Not so shocking: the electric fish of South America

Carlo R. Laing

1 Introduction

You have probably heard tales of electric eels in the Amazon capable of stunning a horse. Or maybe you've heard of fish capable of lighting up a 100 Watt bulb. While these tales are true, there are many less–spectacular South American fish that use also electricity — not to shock their prey, but to navigate, detect their prey, and communicate with one another in water too murky for vision to be useful. These "weakly electric" fish are of much interest in the scientific community, as they provide ideal subjects for the study of questions of general interest, for example: how does an animal make sense of the information it receives about the rest of the world?

2 What is an electric fish?

An electric fish is a fish capable of generating an electric field; these are said to be *electrogenic*. If a fish can detect electric fields, it is said to be *electroreceptive*. Many fish such as sharks, rays and catfish are electroreceptive, but cannot generate electric fields, and are thus not electric fish. This sensitivity to electric fields is utilized in the repulsion of sharks from scuba divers who carry battery–powered repellers. *Strongly electric fish* generate electric fields strong enough to kill or temporarily disable their prey. Typical examples are the Torpedo ray and "electric eels" of the Amazon (these are actually a type of fish, not eel). The electric discharge for these animals can be up to 600 Volts. *Weakly electric fish* (WEF), all of which are found in fresh water, generate electric fields that are too weak to stun prey, but are used for navigation, detection of prey, and communication. Their electric discharges are typically much less than one Volt (this means that you will not receive a shock if you put your hand into a tank containing them!), and can only be detected by humans with appropriate electronic measuring equipment.

Interestingly, many strongly electric fish do not always emit strong electric fields, but sometimes use weak fields to detect prey before using a strong field to stun or kill it.

3 Distribution and History

WEF are found naturally in rivers and lakes in Africa (the Mormyriformes) and South and Central America (the Gymnotiformes). Given the physical separation between the continents, and the genetic differences between African and South American fish, the existence of WEF in both continents seems to be an example of convergent evolution, i.e. two distinct groups of organisms independently evolving the same feature.

In the Americas, WEF have been found from Mexico in the north to Uruguay and Argentina in the south. Some hundred species have been discovered, and new ones are found each year. Out of the South and Central American countries, only Belize and Chile do not have naturally–occurring populations. In Africa there are over 200 species, found through most of the continent (although not in the Sahara, northern Maghreb or southern South Africa); they are most diverse in Central and West Africa.

Strongly electric fish have been known about since ancient times. There are pictures of Nile catfish on the walls of Egyptian tombs, dating from nearly 5000 years ago. The Greeks used shocks from rays as a type of "anesthetic", believing that the electricity would numb the pain of an operation or childbirth; the word "narcotic" comes from the Greek for stingray, "narke", and "torpor" from the name of the Torpedo ray. They were also used by the Romans for the treatment of gout and headaches (perhaps the first from of electroshock treatment?). Doctors from India also used them in the treatment of epilepsy at least a thousand years ago. In more recent times, "electric eels" played an important role in early European investigations into "animal electricity" (you may be familiar with Galvani's twitching frogs' legs). However, it was only in the 1950s that the weakly electric properties of WEF were discovered by Hans Lissmann, who noticed in the London zoo that an electric eel, and a fish thought to have a small electric organ, were both swimming backwards and avoiding obstacles. He subsequently found that the weakly electric fish continuously emitted a high frequency electric field, and could distinguish between objects that differed only in their electrical properties. Since then, much effort has gone into discovering and describing the different species, and more recently, using them as model animals to investigate fundamental questions in neuroscience.

4 How is the electricity generated?

Weakly electric fish (WEF) generate an electric field with their *electric organ*, comprised of modified muscle or nerve cells, which is often located in the animal's tail. For strongly electric fish, the electric organ can form up to 80% of the fish's body mass. There are two types of WEF — "wave type" and "pulse type". This classification refers to the form of their electric organ discharge; see Figure 2. Wave type fish continuously produce as oscillating electric field. The field amplitude varies in an almost sinusoidal fashion (like a "pure tone" in music). The frequency of oscillation varies between about 50 and 1200 Hz, depending on the sex and species of the fish. There are wave and pulse type fish in both Africa and the Americas.

Pulse type fish sporadically emit single electrical pulses. The rate of emission varies a great deal, depending on whether the fish is feeding or communicating with another fish, for example. Determining whether wave discharge has any advantages over pulse discharge is a subject of current investigation.

The electric organ does not spontaneously generate an electrical field, but is controlled by impulses sent from the brain of the fish. The timing of these impulses is determined by the information the fish receives through *electroreceptors* on its skin. Electroreceptors are specialized clusters of cells on the skin of the fish that detect electric fields and send nerve impulses to the brain of the fish which encode the strength of the field. They are spread over the whole body of the fish, but have a greater density around the head.

5 What is the electricity used for?

WEF are both electrogenic and electroreceptive, and thus have an active electrosense. This is similar to echo–location in bats (which emit sounds and listen for the echos), radar (where man–made radio waves are sent out and their reflections detected) and sonar (similarly for sound waves). One use for this electrosense is navigation, i.e. the fish can use it to determine what objects are in its immediate neighborhood. This is particularly useful in many of the water bodies that these fish live in, as they are often so turbid that the visibility is essentially zero. In this way, the fish have a "sixth sense", beyond the usual five (touch, smell, hearing, taste, vision). This is one of the reasons for our fascination with such creatures.

An electric field is generated by the fish's electric organ, and propagates into the immediate environment of the fish. If there is an object in the water whose conductivity is greater than that of water (e.g. a tin can, or worm), current will flow easily through this object, forming a "hot spot" of strong electrical field on the part of the fish's skin closest to the object. Conversely, if there is a nearby object whose conductivity is less that of water (e.g. a rock), the current will be diverted around this object, leading to an electrical "shadow" being cast on the fish's skin. This gives the fish an idea of what is around it. See Figure 1.

Electroreception can be used to detect objects that generate electrical fields themselves. For example, the tiny electrical fields generated by swimming water fleas can be detected by the paddlefish that live in the Mississippi River, and having detected these fields, the paddlefish can catch the fleas. Electroreception can also be used by electric fish (for example, the electric eel) to detect the communication signals of other WEF, which are then eaten by the predator.

The electric sense is also used as a means of communication between fish. Much of this communication takes the form of "chirps", during which wave–type fish change both the amplitude and frequency of their electric organ discharge for a few tens of milliseconds. (These events are called chirps because if the electric field is converted to sound and played though a loud speaker, one hears a “chirp”.) The role of these chirps is not completely clear, but it is known, for example, that a female fish, isolated in an aquarium, can be induced to lay eggs near an electrode that has been placed in the water and which is being used to “play back” chirps that have been recorded from male fish. The rate of chirping is much higher in mating season than not, and chirps are also thought to be a means of warning other fish away from a particular fish’s territory.

A different type of behavior, more well–studied, is the *jamming avoidance response* (JAR). This occurs when two wave–type fish with similar electric organ discharge frequencies come close to one another. Whenever two frequencies are combined, another frequency, equal to the difference between the two original frequencies, is created. This is often known as the “beat” frequency. This phenomenon is used in the tuning of musical instruments: two similar notes are played together and one is changed until the beat frequency disappears — the two notes are then in tune, as the beat frequency (the difference between their two frequencies) is then zero.

For WEF, a low frequency beat apparently disrupts their ability to electrolocate. To avoid this, when two fish with similar frequencies meet, the fish with the lower frequency decreases its frequency, while the other fish moves its high frequency even higher. Since the difference in frequencies is now greater, the beat frequency is higher, and neither fish’s electrolocation abilities are affected. The JAR also occurs when there are more than two nearby fish. An interesting point is that if a fish only knows the beat frequency, it will not know whether it has the higher or the lower frequency out of the pair of fish, and will not know which way to change its own frequency. In order to determine this, both amplitude and phase information about the beat signal must be used. The characterization of the neural circuits used in the JAR is one of the successes in research into WEF.

One of the more commonly studied WEF is *Apteronotus leptorhynchus*, commonly know as the brown ghost knife fish. These are found in the Amazon basin; see Figure 3. The term “knife fish” is a result of the way the fish swim — they remain rigid and swim forwards and backwards several times past a object of interest, in a “sawing” fashion. Their main means of propulsion is the large ventral fin that extends along most of the length of the fish. This is in contrast with most fish, which move by bending their bodies from left to right in an undulating fashion, and which have difficulty swimming backwards. The sawing motion is thought to be related to the way knife fish sense the world — through detecting the electric field on their skin. If their body was not held rigid, they would not only have to take into account the electric field changes due to the object near them, but also the apparent changes simply due to that fact that their electroreceptors (on their skin) were moving as well.

The “ghost” part of the name apparently relates to both their habit of feeding at night, and also the shimmering appearance of their large dorsal fin.

6 Why is it studied?

Why are weakly electric fish so interesting? One attraction is simply that they have a sense that we do not — electrosense. By studying a sense that we do not have we can avoid some of the preconceptions we might have about how the fish use this sense, since we have no experience of it ourselves. Having said this, electrosense is most similar to our auditory sense, and it is hoped that knowledge of its workings may help us understand our own sense of hearing.

WEF are also of interest because they are sensory specialists — their perception of the world is dominated by their electrosense. This means that we can largely ignore the information transmitted in other sensory modalities. In terms of practical applications, WEF are extremely sensitive to weak electric fields. Understanding how their electroreceptors can detect such weak fields may allow us to design similar artificial electric field sensors and employ these sensors to detect, for example, the field generated by a ship passing a submarine. The electric organ discharge of wave–type fish is also very stable, in the sense of not drifting in frequency. Understanding how this is achieved may allow us to better treat problems in heart rhythms and design artificial pacemakers.

On a broader level, why do we study animals at all? One reason is that they are often simpler than us, in terms of the complexity of their nervous systems. Thus it makes sense to investigate and understand simpler organisms before moving on to the one that is of most interest — the human. Also, many organisms are thought to perform general processes, for example, learning, using similar biochemical mechanisms. Thus results for one particular organism are often applicable to many. There is also the broader question of ethics. As a society, we accept that procedures are performed on animals during research that we would not accept being performed on humans.

Some of the researchers currently working on WEF, and their areas of interest are below. Many of them were trained by Walter Heiligenberg, who was instrumental in interesting the scientific community in the electric fish before his tragic death in a plane crash in 1994.

Len Maler and André Longtin, at the University of Ottawa, study the role of neural feedback in electrosensory processing. They want to know how the information that a fish is currently receiving modifies the way it detects and processes information in the future, anywhere from a few milliseconds ahead to minutes ahead. For example, does a prey object near one end of the fish "prime" nearby electroreceptors and make them more sensitive, in preparation for precisely locating the prey?

Carl Hopkins, at Cornell University, studies African weakly electric fish, concentrating particularly on species recognition (how can a fish determine the species and sex of other nearby fish, given that their electric organ discharges are often less than a millisecond long?). He is also interested in the evolution of different species, and has traveled to central West Africa to discover and investigate new species.

Mark Nelson, at the University of Urbana–Champaign, is interested in how an animal's nervous system can extract useful information from the signals received by the sensory organs, at the same time suppressing irrelevant background noise. As part of this, his group has developed techniques for filming and subsequently analyzing the behavior of free–swimming fish capturing single water fleas.

Philip Stoddard, at Florida International University, is interested in the behavior and ecology of WEF, and also the evolution of their electrical signals. One of his findings is that the force of predation seems to have caused WEF to evolve more complex electric organ discharges, in order to reduce the detectability of their electrolocation and communication signals by predators.

Curtis Bell, at the Oregon Health and Science University, studies central processing and memory in WEF. The fish are used because, in a laboratory, their sensory input can be precisely controlled, and because they have been established to have *synaptic plasticity*. Synaptic plasticity refers to changes in the strengths of connections between neurons, and is fundamental to the formation of memory. In the fish, these memories are used to form expectations, which are subtracted from the current sensory input, allowing inputs that are unexpected or novel to stand out more clearly.

Away from North America, there is also a large group of researchers at **Instituto de Investigaciones Biologicas "Clemente Estable"**, in Montevideo. Despite Uruguay's economic problems and a lack of funding for scientific research, much work on various aspects of Uruguayan weakly electric fish is carried out there, particularly in relation to the mechanisms underlying electric organ discharge.

7 Author bio

Carlo Laing has a Ph.D. in applied mathematics from the University of Cambridge, and is currently a research associate at the University of Ottawa, Canada, studying sensory processing and neural feedback in the weakly electric fish *Apteronotus leptorhynchus*. He traveled to Uruguay in 2002 to speak about his work (and to watch candombe and murga music during Montevideo's Carnaval).

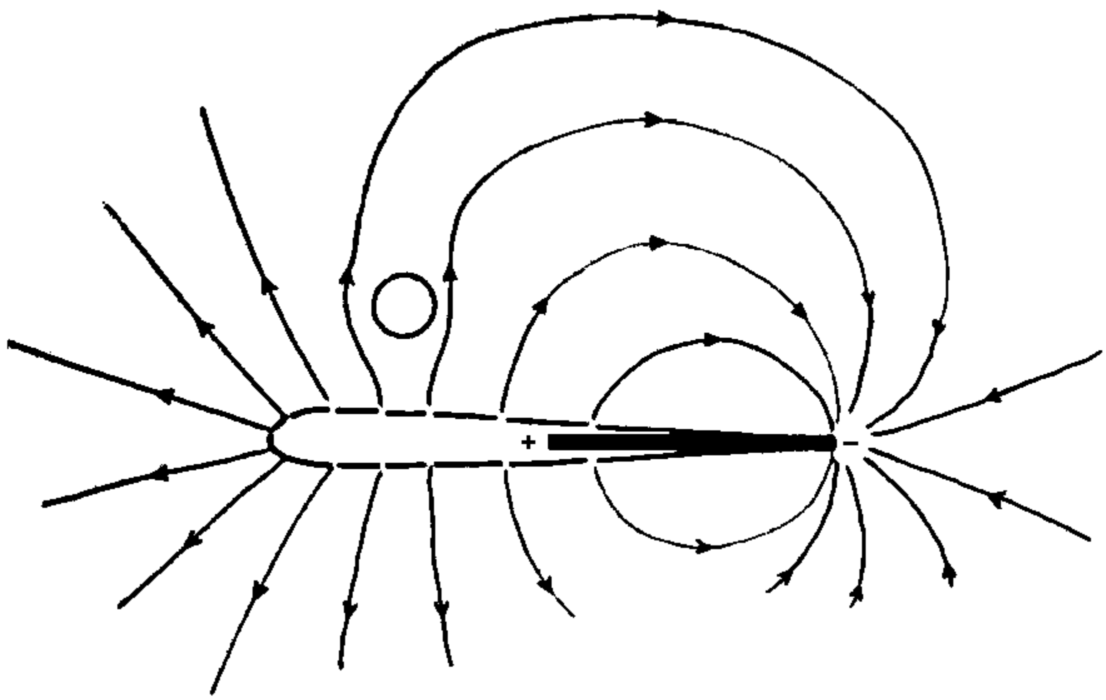

Figure 1: A schematic showing current flowing past an object in the vicinity of an electric fish (as seen from above). The current flows from the head region to the tail, and is deflected around the non–conducting object. The direction of current flow changes at up to 1000 times a second. Picture courtesy of Mark Nelson.

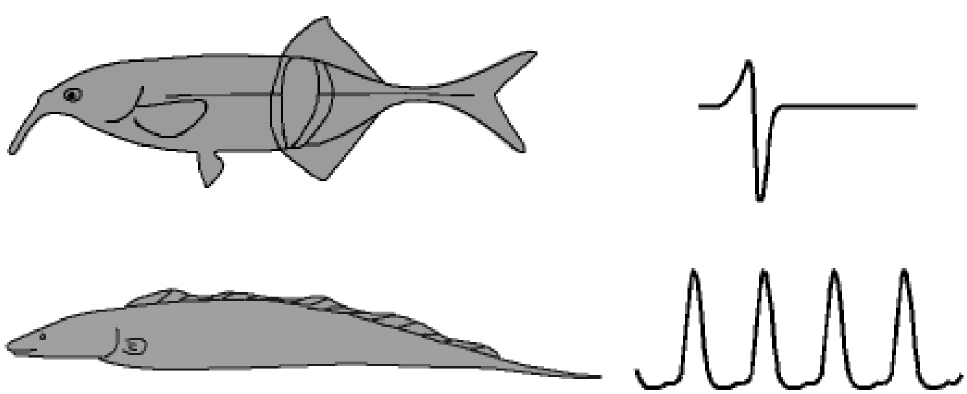

Figure 2: Pulse–type (top) versus wave–type (bottom) fish. On the right are typical electric organ discharges. Picture courtesy of Masashi Kawasaki.

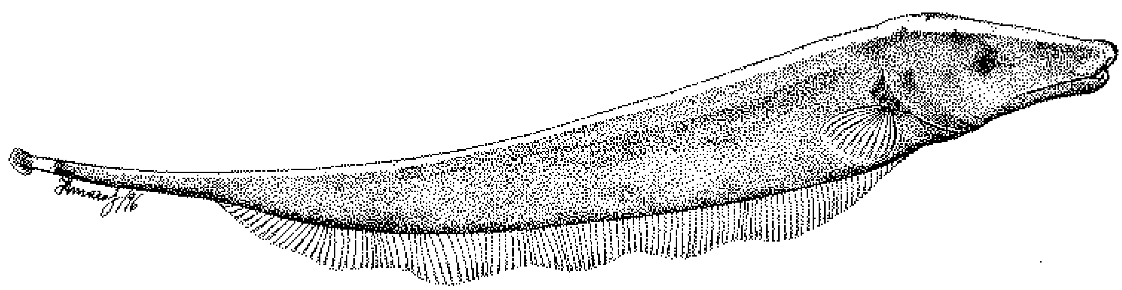

Figure 3: *Apteronotus leptorhynchus* (black ghost knife fish). These fish are typically 10-20 cm long when fully grown. Picture courtesy of Joe Bastian.