 2011;149(4):10–17.
28. Piccolino M, Wade NJ. Carlo Matteucci (1811–1868), the “frogs pile”, and the Risorgimento of electrophysiology. Cortex. 2012;48(6):645–646. DOI: 10.1016/j.cortex.2011.08.002.
29. Moruzzi G. The electrophysiological work of Carlo Matteucci. Brain Research Bulletin. 1996;40(2):69–91. DOI: 10.1016/0361-9230(96)00036-6.
30. Matteucci C. Electro-physiological researches – first memoir. The muscular current. Phil. Trans. R. Soc. 1845;135:283–295. DOI: 10.1098/rstl.1845.0011.
31. Matteucci C. Electro-physiological researches – second memoir. On the proper current of the frog. Phil. Trans. R. Soc. 1845;135:297–301. DOI: 10.1098/rstl.1845.0012.
32. Matteucci C. Electro-physiological researches - Fifth series. Part I. Upon induced contractions. Phil. Trans. R. Soc. 1847;137:231–237. DOI: 10.1098/rstl.1847.0013.
33. Catania KC. An optimized biological taser: Electric eels remotely induce or arrest movement in nearby prey. Brain Behav. Evol. 2015;86(1):38–47. DOI: 10.1159/000435945.
34. Darwin C. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. 6th edition. London: Murray; 1872. 502 p.
35. Robin C. Mémoire sur la démonstration expérimentale de la production d'électricité par un appareil propre aux poisons du genre des raies. J. Anat. Physiol. 1865;23:577–645 (in French).
36. Bennett MVL. Electric organs. Fish Physiology. 1971;5:347–491. DOI: 10.1016/S1546-5098(08)60051-5.
37. Lissmann HW, Machin KE. The mechanism of object location in *Gymnarchus Niloticus* and similar fish. Journal of Experimental Biology. 1958;35(2):451–486. DOI: 10.1242/jeb.35.2.451.
38. Olshanskiy VM. Body-sized electric eye. Science and Life. 2005;11:94–104 (in Russian).
39. Lissmann HW, Machin KE. Electric receptors in a non-electric fish (*Clarias*). Nature. 1963;199:88–89. DOI: 10.1038/199088a0.
40. Bullock TH, Bodznick DA, Northcutt RG. The phylogenetic distribution of electroreception: Evidence for convergent evolution of a primitive vertebrate sense modality. Brain Research Reviews. 1983;6(1):25–46. DOI: 10.1016/0165-0173(83)90003-6.

41. Kalmijn AJ. The detection of electric fields from inanimate and animate sources other than electric organs. In: Fessard A, editor. *Electroreceptors and Other Specialized Receptors in Lower Vertebrates*. Vol. 3/3 of *Handbook of Sensory Physiology*. Berlin, Heidelberg: Springer; 1974. P. 147–200. DOI: 10.1007/978-3-642-65926-3_5.
42. Protasov VR, Bondarchuk AI, Olshanskiy VM. *Introduction to Electroecology*. Moscow: Nauka; 1982. 336 p. (in Russian).
43. Lissmann HW. Electric location by fishes. *Scientific American*. 1963;208(3):50–59. DOI: 10.1038/scientificamerican0363-50.
44. Chagas C, Paes de Carvalho A, editors. *Bioelectrogenesis*. Amsterdam: Elsevier; 1961. 413 p.
45. Bass AH. Electric organs revisited: Evolution of a vertebrate communication and orientation organ. In: Bullock TH, Heiligenberg W, editors. *Electroreception*. New York: Wiley; 1986. P. 13–70.
46. Hagedorn M, Womble M, Finger TE. Synodontid catfish: A new group of weakly electric fish: Behavior and anatomy. *Brain Behav. Evol.* 1990;35(5):268–277. DOI: 10.1159/000115873.
47. Boyle KS, Colleye O, Parmentier E. Sound production to electric discharge: sonic muscle evolution in progress in *Synodontis* spp. catfishes (Mochokidae). *Proc. R. Soc. B*. 2014; 281(1791):20141197. DOI: 10.1098/rspb.2014.1197.
48. Kéver L, Parmentier E, Bass AH, Chagnaud BP. Morphological diversity of acoustic and electric communication systems of mochokid catfish. *The Journal of Comparative Neurology*. 2021;529(8):1787–1809. DOI: 10.1002/cne.25057.
49. Baron VD. *Electric Power Generating Systems of Fish: Evolution and Adaptation Mechanisms*. Moscow: Nauka; 1982. 112 p. (in Russian).
50. Baron VD. Electric discharges of two species of stargazers from the South China Sea (Uranoscopidae, Perciformes). *Journal of Ichthyology*. 2009;49(11):1065–1072. DOI: 10.1134/S0032945209110058.
51. Bullock TH. General introduction. In: Fessard A, editor. *Electroreceptors and Other Specialized Receptors in Lower Vertebrates*. Vol. 3/3 of *Handbook of Sensory Physiology*. Berlin, Heidelberg: Springer; 1974. P. 1–12. DOI: 10.1007/978-3-642-65926-3_1.
52. Hopkins CD. Evolution of electric communication channels of mormyrids. *Behav. Ecol. Sociobiol.* 1980;7(1):1–13. DOI: 10.1007/BF00302513.
53. Hopkins CD. The neuroethology of electric communication. *Trends Neurosci.* 1981;4:4–6. DOI: 10.1016/0166-2236(81)90003-5.
54. Hopkins CD. On the diversity of electric signals in a community of mormyrid electric fish in West Africa. *American Zoologist*. 1981;21(1):211–222. DOI: 10.1093/icb/21.1.211.
55. Hopkins CD, Bass AH. Temporal coding of species recognition signals in an electric fish. *Science*. 1981;212(4490):85–87. DOI: 10.1126/science.7209524.
56. Hopkins CD. Behavior of mormyridae. In: Bullock TH, Heiligenberg W, editors. *Electroreception*. New York: Wiley; 1986. P. 527–576.
57. Heiligenberg W, Bastian J. The electric sense of weakly electric fish. *Annu. Rev. Physiol.* 1984;46:561–583. DOI: 10.1146/annurev.ph.46.030184.003021.
58. Russel CJ, Meyers JP, Bell CC. The echo response in *Gnathonemus petersii* (Mormyridae). *J. Comp. Physiol.* 1974;92(2):181–200. DOI: 10.1007/BF00694505.
59. Dye JS, Meyer JH. Central control of the electric organ discharge in weakly electric fish. In: Bullock TH, Heiligenberg W, editors. *Electroreception*. New York: Wiley; 1986. P. 71–102.
60. Kalmijn AJ. Electric and magnetic field detection in elasmobranch fishes. *Science*. 1982; 218(4575):916–918. DOI: 10.1126/science.7134985.

61. Zakon HH. The electroreceptive periphery. In: Bullock TH, Heiligenberg W, editors. Electroreception. New York: Wiley; 1986. P. 103–156.
62. Brown GR, Ilyinsky OB. Physiology of Electroreceptors. Leningrad: Nauka; 1984. 248 p. (in Russian).
63. Moller P. Electric Fishes: History and Behavior. Dordrecht: Springer; 1995. 584 p.
64. Baron VD. In memory of W. Heiligenberg. Russian Journal of Physiology. 2014;100:891–895 (in Russian).
65. Bullock TH, Heiligenberg W. Electroreception. New York: Wiley; 1986. 722 p.
66. Srivastava CBL, Prasad MS. Tuberos organs in a non-eletric teleosts *Rita rita* (Ham.). Proc. Natl. Acad. Sci. India B. 1984;54(3):187–188.
67. Heiligenberg W. Electrolocation of objects in the electric fish *Eigenmannia* (Rhamphichthyidae, Gymnotoidei). J. Comp. Physiol. 1973;87(2):137–164. DOI: 10.1007/BF01352158.
68. Heiligenberg W. Electrolocation and jamming avoidance in a *Hypopygus* (Rhamphichthyidae, Gymnotoidei), an electric fish with pulse-type discharges. J. Comp. Physiol. 1974;91(3):223–240. DOI: 10.1007/BF00698054.
69. Heiligenberg W. Electrolocation and jamming avoidance in the electric fish *Gymnarchus niloticus* (Gymnarchidae, Mormyriformes). J. Comp. Physiol. 1975;103(1):55–67. DOI: 10.1007/BF01380044.
70. Heiligenberg W. Electrolocation and jamming avoidance in the mormyrid fish *Brienomyrus*. J. Comp. Physiol. 1976;109(3):357–372. DOI: 10.1007/BF00663615.
71. Scheich H, Bullock TH. The detection of electric fields from electric organs. In: Fessard A, editor. Electroreceptors and Other Specialized Receptors in Lower Vertebrates. Vol. 3/3 of Handbook of Sensory Physiology. Berlin, Heidelberg: Springer; 1974. P. 201–256. DOI: 10.1007/978-3-642-65926-3_6.
72. Heiligenberg W. Principles of Electrolocation and Jamming Avoidance in Electric Fish: A Neuroethological Approach. Berlin, Heidelberg: Springer; 1977. 88 p. DOI: 10.1007/978-3-642-81161-6.
73. Heiligenberg W. Jamming avoidance responses: model systems for neuroethology. In: Bullock TH, Heiligenberg W, editors. Electroreception. New York: Wiley; 1986. P. 613–650.
74. Olshanskiy VM. Bionic Modeling of Electrical Systems of Weakly Electric Fish. Moscow: Nauka; 1990. 208 p. (in Russian).
75. Westby GWM. Electric communication in fish and the problem of recognizing very brief waveforms. Journal of Biological Education. 1987;21(3):190–196. DOI: 10.1080/00219266.1987.9654895.
76. Schumacher EL, Carlson BA. Convergent mosaic brain evolution is associated with the evolution of novel electrosensory systems in teleost fishes. eLife. 2022;11:e74159. DOI: 10.7554/eLife.74159.
77. Huang CG, Metzen MG, Chacron MJ. Descending pathways mediate adaptive optimized coding of natural stimuli in weakly electric fish. Sci. Adv. 2019;5(10):eaax2211. DOI: 10.1126/sciadv.aax2211.
78. Nelson ME. Electric fish. Curr. Biol. 2011;21(14):R528–R529. DOI: 10.1016/j.cub.2011.03.045.
79. Mikhailenko NA. On the biological significance of electrical discharges in weakly electric fish species of the Black Sea. Zoological Journal. 1971;50:1347–1356 (in Russian).
80. Baron VD, Mikhailenko NA. *Uranoscopus scaber*: Transitional form in the evolution of electrical organs in fish. Proceedings of the Academy of Sciences of the USSR. 1976;229(4):983–986 (in Russian).

81. Baron VD, Mikhailenko NA. Electrical discharge structure of the sea-fox. *Biophysics*. 1977;22(2):369–371.
82. Orlov AA, Baron VD, Olshanskiy VM. Electrogenenerating activity in synodontis and its modification under weak electric fields. *Proceedings of the Russian Academy of Sciences*. 1993;332(1):108–111 (in Russian).
83. Baron VD, Morshnev KS, Olshansky VM, Orlov AA. Electric organ discharges of two species of African catfish (*Synodontis*) during social behaviour. *Anim. Behav.* 1994;48(6):1472–1475. DOI: 10.1006/anbe.1994.1387.
84. Baron VD, Orlov AA, Golubtsov AS. African *Clarias* catfish elicits long-lasting weak electric pulses. *Experientia*. 1994;50(7):664–647. DOI: 10.1007/BF01952864.
85. Olshanskiy VM, Soldatova OA, Morshnev KS, Nguen TN. Electrical Activity of Asian Catfish *Clarias macrocephalus* (Claridae, Siluriformes) during Spawning Behavior. *Doklady Biological Sciences*. 2009;429:554–558. DOI: 10.1134/s0012496609060210.
86. Olshanskiy VM, Kasumyan AO, Moller P. On mating and function of associated electric pulses in *Clarias macrocephalus* (Günther 1864): probing an old puzzle, first posed by Charles Darwin. *Environmental Biology of Fishes*. 2019;103(1):99–114. DOI: 10.1007/s10641-019-00936-w.
87. Olshansky VM. Elaboration of equipment and methods of continuous recording of electric activity of clariid catfish (Clariidae, Siluriformes) in social and reproductive behavior. *Journal of Ichthyology*. 2010;50(11):1077–1091. DOI: 10.1134/S0032945210110147.
88. Orlov AA, Baron VD, Golubtsov AS. Electric discharges of two African catfishes of the genus *Auchenoglanis* (Claroteidae, Siluriformes). *Doklady Biological Sciences*. 2015;462(1):138–140. DOI: 10.1134/S0012496615030059.
89. Baron VD, Pavlov DS. Discovery of specialized electrogenerating activity in two species of *Polypterus* (Polypteriformes, Osteichthyes). *Journal of Ichthyology*. 2003;43(Suppl. 2):S259–S261.
90. Morshnev KS, Olshanskiy VM. Electrical discharges of Asian catfish *Ompok bimaculatus* (Siluridae). *Proceedings of the Russian Academy of Sciences*. 1997;354(3):419–422 (in Russian).
91. Baron VD, Olshansky VM. Monopolar electric discharges of the catfish *Parasilurus asotus* (Siluridae, Siluriformes). *Journal of Ichthyology*. 2009;49(5):403–408. DOI: 10.1134/S0032945209050063.
92. Olshanskii VM, Baron VD, Wei X. Electrical discharges in Chinese salamander *Andrias davidianus*. *Doklady Biochemistry and Biophysics*. 2016;471(1):447–449. DOI: 10.1134/S1607672916060193.
93. Dunlap KD, Koukos HM, Chagnaud BP, Zakon HH, Bass AH. Vocal and electric fish: Revisiting a comparison of two teleost models in the neuroethology of social behavior. *Frontiers in Neural Circuits*. 2021;15:713105. DOI: 10.3389/fncir.2021.713105.
94. Mashkin PV, Olshansky VM, Volkov SV, Uteshev VK, Wei X. Continuous biological monitoring of water quality in rivers and seas using biosensors: Bivalve mollusks. In: *Topical Issues of Zoology, Ecology and Nature Conservation*. Vol. 5. Moscow: «Sel'skhozya.jstvennyye Tekhnologii»; 2023. P. 133–138 (in Russian).
95. Tomasello DL, Sive H. Noninvasive multielectrode array for brain and spinal cord local field potential recordings from live zebrafish larvae. *Zebrafish*. 2020;17(4):271–277. DOI: 10.1089/zeb.2020.1874.