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On the haptic nature of the active electric sense of fish

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ABSTRACT

Electroreception is a sensory modality present in chondrichthyes, actinopterygii, amphibians, and mammalian monotremes. The study of this non-intuitive sensory modality has provided insights for better understanding of sensory systems in general and inspired the development of innovative artificial devices. Here we review evidence obtained from the analysis of electrosensory images, neurophysiological data from the recording of unitary activity in the electrosensory lobe, and psychophysical data from analysis of novelty responses provoked in well-defined stimulus conditions, which all confirm that active electroreception has a short range, and that the influence of exploratory movements on object identification is strong. In active electric images two components can be identified: a "global" image profile depending on the volume, shape and global impedance of an object and a "texture" component depending on its surface attributes. There is a short range of the active electric sense and the progressive "blurring" of object image with distance. Consequently, the lack of precision regarding object location, considered together, challenge the current view of this sense as serving long range electrolocation and the commonly used metaphor of "electric vision". In fact, the active electric sense shares more commonalities with human active touch than with teleceptive senses as vision or audition. Taking into account that other skin exteroceptors and proprioception may be congruently stimulated during fish exploratory movements we propose that electric, mechanoceptive and proprioceptive sensory modalities found in electric fish could be considered together as a single haptic sensory system.

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1. Introduction

Many aquatic species have developed electroreceptors that are able to specifically sense the drop of voltage across the skin (Bullock et al., 1982, 1961). Using electrosensory signals many species of fish, amphibia and monotremata are able to explore their environment and, in some cases, to communicate.

Abbreviations: E_b, Basal field; EO, Electric organ; EOD, Electric organ discharge; E_s, Global electromotive force of the scene; F, Shape factor; R_o, Object's resistance; R_w, Longitudinal resistance of the water volume displaced by the object; ROC, Receiver operating characteristic; R_s, Global resistance of the scene; S_{probe}, Stamp of the object

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Discovery of this non intuitive sensory modality has contributed to the rational understanding of sensory systems in general and also to develop a theoretical framework of image generation and processing (Caputi, 2004; Caputi and Budelli, 2006). In addition, understanding active and passive electric sense of animals has recently inspired the development of artificial senses to be used for robotic object exploration and guiding in murky water (Bai et al., 2012; Boyer et al., 2012, Gottwald et al., 2011; Lebastard et al., 2013; Silverman et al., 2012; Snyder et al., 2012, Solberg et al., 2008) or for medical purposes (Metzen et al., 2012).

Here we review the characteristics of the active electric sense and compare it with other sensory modalities. First, we made a general consideration of the role of the sensory carrier and its origin for setting the characteristics of a sense. Second, the core of the review focuses on electric sense and the aspects of active electroreception that likens this sensory modality as a kind of "active electric touch" rather than the more accepted metaphor of "electric vision". Finally we compare the skin senses of electric fish (including the lateral line and electroreceptive mosaics) with other active, short range and multimodal systems as touch and taste. We conclude that the active electrosensory system of electric fish is part of a haptic sensory system.

2. The importance of the sensory carrier type and its origin

A sensory system is classically associated with a characteristic carrier of signals (light, sound, pressure, gravitational fields, electric fields, chemical agents, etc.—Müller, cited by Fulton, 1946). From the four known fundamental forces of nature, just two are useful for sensory systems. Only gravitatory and electromagnetic fields meet living beings' dimensions (Sears et al., 2005). Photoreceptors are able to sense electromagnetic fields directly, triggering a redox chemical reaction in the presence of a given frequency band of light (Wald et al., 1950). There is not a known receptor able to directly sense gravitational fields.

All other types of energy different from electric or gravitatory fields depend on the interaction between the mass and/or the charge of material elements in the presence of these two fields. Consequently, all other senses rely on "secondary" energy fields that require a material substrate for propagation. In those senses signals are carried by either (a) spatial dispersion of specific molecules to which the transducer chemically reacts (e.g. olfaction); (b) a pressure wave transmitted through the interaction between molecules of the media (e.g. sense of vibration and audition); (c) the combined gravitatory, and inertial effects on pre-receptor structures (e.g. vestibular) and, the electromagnetic contact and self-generated forces and external loads (e.g. proprioception and touch). In the case of the focus of this review, electroreception, electromagnetic fields cause ionic currents through the water that in turn provoke transmembrane voltage resonance phenomena (Bennett, 1967; Cilleruelo and Caputi, 2012).

Since different types of energy are differently propagated in space and time, images carried by the different types of energy are able to represent the same external reality differently. Thus, the sensory repertoire of an animal or an artificial agent provides a framework, and ultimately sets the limits on the way that such agent behaves. This section focuses on the properties of the sensory carrier that determine the spatiotemporal range in which an object can be detected with more or less sensitivity and in which object attributes and position may be discriminated more or less precisely. We pay particular attention to the self- or allo-generation of the carrier.

2.1. *Active vs. passive re-afferent sensory systems*

An essential issue for understanding the role of the energy carrier for shaping differences between sensory systems is to consider the origin of the carrier as either self- or allo-generated by the sensory agent.

The effective stimulation of a sensory surface by an energy field is a function of two kinds of variables: (a) those for which an animal's actions are necessary and (b) those that represent the pure external influences either on animal actions or directly on receptors. To be precise with nomenclature used in this article we must recall the "reafference principle" (von Holst and Mittelstaedt, 1950) and the terminology that is derived from considering the different forms of reafference. Reafference was defined as the "afference… evoked through the effectors and receptors by the efference" (von Holst and Mittelstaedt, 1950), while exafference was defined as "the alteration of afference which is not a direct consequence of an efference but arises through external influences" (von Holst and Mittelstaedt, 1950).

There are three ways for generating reafference: (i) carrier generation, (ii) receptive surface orientation and (iii) pre-receptor signal conditioning (Caputi, 2004).

First, in many sensory systems, physical images of the world result from the interaction of a self-generated carrier with the impedance of the neighbor objects. These systems were called "active sensory systems" (Bennett, 1971) or more precisely "energy emitted sensory systems" (Camhi, 1984). The first term is the one generally used in the field of electroreception and for the sake of simplicity we will use it throughout this article.

Despite the generalized use of the term "active" referring to the self-generation of the sensory signal carrier, the generation of stimulating energy specific for a sensory modality is not the only way of affecting sensory images by self-generated actions. Sensory surface reorientation (as eye, head and finger movements, in vision, hearing and touch, respectively) and control of pre-receptor mechanisms conditioning the sensory signals (as accommodation, and motor control of the middle ear or intrafusal muscles) are clear examples of the other two ways of generating re-afference: receptive surface orientation and pre-receptor signal conditioning respectively.

In this article we refer to as "re-afferent sensory systems" to the systems in which self-generated actions are involved. It must be remarked that under this nomenclature the category "active sensory systems" is a subset of the "reafferent sensory systems". With few exceptions (as the light control of circadian rhythms) one can say that almost all