Electric images of two low resistance objects in weakly electric fish

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Abstract

Electroreceptive fish detect nearby objects by processing the information contained in the pattern of electric currents through their skin. In weakly electric fish, these currents arise from a self-generated field (the electric organ discharge), depending on the electrical properties of the surrounding medium. The electric image can be defined as the pattern of transepidermal voltage distributed over the receptive surface. To understand electrolocation it is necessary to know how electric image of objects are generated. In pulse mormyrids, the electric organ is localized at the tail, far from the receptors and fires a short biphasic pulse. Consequently, if all the elements in the environment are resistive, the stimulus at every point on the skin has the same waveform. Then, any measure of the amplitude (for example, the peak to peak amplitude) could be the unique parameter of the stimulus at any point of the skin. We have developed a model to calculate the image, corroborating that images are spread over the whole sensory surface and have an opposite center-surround, "Mexican-hat" shape. As a consequence, the images of different objects superimpose. We show theoretically and by simulation that the image of a pair of objects is not the simple addition of the individual images of these objects.

Keywords: Electric image; Object interaction; Electrolocation; Perception; Electric fish

1. Introduction

Electroreceptive fish detect nearby objects by processing the information contained in the pattern of electric currents through their skin. These currents, in weakly electric fish, result from a self-generated field (the electric organ discharge), depending on the relative positions of different parts of the animal (as for example body bending, tail position, etc.) and the electrical properties of the surrounding medium. The electric image can be defined as the pattern of transepidermal voltage (Bastian, 1986; Bell, 1989). 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 in a complex environment. Electric images of isolated objects have been measured in certain specific cases (Aguilera et al., 2001; Hoshimiya et al., 1980; Rasnow, 1996; Rasnow et al., 1993; Rasnow and Bower, 1996; von der Emde and Bleckmann, 1992; von der Emde et al., 1998), but this approach,

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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 with acceptable accuracy the electrosensory stimulus (Assad, 1997; Budelli and Caputi, 2000; Caputi and Budelli, 1995; Caputi et al., 1998; Heiligenberg, 1973; Lissmann and Machin, 1958; Rasnow, 1996). When the image is calculated by these computational models, an unique object is placed either in an infinite environment or in a tank. Experimentally, the image of an object is calculated by the difference in the transcutaneous voltage between two scenes (i.e. the fish and all the objects in the environment) in which the only difference is the pres- ence or absence of that object. But usually the fish is moving in a complex medium with several objects of interest.

We argue in this paper that when including several objects, the resulting image of the scene is not the addition of the images of the individual objects: by the contrary, the presence of an object distorts the image of others, if close enough. As a consequence, when we determine the image of an object as the difference between the current densities in the presence and absence of the object, the result depends on the context; i.e. the presence and characteristics of other objects and the active changes of the field direction related to the orientation of the skin.

2. The model

We developed a program to determine the electric image in weakly electric fish using the Boundary Element Method (BEM; Hunter and Pullan, 2001) as proposed by Assad (1997). The program allows the determination of the electrosensory images of weakly electric fish in a given environment (scene). It allows to model fishes of different species, placed in specific po- sitions in an environment with objects, and calculates the currents through the skin. The program, includ- ing the user's manual is available for any interested researcher (request: ruben@biomat.fcien.edu.uy). A scene is defined by setting the geometry and location of one or more electric fish and objects. Water and internal conductivity can be set at will. The transcu- taneous resistance at different regions of the skin can be set using a graphic interface. Complex shapes, including the fish body, are approximated by a surface composed by triangles with the help of two orthogonal pictures. The shape of the fish might be modified, although it is kept constant throughout this presentation. Once the scene is determined, the potentials and current density through the skin of the fish and the borders of the objects are calculated. The graphic presentations are made by Matlab standard subroutines.

In this study the interaction between two conductive cubes placed close to the fish was examined. The cubes were placed either along a horizontal line perpendicular to the main axis of the fish or parallel to such axis. In different simulations cubes were separated by different distances and the effect of two extreme values of water conductivity (50 and 500 μS) was explored. Two sources in the tail were set to 1 and 1, and consequently the current densities are expressed in arbitrary units.

To calculate the field around the fish we used a model described in previous studies (Budelli and Caputi, 2000).

3. Results

3.1. Theoretical considerations

When an object is placed in a basal electric field (F_0), it distorts the field in a way (F_d) that depends on the object (O), the basal field (F_0) and the other elements in the environment (E). The resulting field is then $F = F_0 + F_d(F_0, E, O)$. Only in very special cases (as for example a sphere in a uniform field) the perturbation of the field is the same as that produced by a dipole (Rasnow, 1996). When the object is far from the fish, the resulting field perturbation is similar to that produced by a dipole.

When two objects (O_1 and O_2) are placed in a basal electric field, the situation is more complex. In this case the perturbation produced by one object changes the field in which the other object is immersed. Then, the resulting field is:

$$F = F_0 + F_{d2}(F_0 + F_{d1}, E_1, O_1) + F_{d1}(F_0 + F_{d2}, E_2, O_2).$$

When the objects are far enough, we may approximate F_{d1} by the field produced by a dipole.

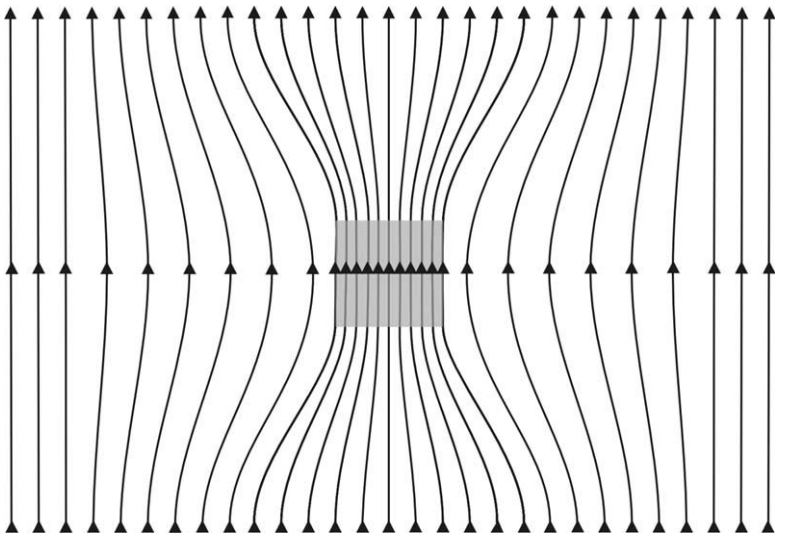

Fig. 1. The distortion of a uniform field produced by a high conductance cube. The field lines are closer in the direction of the field (indicating a stronger field) and more apart in the direction perpendicular to the field (indicating a weaker field).

Furthermore, if the objects are also far from the fish, we may consider the field in which the object is immersed to be uniform.

We will follow Faraday's intuitive approach (also used by Sears and Zemanski, 1955) evaluating changes in the field intensity by changes in the density of the field lines. A conductive object distorts the field lines producing an increase of density along them and a de- crease in the perpendicular plane (Fig. 1). Therefore, if a new object is placed close to a high conductivity object along the basal field lines, the field in which it is immersed will be $|F_0 + F_{d1}|$ (with $|F_0 + F_{d1}| > F_0$) and consequently, the distortion of the field produced by this new object will be larger than the one produced in the absence of the old object. The opposite occurs when the new object is placed on the surface perpen- dicular to the field lines. Consequently, the image of an object (i.e. the distortion of the currents through the fish skin, produced by the presence of the object) depends on the position relative to other objects: it is larger than in basal conditions when the new object is in the direction of the field lines and smaller if in the perpendicular surface.

Consequently, if two high conductive objects are placed close and along the basal field, each object will produce a distortion of the field lines which is larger than the one produced in the absence of the other. Then, the image of two objects in this disposition should be larger than the addition of the images of each object alone. By the contrary, when the objects are placed in a plane perpendicular to the field lines the image of the two objects should be smaller than the addition of the images of each object alone. The opposite should occur with two high resistivity objects. The situation is more complex when one object has conductivity larger than the conductivity of the water and the other smaller.

3.2. Simulations

In the absence of objects, the distribution of transepidermal voltages is the basal stimulus for the sensory surface. In pulse mormyrids, the electric organ is localized at the tail, far from the receptors and fires a short biphasic, almost synchronous discharge. Consequently, if all the elements in the environment are resistive, the stimulus in every point of the skin has the same waveform. Then, any measure of the amplitude (for example, the peak to peak amplitude) could be the unique parameter of the stimulus at any point of the skin. We posed the general problem of image generation calculating numerically the electric image. The image of an object is the difference of the distributions of the currents produced by the presence

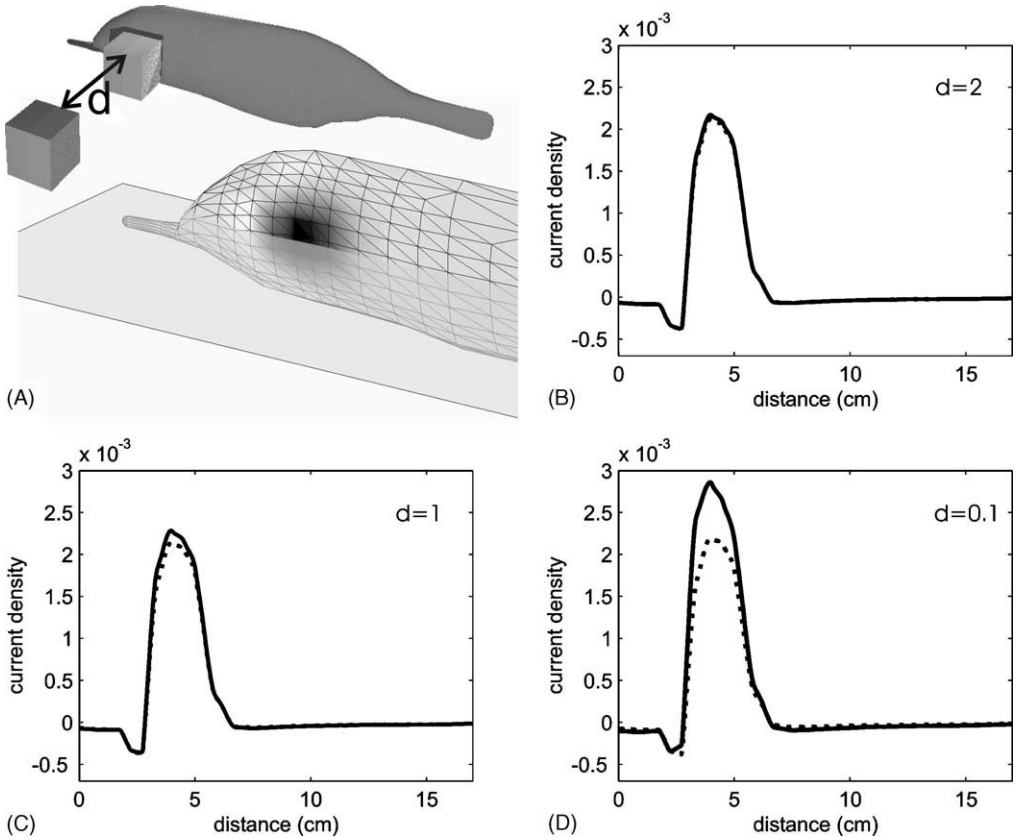

Fig. 2. The image of two cubes placed perpendicularly to the fish axis (along the field line). Water conductivity: 500μS. (A) The image of the two cubes in a gray scale. Inset: the position of the cubes. (B, C, and D) The additive image (dotted line) and the composed image (solid line), when the cubes are 2, 1, and 0.1 cm apart. Abscises: distance along the section shown in A, facing the cubes; rostral (0 cm) to caudal. Ordinates: peak to peak current density in arbitrary units.

of such object, i.e. the difference of the scene images with and without the object, the rest of the scene unchanged. However, when there are two objects the image of both (the composed image) is the difference in the current distribution produced by the presence of both objects. Theoretical arguments predict that the composed image is different than the addition of the images of the individual objects (the additive image).

We studied the difference between the additive and the composed images. Since water resistance is several orders of magnitude larger than the internal resistance of the fish and the electric organ is placed in the tail, the field close to the fish side is almost perpendicular to the skin. Then, to study two extreme situations (objects along or perpendicular to the field lines) we place objects close to the fish side in the direction perpendicular or parallel to the fish axis.

Fig. 2 shows the case for two metallic cubes placed along a horizontal line perpendicular to the antero-posterior axis. One of the cubes remains on the same location about 3 mm from the skin, while the other is placed at 0.1, 1 and 2 cm apart from the first one (Fig 2A, inset). Fig. 2A shows the composed image when the cubes are 3 cm apart. In this case, the composed and the additive images are almost identical, showing a peak surrounded by a trough ("Mexican hat" profile, Kohonen, 1984; Caputi et al., 1998; von der Emde et al., 1998). When the distance between the cubes diminishes, the composed image becomes progressively larger than the additive. To better quantify such differences we present the section

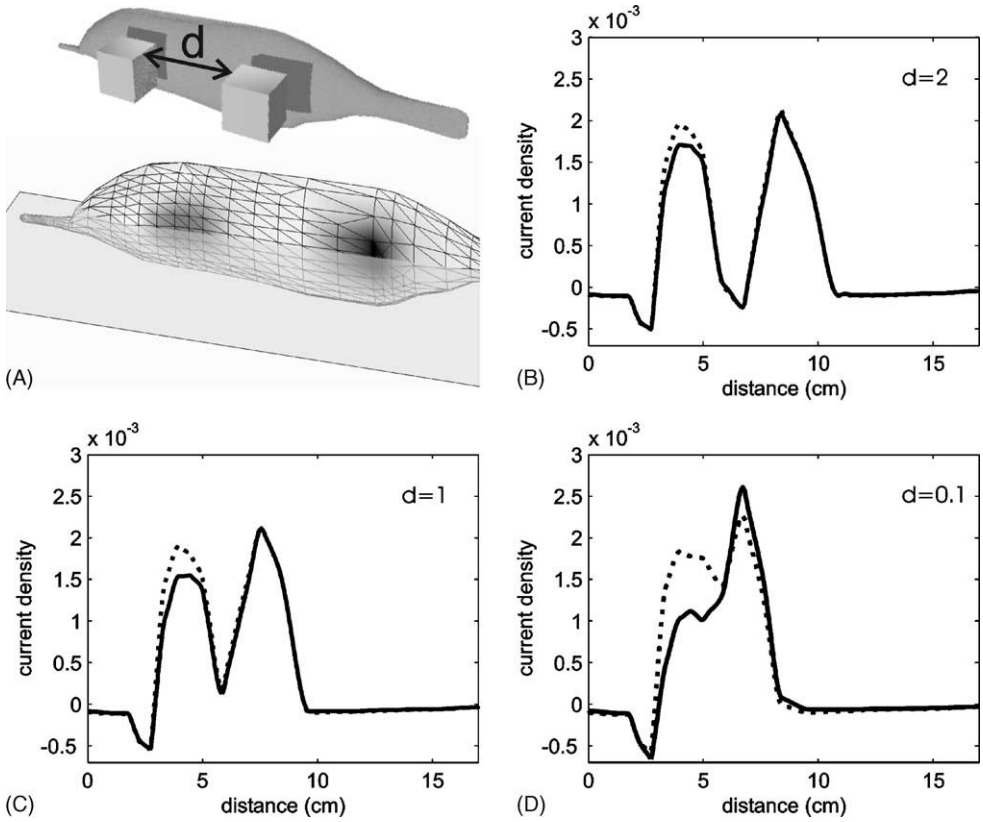

Fig. 3. The image of two cubes placed parallel to the fish axis (perpendicularly to the field lines). (A) The image of the two cubes in a gray scale. Inset: the position of the cubes. (B, C, and D) The additive image (dotted line) and the composed image (solid line), when the cubes are 2, 1, and 0.1 cm apart. Axis and water conductivity as in previous figures.

of the images along a line on a horizontal plane, by the center of the cube (Fig. 2A). A separation of 2 cm renders a just noticeable difference (Fig. 2B). Fig. 2C and D show the profiles for cubes separated by 1 and 0.1 cm. In each case the composed image is not proportional to the additive: peak values increase and the depth of the trough at the rostral side decrease.

Fig. 3 shows the case of two metallic cubes placed along a line parallel to the antero-posterior axis. One of the cubes remains on the same location about 3 mm from the skin, while the other is placed caudally at 0.1, 1 and 2 cm. Fig. 3A shows the composed image when the cubes are 4 cm apart. In this case, the composed and the additive images are almost identical, show- ing two peaks, each one corresponding to each cube. When the distance between the cubes diminishes, the profiles of the additive and composed image change in different ways. The peak of the composed image facing the rostral cube diminishes progressively. When the cubes are 2 cm apart (Fig. 3B), the peak of the composed image facing the caudal cube is smaller than the peak of the additive one. At 1 cm they are almost equal (Fig. 3C). At 0.1 cm, the peak of the composed image is larger (Fig. 3D).

The increase of the composed peak when the objects are aligned perpendicularly to the fish and the decrease of the rostral peak of the composed image when the objects are aligned parallel to the fish, are expected by the theoretical arguments under the assumption that the field is perpendicular to the fish. However, the differences on the caudal peak cannot be understood under this assumption. We propose that a longitudinal component of the field could be responsible for the changes observed in this peak. In fact, as shown in

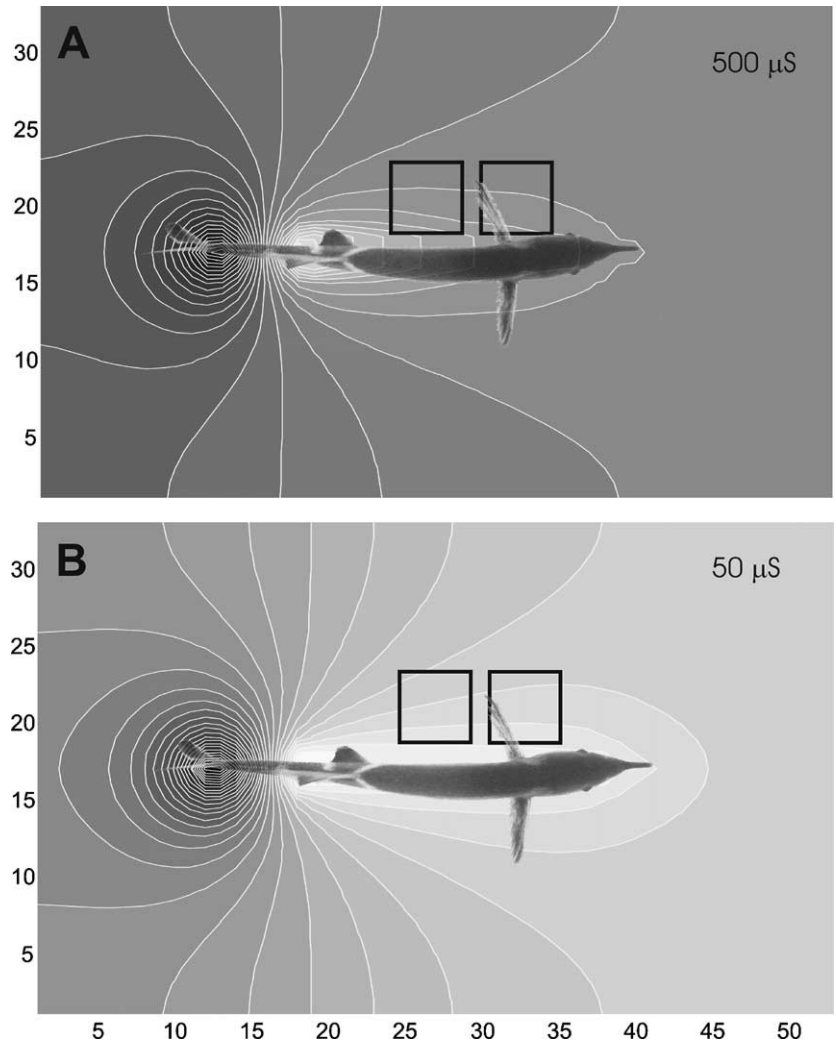

Fig. 4. The field produced by fish in water of two different conductivities. (A) The water conductivity was 500**μ**S, as in previous figures. (B) The water conductivity was 50 **μ**S. The white lines represent horizontal sections of equipotential surfaces. The squares indicate the position of the cubes in Fig. 3.

Fig. 4A, close to the skin the longitudinal component of the field is significant: in the neighborhood of the fish the equipotential lines are not parallel to the skin. To check that the longitudinal component of the field can be responsible for the increase of the caudal peak of the composed image, we study the image generated by the cubes in the presence of a longitudinal field imposed externally. Fig. 5A shows the composed (gray line) and additive (dotted line) images. The difference between them (solid line) is bimodal with the negative peak at the position of the rostral peak and the positive one at the position of the caudal peak. This effect tends to decrease the rostral peak and to increase the caudal one, generating the unexpected re- sult of Fig. 3D.

The direction and magnitude of the longitudinal field can be modified by changes in water conductivity. Fig. 4B shows the field when water conductivity was decreased 10 times (50 **μ**S). In this case the equipotential planes are parallel to the skin and consequently, the field perpendicular to the skin. Fig. 6 shows the additive and composed images when the

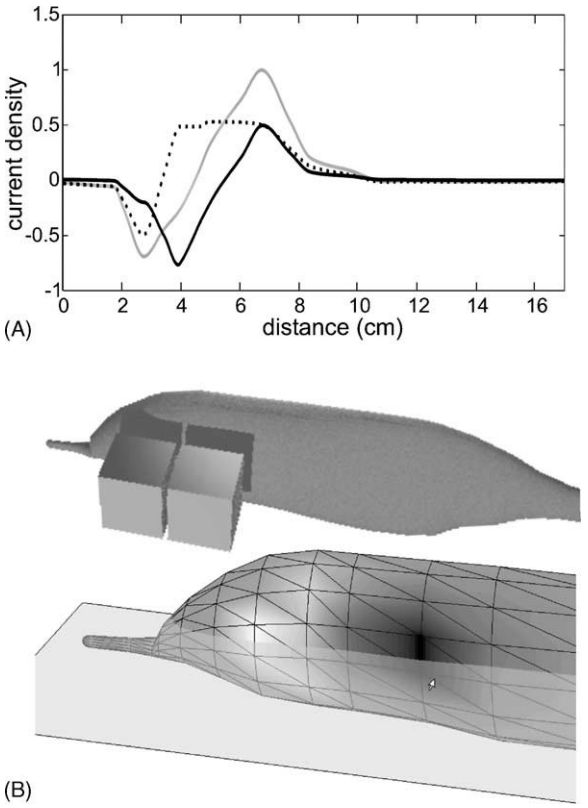

Fig. 5. The normalized images of two cubes by a longitudinal field. (A) The additive and the composed images (dotted and gray lines, respectively) and their difference (solid line). The last curve is the component of the composed image added by the longitudinal field. (B) The composed image. The plane indicates the line corresponding to the profiles in A. Inset: position of the cubes.

cubes are along a longitudinal axis. As suggested by the theoretical arguments, both peaks of the additive image are larger than those of the composed image. When increasing the water conductivity, the opposite result was obtained (not shown).

4. Discussion

Since Aristotle, it is accepted that perception is the process that, using the information provided by the senses, constructs mental representations of the world around us (scenes). Since shaped by evolution, perception has to produce a useful representation of reality from the sensory input. It must extract interesting particularities of the environment from a given image (the representation of a scene at the receptor level): e.g. the distance or shape of an object. Vision is the paradigmatic sense for the study of perception, while perception is not well understood even in senses as important for life as audition. Bregman (1990) maintains that "We came to know about the puzzles of visual perception through the arts of drawing and painting. The desire for accurate portrayal led to an understanding of the cues for distance and certain facts for about projective geometry." He also suggest that "The earlier development of sophisticated think- ing in the field of visual perception may also have been due to the fact that it was much easier to create a visual display with exactly specified properties than it was to shape sound in equally exact ways." Thus it is important to explore different sensory systems to understand the general rules of image formation and how different pathways of the nervous systems are organized to extract information from those images.

In vision, the physical image is defined as the distri- bution of incident light on the retina. By extension, in sensory physiology, a physical image is a distribution of a stimulus on a sensory surface (a set of sensory re- ceptors). This has to be distinguished from the neural representation of the physical image (sensory or neu- ral image). The stimulus for a sensory receptor is ei- ther the concentration of a substance (taste and smell) or a specific form of energy. The electrical image may be defined as the distribution of the dissipated electri- cal energy. The dissipated energy, the transcutaneous voltage, the current density and the electric field are equivalent variables since each of them can be deter- mined from the others by simple calculations.

In this paper we show that in electrolocation the composed image of several objects is not the addition of the images of the individual objects. This fact is shared by other sensory systems. In hearing the sound of a string depends on the resonance box of the played instrument: echoes are constitutive elements of the image of a scene, essentials for the determination of the distance of the source (Zahorik, 1996). In vision, objects intercept the illumination producing shadows, and reflect the light acting as secondary sources (where an extreme case is the presence of a mirror). For elec- trolocation a very high conductive plate acts as a mir- ror: its presence distorts the field produced by a source as would do another source of the same magnitude

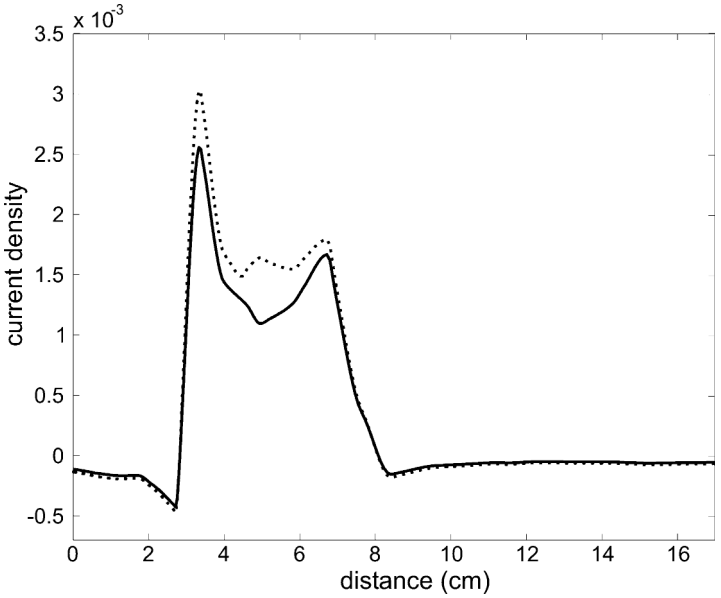

Fig. 6. The image of two cubes placed parallel to the fish with a water conductivity of 50 μS. The additive image (dotted line) and the composed image (solid line). Compare with Fig. 3D.

and opposite sign placed symmetrically in relation to the metallic plane (Jackson, 1975).

Theoretical and modeling results indicate that interaction can either potentiate or depress local stimuli depending on the direction of the field with regard to the orientation of the skin surface. We explored the interaction maintaining one of the objects in the same location, very close to the fish. In this way, the field interacting with this object is almost perpendicular to the skin. The presence of a second object aligned in the direction of the field (perpendicular to the skin) enhances the stimulus at the region of skin facing the first object. This enhancement occurs because the sec- ond object funnels the current through the first one. The presence of a second object aligned perpendicu- larly to the field (parallel to the fish axis) reduces the stimulus on the skin facing the first object. This recip- rocal depression occurs because both objects compete for the current. This is clear when the water conduc- tivity is low and the field is almost perpendicular to the skin.

However, with water of higher conductivity a second effect may be present. In this case the longitudinal component of the field becomes more important and the depressant effect is associated to a potentiation effect due to the funneling of longitudinal currents. This causes a larger reduction of the image facing the ros- tral object and smaller reduction or even an increase of the image facing the caudal object.

In vision, the presence of a flat mirror reflects the light coming from an 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 images. In hearing, the images of different sources of noise usually not only add on the same places of the cochlea but they also interact by masking effects (Yost, 1991). In electrolocation, these effects are more important: every low resistance object acts like a mirror generating new images and affecting the current through the other objects. Thus, the image of the scene is different from the superposition of the images of individual objects.

Rather than generating ambiguity, the presence of a second object may help to identify the first one when performing natural motor behaviors, as tail movements or body bending. These movements may affect the direction of the field and the position of the surface of the skin, altering in these ways the composed image. The changes in images caused by

active movements may be informative because fish have a well-developed proprioceptive system that pro- vides information on tail and body posture and help to decode the electrosensory input in the central ner- vous system. As in other systems the context and its changes in response to self-generated actions could be fundamental for perception.

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