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THE ELECTRIC IMAGE IN WEAKLY ELECTRIC FISH: PERCEPTION OF OBJECTS OF COMPLEX IMPEDANCE

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Summary

Weakly electric fish explore the environment using electrolocation. They produce an electric field that is detected by cutaneous electroreceptors; external objects distort the field, thus generating an electric image. The electric image of objects of complex impedance was investigated using a realistic model, which was able to reproduce previous experimental data. The transcutaneous voltage in the presence of an elementary object is modulated in amplitude and waveform on the skin. Amplitude modulation (measured as the relative change in the local peak-to-peak amplitude) consists of a 'Mexican hat' profile whose maximum relative slope depends on the distance of the fish from the object. Waveform modulation depends on both the distance and the electrical characteristics of the object. Changes in waveform are indicated by the amplitude ratio of the larger positive and negative phases of the local electric organ discharge on the skin. Using the peak-to-peak amplitude and the positive-to-negative amplitude ratio of this discharge, a perceptual space can be defined and correlated with the capacitance and resistance of the object. When the object is moved away, the perceptual space is reduced but keeps the same proportions (homothetically): for a given object, the positive-to-negative amplitude ratio is a linear function of the peak-to-peak amplitude. This linear function depends on the electrical characteristics of the object. However, there are 'families' of objects with different electrical characteristics that produce changes in the parameters of the local electric organ discharge that are related by the same linear function. We propose that these functions code the perceptual properties of an object related to its impedance.

Key words: perception, electroreception, capacitance detection, electric image, weakly electric fish, mormyrid.

Introduction

Electroreceptive fish are able to detect nearby objects by processing the information contained in the pattern of electric currents through their skin. In weakly electric fish, these currents result from the distortion of an electric organ discharge (EOD). The electric image of an object can be defined as the changes caused by the object in the pattern of transepidermal voltage (Bastian, 1986; Bell, 1989). To understand how this electrolocation sensory system works, it is necessary to assess not only the activity of the neural elements in the skin of the fish in the presence of different objects but also the electric image of those objects on the skin. This problem has been approached both experimentally (Hoshimiya et al., 1980; Rasnow et al., 1993; Rasnow, 1996; Rasnow and Bower, 1996; von der Emde et al., 1998) and theoretically (Lissmann and Machin, 1958; Heiligenberg, 1973; Bacher, 1983; Caputi and Budelli, 1995; Caputi et al., 1995, 1998).

In our previous work, we have shown how the electrogenic properties of the electric organ and the post-effector mechanisms (filtering of the EOD by the non-electrogenic tissues) determine the electric image. We showed that a simple resistive object can be represented by an equivalent dipole that varies proportionally with the EOD. Consequently, the local EOD on the skin (LEOD) is not distorted but is modulated in amplitude by resistive objects. On the basis of these results, a set of rules for understanding electroreception was proposed (Caputi et al., 1995, 1998; Rasnow, 1996). Some of these rules were verified experimentally (von der Emde et al., 1998).

Electric fish can discriminate between capacitative and resistive objects (von der Emde, 1991; Meyer, 1982). For capacitative objects, the LEOD waveforms are different from the EOD waveform for a range of capacitances. Comparing the distortion of LEOD waveforms with discrimination performance, von der Emde (1991) showed that the range of capacitance detection corresponds to the range of capacitative objects that distort the LEOD waveform. These waveform distortions are not unequivocally related to the change in LEOD peak-to-peak (PP) amplitude, but the ratio between the positive

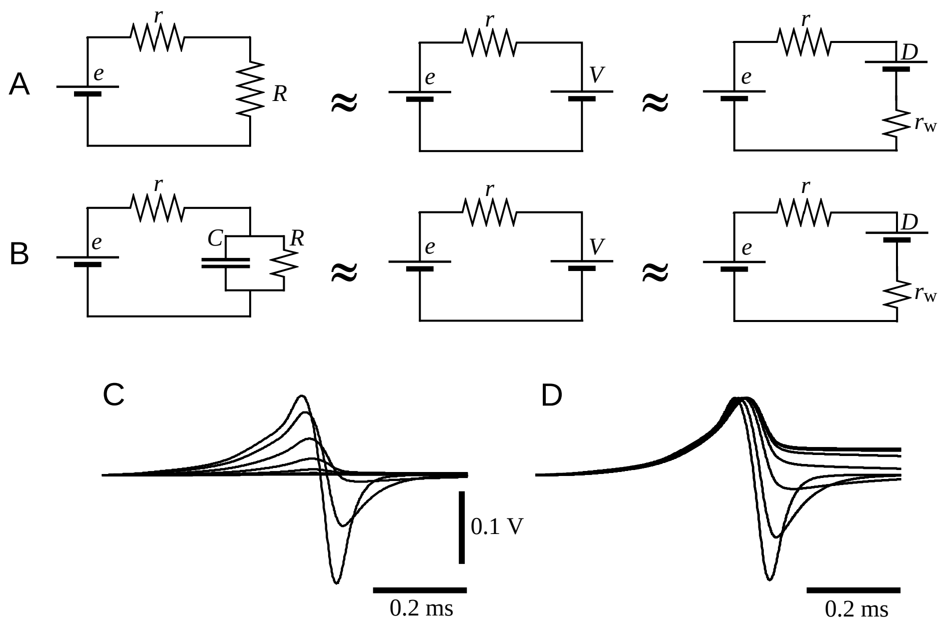

Fig. 1. Determination of the equivalent dipole. (A) The Thevenin equivalent of the fish and the surrounding medium connected to a resistive object (left), to a pure voltage source equal to the voltage (V) between the nodes of the object (middle) and to a source with an electromotive force equal to the equivalent dipole (D) in series with the resistance (r_w) of a water element (right). R is the resistance of the object; r and e are, respectively, the equivalent series resistance and electromotive force of the fish source 'seen' from the object. (B) The same as in A, but with a complex object (R is the resistance and C is the capacitance). (C) Voltage amplitude as a function of time for pure capacitances (C=0.1, 0.3, 1, 3, 10, 30 and 100 nF from the smallest to the largest). (D) Voltage waveform: normalized voltage amplitude as a function of time.

and negative peaks of the LEOD (P/N) is an accurate measure of waveform distortion (von der Emde, 1991). However, what the relevant parameters of the LOED are for the detection of capacitance-induced signals is still an open question.

In this paper, we address the problem by calculating the image of elementary objects of complex impedance using a three-dimensional model. We describe a numerical method for calculating the equivalent dipole and LEOD when the EOD field is distorted by a capacitative object. We studied the distribution of different putative relevant parameters of the LEOD waveform to draw two conclusions: (i) distance discrimination might be achieved from the spatial profiles of any of those parameters, but not from the PP–P/N relationship; and (ii) impedance discrimination can probably be achieved from the identification of families of objects producing corresponding variations in LEOD amplitude and waveform, and not from the LEOD spatial profiles.

The model

The model strategy was described by Caputi et al. (1998). The mathematical bases are presented in the Appendix. Briefly,

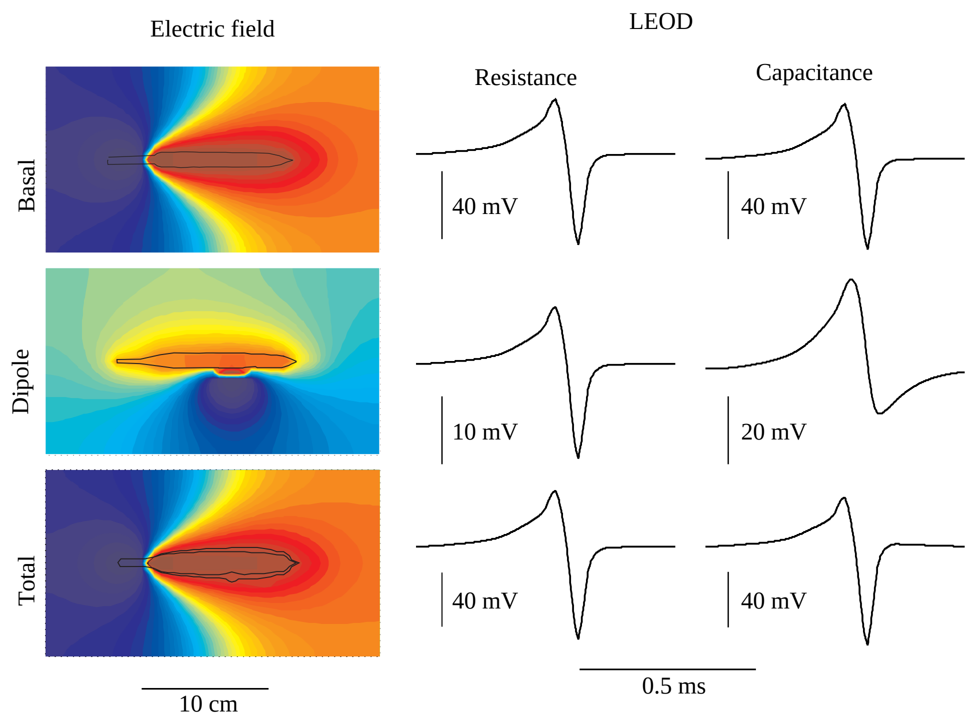

Fig. 2. Determination of the electric field and local electric organ discharge at the skin (LEOD). The left-hand column shows the electric fields generated by unitary sources located at the electric organ (top), at the position of an elementary object (middle) and the total field (bottom) obtained as a linear combination of the first two. Black lines correspond to arbitrary isopotential lines close to the skin; at the tail region, these lines were substituted by others following the fish profile. In the total field, two isopotential lines were drawn to emphasize the effect of the object, which causes an increase in the distance between them. Columns on the right show the LEOD produced by the electric organ discharge (top), by the equivalent dipole (middle) and by the addition of the two (bottom). The central column corresponds to a purely resistive object (resistance R=0 Ω) and the right-hand column corresponds to a purely capacitative object (capacitance C=3 nF).

we simulate a fish 13 cm long in the centre of a three-dimensional tank (17 cm×27 cm×17 cm; width×length×depth). This volume was divided into cubes with sides of 0.5 cm. The center of each cube was a node of the electric network. Contiguous nodes aligned parallel to the edges of the tank were connected by resistances according to the resistivities of the interposed elements. The differences in specific resistance of the skin described by Caputi et al. (1998) were taken into account. The calculation of the field is then reduced to solving a system of equations in which each equation corresponds to Kirchoff's law of nodes, for each node. A more detailed description is given by Caputi et al. (1998).

It has already been demonstrated that the changes in transcutaneous currents produced by an elementary object are the same as those produced by an equivalent dipole (Lissman and Machin, 1958; Bacher, 1983; Caputi et al., 1998). An elementary object is defined as spherical and small in relation to the radius of curvature of the field. The requirement for the object to be spherical is abolished if its effects are not studied too close to the object. Fig. 1A illustrates the Thevenin equivalent circuit in this case, where R is the resistance of the object, r and e are, respectively, the equivalent series resistance and electromotive force of the fish source 'seen' from the object. e is the voltage when the resistance was assumed to be infinite. The Thevenin resistance, r, is the ratio between e and the current through the object, when R is assumed to be zero. V is the voltage at the object nodes. D is the magnitude of the equivalent dipole. In the case of a resistive object, the magnitude of the equivalent dipole (D) is proportional to the instantaneous magnitude of the EOD.

In the case of capacitative objects, the equivalent dipole is no longer proportional to the instantaneous magnitude of the EOD. At the beginning of the EOD, the potential through the object (V) remains negligible, because almost all the current goes through the capacitor. Fig. 1B shows the equivalent circuit of an object as a capacitor and a resistance in parallel. When the capacitor starts charging, current starts to circulate through the resistance, generating a potential between the nodes of the object. For very small capacitances, the capacitor charges and discharges very quickly [$\tau_c=C\times r$ and $\tau_d=C(r\times R)/(r+R)$ are very small] and the object behaves as the resistance R alone (C is capacitance and τ_c and τ_d are time constants; see Appendix). When the capacitance is very large, the voltage between the nodes remains negligible and the object behaves like a short circuit. For intermediate capacitance values, the charge in the capacitor modifies the voltage waveform between the nodes of the object. The waveform spreads to the right, the zero crossing time is delayed and the positive-to-negative ratio (P/N) increases as capacitance increases (Fig. 1C,D).

The calculation of the potentials inside the tank (including the fish) is illustrated in Fig. 2. First, we determine the potential fields generated by unitary sources located at the positions of the electric organ and the object. Next, we obtain the total field as a linear combination of these two fields. To obtain the total field, it is necessary to add the voltages generated by the electric organ without an object (basal field) to the voltages generated by the dipole (dipole field). In Fig. 2 (total electric field), the presence of the object can be detected by a small distance increment between the contiguous isopotential lines (in black). The basal field is proportional to the EOD, and the dipole field is proportional to the magnitude of the equivalent dipole. Since, for capacitative objects, the dipole is not proportional to the EOD, the relative weight of each term in the sum varies over time. The LEOD waveforms were also obtained as weighted sums of the normalized waveforms of the EOD and the dipole. Fig. 2 shows the waveforms generated by the EOD (basal), the equivalent dipole (dipole) and the weighted sum of the two (total) as a function of time for a resistive object (middle column, R=0 Ω) and for a capacitative object (right-hand column, C=3 nF).

To test the accuracy of the model, we simulated the effect of cylindrical objects similar to those used by von der Emde (1991). These were plastic (non-conducting) tubes whose ends were blocked by carbon plugs; inside the tube, the carbon plugs were connected by a variable resistance/capacitance circuit. In this case, the tube may be considered as part of a non-uniform medium, and we therefore cannot compare the waveform distortion with a basal EOD. To calculate the total field, we add the field obtained by short-circuiting the extremes of the tube to the field produced by an electromotive force equal to the voltage across the extremes of the tube when a load is connected. This procedure is equivalent to that described previously in the case of elementary objects.

Results

Two experimental situations were modeled. First, we simulated the conditions described by von der Emde (1991, 1993) and von der Emde and Bleckmann (1992a,b). The results obtained in these conditions allow us (i) to make a complete description of the field potentials, (ii) to calculate the electric image of an object similar to that used by von der Emde (1991), (iii) to study how the temporal waveforms of LEODs are distorted by capacitative objects, and (iv) to determine the accuracy of the model. Second, we followed a more general and formal approach, determining fields and images of elementary objects placed at different distances from the fish. This approach allowed us to find a distance-invariant property of the image defining 'families' of objects.

Distortion of LEOD temporal waveforms by cylindrical objects

We accurately reproduced the experimental recordings of von der Emde (1991) and von der Emde (1993) of the fall in voltage between two recording electrodes placed in the direction of the current, perpendicular to the skin. Since water resistivity is known, these drops in voltage are proportional to transcutaneous currents. The resulting LEODs in front of objects of different impedance are shown in Fig. 3 (upper row). Lissajous plots (Fig. 3, lower row), showing LEOD *versus* EOD, stress phase differences. For very high and very low

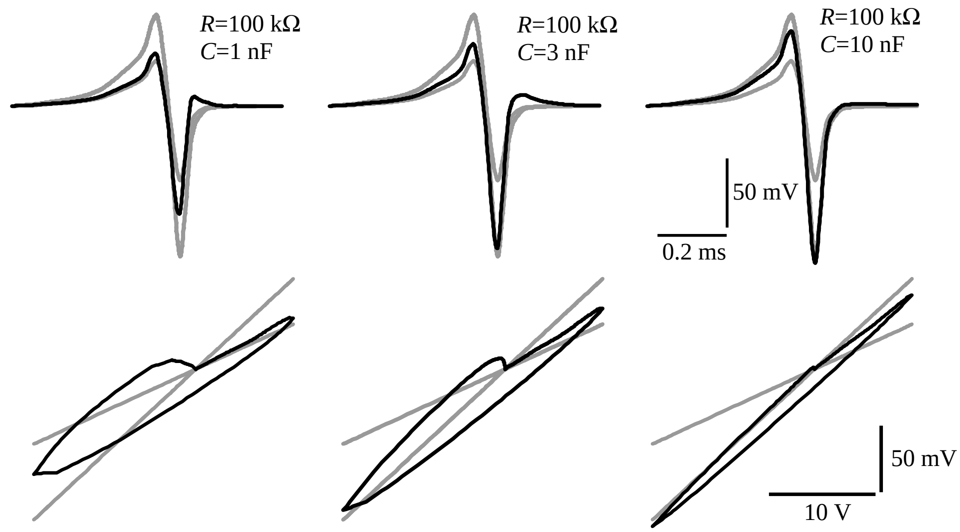

Fig. 3. Local electric organ discharge (LEOD) waveforms for objects of differing impedance. Upper row, LEODs for objects of differing capacitance (*C*) (1, 3 and 10 nF) and 100 kΩ resistance (*R*). Gray waveforms (included for comparison) correspond to 0 and ∞ Ω pure resistance. Bottom row: Lissajous plots showing electric organ discharge *versus* LEOD; the straight gray lines correspond to the Lissajous plots of the gray waveforms in A.

capacitance, the object acts as a resistance of 0 and 100 kΩ, respectively. The LEODs are then proportional, and the Lissajous plots reduce to straight lines (in gray in Fig. 3). Non-proportionality generates the loops seen for intermediate capacitances.

Following von der Emde (1991, 1993), we studied the peak-to-peak amplitude (PP) and the positive-to-negative ratio (P/N) of the LEOD as a function of the resistance and capacitance of the object. Fig. 4A,C shows the PP values as functions of the resistance of the object for two water resistivities. As in the experimental results, the PP value decreased monotonically with object resistance and was smaller for water with lower resistivity. Fig. 4B,D shows the PP and P/N values as functions of the capacitance of the object for two water resistivities. In this case, the PP values also decreased with capacitance and were smaller for lower resistivity. P/N values show a U-shaped dependence on capacitance, reaching maximal values at both extreme capacitances. All the simulation results reproduced those obtained experimentally. Fig. 5 shows the PP and P/N values for different combinations of resistances and capacitances. As for the experimental results obtained by von

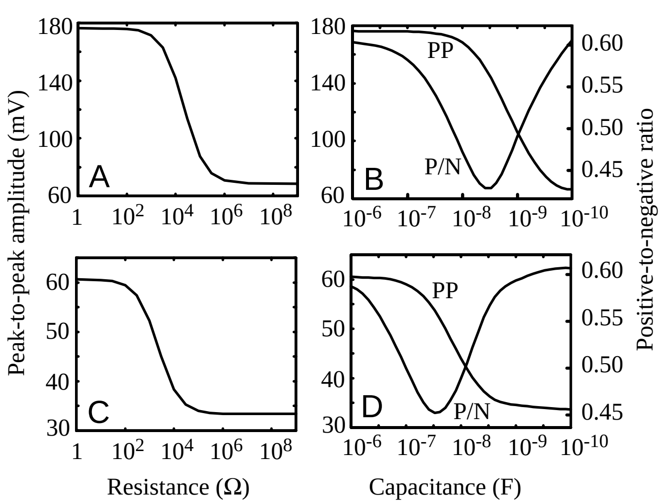

Fig. 4. Reproduction of experimental measurements made by von der Emde (1991). (A,C) Peak-to-peak amplitude (PP) of the local electric organ discharge (LEOD) as function of the resistance of the object for two water resistivities (A, 20 kΩ cm; C, 2 kΩ cm). The ratio between the positive and negative peaks of the LEOD (P/N) is not changed by pure resistive objects. (B,D) PP and P/N values of the LEOD as functions of the capacitance of the object for the same two water resistivities. The object is 0.5 cm away from the skin, and the recording electrodes (0.3 cm apart) are between the object and the skin.

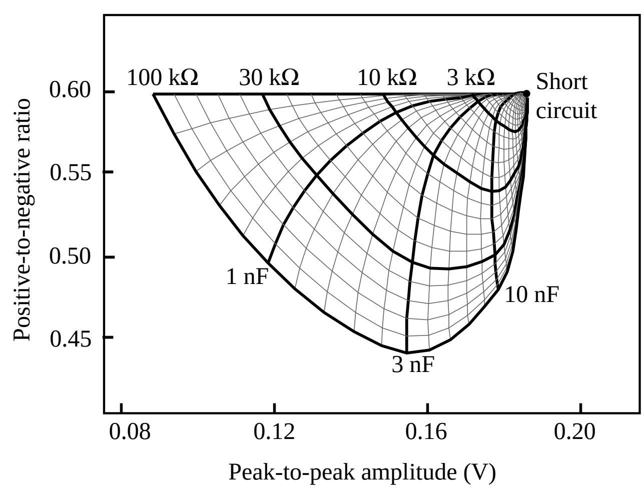

Fig. 5. PP–P/N perceptual space. PP is the peak-to-peak amplitude of the local electric organ discharge (LEOD) and P/N is the ratio between the positive and negative peaks of the LEOD. The LEOD in front of an object was calculated for different resistance (Ω) and capacitance (nF) values of an object. PP–P/N pairs fall within a closed surface limited by the curves corresponding to purely capacitative (U-shaped curve at the bottom) and purely resistive (upper horizontal line) objects. The area between these two curves (the ‘perceptual space’ of von der Emde, 1991) includes all values of complex resistive/capacitative objects. The object is 0.5 cm away from the skin.

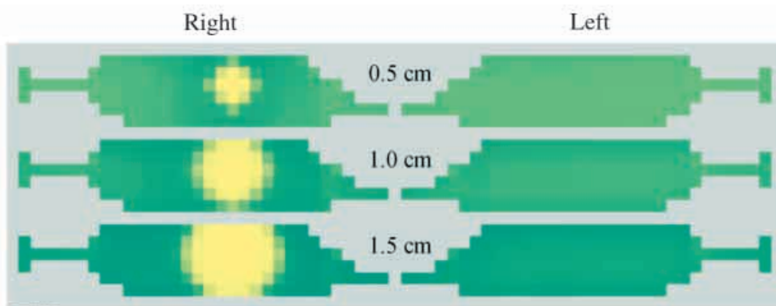

Fig. 6. The transcutaneous voltage spatial profiles generated by a unitary dipole at three different distances. The diagrams show, in a color scale map, the transcutaneous voltage profiles normalized for peak amplitude generated by an elementary dipole 0.5, 1 and 1.5 cm away from the skin on the left and right sides of the fish. The profile resembles a 'Mexican hat' and remains almost ipsilateral to the object. Note that the image spreads out as the object is moved away and that the region of negative modulation (in dark green) is mainly concentrated on the ipsilateral side of the fish. The fish is 13 cm long.

der Emde (1991, 1993), the curves for fixed capacitance have a positive slope and a negative curvature, while those for fixed resistance are U-shaped. These results confirm the existence of a range of capacitance that could be detected as different from resistance and that this range depends on water resistivity. The characteristics of the 'perceptual space' (the set of PP–P/N pairs that can be obtained by changing the electrical properties of an object) defined by von der Emde (1991, 1993) were accurately reproduced by the simulation. The similarity between the simulations and the experimental results validates our model.

Spatial profiles produced by a dipole

We term spatial profile the distribution of any parameter on the fish skin. A given profile may constitute the whole electric image or only part of it. For example, the PP profile is the complete image of a resistive object (Caputi et al., 1998), but not of a capacitative one (as shown below). LEOD spatial profiles produced by an elementary object are equivalent to those produced by a time-dependent dipole placed at the location of the object. Although the magnitude of the equivalent dipole for an elementary object is time-dependent, the normalized spatial profile of transcutaneous currents, for any dipole placed at the object site, is not.

The direction of the equivalent dipole of an elementary object coincides with the direction of the field. When the object is close to the side of the fish, where the skin surface is relatively planar, the current flows perpendicular to the skin and, consequently, the equivalent dipole is placed perpendicular to the skin. Then, the maximum change in the LEOD occurs just in front of the dipole (i.e. on a line perpendicular to the skin of the fish through the object) and will produce a center–surround ('Mexican hat') spatial profile (Caputi et al., 1998; Sicardi et al., 1998). In Fig. 6, the 'Mexican hat' profile is presented by a yellow (positive) region, surrounded by a dark green region (negative). In general, objects producing the maximum effect at a given point on the skin (projection point) are on a line referred to as the electrosensory field line. Far from the fish, these lines may curve depending on the geometry of the fish and the surrounding medium. Then, the position of an elementary object is determined by the projection point (x,y) and by the distance (d) along the electrosensory field line.

Using a three-dimensional model, this study confirms previous results which indicate that spatial profiles generated by dipoles, and thus by elementary objects, spread out as a function of the distance from the skin. We have hypothesized that the relative slope of the image was a cue for distance detection (Caputi et al., 1998). The consequences of this hypothesis have been confirmed behaviorally (von der Emde et al., 1998). Fig. 6 shows, in a color-scale map, the transcutaneous voltage spatial profiles on the two sides of the fish (left and right) when an elementary dipole was placed 0.5, 1 and 1.5 cm from the skin, on the left of the fish. The image resembles a 'Mexican hat' and remains almost entirely ipsilateral to the object. Note that, surrounding the yellow region (positive modulation), there is a dark green area (negative modulation). Fig. 7A shows these profiles represented as functions of the longitudinal rostro-caudal axis, for different horizontal levels, covering the top-to-bottom depth of the fish body. Fig. 7B shows the peak of the profiles as a function of the distance to the object. When this distance increases, the peak amplitude of the image diminishes and that of the center region increases. To characterize the shape of the profile, we use the maximum of the relative slope as defined by von der Emde et al. (1998) (relative slope=maximum slope/maximum amplitude). The relative slope is a measure of the sharpness of the image. Since it decreases with distance to the object (as established experimentally and corroborated by the simulation in Fig. 7C), it was proposed that the fish uses this calculated parameter as a cue for distance discrimination.

Spatio-temporal pattern of transcutaneous voltage determined by elementary objects of complex impedance

For purely resistive objects, the LEOD waveforms are proportional to the EOD waveform at any point on the skin. Thus, the information in the LEOD at the projection point is given by a single parameter (e.g. the peak-to-peak amplitude, PP). Since the threshold of the electroreceptors depends on the amplitude of the LEOD in the absence of objects, the signal detected by the electroreceptors is the modulation of the LEOD amplitude caused by the object (Bennett, 1971; Bell, 1989). Using this reasoning, we use the LEOD modulation to compare the signals received by receptors spread over the skin. Fig. 8 compares two PP modulation profiles generated by two elementary objects of different resistance when placed at the appropriate distance to produce the same PP LEOD at the projection point. Because the objects had to be placed at

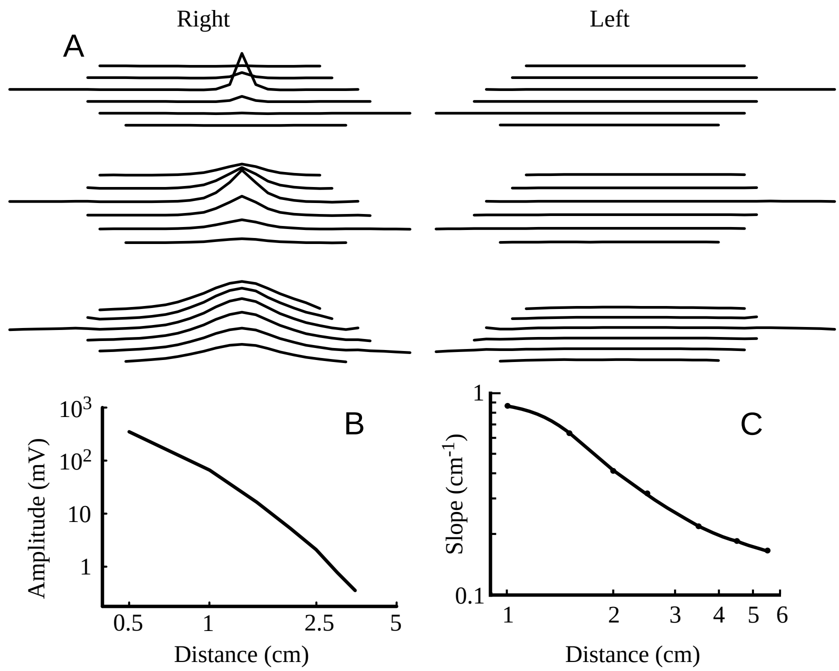

Fig. 7. Voltage profiles generated by dipoles at different distances from the fish. (A) Profiles as a function of the longitudinal rostro-caudal axis, for different horizontal levels, when the dipole is (top to bottom) 0.5, 1 and 1.5 cm away. (B) Amplitude of the profile at the projection point as a function of the distance to the dipole. (C) Maximum relative slope of the profile as a function of the distance to the dipole. Note that, close to the fish, the function relating slope and distance cannot be estimated accurately because of the spatial resolution of the model. The fish is 13 cm long.

different distances from the fish, this demonstrates that, for resistive objects, the PP LEOD at the projection point does not code distance. Two objects may have the same PP LEOD at the same projection point, while being at different distances and having different resistances.

When considering capacitative objects, the LEOD waveform can be described completely by the EOD and at least three further parameters (see Appendix). These parameters might be the time constants (of the charge τ_c and discharge τ_d of the capacitance) and the distance (*d*) or any other set of parameters that allows one to calculate them (e.g. object capacitance, object resistance, water resistance and distance, see Appendix). Conversely, three independent parameters of the LEOD, at the projection point, allow the determination of τ_c, τ_d and *d*. It is important to note that, to calculate the resistance and capacitance of the object from these time constants, it is necessary to know water resistivity.

We do not know which, and how many, parameters the fish are able to extract from the LEOD at the projection point. The pair of PP–P/N values at the projection point was proposed by von der Emde (1993) 'as a waveform cue' for capacitance detection. However, these parameters do not provide complete information about the electrical characteristics and position of the elementary object in water of a given conductivity.

The 'PP–P/N perceptual space' depends on the distance between the object and the fish. PP–P/N pairs for purely capacitative objects (U-shaped black curves) located 0.5, 1 and 1.5 cm from the skin are represented in Fig. 9A. The horizontal black line is the superposition of PP–P/N pairs for purely resistive objects placed at the same distances. The horizontal and U-shaped lines limit the 'PP–P/N perceptual spaces' for each object distance. PP–P/N pairs corresponding to combinations of resistance and capacitance will be represented between these two curves. Three similar (mathematically homothetic) curves, scaled differently with regard to a common center (corresponding to the basal PP–P/N pair in the absence of an object; black arrowhead), are presented. The largest curve corresponds to the smallest distance, the smallest curve to the largest distance. Objects having the same combination of resistance and capacitance, but placed at different distances, are represented by points on straight lines (not shown) passing through the PP–P/N pair corresponding to the basal LEOD (black arrowhead). Objects 0.5 cm from the skin, having a constant resistance (R=42 kΩ), are represented by the gray U-shaped curve, and those having a constant capacitance (C=0.7 nF) are represented by a downward concave gray curve. The intersection of these gray curves

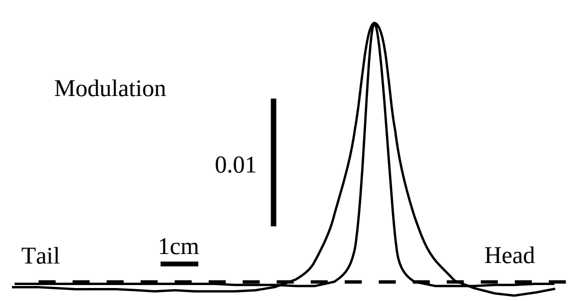

Fig. 8. Distance is coded by the spatial peak-to-peak (PP) amplitude profile but not by the PP amplitude at the projection point. The graph compares two PP modulation profiles generated by two elementary objects of different resistance when placed at the appropriate distance to produce the same local electric organ discharge (LEOD) at the projection point. Note the difference in relative slope.

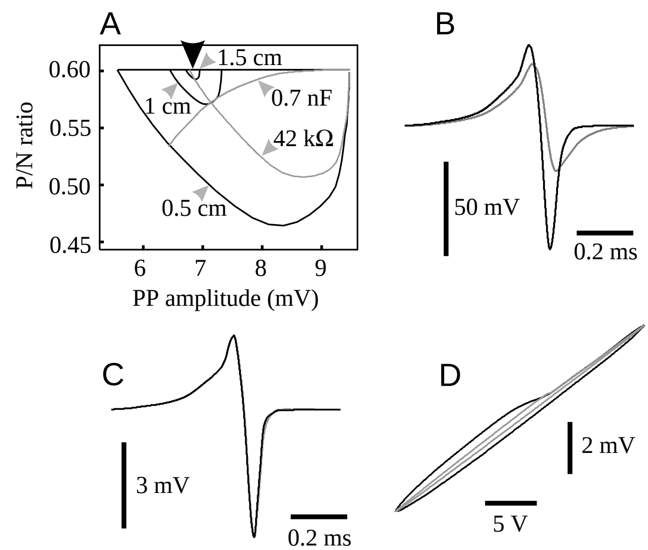

Fig. 9. The perceptual space as a function of the distance of the object from the fish. (A) The boundaries of the perceptual space calculated for three different distances are superimposed. Three homothetic (similar) figures, scaled differently with regard to a common center (corresponding to the basal PP–P/N pair in the absence of an object, black arrowhead), are observed. PP is the peak-to-peak amplitude of the local electric organ discharge (LEOD) and P/N is the ratio between the positive and negative peaks of the LEOD. The largest curve corresponds to the smallest distance and the smallest curve to the greatest distance. (B) The equivalent dipole waveforms for two objects placed at different distances from the fish's skin and having different electrical characteristics (R=42 kΩ, C=0.7 nF, d=0.5 cm: black outline, and C=4 nF, R=∞ Ω, d=1 cm: gray outline; C, capacitance; R, resistance; d, distance) are represented. (C) LEODs as functions of time, for the same objects as in B. Note that it is almost impossible to differentiate the two curves in this plot. (D) Lissajous plots (LEOD against EOD) for the same objects.

corresponds to a resistive/capacitative object (R=42 kΩ and C=0.7 nF) located at 0.5 cm. The same PP–P/N pair corresponds to a purely capacitative (C=4 nF, R=∞ Ω) object at 1 cm distance. Therefore, a single PP–P/N pair does not determine the electrical characteristics of the object independently of the distance.

Fig. 9B shows the equivalent dipole waveform for two objects with different electrical characteristics placed at different distances from the fish's skin, which nevertheless produce an LEOD with the same PP and P/N values (Fig. 9C). The dipole waveforms are clearly different, and the resulting LEODs are almost identical. The small difference between the two curves can be better perceived in the Lissajous plot (Fig. 9D) by the presence of a loop. These LEODs differ in other parameters, but we were not able to identify any that might produce a significant change in the response of the receptors (Bell, 1990; von der Emde and Bleckmann, 1997). Three putative parameters were investigated: the zero crossing delay, the peak-to-peak time and the time derivative. These parameters seem to be easily detected by the receptors and independent of PP and P/N. Nevertheless, their variations for

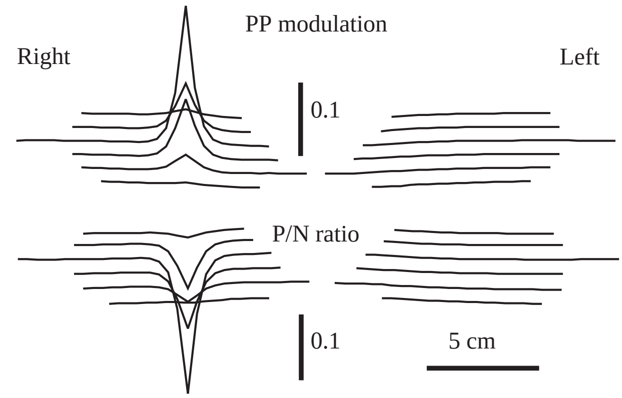

Fig. 10. Spatial distribution of the local electric organ discharge (LEOD) parameters on the left and right sides of the fish. PP modulation (top) and P/N profiles (bottom) are compared for an elementary object (C=3 nF, R=∞ Ω; C, capacitance; R, resistance) 1 cm away from the fish. PP is the peak-to-peak amplitude of the local electric organ discharge (LEOD) and P/N is the ratio between the positive and negative peaks of the LEOD.

objects having the same PP–P/N pair were not significant. For example, the maximum change in the zero crossing value was of the order of 1 μs.

To study whether the spatial distribution of PP and P/N values can also provide the fish with information about the impedance of an object, we compared PP and P/N spatial profiles. For a resistive object, the PP and dipole profiles are similar (Caputi et al., 1998). Figs 6 and 10 (top) show that the profile produced by a dipole (and consequently by a resistive object) is similar to the PP profile produced by an object of complex impedance. Thus, as for purely resistive objects, the distance of capacitative objects from the fish can also be determined from the PP profiles using the relative slope value. The relative slope of the profile may be the third parameter necessary for impedance determination. PP and P/N profiles (Fig. 10) are line-to-line '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. 11A,B), in which it can be seen that, for each object, the PP–P/N pairs fall on a straight line. Lines corresponding to different objects diverge, intersecting at a single point defined by the basal PP–P/N pair. Fig. 11A shows plots for objects with a resistance of 100 kΩ and of varying capacitance. Fig. 11B show plots for objects with a capacitance of 3 nF and of varying resistance. Since the points fall on straight lines, all intersecting at the basal PP–P/N pair, we may describe the set of PP–P/N points corresponding to a given object by the slope of the line. The slope depends on the capacitance and resistance of the object. When the object is purely resistive, the line is horizontal, irrespective of its value (not shown). Moreover, as shown in Fig. 11A,B, there are objects with different resistive–capacitative impedances that produce images sharing exactly the same curve. Note, for example, that the slope for

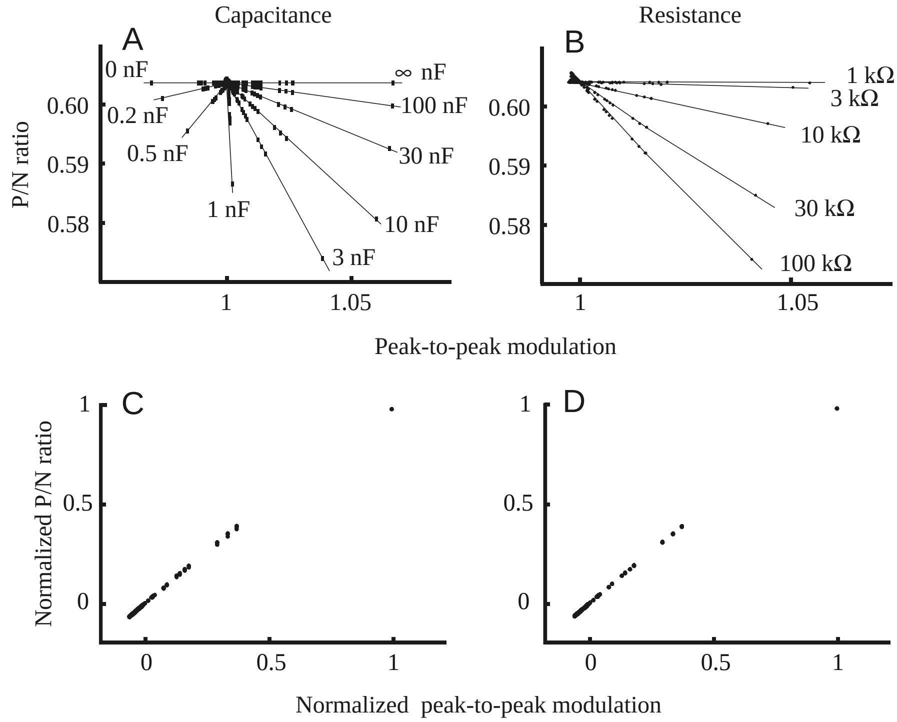

Fig. 11. The PP–P/N relationship codes a perceptual property of the object. PP is the peak-to-peak amplitude of the local electric organ discharge (LEOD) and P/N is the ratio between the positive and negative peaks of the LEOD. (A) Points on each straight line corresponds to the PP–P/N pairs at different points on the skin for an object with a resistance of 100 kΩ and with varying capacitance (nF) placed 1 cm away from the skin. (B) The same as in A, but for an object with a capacitance of 3 nF and with varying resistance (kΩ). (C,D) Normalized superimposed graphs for the same values as in A and B respectively. Both variables were normalized with regard to the range between the basal values (0) and their maxima (1). Note that the individual points are superimposed, indicating that profiles of different objects located at the same site are nearly identical.

an object of 100 kΩ and 10 nF (Fig. 11A) is similar to the slope for an object of 30 kΩ and 3 nF (Fig. 11B).

In addition, the same pattern of points occurs in all the lines (Fig. 11A,B). The maximum value of PP and P/N corresponding to the projection point is far from the others, the surrounding four points are grouped in a triad of lower value (two pairs superimposed), etc. When plotting PP–P/N relationships normalized to their maxima, the relative values for the same points on the skin are superimposed. Fig. 11C,D shows superimposed the normalized PP–P/N scattergrams for the same objects considered in Fig. 11A,B, respectively. This superposition indicates that the shape of the spatial profile is not dependent on the impedance of the object. Consequently, profiles alone do not code impedance.

However, the PP–P/N pairs of an object fit a single straight line, indicating a relationship that is independent of the position of the object with respect to the fish. As shown in Fig. 12A, PP–P/N pairs from images of the same object at two different distances fall on the same line. Fig. 12B shows that PP–P/N pairs derived from images of the same object at the same distance, on two different electrosensory field lines, are related by the same linear function. Thus, the results show that the relationship between PP and P/N codes a perceptual property of the object. The qualitative properties of the objects, such as color, are represented by the ratios between the activities of receptors of different type. In human vision, three receptors generate two independent ratios; colors can therefore be represented on a two-dimensional surface. In mormyrids using active electrolocation, there are two electroreceptor types determining a single ratio. Consequently, ‘electric color’ can be represented on a line (or color bar).

Discussion

The model accurately reproduces experimental results obtained under a variety of conditions for objects at varying distances from the fish and with varying impedance (von der Emde, 1991, 1993; von der Emde et al., 1998).

The present results are qualitatively similar to those obtained using a two-dimensional model and confirm the physical rules for understanding electrolocation proposed in a previous paper (Caputi et al., 1998). In the previous study, we measured the impedance of the skin and found that there is a capacitative component of the skin. This component varies over the surface of the fish, reaching a maximum ($45\,nF\,cm^{-2}$) at the head region. In the previous and the present studies, we have neglected both this capacitative component and the details of the head; this might be an oversimplification. In fact, unpublished experimental data (S. Schwartz, personal communication) suggest that the complex impedance of the skin may have some effect in the head region.

The present study suggests that the geometrical (shape and position) and electrical properties of an object might be perceived independently by the fish. To discuss different aspects of electrolocation, we will compare the electric sense with human vision, a sensory modality for which we have a clearer subjective knowledge.

An elementary object can be considered as a point source of light. The spatial profiles of light intensity projected onto a surface depend on the distance and spectral properties of the light source. A candle placed close to a surface projects a small, sharp, bright spot. Candles made with different waxes produce lights of different colors. When the candle is moved away from the surface, the light spreads out and the spot becomes larger, dimmer and blurred. When a close object interferes with the

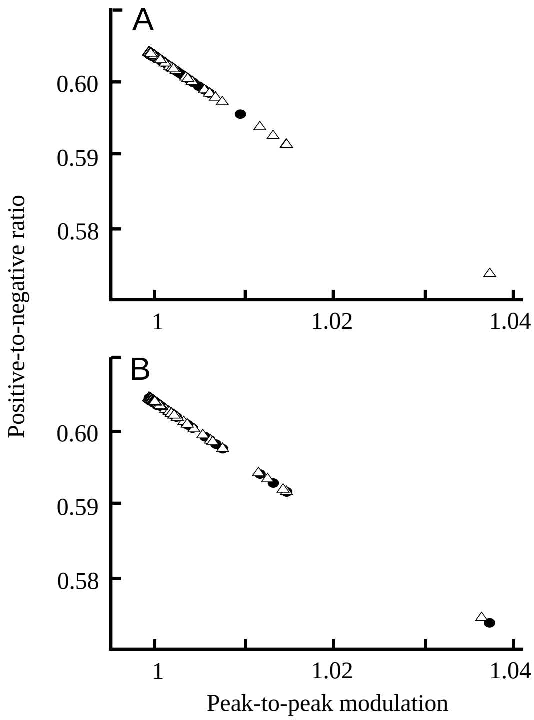

Fig. 12. The PP–P/N relationship codes a perceptual property of the object. PP is the peak-to-peak amplitude of the local electric organ discharge (LEOD) and P/N is the ratio between the positive and negative peaks of the LEOD. (A) PP–P/N pairs from different points on the skin of the fish, produced by the same object placed 1 cm (open triangles) and 1.5 cm (filled circles) away from the skin. (B) PP–P/N pairs from different points on the skin of the fish, produced by the same object located on different electrosensory field lines passing through projection points 2 cm apart. Both objects were placed 1 cm from the skin.

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 terms of electric images, when small objects with an impedance different from that of the medium interfere with an electric field, they behave as dipoles. In the following sections, we will discuss how these dipoles produce currents through nearby surfaces and how similar rules to those in the example of the candle can be applied to electroreception.

Distance discrimination

Images produced by purely resistive objects depend on the distance to that object. As in the example of the candle, the image of an elementary object spreads out, dims and blurs with distance. Objects of differing resistance (such as candles of differing brightness) may produce images of the same maximal amplitude when placed at the appropriate different distances (Fig. 8). Conversely, objects of differing resistance, placed at the same distance, produce similar profiles of different intensity. Therefore, as reported previously, the spatial profile (and not the intensity of the image) is the relevant cue for distance discrimination (Caputi et al., 1998). It is important to note that a similar spatial profile can be produced by objects of different shape placed at different distances (von der Emde et al., 1998).

In contrast to the case of purely resistive objects, we have shown that the distortion of the LEOD waveform at the projection point theoretically contains enough information to allow the distance of elementary objects with complex impedance to be estimated (see Appendix). At least three parameters must be detected and computed to extract distance information from the LEOD/time waveform. We do not know whether the fish can accomplish this task. Nevertheless, there are two types of receptor, projecting to different zones of the electrosensory lateral line lobe in the medulla, which respond differentially to the LEOD (Bell, 1990; von der Emde and Bleckmann, 1992a,b, 1997; von der Emde and Bell, 1994). Type A afferents respond to the amplitude of the LEOD independently of the LEOD waveform, while type B afferents respond to both the amplitude and waveform of the LEOD. These results indicate that fish probably use PP amplitude as one of the LEOD parameters. We do not yet know which other parameters are used in electrolocation. However, it has been shown that a parameter related to the P/N ratio is used as a ‘waveform cue’ (von der Emde and Bleckmann, 1997). No significant variation was found in any of the other parameters (zero crossing, peak-to-peak time, maximum derivative) that, it has been suggested, might serve as cues for the detection of LEOD waveform modulation. Thus, we conclude that distance is probably not encoded by the LEOD waveform at the projection point, but by the spatial profiles, as in the case of resistive objects.

Impedance discrimination

For elementary objects of complex impedance, three parameters are needed to determine the relationship between the LEOD and the EOD. As explained in the Appendix, there is a linear transformation between the EOD and the LEOD. The transfer function of a system whose input is the EOD and whose output is the LEOD at a given point on the skin depends on the position of the object and on two time constants (corresponding to the charge and discharge of the capacitor). These time constants result from multiplying the capacitance by the charging resistance and by the discharging resistance, respectively. Both resistances (and therefore the time constants) depend on the position of the object, but only one (the discharge time constant) depends on the resistance of the object. Mathematically, one can conceive three other parameters equivalent to those resulting from this analysis. Any system able to determine three parameters from the relationship between the LEOD and EOD may estimate accurately the distance and impedance of an elementary object by making the appropriate computation.

However, physiological data suggest that only two parameters are detected by mormyrids: (i) the PP of the LEOD and (ii) some other parameter related to the P/N ratio (von der Emde and Bleckmann, 1997). In addition, we have not been able to identify any other LEOD parameter likely to be detected by fish electroreceptors. The P/N ratio is a measure of the change in waveform and allows one to determine a 'perceptual space' for capacitance detection (von der Emde, 1991). The P/N ratio of the LEOD is equal to the P/N ratio of the EOD in only three circumstances: (i) when the object is purely resistive; (ii) when the capacitance of the object is large enough to pass the EOD frequencies without attenuation (for instance, in the case of a short circuit); and (iii) when the capacitance of the object is small enough to block all the EOD frequencies (the impedance of the object is mainly resistive).

As shown in Fig. 9, PP–P/N pairs can correspond to different objects at different distances from the projection point. Thus, a single PP–P/N pair is not enough to represent accurately the impedance of an elementary object. Confirming the results of von der Emde and Bleckmann (1997), we have found no third waveform parameter likely to be detected by the sensory system that could solve the ambiguity between impedance and distance. It could be argued that, as in the case of distance discrimination for purely resistive objects, the third parameter arises from any of the spatial profiles. Fish could determine distance from a profile and, by integrating this estimation with two other parameters of the LEOD waveform, compute the resistance and capacitance of the object. However, this does not appear to be the case in *Gnathonemus petersii.* Fish possess a 'city block perceptual metric', suggesting that only two parameters related to object impedance are perceptually separable by the fish (von der Emde and Ronacher, 1994). Moreover, fish confuse two objects of different impedance if they are 'similarly different' from the training object. Therefore, it is possible that fish might detect a distance-invariant property of the object related to the impedance.

In the candle example, the color of the light results from 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 color can be achieved using candles of different chemical composition. By analogy, the distance-invariant property or 'electric color' can be related to a whole family of capacitative–resistive objects.

For a given distance, the 'PP–P/N perceptual space' (von der Emde, 1991) is biunivocally related to the impedance of the object at any given point of the skin, but this relationship changes when the object is moved away. We found that 'PP–P/N perceptual spaces' change homothetically with distance; this means that 'PP–P/N perceptual spaces' have a similar shape and can be scaled according to a function of the object distance (Fig. 9).

In addition, we found that there is a function relating the PP and P/N profiles produced by the same object; this function is not dependent on distance. When P/N ratio is plotted against PP amplitude for all points on the skin, the result is a straight line. If the object is moved away, the corresponding PP–P/N pair at a given point on the skin moves along the line. If such lines are considered together with the possible 'perceptual spaces', families of objects can be identified defined by their ability to produce the same PP–P/N relationships. The line for each family is constant regardless of the object distance. A single object will produce PP–P/N pairs pertaining to the same line, irrespective of the position. All the objects in the family will reproduce the same PP–P/N line. Objects pertaining to a family will not produce, in any circumstances, a PP–P/N pair on a line corresponding to that of 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 hypothesise that such curves define a distance-invariant perceptual property or 'electric color' for families of capacitative objects. Although further experimental confirmation is required, behavioral data reported by von der Emde and Ronacher (1994) are in agreement with our hypothesis.

Four main conclusions can be drawn for the perception of elementary objects. (i) PP and PN spatial profiles encode the distance to the object, even for objects of complex impedance. (ii) Single spatial profiles are unlikely to encode impedance. (iii) A given PP–P/N pair does not encode the object of complex impedance as conceived by humans. Only when distance is constant is there a one-to-one reciprocal relationship between the PP–P/N pair and the resistance/capacitance pair. (iv) We hypothesise that there are sets of parameter pairs that are perceived as equivalent by fish, independent of distance from the object. Each of these sets would be related one-to-one with a perceptual property of the object. We term such a perceptual property the 'electric color of the object'.

Appendix

The voltage (V) through an elementary object of capacitance C and resistance R consists of the filtered shape of the electric organ discharge (EOD) (Fig. 1C) and can be calculated from the equation:

$$\mathrm{d}V/\mathrm{d}t = -V/\tau_\mathrm{d} + e \times \mathrm{EOD}/\tau_\mathrm{c}\,, \qquad (1)$$

where t is time, $\tau_\mathrm{c}=C\times r$, $\tau_\mathrm{d}=C(r\times R)/(r+R)$, e is the Thevenin electromotive force and r is the resistance 'seen' from the object.

The solution to this equation can be expressed by the solution to the normalized equation:

$$\mathrm{d}V_0/\mathrm{d}t = -V_0/\tau_\mathrm{d} + \mathrm{EOD} \qquad (2)$$

multiplied by e/τ_c:

$$V = (e/\tau_\mathrm{c}) \times V_0\,. \qquad (3)$$

The parameter τ_d determines the voltage waveform (V_0) and, given the waveform, the parameter e/τ_c determines voltage amplitude with regard to V_0.

The magnitude of the object equivalent dipole D is:

$$D = (1 + r_\mathrm{w}/r)V - (r_\mathrm{w} \times e/r)\mathrm{EOD}\,, \qquad (4)$$

where r_w is the resistance between the nodes of the object when it is assumed to have the same resistivity as the tank water. Note that the coefficient of EOD ($r_\mathrm{w}\times e/r$) depends on e and r

(and consequently on the position) and not on the electrical parameters of the object.

The waveform of the local EOD on the skin (LEOD) is the temporal course of the transcutaneous current density generated by the EOD at a point (x,y) on the skin. It results from the weighted sum of the voltages at the nodes of the object (V) and the EOD waveforms:

$$\mathrm{LEOD}(x,y,t) = A(x,y,p)\mathrm{EOD}(t) + B(x,y,p)V(t)\,, \tag{5}$$

where (x,y) are the coordinates on the fish skin, t is time, A is the transcutaneous voltage profile in the presence of a short-circuit object when the EOD is substituted by a unitary dipole, B is the transcutaneous voltage profile when the voltage between the nodes of the object is set to 1 V, and p is the position of the object.

The LEOD produced by a given object at a given point (x_1,y_1) depends on three independent parameters: (i) p, which determines the weighting factors $A(x_1,y_1,p)$ and $B(x_1,y_1,p)$, (ii) τ_d, which determines the voltage waveform V_0 and (iii) τ_c, which, operating with e (depending in turn on the position of the object p), determines the relative amplitude of V. Note that the position of the object can be determined by the projection point (x_0,y_0) and the distance (d) along the electrosensory field line.

Using equations 4 and 5, the LEOD on the skin of the fish can be calculated as the weighted sum of a unitary equivalent dipole (D) at the nodes of the object and the EOD waveforms:

$$\mathrm{LEOD}(x,y,t) = F(x,y)\mathrm{EOD}(t) + G(x,y,p)D(t)\,, \tag{6}$$

where F is the basal profile and G is the dipole profile. Note that F does not depend on p.

When the object is resistive (C=0), from Fig. 1A and equation 4 we obtain:

$$D = e(p)\{(R - r_\mathrm{w})/[r(p) + R]\}\mathrm{EOD}\,, \tag{7}$$

$$\mathrm{LEOD} = [F(x,y) + G(x,y,p)e(p)] \times \{(R - r_\mathrm{w})/[r(p) + R]\}\mathrm{EOD}\,. \tag{8}$$

Then, since the EOD and D waveforms are equal, the LEOD is proportional to the EOD. In this case, the significant parameters are (x,y,p) and R. For an elementary object projecting on a given point (x_0,y_0), there are different combinations of R and d giving the same LEOD at the point (x_0,y_0).

In the case of elementary capacitance objects, the situation is different. Two objects on different electrosensory field lines can be discriminated since the projection point is different. Consider, now, two objects placed on the same electrosensory line at two different distances (p_1,R_1,C_1) and (p_2,R_2,C_2). If the LEODs (LEOD_1 and LEOD_2) at the projection point (x_0,y_0) are equal, the position and electrical characteristics of the object are the same. Let us assume that the objects are placed at two different positions. Then:

$$\mathrm{LEOD}_1(x_0,y_0,t) = F(x_0,y_0)\mathrm{EOD}(t) + G(x_0,y_0,p_1)D_1(t) \tag{9}$$

$$\mathrm{LEOD}_2(x_0,y_0,t) = F(x_0,y_0)\mathrm{EOD}(t) + G(x_0,y_0,p_2)D_2(t)\,. \tag{10}$$

If the two LEODs are equal, subtraction will give:

$$\mathrm{LEOD}_1(x_0,y_0,t) - \mathrm{LEOD}_2(x_0,y_0,t) = G(x_0,y_0,p_1)D_1(t) - G(x_0,y_0,p_2)D_2(t)\,, \tag{11}$$

but if:

$$\mathrm{LEOD}_1(x_0,y_0,t) - \mathrm{LEOD}_2(x_0,y_0,t) = 0 \tag{12}$$

then:

$$G(x_0,y_0,p_1)D_1(t) - G(x_0,y_0,p_2)D_2(t) = 0\,. \tag{13}$$

Equation 13 implies that $D_1(t)$ is proportional to $D_2(t)$. These equations also imply that the waveforms $V_{0,1}$ and $V_{0,2}$, are equal. But $V_{0,1}$ and $V_{0,2}$ depend on τ_{d1} and τ_{d2}, which in turn depend on the Thevenin equivalent resistances (r_1 and r_2, respectively), which (with objects with a capacitance different from zero) vary with distance to the object. Consequently, the LEOD at the projection point corresponding to a given capacitative object cannot be reproduced by any other object placed on the same electrosensory field line. Therefore, the LEOD at the projection point contains all the information necessary for determining the capacitance, the resistance and the distance of a non-purely resistive elementary object placed along the electrosensory field line corresponding to such a projection point.

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