The electric image in *Gnathonemus petersii*

R. Budelli[a,*], A. Caputi[b], L. Gomez[a], D. Rother[a], K. Grant[c]

[a]*Secciones Biomatemática y Neurociencias, Instituto de Biología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo, Uruguay*
[b]*Department Neurofisiología Comparada, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay*
[c]*Unité de Neurosciences Intégratives et Computationnelles, CNRS-UPR 2191, Gif sur Yvette, France*

Abstract

We review modelling and experimental work dealing with the mechanisms of generation of electric image. We discuss: (1) the concept of electric image in the context of the reafference principle; (2) how waveform codes an impedance related qualia of the object image, referred to as "electric colour"; (3) that some characteristics of the spatial profiles generated by pre-receptor mechanisms are suitable for edge detection; (4) which parameters of the spatial profiles provide information for distance discrimination; (5) that electric images are distributed representations of the scene.
© 2003 Elsevier Ltd. All rights reserved.

Keywords: Edge detection; Distance discrimination; Electrolocation; Distributed representation

1. Introduction

Electroreceptive fish are able to detect nearby objects by processing the information contained in the pattern of electric currents through the skin. In weakly electric fish, these currents result from a self generated field (the electric organ discharge: EOD), depending on the relative positions of different parts of the animal and the electrical properties of the surrounding medium.

The electric image can be defined as the pattern of trans-epidermal voltage [3,4]. From this image the brain constructs a representation of the external world. To understand electrolocation it is necessary to know how electric images of objects are generated. Electric images have been measured in certain specific cases [1,20,28–30,36,38], but this approach, having the strength of empirical data, lacks the flexibility for describing different scenes and circumstances. Complementing these experimental studies, theoretical analysis of image generation has yielded realistic models that predict the electrosensory stimulus with acceptable accuracy [1,10–12,19,23,28].

Modeling can serve research in two different ways. A model is actually a complex hypothesis about a given system: it includes only the parameters and relations considered relevant for the system. Model development is a continuous task, allowing the understanding of the role of different parameters in the construction of the image. It provides a tool to calculate electric images in diverse circumstances and then to determine the stimulus that the brain is processing. However, a model reproduces features with a precision determined by the question posed. The exact representation of the whole system under all possible conditions would not only be difficult to achieve, but would also be of minimal usefulness. Models, like maps, are only useful if they present a simplified version of reality [9].[1]

---

[1] "...En aquel Imperio, el Arte de la Cartografía logró tal Perfección que el mapa de una sola Provincia ocupaba toda una Ciudad, y el mapa del imperio, toda una Provincia. Con el tiempo esos Mapas Desmesurados no satisfacieron y los Colegios de Cartógrafos levantaron un mapa del Imperio, que tenía el tamaño del Imperio y coincidía puntualmente con él. Menos Adictas al Estudio de la Cartografía, las Generaciones Siguientes entendieron que ese dilatado Mapa era Inútil y no sin Impiedad lo entrergaron a las Inclemencias del Sol y de los Inviernos. En los desiertos del Oeste perduran despedazadas Ruinas del Mapa, habitadas por Animales y por Mendigos; en todo el País no hay otra reliquia de las Disciplinas Geográficas". *Translation by the authors*: "...In that Empire, the Cartographic Art reached such a Perfection that the map of a single Province occupied a whole City, and the map of the Empire, a whole Province. As time went on, these Disproportionate Maps failed to satisfy and the Cartographic Academy produced a map of the Empire, having the size of the Empire and coinciding point to point with it. Following Generations, Less Devoted to the study of Cartography, understood that this vast map was useless and not without impiety they delivered it to the inclemency of the sun and the winters. In the deserts of the West, broken Ruins of the Map remain, inhabited by Animals and Beggars: in the whole country, there is no other vestige of the Cartographic Disciplines."

* Corresponding author.
E-mail address: ruben@biomat.fcien.uy (R. Budelli).

We review here results obtained with models and experimental results that were predicted by the model. We examine the information, coding temporal and spatial aspects of the reafferent stimulus, that can be transmitted.

2. The reafferent image in electrosensory systems

The concept of image is historically and intuitively based on visual images. In vision, the physical image is defined as the distribution of incident light on the retina. When the eye is focusing an object, its optical image, generated by the optical system of the eye, is on the retinal surface; thus, it coincides with the physical image. When the object is not in focus, the optical image is not generated on the retina and does not coincide with the physical image. In this case the physical image is a blurred version of the optical image. By extension, in sensory physiology, a physical image is a distribution of a stimulus on a sensory surface (a set of sensory receptors). This has to be distinguished from the neural representation of the physical image (the sensory or neural image). Most of this review refers to the physical nature of electric images, although references to other sensory modalities are used to stress the significance of mechanisms of physical image generation for sensory performance.

The stimulus for a sensory receptor is either the concentration of a substance (taste and smell) or a specific form of energy. In either case the stimulus is a local parameter: it can be the local concentration of some substance or the energy dissipated at the level of the receptor cell. It cannot be, for example, the difference in concentration or voltage between a point close to the receptor and a fixed point in the environment. In the case of electro-reception the stimulus may be defined as the electrical energy dissipated by a unit of skin surface. However, it is difficult to measure the magnitude of this. It can be calculated by: (1) $V.J$, where V is the transcutaneous voltage and J is the current density through the skin; (2) $\rho.J^2$, where ρ is the resistance by surface unit of the skin; or (3) V^2/ρ. It is easy to measure the voltage V, but not the current density or the specific resistance of the skin. But since the resistance of the skin at a given point is constant, either V or J determine the dissipated energy and, consequently they are definitions of the stimulus equivalent to the energy. Furthermore, they are related by $V = \rho.J$, and consequently equivalent.

In previously published works [10,11] we used the transcutaneous voltage V to define the image. However, since the voltage drop across the skin is proportional to the current density, the current density distribution can be considered as the electric image. Since, the resistance of the water is high compared to the fish's internal resistance, at the skin interface current density is almost perpendicular to the receptive surface [11,13,33,39].

Thus we use the current density normal to the interface (J_n) to describe the electric image. The current density in the vicinity of the skin is equal to the electric field times the water resistivity. In conclusion, the electrical image may be defined either by the dissipated energy, or the transcutaneous voltage, or the current density, or the electric field seen locally at a given point on the skin. All these definitions are equivalent since they can each be determined from the others by simple calculations.

In a static environment and when the animal does not move, visual images are distributions of arriving photons. When input information is completely determined by the environment and the optic apparatus of the eye, sensory signals are called ex-afferent [40]: they originate from a stimulus external to the individual. This is close to the case in the eye in a quiet insect, where the signal is almost completely determined by the environment. In vertebrates the efferent control of pre-receptor mechanisms (iris and lens) also contributes to image generation. In addition, vertebrates have sophisticated mechanisms for controlling gaze that allow the animal to explore in detail critical aspects of the scene. The images resulting from the interaction of the external stimulus and individual exploratory actions are called re-afferent signals. The concepts of reafference and exafference were introduced by von Holst and Mittelstadt [40]: they refer to the "afference...evoked through the effectors and receptors by the efference" as a *reafference,* and to "the alteration of the afference which is not a direct consequence of an efference but arises through external influences (through proprioceptors or exteroceptors)" as an *exafference*. Weakly electric fish explore the environment by generating the energy that will carry the electrosensory signals and also by directing an electric fovea towards interesting objects [13,14,39]. A uniform environment containing no objects with different electrical properties represents the basal stimulus for the sensory surface. Thus, in the case of the electric image, we can distinguish the *reafferent image* of a given object, resulting from the interaction of the electric organ discharge (EOD) with the environment, from the exafferent image that is the change of the basal *reafferent image* when a novel object is introduced in the neighborhood. This theoretical framework matches the processing mechanisms used by Mormyrids: plasticity in the ELL is a mechanism suitable to extract the ex-afferent image.

Usually, the stimulus at a point on the receptive surface is defined by a time function. This function can be constant in the period considered. This happens, for example, when we are looking a static image: for example a picture, fixing the gaze on a certain point. But this is not the usual situation; generally, the stimulus changes in time, either because something is changing in the environment or because the receptor (the eye, for example) is moving. In this case the stimulus at each instant is defined by a function of the dynamical evolution of the

image. In vision the physical image can be considered as a continuous signal. Visual representation results from temporal integration of visual stimuli over several milliseconds, with the result that discrete images presented as a fast sequence are perceived as a continuous signal. In pulse Mormyrids the physical image results from pulses self-generated at irregular intervals. Thus, the stimulus is intermittent, like a scene illuminated by a series of flashes. In addition, each pulse has an intrinsic temporal evolution whose waveform is coded by the electroreceptors [36], opening the possibility of a kind of electric colour perception in these fish.

3. Coding waveform and extracting colour

In pulse mormyrids, the electric organ (EO) is localised at the tail, far from the receptors and fires a short bi- or triphasic, discharge. If all the elements in the environment are purely resistive, the resulting stimulus at every point of the skin has the same waveform. In this case, the unique parameter of the stimulus at a given point of the skin is the local amplitude of the electric organ discharge (measured for example as the peak to peak amplitude: PP). The presence of a resistive object causes only changes in PP. However, the presence of a capacitive (parallel RC) object may change both: PP and the waveform.

We have studied how the impedance of elementary objects affect local EOD (LEOD) waveform. We found that waveform changes also depend on the relative position of the object and the fish. The LEOD depends on at least three parameters: resistance, capacitance of the object and the resistance between the connectors of the capacitor (environment resistance) [10]. Since the fish's internal resistance is less than that of the water, when the object is close to the fish the environmental resistance will be small. When a generator is connected to the capacitor, more current will tend to follow the lower resistance pathway through the fish body: the fish acts as a short circuit in the path of the current. When the object is far away then the environmental resistance will be greater. Consequently, the same object in different positions relative to the fish's body generates different LEOD waveforms because of the different resistance of the local environment.

To evaluate changes in waveform, von der Emde [35] introduced the positive negative quotient parameter (P/N). A capacitance is charged during the initial phase, reducing the first LEOD peak, and discharges during the second phase adding its effect to the EOD and increasing the second peak. When the capacitance is small enough, it is negligible and it does not modify the effect of the parallel resistance. When it is large enough, it acts as a short circuit shunting the parallel resistance. Thus at the extreme cases, P/N is the same as the basal EOD, while there is a maximal change in waveform at intermediate values.

PP and P/N are two of the three parameters necessary to define the LEOD. Using the model for calculating LEOD in different situations, we did not find a third parameter whose changes could be easily detected by electroreceptors. The responses of type A mormyromast electroreceptors depend only on PP, while type B receptor responses depend on both PP and P/N. Then, from the responses of both types of receptors, it is possible to determine PP and P/N. In the present state of knowledge, no third parameter coded by the nervous system has yet been identified (see von der Emde and Schwarz [39]). With these two parameters, von der Emde [35] defined the perceptual space for stimulus waveform as the set of pairs (PP, P/N) that can be produced by a RC object. This space depends on the characteristics of the object, for example, distance, size and shape. For elementary objects, this space is a crescent shaped area limited by a horizontal line (P/N = 0.6, corresponding to resistors) and a U-shaped curve (corresponding to capacitors) (Fig. 1). The parameters of the LEOD produced by RC objects with fixed capacitance fall on a curve joining the bounding U-shaped curve and the upper right corner of the horizontal line at P/N = 0.6. The parameters of the LEOD produced by objects with fixed resistance fall on the U-shaped curves.

The perceptual space change in size with distance maintaining its shape. Its maximum size corresponds to the object close to the skin and contracts to a point (the basal (PP, P/N)) for large distances. The pair (PP, P/N) generated by a given object moving away from the fish moves along a straight line passing through the basal (PP, P/N) pair. Different objects, placed at different distances may have the same (PP, P/N) and when moved share the same straight line.

If such lines are considered together with the possible "perceptual spaces" one can identify families of objects defined by the ability to produce the same (PP, P/N) relationships. Each family is constant regardless of the object distance. Objects pertaining to a family will not produce in any circumstance a (PP, P/N) pair on a line corresponding to another family. Therefore, objects pertaining to different families will be discriminated; and objects pertaining to the same family will be confused. In conclusion, we can hypothesize that such curves are defining a distance-invariant perceptual property (quale) for families of capacitive objects. Although, further experimental confirmation is required, behavioural data reported by von der Emde and Ronacher [37] is in agreement with our hypothesis.

For the visual system, an elementary object can be considered as a point source of light. A candle, placed close to a white surface projects a small, sharp, bright spot. Candles made with different waxes produce lights of different colours. The colour is the quale of the light
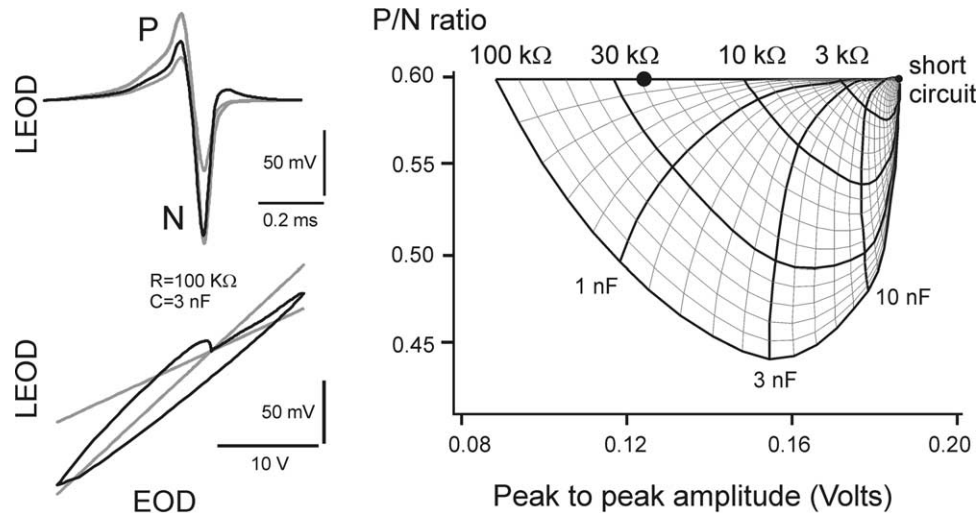
Fig. 1. Left-top: waveform of the LEOD generated by an parallel RC object (3 nF, 100 KΩ, black curve) compared with those produced by an open circuit (the smaller gray curve) and a short circuit (the larger gray curve). Left-bottom: the same LEODs plotted against the EOD. Right: the perceptual space (P/N, PP pairs). U-shaped curves correspond to objects having the same resistance and negatively concave curves to objects having the same capacity. Modified from [10].

stimulus, reflecting the combination of the emission spectra of the substances in the flame. It does not vary when the candle moves with respect to the surface. However, the same light colour can be achieved using candles of different chemical composition. Analogous to vision, the distance-invariant property related to impedance can be denominated "electric colour" [39].

4. Coding profiles: detecting edges and extracting distance

Again using the example of the candle when a object interferes with the source, it may attenuate and/or reflect the light on the surface, modifying the illumination pattern. The change in luminosity caused by the object diminishes in sharpness and contrast as the object is moved away. Thus, an object interfering with an energy field can be treated as a source of energy. In this section, we discuss how rules similar to those in the example of the candle can be applied to electroreception.

In the case of resistive objects, the only parameter that changes with the presence of the object is PP. As we discussed above, PP can be measured as transcutaneous voltage, current or electric field. For the pure resistive case, the stimulus can be also measured as the modulation of any of these variables, defined as the quotient of PP in the presence of objects and in their absence (basal stimulus). One advantage of defining the stimulus by the modulation rather than in absolute values, is that this is the same whether calculated from the transcutaneous voltage, the current density or the electric field.

This chapter deals with coding of object features by spatial profiles. The general problem was posed by

Sicardi et al. [33] who calculated numerically the electric image of revolving objects on a plane separating two different media in the presence of a field perpendicular to the plane. Numerical simulations indicated that the shape of the profile depends not only on distance, but also on the shape, the size and the conductivity of the object. In addition, we found that, whatever the object-stimulus, the image profile has an opponent center-surround "Mexican-hat" shape. The importance of this "Mexican-hat" profile and the role of the relative slope as a cue for distance discrimination are discussed in detail.

4.1. The Mexican-hat effect

A center-surround effect is present in every case when an object interacts with a field. It is enhanced when the object is close to a interface separating media of different conductivity [12,33]. These physical constrains are applicable to the generation of electric images as shown by realistic models and experiments [10,12,38] (Fig. 2).

In *G. petersii* the Mexican hat effect is asymmetric because of the caudal-to-rostral decreasing gradient of transcutaneous current. As an example, at the mid body region, metal objects funnel currents through the nearby skin causing, a larger surround effect at the rostral regions. The monotonic relationship observed experimentally between LEOD amplitude and sensory primary afferent activity [5,6], and described by modelling studies [10,12,31,33] predicts that the Mexican hat effect should also be observed in the primary afferent neuronal code. Some pioneering works in Mormyrids [34] and also in Gymnotids [17] have shown primary afferent recordings compatible with this effect. However, this

pre-receptor mechanism has been the object of a recent controversy after the studies of Rasnow [28], Assad [2] and Nelson and MacIver [27].

To address the encoding of the Mexican hat effect in the early stages of neuronal sensory processing, we have studied the sensory response as a function of the position of the object (Fig. 3). Since it is not possible to record a sensory response over the entire electrosensory lobe simultaneously, we took the alternative of studying the effect at a fixed recording site as an object was positioned statically at different points in the environment relative to the receptive field. In these experiments, a cylinder (either metal or plastic) was placed sequentially along a parasagittal line 2 mm away from the skin. The cylinder axis was perpendicular to the skin. When recording in a given point of the ELL, the response corresponds to the LEOD at the center of the receptive field. Depending on the position of the object, the center of the receptive field could fall either within the center or within the periphery of the Mexican hat profiled stimulus. The latency of afferent unit action potentials and the area of the negative field potential response, plotted as a function of the distance between the object axis and the center of the receptive field also produced an enhanced Mexican hat profile (Fig. 3). Note that the increase in unit latency produced by a plastic cylinder at the center of the receptive field is smaller than the increase produced by a similar metal cylinder at the periphery, showing that the Mexican hat effect can not be considered negligible.

The "Mexican hat" effect is a well known mechanism for edge detection [21,24]. It is usually instrumented by neural circuits based on lateral inhibition [18,22]. In the mormyrid electrosensory system, however, the center-surround profile is further enhanced centrally by lateral inhibition circuits [8,16,25,26]. Peripherally generated center-surround effects have also been described in the mechanosensitive lateral line system [15]. These

pre-receptor is preserved at the primary afferents level by the latency code of and further enhanced centrally by lateral inhibition circuits. Thus, this important edge detection mechanism is implement by a synergistic chain of independent processes in pulse Mormyrids.

4.2. The relative slope as a cue for distance discrimination

Behavioral studies have shown that Gnathonemus petersii is able to discriminate distance independently of object size and conductivity [32,38]. Two parameters: the width and relative slope of the image, have been proposed as candidates for coding object distance [12,28]. Theoretical analysis [33], experimental recordings of local fields and primary afferent discharges [12,38], and behavioural studies [32,38] all indicate that the relative slope (the maximal slope at the rostral edge of the image/maximum amplitude) of the spatial profile is the best candidate as the parameter used by the fish to measure distance [39].

The effect of shape, distance, size and conductivity of different objects on the image were analysed by Sicardi et al. [33]. Larger cylinders generate wider profiles with similar relative slopes. However, when the radius/distance ratio of the object is smaller than 3, the slope
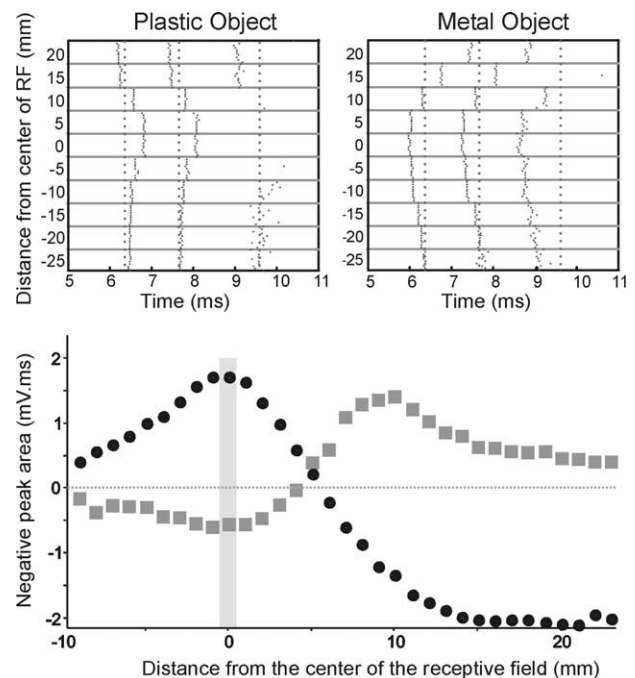
Fig. 3. Mexican hat profile in primary afferent activity. Top: unit action potential firing as a function of the longitudinal position and conductivity of the object (plastic on the left and metal on the right). A group of 10 raster diagrams represent the latency of primary afferent spikes when an object was positioned in steps of 5 mm along a parallel line close to the fish. Bottom: area of the negative peak of the sensory field potential response evoked by a plastic (gray squares) and metal (black circles) cylinder placed at different distances from the mouth. The gray bar indicates the center of the receptive field.
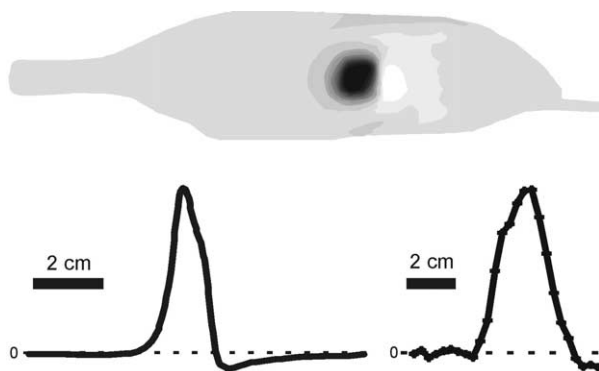

Fig. 2. Mexican hat: LEOD. Top: the image produced by a (1 cm side) cube obtained by simulation with the model. Bottom Left: profile of a (1 cm side) cube simulated with the model. Bottom Right: profile of a metal cube (2 cm side) determined experimentally (this last curve is modified from [38]).

increases (Fig. 4). The profile shape is also dependent of the object conductivity. High resistivity objects have narrower profiles than low resistivity objects of the same size (indicated by dotted and solid lines, respectively). In contrast to width, relative slope is very similar for different objects placed at the same distance (inset).

The width of the image increases with the distance of the object, showing different curves for objects of different shape. However, it also increases with the size and the conductivity of the object [33]. For this reason, width alone is not a good candidate for coding distance. In contrast, the relative slope of the physical image decreases with distance and is much less affected by conductivity and size of the object. Note that, in spite of the fact that metal and plastic objects do not have exact mirror images, their relative slopes are similar (Fig. 4, inset). Furthermore, for different objects (a cube and sphere in Fig. 5) the relative slope decreases with distance, and these changes are translated in the pattern of primary afferent activity (Fig. 6). Thus, relative slope is a more reliable parameter for coding distance.

Profiles generated by a cylinder are clearly different from those generated by a sphere (Fig. 5). One can say, in general, both the sharpness of the profile and its width depend on the curvature of the object facing the sensory surface. The shape of the profile of nearby objects depends on the shape of the object: the image of the cylinder is wider than the image of the sphere. As a consequence the relative slope increases and the surrounding trough is more marked. The shape of these

patterns change when the object is moved away from the sensory surface tending progressively towards a common profile: the Mexican-hat generated by a small sphere.

If fish is using the relative slope as a cue for distance discrimination it should interpret that a cube is closer than a sphere placed at the same distance. This theoretical prediction was confirmed experimentally [38]. This provides an additional support to the hypothesis that fish discriminate object distance by measuring the relative slope of the image [12,38].

5. Parameter profiles and distributed representation of the scene

In the case of capacitive objects, there are two profiles of interest: PP and P/N. To study whether the spatial distribution of P/N adds new information about the object, we compared PP and P/N spatial profiles. The profile produced by an elementary resistive object is
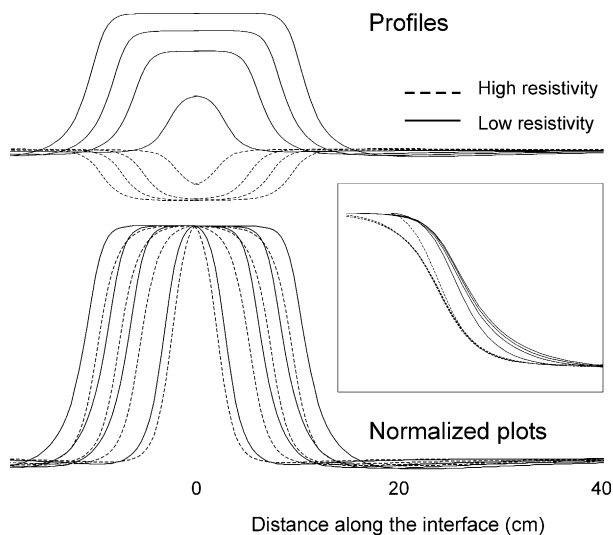

Fig. 4. Image profiles produced by cylindrical objects of different sizes and resistivities. Top: profiles produced by cylinders of high and low resistivity projected on the sensory interface. 0 corresponds to the center of the object. The distance of the object from the sensory surface is 2.5 cm and the radii of the cylinders are 3.5, 7.5, 10 and 12.5 cm. Bottom: normalized profiles (dashed lines: high resistivity objects; black lines: low resistivity objects. Inset: Normalized profiles shifted horizontally to compare relative slopes. Modified from [33].
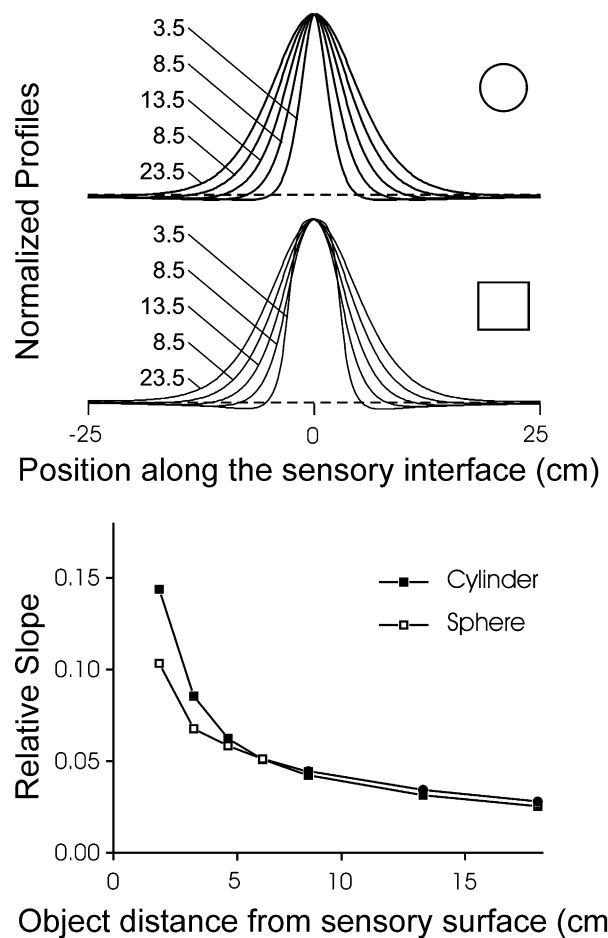

Fig. 5. Profiles depend on object shape. Top: image profiles of 7 cm wide spherical (upper) and cylindrical (lower) objects placed at different distances from the receptive surface (the numbers correspond to the distance in cm). Bottom: the relative slope of the profiles as a function of the object distance. Modified from [33].
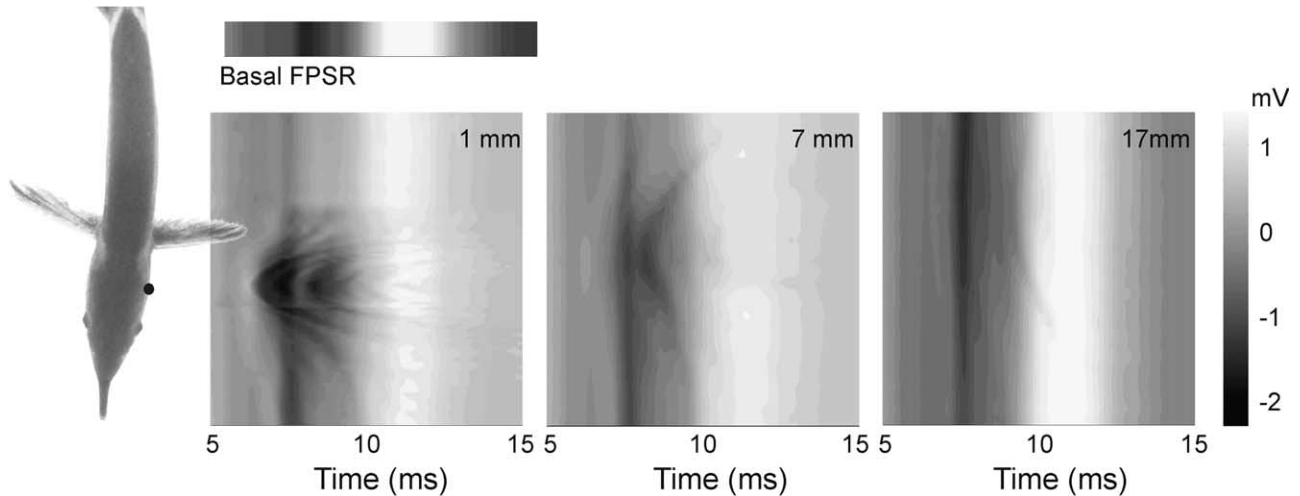
Fig. 6. Effect of distance on field potential sensory responses. The field potential sensory response recorded in the ELL granular layer for a metal cylinder placed at different positions along the side of the fish is plotted using a gray scale. The response was calculated by subtracting the field potential recorded in the curarized fish (produced by the corollary discharge: [7]), from the field potential following the normal EOD. The fish on the left indicates the position of the cylinder along the body, corresponding to the records on the same horizontal line. The black dot indicates the center of the receptive field.

similar to the PP profile produced by an elementary object of complex impedance. Thus, in both cases, the distance can be determined from the PP profiles, using the relative slope. In Fig. 7, PP and P/N profiles are "mirror images". This is the case when the PP at the projection point is larger than the basal PP. In the opposite case, the profiles are similar. In both cases, the PP/P/N relationship, for different points on the skin, should be linear. This is demonstrated from the plot of (PP, P/N) pairs (Fig. 7), where it can be seen that for each object, the (PP, P/N) pairs fall close to a straight line. In the case of elementary objects, points fall on the straight line defining the electric colour of the object. Lines corresponding to objects of different colours are divergent, intersecting at a single point [the basal (PP, P/N) pair].

Complex objects will produce dissimilar PP and P/N profiles. Elementary objects, such as punctual light sources in vision, have a defined color and their images
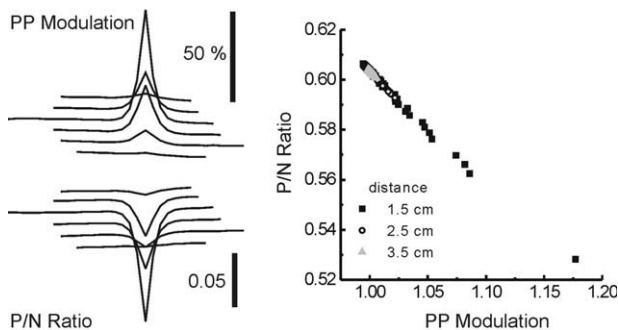

Fig. 7. Left: spatial profiles (PP, top; P/N, bottom) generated by a parallel RC elementary object (100 KΩ, 3nF). Right: P/N vs PP for different points on the surface and 3 distances. Modified from [10].

are defined only by the position in relation to the sensory surface. However, interaction of different stimuli on the sensory surface in vision and electroreception are not alike. In vision, the image of a complex object is its central projection on the retina: the image of a small object is reduced to a small region of the retina. If a new opaque object is introduced in the scene and it does not hide the first one, the image of the first one remains intact. Each of these objects produces a distinct image at different spots on the retina: we say that the representations of the objects are in apposition. There is a one to one correspondence between the points seen by the eye and the points of the image on the retina.

In contrast, in electrolocation, each point of an external object generates an image spread over the whole skin. Then, each point on the image results from the superposition of the images generated by each point of the surrounding medium: the representation of the objects are in superposition. Consequently, the information on each object is distributed in the whole pattern of stimulation on the electroreceptive surface.

Furthermore, in vision, the presence of a flat mirror reflects the light coming from the object, generating a second image. Almost every surface reflects the light coming from other sources changing the illumination of the objects. More than one flat mirror, or curved mirrors, multiply the images. In hearing, the images of different sources of sound usually not only add at the same places in the cochlea but they also interact, producing masking effects [41]. In electrolocation, these effects are more important: every object acts like a mirror generating new images and affecting the current through the other objects. Thus, objects are not only represented in superposed images, but also the image of the whole

scene is different from the superposition of the images of individual objects.

Acknowledgements

This work was partially financed by grants from the French ministry of Foreign Affairs: ECOS No. U97B03, CSIC (University of Uruguay) and Premio Clemente Estable 4014 for partial support.

References

[1] P.A. Aguilera, M.E. Castello, A.A. Caputi, Electroreception in Gymnotus carapo: differences between self-generated and con-specific-generated signal carriers, J. Exp. Biol. 204 (2001) 185–198.

[2] C. Assad, Electric Field Maps and Boundary Element Simulations of Electrolocation in Weakly Electric Fish. PhD thesis, California Institute of Technology, Pasadena, California, 1997.

[3] J. Bastian, Electrolocation, in: T. Bullock, W. Heiligenberg (Eds.), Electroreception, Willey, New York, 1986.

[4] C.C. Bell, Sensory coding and corollary discharge effects in mor-myrid electric fish, J. Exp. Biol. 146 (1989) 229–253.

[5] C. Bell, Mormyromast electroreceptor organs and their afferent fibers in Mormyrid fish II. Intra-axonal recordings show initial stages of central processing, J. Neurophysiol. 63 (1990) 303–318.

[6] C.C. Bell, Mormyromast electroreceptor organs and their afferent fibers in Mormyrid fish III. physiological differences between two morphological types of fibers, J Neurophysiol 63 (1990) 319–332.

[7] C.C. Bel, K. Grant, Sensory processing and corollary discharge effects in the mormyromast regions of the mormyrid electro-sensory lobe. I. Field potentials, cellular activity in associated structures, J. Neurophysiol. 68 (1992) 843–858.

[8] C.C. Bell, A.A. Caputi, K. Grant, Physiology and plasticity of morphologically identified cells in the mormyrid electrosensory lobe, J. Neurosci 17 (1997) 6409–6423.

[9] J.L. Borges, Del rigor en la ciencia, in: Historia universal de la infamia, Emecé, Buenos Aires, 1954.

[10] R. Budelli, A.A. Caputi, The electrical image in weakly electric fish: perception of complex impedance objects, J. Exp. Physiol 203 (2000) 481–492.

[11] A.A. Caputi, R. Budelli, The electric image in weakly electric fish: I. A data-based model of waveform generation in Gymnotus carapo, J. Comput. Neurosci. 2 (1995) 131–147.

[12] A. Caputi, R. Budelli, K. Grant, C. Bell, The electric image in weakly electric fish: II. Physical images of resistive objects in Gnathonemus petersii, J. Exp. Biol. 201 (1998) 2115–2128.

[13] A.A. Caputi, M. Castelló, P. Aguilera, O. Trujillo-Cenóz, Electrolocation and electrocommunication in pulse gymnotids: signal carriers, pre-receptor mechanisms and the electrosensory mosaic. J. Physiol. Paris 96 (2002) PII: S0928-4257(03)00005-6, this issue.

[14] M.E. Castelló, P. Aguilera, O. Trujillo-Cenóz, A.A. Caputi, Electroreception in Gymnotus carapo: pre-receptor processing and the distribution of electroreceptor types, J. Exp. Biol. 203 (2000) 3279–3287.

[15] S. Coombs, J.G. New, M. Nelson, Information-processing demands in electrosensory and mechanosensory lateral line systems. J. Physiol. Paris 96 (2002) PII: S0928-4257(03)00013-5, this issue.

[16] K. Grant, J. Meek, Y. Sugawara, M. Veron, J. Denizot, T. Hafmans, J. Serrier, T. Szabo, Projection neurons of the mor-myrid electrosensory lateral line lobe—morphology immunohis-tochemistry, and synaptology, J. Comp. Neurol. 375 (1996) 18–42.

[17] S. Hagiwara, H. Morita, Coding mechanisms of electro-receptor fibers in some electric fish, J. Neurophysiol 26 (1963) 551–567.

[18] H.K. Hartline, Inhibition of activity of visual receptors by illu-minating nearby retinal elements in the Limulus eye, Fed. Proc. 8 (1949) 69.

[19] W. Heiligenberg, Electrolocation of objects in the electric fish Eigenmannia rhamphichthyidae, Gymnotoidei, J. Comp. Physiol. 87 (1973) 137–164.

[20] N. Hoshimiya, K. Shogen, T. Matsuo, S. Chichibu, The Apter-onotus electric organ discharge field waveform and electric organ discharge field simulation, J. Comp. Physiol 135 (1980) 283–290.

[21] T. Kohonen, Self-organization and Associative Memory, Springer-Verlag, Berlin, 1984.

[22] S.W. Kuffler, Discharge patterns and functional organization of mammalian retina, J. Neurophysiol 16 (1953) 37–68.

[23] H.W. Lissmann, K.E. Machin, The mechanisms of object loca-tion in Gymnarchus Niloticus and similar fish, J. Exp. Biol. 35 (1958) 457–486.

[24] D. Marr, Vision, Freeman, NY, 1982.

[25] J. Meek, K. Grant, Y. Sugawara, T.G. Hafmans, M. Veron, J.P. Denizot, Interneurons of the ganglionic layer in the mor-myrid electrosensory lateral line lobe: morphology, immunohis-tochemistry, and synaptology, J. Comp. Neurol. 375 (1996) 43–65.

[26] J. Meek, T.G. Hafmans, V. Han, C.C. Bell, K. Grant, Myeli-nated dendrites in the mormyrid electrosensory lobe, J. Comp. Neurol. 431 (2001) 255–275.

[27] M.E. Nelson, M.A. MacIver, Prey capture in the weakly electric fish Apteronotus albifrons: sensory acquisition strategies and electrosensory consequences, J. Exp. Biol. 202 (1999) 1195–1203.

[28] B. Rasnow, The effects of simple objects on the electric field of Apteronotus Leptorhynchus, J. Comp. Physiol. A 178 (1996) 397–411.

[29] B. Rasnow, C. Assad, J.M. Bower, Phase and amplitude maps of the electric organ discharge of the weakly electric fish, Apteronotus leptorhynchus, J. Comp. Physiol. A 172 (1993) 481–491.

[30] B. Rasnow, J.M. Bower, The electric organ discharges of the Gymnotiform fishes: I. Apteronotus leptorhynchus, J. Comp. Physiol. A 178 (1996) 383–396.

[31] H. Scheich, T.H. Bullock, The role of electroreception in the animal life. II The detection of electric field from electric organs, in: A. Fessard (Ed.), Handbook of Sensory Physiology, vol. III/3, Springer Verlag, Berlin, 1974, pp. 201–256.

[32] S. Schwarz, Entfernungsmessung mit Hilfe der Elektroortung beim schwach-elektrischen Fisch Gnathonemus petersii. Diplo-marbeit, Zoological Institute, University of Bonn, Bonn, 1997.

[33] E.A. Sicardi, A.A. Caputi, R. Budelli, Physical basis of distance discrimination in weakly electric fish, Physica A 283 (2000) 86–93.

[34] T. Szabo, S. Hagiwara, A latency-change mechanism involved in sensory coding of electric fish (mormyrids), Physiol. Behav 2 (1967) 331–335.

[35] G. von der Emde, Discrimination of objects through electroloca-tion in the weakly electric fish, Gnathonemus petersii, J. Comp. Physiol. A 167 (1990) 413–421.

[36] G. von der Emde, H. Bleckmann, Differential responses of two types of electroreceptive afferents to signal distortions may permit capacitance measurments in a weakly electric fish, Gnathonemus petersii, J. Comp. Physiol. A 171 (1992) 683–694.

[37] G. von der Emde, B. Ronacher, Perception of electric properties of objects in weakly electric fish: two-dimensional similarity scal-ing reveals a City-Block metric, J. Comp. Physiol. A 175 (1994) 801–812.

[38] G. von der Emde, S. Schwarz, L. Gomez, R. Budelli, K. Grant, Electric fish measure distance in the dark, Nature 395 (1998) 890–894.

[39] G. von der Emde, S. Schwarz, Imaging of objects through active electrolocation in *Gnathonemus petersii*. J. Physiol. Paris 96 (2002) PII: S0928-4257(03)00021-4, this issue.

[40] E. von Holst, H. Mittelstadt, Das Reafferenzprinzip Wechselwir-kungen zwischen Zentralnervensystem und Peripherie, Nat-urwissenschaften 37 (1973) 464–476, (Translated in: "The behavioral physiology of animals and man". Selected papers from E. von Holst. University of Miami Press, Coral Gables, 1973).

[41] W.A. Yost, Auditory image perception and analysis: the basis for hearing, Hearing Res. 56 (1991) 8–18.