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Review Paper

Computational modeling of electric imaging in weakly electric fish: Insights for physiology, behavior and evolution

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ABSTRACT

Weakly electric fish can sense electric signals produced by other animals whether they are conspecifics, preys or predators. These signals, sensed by passive electroreception, sustain electrocommunication, mating and agonistic behavior. Weakly electric fish can also generate a weak electrical discharge with which they can actively sense the animate and inanimate objects in their surroundings. Understanding both sensory modalities depends on our knowledge of how pre-receptorial electric images are formed and how movements modify them during behavior. The inability of effectively measuring pre-receptorial fields at the level of the skin contrasts with the amount of knowledge on electric fields and the availability of computational methods for estimating them. In this work we review past work on modeling of electric organ discharge and electric images, showing the usefulness of these methods to calculate the field and providing a brief explanation of their principles. In addition, we focus on recent work demonstrating the potential of electric image modeling and what the method has to offer for experimentalists studying sensory physiology, behavior and evolution.

Contents

1. Introduction

The various forms of life that inhabit the planet are constantly exposed to different forms of energy. Organisms have evolved the ability to obtain data from the environment sensing changes in the different types of energy. Muscle and nervous tissue generate electric potentials which can be detected in conductive mediums such as water. Several aquatic animals have evolved the capacity to sense these electric potentials allowing them to detect other animals, whether they are conspecifics, preys or predators. The capability to locate electrogenic sources or objects with distinct electrical properties is called passive electrolocation.

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Among the fishes that have this electric sense there is a subgroup of species from America and Africa that convergently evolved the capacity to generate electric fields by means of a specialized structure called the Electric Organ (EO) (Hopkins, 2005; Lavoué et al., 2012; Lissman, 1951; Lissmann and Machin, 1958). They also evolved specialized electroreceptors and neural structures devoted to detecting and processing these self produced fields. These specializations confer the ability to detect the perturbations in the field resulting from the presence of objects whose conductivity contrasts with that of the medium. This results in an active sensory modality in which electric fields can be used to sense both, living organisms and inanimate objects. This submodality of electric sense is termed active electroreception and the animals with this ability are called weakly electric fish (in contrast to other electric fish which produce strong electrical discharges that serve different purposes).

Lissmann and Machin (1958) coined the term unperturbed (or basal) field for the field generated by the EOD in the absence of objects and the term perturbed field for the electric field generated in the presence of objects. The perturbation is the difference between the perturbed and basal electric field. They also named imprimence to the properties of the object responsible for the perturbation. The electric image of the object was defined as the transcutaneous voltage (or current density) through the skin of the fish produced by the perturbing field, which is sensed by an array of electroreceptors.

The concept of electric image determines one important technical drawback to the experimental study of electroreception: we should be able to measure precisely the electric basal and perturbed fields on the sensory surface in order to obtain the sensory image. To quantify the stimulus we should measure transepidermal voltages or current densities on the fish skin. This precise measurement are technically very difficult for many positions at the same time. They have been achieved only for a single position on a immobile fish (Chen et al., 2005) and on a freely moving one (Fotowat et al., 2013). Those experimental difficulties to determine the electric image highly increase when the scene (the ensemble of "physical objects" present: one or more fish, one or several objects and their relative positions, etc.) is complex and/or the fish is moving. Measuring the spatial pattern of the electric image in a naturally behaving fish is still a long-shot, since it would require implanting an array of electrodes on the skin of the fish which needs to remain a healthy behaving animal. The development of computational methods, to determine fields and images in electric fishes, helps to overcome the above mentioned difficulties of experimental approaches.

The basic physical laws of electric field generation are well known and in simple cases, the differential equations that express those laws can be solved analytically. In the case of weakly electric fish the fields generated depend on the activation of the EO which can take two forms: simple: a spatially compact organ activated synchronically; or complex: a spatially extended organ with temporally asynchronous activation. Furthermore, there are pulse and wave type fishes, whose activation could be different. The spreading of the field generated by the electric organ is always through a non-homogeneous medium composed by the fishs own body (that is in itself non-homogeneous) and the external medium whose basal conductivity in normal conditions remains rather constant but can vary seasonally due to the rain, for example. The external medium conductivity is also locally modify by the presence of objects with conductivity different than that of the surrounding water, which is the basis for the electric image generation mentioned before. To resolve the resulting field of this complex physical system through analytical approaches is not possible, unless some important simplifications are introduced. The partial differential equations that express this temporally changing and spatially inhomogeneous system can only be solved numerically by computational modeling.

This review focuses on the vast potential of several computational models of electroreception developed over the last 40 years by many research groups as well as the most recent developments in this field and the perspectives that unfold for this type of modeling. Computational modeling studies of the EO discharge (EOD), to determine the transcutaneous currents and electric images, started with simple models using the Finite Element Method (FEM) in 1975 (Heiligenberg, 1975; Hoshimiya et al., 1980). The use of the Boundary Element Method (BEM) proposed by Assad and Rasnow (Assad, 1997; Assad et al., 1999) started around the turn of the century.

2. Approaches to electric field modeling

Four main modeling methods have been used to calculate the fields involved in active electroreception: analytical, finite difference, Finite Elements Method (FEM) and Boundary Elements Method (BEM). Since our problem can be treated as static (Bacher, 1983), we can solve the equations for every instant independently, regardless of the method.

The use of analytical methods to calculate the electric fields produced by the EOD are based on the mathematical expressions of the field generated by a charge. Bacher (1983) proposed to simulate 3-dimensional scenes using line charges to model the unperturbed EOD, and a dipole for the object. For the calculation, he assumed the sources to be in a homogeneous medium and that the object (simulated by a dipole) is a sphere. Rasnow and colleagues (Assad et al., 1999; Rasnow, 1996) calculated the perturbed field determining the basal field in the position of a sphere, assuming that the field is almost uniform in this region, and calculating the field generated by a sphere in a uniform field. Sicardi et al. (2000) used the analytical method to calculate the image of a small sphere close to an almost flat fish skin, where the field is almost uniform. Results rendered by these methods lack enough precision specially when scenes are not simple and the geometries of the sources and the objects are not related through simple laws. Besides, they do not consider the effect of the fish body, actually an object, which, having imprimence, modifies the perturbing field (Migliaro et al., 2005). However, Chen et al. (2005) obtained a very precise approximation to the basal field, selecting a line of poles to simulate the sources generated by the fish. Note that the sources are in the water and not inside the fish: they correspond to a simulation of the sources of the whole fish (not the EO) as a generator.

All the simulation methods are approximate, but in the most powerful ones (as those that follow) the error can be reduced considerably by refining the model. For example, in these methods, if an approximate solution is found on a discrete set of points (or sections), an increase in the number of points in the set (as for example, by interpolation), will decrease the error; and in the limit, this error will tend to zero.

Finite-difference models consist in solving the physical equations that rule the same equations solved by the analytical methods, but only on the points of a rectangular grid (Fig. 1B). This method was implemented mostly in two-dimensions. Using this method, Heiligenberg (1975) described electric images, showing the short range of electric sense. In the first papers of our group we simulated the fields produced by the African fish *Gnathonemus petersii* with a 2D model, dividing the space in a rectangular grid of points (Caputi et al., 1998). Results of this model suggest rules for electrolocation: (1) the object's position is indicated by the point of maximum modulation of the transcutaneous voltage; (2) the degree of focus of the image indicates the distance to the object.