BRAIN RESEARCH 1434 (2012) 102–114

available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research Report

Encoding electric signals by *Gymnotus omarorum*: Heuristic modeling of tuberous electroreceptor organs

*Esteban R. Cilleruelo, Ángel Ariel Caputi**

Instituto de Investigaciones Biológicas Clemente Estable, Av. Italia 3318 Montevideo, Uruguay

ARTICLE INFO

Article history:
Accepted 6 July 2011
Available online 12 July 2011

Keywords:
Active electroreception
Secondary qualities
Color
Parallel encoding
Electric fish

ABSTRACT

The role of different substructures of electroreceptor organs in signal encoding was explored using a heuristic computational model. This model consists of four modules representing the pre-receptor structures, the transducer cells, the synapses and the afferent fiber, respectively. Simulations reproduced previously obtained experimental data. We showed that different electroreceptor types described in the literature can be qualitative modeled with the same set of equations by changing only two parameters, one affecting the filtering properties of the pre-receptor, and the other affecting the transducer module. We studied the responses of different electroreceptor types to natural stimuli using simulations derived from an experimentally-obtained database in which the fish were exposed to resistive or capacitive objects. Our results indicate that phase and frequency spectra are differentially encoded by different subpopulations of tuberous electroreceptors. A different type of receptor responses to the same input is a necessary condition for encoding a multidimensional space of stimuli as in the waveform of the EOD. Our simulation analysis suggested that the electroreceptive mosaic may perform a waveform analysis of electrosensory signals. As in color vision or tactile texture perception, a secondary attribute, "electric color" may be encoded as a parallel activity of various electroreceptor types.

This article is part of a Special Issue entitled Neural Coding.

1. Introduction

Active electroreceptive fish are able to extract information about objects that modulate the waveform of a self-generated electric carrier and project electric images on an electroreceptor mosaic on the skin of these fish (Lissmann, 1958; Lissmann and Machin, 1958; see Bullock et al., 2005).

As in any other active sense, neural encoding of electric images depends on: a) the characteristics of the self-emitted, species-specific, electrosensory carrier, b) the imaging rules and c) the distribution and responsiveness of electroreceptors. This study deals with electroreceptor responsiveness in *Gymnotus omarorum*. We provide some background about such image encoding factors giving predominance to electroreceptors, the focus of this article.

Some species emit a carrier consisting of a sine-wave-like continuous electric discharge having a predominant species-specific frequency (wave species). Other species emit brief electric pulses covering a broad species-specific frequency spectrum range (pulse species). The two main groups of electric fish (Mormyriforms from Africa and Gymnotiforms from America) may use one or the other signal emission

* *Corresponding author.* Fax: +598 24875548.
E-mail address: angel@iibce.edu.uy (Á.A. Caputi).

0006-8993/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2011.07.012

strategies and provide an example of evolutionary convergence in this regard (pulse and wave, Moller, 1995). Pulse gymnotiforms have a characteristic "distributed" electric organ. In *G. omarorum*, one of the best studied species of pulse gymnotiforms, the electric organ discharge consists of a spatiotemporal pattern which in the absence of objects stimulates the skin with site-specific waveforms (Aguilera et al., 2001; Caputi, 2011; Caputi et al., 2002). These site-specific waveforms are modulated by the presence of nearby objects in the environment giving origin to what are termed electrosensory images.

Electric imaging rules depend on the propagation of the carrier energy. Objects having impedance differing from water are polarized by the self-generated electrosensory carrier. Because of this polarization, objects behave as virtual secondary electric sources. Similarly as the Moon reflects sunlight and appears to be a light-emitting object illuminating the Earth, polarized objects appear to be electric sources projecting an electric image on the mosaic of skin electroreceptors. These images provide clues about different attributes of surrounding objects (such as shape, surface, size or electric impedance) as well as about their position and distance relative to the skin (Caputi et al., 2008; Caputi and Budelli, 2006; Pereira and Caputi, 2010).

Electroreceptors of gymnotiforms are classified as two main types. One group responds to low frequency electric fields (ampullary receptors) and the other specifically senses the self-generated field (tuberous electroreceptors, see Kawasaki, 2005; Zakon, 1986). The electrosensory mosaic of the mormyrid and gymnotid groups has several types of tuberous receptors distributed in a heterogeneous way. Electric fish show an increase of electroreceptor density and variety in the perioral region which in turn has the most important central representation (Bacelo et al., 2008, Castelló et al., 2000). This region has been likened to an "electroreceptive fovea" (Castelló et al., 2000). Interestingly, a mormyrid species (*Gnathonemus petersii*) has this sensory structure on a mobile finger-like appendix below the mouth (Engelmann et al., 2009). As in most electric fish species, tuberous electroreceptors of *G. omarorum* are heterogeneously distributed on the skin of the fish. The maximal density of distribution of the different types of tuberous electroreceptors is in the jaw region (foveal region) with two additional maxima on the dorsal region of the snout (parafoveal region). The foveal and parafoveal regions have a relatively large number of electroreceptors and together contribute ca. 50% of the electrosensory map at the electrosensory lobe (Caputi et al., 2002; Castelló et al., 1998, 2000).

There are two types of receptors that can be distinguished by size, morphology and innervation pattern. Small size (type II) electroreceptors are much more abundant than large (type I) electroreceptors. Type I electroreceptors occur exclusively on the head and rostral trunk regions, while type II electroreceptors are on up to 90% of the fish body (Caputi et al., 2002; Castelló et al., 2000; Echagüe and Trujillo-Cenóz, 1980; Szabo, 1965).

Schematically, the tuberous electroreceptor anatomical structure consists of three parts: a spherical bulb-like portion (the bulb) connected to the external medium by a column of epithelial cells (the plug), a group of receptor cells that transduces the physical stimulus and a single nerve fiber synaptically in contact with these cells. The cavity of the spherical bulb is filled with these receptor cells. These pear-shaped sensory cells vary in number from 10 to 100 (Fig. 1, inset). The apical and lateral cell membranes of the sensory cells project into an extracellular space. The basal region of these cells is in synaptic contact with a single afferent fiber that innervates all (Bennett, 1967; Caputi et al., 2002; Echagüe and Trujillo-Cenóz, 1980; Kawasaki, 2005; Szabo, 1965, 1974; Zakon, 1986).

Earlier studies by Hagiwara et al. (1962); Hagiwara and Morita (1963); Szabo (1965; 1974), Bennett (1967) and Suga (1967), further extensive research by Bastian and coworkers (Bastian, 1976; 1977; Watson and Bastian, 1979) and more recently studies by Hopkins and coworkers (McKibben et al., 1993; Yager and

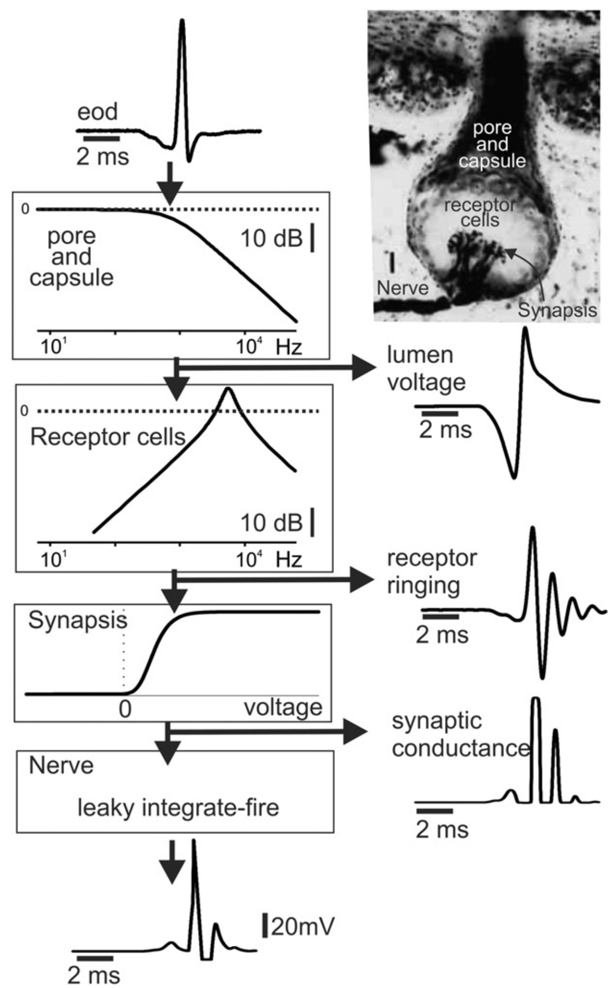

Fig. 1 – The hypothesis underlying the computational model. Encoding local signals involves four main sequential modules: a) pre-receptor structures (pore and capsule) providing receptor cells a filtered version of the transcutaneous voltage (lumen voltage), this was modeled as a low pass filter; b) a transducer represented by a group of receptor cells sensitive to the electrical stimulus, this was modeled as a second order differential equation yielding a band pass filtered ringing response; c) a synaptic module rectifying receptor response; and d) a neural encoding module, corresponding to the peripheral tree of terminals of a single nerve fiber synaptically in contact with the group of transducer cells. This was a leaky-integrate-and-fire model. Inset: Micrograph of a tuberous electroreceptor.