THE NATURE OF ELECTROSENSING IN THE FISH

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ABSTRACT An evaluative review of the electrosensing literature was pursued with the intention of determining the nature of the electrosensing mechanism and its sensitivity. The biological data base, although weak, was useful in development of a mathematical model and in analyses of the sense mechanisms and their functions. During the analyses, we suggest a working hypothesis on the nature of the sense mechanism. We also collapse the various sensor coding schemes that have been proposed into one scheme. The function of the mathematical model of the sensor that was developed was explored with the use of a computer. The fishes' function at the system level was also considered and possible mechanisms defined.

INTRODUCTION

Only a short period has elapsed since certain fish were identified as having a previously unknown sensing system, an electrosensing system. It was observed that these fish apparently detect and classify objects that enter into and perturb a weak electrical field generated by the fish. Further investigation revealed that this sense is more generally found among fish than was first thought. Some fish, such as the shark and catfish, apparently use a passive electrosensing system in that the fish does not seem to generate its own electrical field. Rather, it detects electrical signals, possibly muscle potentials, generated by objects entering its area.

Although there is now a fairly substantial data base, very little can be used in developing an understanding of sense mechanism and sensitivity. This is in part due to the fact that pioneering data in this area, as they are in most areas, tend to have faults no matter how competent the investigators. Further, there is little information on system sensitivity and function due to limited behavioral investigation.

In sum, though there are investigators contributing useful data, as a whole the data base is weak. Thus, we have undertaken several tasks which may allow an assessment of the fishes' electrosensing mechanism and capability, using available data.

First, through limited experimental work with electrical fields, sensors, and objects in various size bodies of water, we have gathered data which, when taken with the mathematical analysis, allow us to interpret much of the data now available. This analysis also provides specifications for tank size, fish location, and attachments that will yield valid data in future studies.

Second, we suggest a working hypothesis of electrosensor mechanism. This hypothesis is subject to test and may provide a means for collapsing the current multiple crude categorizations of the receptors. The hypothesis may also provide a basis for analyzing higher interactions in the fishes' nervous system and thereby increase our understanding of the sense.

Third, we indicate the linkage among the various neural coding schemes suggested for the fish and show their essential identity.

Fourth, we develop a mathematical model of the fish based upon the usable experimental data. The mathematical model is analyzed by a computer to ascertain the sensitivity requirements of the fish at the receptor and to determine the effects of manipulating a number of variables. These variables include fish size, object size, object electrical characteristics, object distance from the fish, direction and angle of the object from the fishes' axis, etc.

We briefly discuss the fishes' function at the systems level and close with our conclusions concerning the electric sense.

SYMBOLS

θ	The angle between the y axis and the radius vector from the positive charge to an arbitrary point in space.
θ_0	The angle between the y axis and the radius vector from the charge to the center of the perturbing object.
R	The radius vector from the positive charge to an arbitrary point in space.
R_0	The radius vector from the positive charge to the center of the perturbing object.
ϕ	The angle between the x axis and the x-z projection of the radius vector from the positive charge to an arbitrary point in space.
ϕ_0	The angle between the x axis and the x-z projection of the radius vector from the positive charge to the center of the perturbing object.
Q	The charge on either side of the dipole.
L	The length of the dipole.
ϵ_w	The dielectric of water.
ϵ_x	The dielectric of perturbation.
U_x	The potential due to the interaction between the dipole field and the perturbation.
w	A coordinate centered at the perturbation opposed to the vector E_0 and in the $-y$ axis $-R_0$ plane.
m	A coordinate perpendicular to the w axis in the y–P_0 plane originating at the center of the perturbation.
β	The angle between E_0 and a line parallel to the y-axis at the center of the perturbation.
ρ	A radius vector in the w, m coordinate system to an arbitrary point in space.
α	The angle between the radius vector and the coordinate w.
U_0	Potential due to uniform approximation of the dipole field.
U_1	Potential inside sphere due to uniform approximation of dipole field.
y	End point of charge path.
a	Radius of sphere in dipole arrangement.
I	Current.
P	Macroscopic polarization.
N	The number of molecules per volume.

χ_e	The electric susceptibility.
E	Storing force.
P_{ind}	Induced dipole moment.
T	Threshold function.
T_{max}	Maximum threshold.
T_{min}	Minimum threshold.
T_c	Exponential time constant.
V	Absolute voltage.
v	Voltage.
C	Capacitance.
A	A constant to be determined from the boundary conditions.
B	A constant to be determined from the boundary conditions.
X	Reactance.
L	Inductance.
U	Potential in terms of the coordinate system.
ω_0	Radian frequency of harmonic oscillation.

NATURE OF THE BIOLOGICAL SYSTEM

Marine and freshwater species of strongly and weakly electric fish have evolved. Strongly electric fish are defined as those that discharge their electric generating organs reactively to stun prey or resist capture. Weakly electric fish are defined as those that detect and classify objects which perturb a normally continuous self-generated electric field. This electric field is not strong enough to stun other fish.

There are numerous species of weakly electric freshwater fish but most can be classified as either gymnotids which are South American in origin or mormyrids which are common in Africa. The two groups have many similarities and some differences in physical structure and in the function of their electric generator and receptor organs. Other weakly electric fish include the African *Gymnarchus* and the South American sternarchid which are probably related to the mormyrids and gymnotids, respectively.

Generator Organ

An understanding of the structure and function of the electric generator organ is of importance in understanding receptor function. Thus, generator function will be considered first.

The cells of the generating organ are referred to in the literature as electroplaques, electroplax, electroplates, or electrocytes. We shall follow Bennett (1970) and use the term electrocytes. The electrocytes of all known weakly electric fish except sternarchids are derived from the mesoderm (Szabo, 1966). The origin of the electrocytes of the sternarchids is ectoderm (Steinbach, 1970).

Electrocytes of mesodermal origin are typically disc shaped, but may also be drum shaped or tubular. Electrocytes of ectodermal origin are U-shaped processes from the spinal cord. The electrocytes of the gymnotid, *Hypopomus*, are between 300 and

500 μ in diameter and about 200 μ thick. The electrocytes of *Sternopygus*, on the other hand, are rod shaped and much longer than those of *Hypopomus*. They are about 1–2 mm in the anterior-posterior direction and 200 μ in diameter. These cells are packed together tightly with little extracellular space, whereas the electrocytes of *Hypopomus* are separated by a considerable amount of extracellular space.

The electrocytes are "stacked" in columns in the rear portion of the fish's body to form the electric generating organ. For example, the electric organ of *Gnathonemus*, a mormyrid, is located just in front of the tail fin and extends forward less than one-fifth of the fish's body length. *Gymnarchus*'s electric generating organ extends from the tail fin to nearly the midpoint. The generating organs of the gymnotid, *Gymnotus*, and of *Sternarchus* extend further from the tail fin almost to the back of the head.

The weakly electric freshwater fish can be categorized in terms of patterns of discharge: those with variable frequency and those with constant frequency. Constant frequency fish are defined as those that discharge their electric generating organs at a virtually constant rate even when strongly stimulated by an experimenter, i.e., 2–2000 pulses per second depending on species. Some of these are *Eigenmannia*, *Sternopygus*, and the sternarchids. Fish that are reported to emit at variable frequency generally increase their discharge rate markedly when stimulated. Fish that exhibit this characteristic are the mormyrids (Mandriota et al., 1965), *Hypopomus*, *Steatogenys*, and *Gymnotus* (Larimer and McDonald, 1968). It should be noted that constant frequency fish do vary their frequency under certain circumstances, i.e., the presence of another signal of a similar frequency. *Gymnarchus*, on the other hand, temporarily ceases its discharge entirely when presented with a signal mimicking another *Gymnarchus* or when startled (Bennett, 1970).[1,2]

The mechanisms controlling electric organ output are in the medullary portion of the brain and appear similar among weakly electric fish. A small group of cells in the medulla are autoactive and fire synchronously, apparently acting as a pacemaker. Their discharge appears to trigger another group of cells in the medulla commonly referred to as medullary "relays." Axons from the medullary relay cells descend as part of the spinal cord to synapse on spinal relay neurons. These in turn communicate the signal to the electrocytes. The electrocytes of the electric generating organ fire snychronously because of one or more compensatory mechanisms in the relay pathway from the pacemaker cells. These mechanisms include variation in path length and conduction velocities.

Several investigators have measured the voltage output of the generating organ. *Hypopomus* is reported to generate a voltage of 8 v peak-to-peak when electrodes are placed on the head and tail with the fish more or less out of the water. The same fish

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[1] Each type of fish has a wave form that is specific to itself. Therefore, although *Gymnotus* and *Steatogenys* have the same frequencies, their wave forms are different. These differences in wave form may be functions of the various experimenters' analyzing methods or equipment.

[2] If a passive electric sense is more common than is thought, this could be protective reaction.

in water is reported to generate a voltage of from 10 to 200 mv. The in-water measurements were taken with two stainless steel electrodes, one placed in front of the fish and one placed behind the fish. The distance between the electrodes was not given nor was the distance between the electrodes and the fish given. In general, inadequate information is given in the reports of voltage measurements of the electric organ output.

In measurements in our laboratory simulating the reported data, we found that the water acts as a very high distributive resistance. When an oscilloscope is used in the typically reported fashion to measure the fishes' voltage output, the input impedance of the scope is being placed in parallel with the resistance of the water. Even when a high input impedance scope is used, there is a loading effect upon the circuit. Thus, we believe, based upon our measurements and the techniques reported, that the investigators have inadvertently loaded the fish's electric field generator through the use of their measuring devices.

We can summarize the salient points by saying that these fish generate a pulsed electrical field in the water. The generator is located in the posterior portion of the body. The generator components have their outputs synchronized by a clock. In some species the clock is more or less invariant, in others it varies, in part, as a function of external events. The reason for this difference among species is unknown. The voltage output of the generator and the effective range of the field are unknown due to inadequate measurement technique.

Receptor Organ

The weakly electric freshwater fish are reported to have both active and passive sensory systems. The active system primarily detects disturbances in the fish generated E field. The passive system is primarily sensitive to energy provided by extrinsic sources. We are not so sure that the data really indicates two such systems in the same fish, but we shall follow this convention for the time being. There is better evidence that there are a number of organisms, such as sharks and catfish, which have good passive electrosensing systems but no active system. The passive systems in these organisms are not considered in this paper.

Gymnotid Receptors. There are two basic types of electroreceptor organs reported in the literature. As indicated the differences may be more apparent than real in terms of function.

The ampullary organs are believed to be the passive system sensors. They consist of cells that maintain a continuous rhythmic background firing. Thus, they are referred to as tonic receptors. This background firing appears to be unrelated to electric organ discharge.

The background firing shifts smoothly to a higher or lower rate in response to electrical sources moving into the fish's range. The response to a brief stimulus, for example, is rate increase followed by a decrease. The rate increase phase can outlast the stimulus and according to Bennett (1970) there is accommodation to maintained stimuli. These receptors are sensitive to low frequency electrical fields and to changes in a DC field. Their response to an applied current is a monotonic increase.

The active system sensors are called tuberous organs. They are more rapidly adapting than tonic receptors. They are sensitive to relatively high frequency stimuli and are insensitive to applied DC. Their firing is related to electric organ discharge in that they respond with a train of pulses to each electric organ discharge. Thus, they are referred to as phasic receptors.

As seen on the skin, the ampullary and tuberous organs differ. They also differ in appearance from mechanoreceptors, i.e., canal organs and free neuromasts. The tuberous organ appears on the skin surface as a single pore, even though it has no opening. The ampullary organs appear as a group of small pores. As an indication of the number of receptors found on a fish, it can be noted that Lissmann and Mullinger (1968) found that there were 2000 ampullary and tuberous organs on a 6 cm long *Steatogenys*. Most receptors, about 95 %, are phasic according to Lissmann and Mullinger (1968).

In considering the fine structure of the receptor organs, it can be noted that the ampullary organ (Fig. 1 A) has the appearance of a flask with a narrow duct (5–20 μ in diameter) leading from the skin surface to a cavity (30–40 μ in diameter) located 100–500 μ within the skin. Embedded in the cavity wall with a small surface exposed are the sensing cells of the organ. These sensing cells are 10–15 μ in diameter with each organ containing two to eight of them. Some microvilli 0.8 μ long are irregularly distributed on the exposed surface of the sensing cells. Filling the duct and cavity is a jelly-like substance with no known function. All sense cells in one organ feed their signals to the same myelinated nerve fiber. The nerve is unmyelinated within the organ, having lost its myelin sheath and dividing before entering the organ.

There are many clusters of 5–15 ampullary receptor cells on the head. On the body there are fewer clusters, and they tend to be restricted to three bands that extend longitudinally along the fish.[3]

The tuberous organ consists of a bulb-shaped invagination of the skin as shown in Fig. 1 B. The side of the bulb is composed of 10–50 layers of flattened cells for a total thickness of 2–5 μ. The bottom of the bulb is made up of supporting cells upon which the numerous sensing cells rest. The sensing cells are 25–30 μ long and project somewhat like rods into the bulb cavity. They are ordered such that the gap between adjacent sensory cells is relatively constant. Each sensory cell is covered on the cavity end with microvilli 0.7 μ long. The cavity is filled with a fluid or possibly jelly-like substance. Loose epithelial-like cells fill much of the cavity above the sensory cells and appear to plug the pore to the surface. The sensory cells feed their signals

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[3] The fish being described is *Hypopomus artedi*, a species of gymnotid. Details vary slightly from species to species.

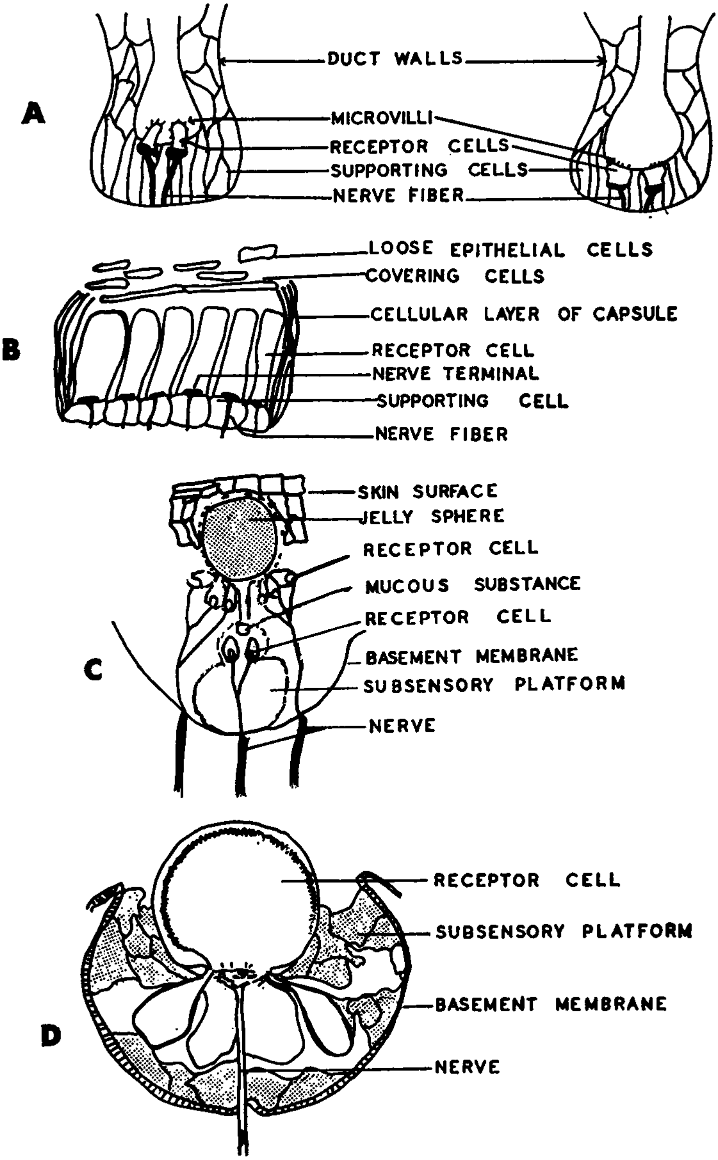

FIGURE 1 (A) Schematic drawing of the two types of ampulla of gymnotids, (B) schematic drawing of the tuberous organ of the gymnotid, (C) schematic drawing of the mormyromast of the mormyrid, (D) schematic drawing of the tuberous organ of the mormyrid.

to a single nerve which, in most cases, loses its myelin sheath as it passes into the tuberous organ. In a small proportion of the tuberous organs, the myelin sheath is retained until the nerve fiber enters the sensory cell. The tuberous organs appear to be randomly distributed on the head and on the anterior portions of the body where they are most numerous. On the posterior half of the body they are found in four longitudinal bands.

Mormyrid Receptors. In mormyrids, the electroreceptors are referred to as mormyromasts and Knollenorgans (Szabo, 1966). The mormyromast is a two level organ that contains at the surface level sensory cells (type A) similar to the ampullary sensory cells and at the second level sensory cells (type B) similar to the sensory cells of the tuberous organ of the gymnotids. Types A and B sensory cells are always separately innervated.

The type A sensory cells form one or two concentric aureoles at the base of a "jelly sphere" located near the surface of the skin as shown in Fig. 1 C. In the center of this aureole, a small duct leads to a more deeply situated sensory chamber in the skin within which the type B cells are located. The inner surface of the duct wall bears tiny microvilli. The duct as well as the lower sensory chamber is filled with a mucous substance.

Two to five sensory cells occupy the lower sensory chamber. The type B cells with their supporting cell platform, though similar to the tuberous organ are smaller. They do not completely fill up the sensory chamber and their free surfaces bear a large number of microvilli.

The type B sensory cells in a mormyromast are innervated by a single nerve fiber which splits immediately after penetration through the supporting cells into several branches to serve the sensory cells. Where the nerve joins the type B sensory cell membrane a rodlike projection, 0.5 μ in size, occurs within the sensory cell.

Each type A sensory cell is encircled by several accessory cells. The sensory cells and their accessory cells are bottle shaped. The apical or tip portion of both sensory and accessory cells contact the jelly sphere. The nerve fibers innervating type A cells lose their myelin sheath before entering the receptor organ and pass among the accessory cells to contact the sensory cells. As with type B cells, where the nerve joins the sensory cell, there is a rod present at the sensory cell membrane.

The mormyrids also have receptor organs, Knollenorgans, which are somewhat similar to the tuberous organs of the gymnotids. Derbin and Szabo (1968) describe them as being composed of three or four sensory cell complexes one of which is shown in Fig. 1 D. Each complex is a single sensory cell attached to a highly differentiated supporting platform of cells. The organ is innervated by a single nerve fiber which is derived from a nerve that appears to serve many sensory cells.

The sensory cell lies in and amost completely fills a cavity in the skin at the surface. The wall of the cavity is formed by flattened epithelial cells. The interior epithelial cells have microvilli-like processes which densely pack the space about the sensory cell. The cavity has a relatively large opening toward the supporting cells through which the sensory cell contacts the nerve endings and supporting cells. The sensory cell itself is 35–40 μ in diameter.

In sum then, the weakly electric fishes of South America, the gymnotids, and of

Africa, the mormyrids, both seem to have receptor organs that are similar in some respects but differ in other respects. Though there are structural differences in receptor organs within and between species, the evidence suggesting that there are differences in function is rather weak.

System Function, Measurement Technique, and Sensitivity

In this section we will discuss the three primary techniques that have been used to obtain data on function, discuss their deficiencies, and estimate from the data the probable system function and sensitivity. Two of the techniques are electrophysiological and the third is behavioral.

Electrophysiological and Behavioral Techniques. In one electrophysiological technique (Szabo and Hagiwara, 1967) an anesthetized fish is affixed to a wooden plate in the normal swimming position. The wooden plate is tilted into the water so that the body is submerged and the head exposed. Regular respiratory movements and oxygenation are maintained by spraying a fine jet of water into the fish's mouth. The dorsal branch of the lateral line nerve which lies immediately under the dorsal skin at the head is then surgically exposed. After desheathing, fine nerve strands are separated by microdissection. Then silver-silver chloride electrodes are applied to a strand and single nerve fiber responses are recorded under various stimulation conditions.

The other electrophysiological technique involves restricting the fish's movement by placing it in 3–5 inches of water in a small glass or plastic tank. Electric discharges are then detected with monitoring equipment connected to the water via electrodes suspended in the experimental tanks.

The data obtained by the above provide insight into system operation but are not very useful in evaluating the function or sensitivity of the receptors or systems. First, in those cases where anesthesia was used, questions can be raised concerning its effect on neural function. Second, investigators were studying isolated sensor signal under grossly abnormal conditions. Third, isolated sensor data, even if collected under reasonably normal stimulation conditions, reveal little about system function. Fourth, the engineering is typically questionable for one reason or another. This engineering question is also the prime problem with the yet to be described behavioral technique. For example, Agalides (1965) did extensive work on these fish, much of it being excellent. He, however, used a small tank which would distort the fishes' field, he did not control impedance within normal limits, and he had extraneous objects in the fishes' field. Clark and Granath (1967) and Minkoff et al. (1967) used stainless steel electrodes which may distort the fishes' field. Hagiwara et al. (1965, 1967) all show wave forms in their reports which appear to be riding on an increasing DC potential. It appears as though their electrodes underwent a significant polarization during the experiment. The experimenters will not offer an explanation for this observation. Mandriota's investigations (Mandriota et al.,

1965) are characterized by very poor experimental techniques. Not only did he use silver electrodes, a small tank, etc., but he used as a punishment with his behavioral training technique an electrical shock sufficient to jerk the fish visibly.

The foregoing is sufficient indication of the deficiencies encountered. We shall turn now to the behavioral technique that has been used, the technique that can most directly answer the question of sensitivity. In this technique, the free swimming fish is conditioned to respond to a certain stimulus. When it responds correctly, it is rewarded. The stimuli used have been an applied voltage gradient across the fish's tank or objects of different conductivity hidden within clay pots. With this technique, the sensitivity and function of the entire system can be tested.

The limits of sensitivity found can best be summed up by stating that the fish could detect the presence of a glass rod 2 mm in diameter in a clay pot but would fail to respond to a glass rod of 0.8 mm in diameter in the pot (Lissmann and Machin, 1958). This limited statement of sensitivity is as much as the state of the art provides, and even this statement can be questioned since the tank used does not appear to meet the specifications discussed below.

Somewhat akin to this behavioral technique have been the limited number of data-gathering expeditions into the fishes' natural environment. The published results are rather limited. About the only thing that has been found is that the fish have about the same pulse repetition rate in natural conditions as they do in the laboratory. It has also been found that the weakly electric fish are nocturnal creatures. Other results are ambiguous due to engineering deficiencies.

We can conclude very little about sensitivity and system function from the available data. About all that can be said is that the fish is reported to be quite sensitive and qualitative observations would seem to bear this out; but there is no adequate quantitative data.

Size of Tank Required for Valid Experimental Data. One of the prime deficiencies in the reported work is the use of a tank of inadequate size or with extraneous objects in the field. These can distort the field and seriously affect the data obtained.

We have experimentally explored the effect of various objects and tank size on a simulated fish field and found that all objects and even the walls of small pools distort the field to some extent. A quantification of this effect is defined in the calculations presented below in which we determine the specification of the tank needed for acceptable experimental work.

We assume that the fish is located centrally within a cylinder. With this assumption, we study how the potential varies as a function of cylinder length assuming an infinite radius for the cylinder. Next, we assume the cylinder has infinite length and see how current varies with radius. With this information, we will be able to determine reasonable lengths, widths, and depths for experimental containers for electric fish research. We will disregard all interfaces in this development because our ultimate intention is to determine when these interfaces can be disregarded.

The equations which express potential as a function of distance are:[4]

$$\text{for}\quad y > \frac{L}{2} + a, \qquad V = \frac{Q}{4\pi\epsilon}\left[\frac{L}{\left(y - \frac{L}{2}\right)\left(y + \frac{L}{2}\right)}\right];$$

$$\text{for}\quad \frac{L}{2} - a > y > -\frac{L}{2} + a, \qquad V = \frac{Q}{4\pi\epsilon}\left[\frac{2y}{\left(\frac{L}{2} - y\right)\left(\frac{L}{2} + y\right)}\right];$$

$$\text{for}\quad -\frac{L}{2} - a > y, \qquad V = \frac{Q}{4\pi\epsilon}\left[\frac{L}{\left(\frac{L}{2} - y\right)\left(\frac{L}{2} + y\right)}\right].$$

Plotting for different values of L in Fig. 2 A, we obtain the required cylinder length. Only the positive direction is plotted because the negative direction is identical except that the sign is reversed. How long the cylindrical tank should be is difficult to determine precisely. As a minimum, though, we can say that there should be five electric organ lengths of water in front and in back of the fish at all times during the experiment.

To determine the cylinder radius required for the tank w, we can modify the limits on the integral expressing the current I in equation 19 of our later development. This equation is:

$$I = \int_0^{\infty}\left[\int_0^{2\pi} \frac{QL\sigma R}{4\pi\epsilon\left(R^2 + \frac{L^2}{4}\right)^{3/2}}\, d\phi\right] dR.$$

The only limit which needs to be modified is the infinity symbol. We replace this with w and solving as before we find the current to be:

$$I = \frac{QL\sigma}{2\epsilon}\left[\frac{2}{L} - \frac{1}{\left(w^2 + \frac{L^2}{4}\right)^{1/2}}\right]. \tag{1}$$

The maximum current is expressed in equation 20 of the later development as:

$$I = \frac{Q\sigma}{\epsilon}.$$

By letting $w = Ln/2$ and solving equation 2 for different values of n, we have ob-

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[4] The five unnumbered equations used in this section are developed in a later section. They are numbered in the later section as 10 *a*, 10 *b*, 10 *c*, 19, 20, but appear in this order in the text due to logical considerations. Definitions of symbols can be found in symbols.

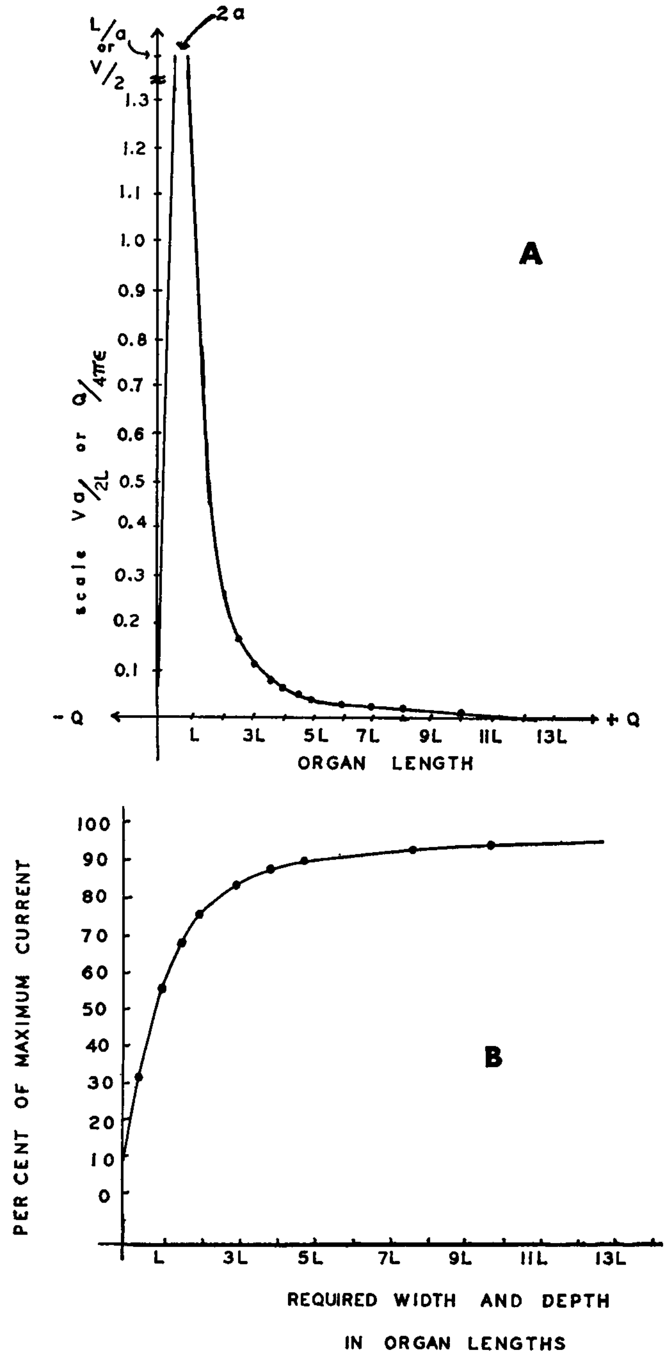

FIGURE 2 (A) This illustrates the potential on the positive side of the dipole electric generating organ. The potential on the negative side is the negative reflection of this. (B) This indicates the per cent of maximum electric generator current which will flow between the positive and negative ends of the organ as a function of the width and depth of the tank, assuming a free field expression for the current generated.

tained a plot of current as a function of width and depth. This plot is shown in Fig. 2 B. To obtain 90% of the maximum current requires five electric organ lengths on each side of the fish; to get 95% would require 10 lengths. More than 95% of the maximum current would be almost impossible to obtain in the laboratory.

Thus, for experimental results to be considered valid there should be at least five electric organ lengths of water surrounding the fish. For free swimming experiments, it would be best to have at least 10 electric organ lengths about the fish. When the fish must be restrained near the surface, 10 organ lengths of water in all other directions should be the minimum. It should also be noted that to simulate infinity in research, the tank must be connected to earth ground and made to conduct.

POSTULATED RECEPTOR MECHANISM AND NEURAL CODING

The possible mechanism discussed below cannot be said to be the mechanism that the fish actually uses in its detection and classification of objects. It is, however, derived from our review and analysis of the available data, from results of the limited experimentation that we carried out to clarify some of the available data, and from our knowledge of auditory and labyrinthine system function. Postulating on this mechanism, viewing the electroreceptors and auditory receptors as evolutionary derivations of the same primitive receptor, provides a testable hypothesis of function. It also provides a basis that can be of assistance in determining sensitivity.

Mechanism

The inner ear is a fluid-filled cavity with a complex membrane structure. It is notable for the complex electrical fields that are generated within it by external events and its organized bands of hairlike sensing cells. Early concepts of pressure waves in the fluid bending by hair cells and thereby triggering signals to the brain are very much in question. Some of the newer concepts implicate an intermediate electrical field sensing mechanism in the hair cells. The precise nature of this is not clear, but elements of O'Leary's (1970) recent work on the labyrinthine system appear quite applicable to the weakly electric fishes' sensing system. These elements combined with other information on auditory and balance sensor function will be discussed below to the extent that they have bearing on the fishes' sensing system.

Since Dohlman (1960) has shown that hair cell membranes are apparently impermeable to ions, O'Leary assumes that the detection of fields is due to electrostatic forces as opposed to ionic current. In his analysis, he points out that dissipative energy losses of an electric field in a dielectric are generally associated with the motion of charge carriers resulting in an effect called polarization. van Beek (1967) pointed out that the average molecular dipole moment P_{mol} in a heterogeneous system is the vector sum of induced (electronic) polarization resulting from the relative displacement of electrons and nuclei, dipolar polarization resulting from the partial alignment in the direction of the field of molecules with permanent dipole moments and interfacial (Maxwell-Wagner) polarization occurring at boundaries between the components of a heterogeneous system. Jackson (1962) indicated that P_{mol} is related to the macroscopic polarization P (electric dipole moment per unit volume) and the macroscopic electric field E by

$$P = N(P_{mol}) = \chi_e E, \tag{2}$$

where N is the number of molecules per unit volume and χ_e is the electric susceptibility.

From this and his own experiments, O'Leary (1970) suggests that a weak electric field in the fluid-filled inner ear might be detected by hair cells because of induced polarization in long chain filaments of polyatomic molecules in the cilia. van Beek's (1967) studies of dielectric behavior of colloidal solutions indicate that polystyrene particles are frequently surrounded by electric double layers when they are dispersed in dilute KCl solutions. Thus, it is conceivable that low frequency electric fields polarize molecules by inducing dipole moments in double layers. There is also evidence along this line from Heller et al. (1960) and Saito et al. (1966). Polarizacan also occur by a mechanism suggested by Frohlich's observation (1958) that large molecules can have CH_3, C=O, or OH groups that are in themselves dipolar but have a net dipole moment of zero. These molecules then behave like nonpolar molecules in that their polarization is of the induced (electronic) type with resonant frequencies in the optical range.

With these possible polarization mechanisms, O'Leary develops a theoretical basis for accepting an electric field sensing mechanism. This mechanism encompasses more data than a mechanical model.

Starting with Jackson's (1962) observation that a charge e which is displaced a distance x is bounded by a restoring force F given by

$$F = -m\omega_0^2 x, \tag{3}$$

where m is the mass of the charge, and ω_0 is the radian frequency of harmonic oscillation. He goes on to consider the effect of a field on a charge. The action of the field E causes the charge to be displaced a distance x from its equilibrium position. From Newton's third law we know

$$eE = m\omega_0^2 x. \tag{4}$$

The induced dipole moment is then defined for one electron as

$$P_{ind} = ex = \frac{e^2 E}{m\omega_0^2}\,. \tag{5}$$

If there are Z electrons per molecule with f_j of them bound by a restoring force

$-m\omega_j^2 x$, then the induced dipole moment is

$$P_{\text{ind}} = \frac{e^2}{m} \sum_j \frac{f_j}{\omega_j^2} E, \tag{6}$$

where $Z = \sum_j f_j$.

Temperature is not a variable in equation 6 so the induced polarization would not be disrupted by thermal agitation. Thus, the sensitivity of this effect for the detection of weak E fields would be limited by quantum considerations rather than by the classical limit of kT.

O'Leary suggests that this polarization mechanism has great sensitivity. He estimates it for the inner ear with the following argument. If the behavioral threshold for stimulus energy is indeed close to 1 $kT \simeq 4 \times 10^{-14}$ ergs/molecule as suggested by de Vries (1949), the corresponding wave number $1/\lambda$ for an energy transition of 1 kT.

$$hc/\lambda = kT, \tag{7}$$

would be $1/\simeq 200$ cm^{-1} if this energy were entirely absorbed by a single molecule. The threshold energy would probably be distributed among numerous molecules. Thus, the polarization of a single molecule would occur for energies much smaller than kT, i.e., for transitions of far less than 200 cm^{-1}.

The occurrence of hyperfine splittings in the Stark effect suggests that a transductive mechanism based on polarization would be sufficiently sensitive for the detection of threshold stimuli. Herzberg (1950) and others have studied spectroscopically the splitting of energy levels by an electric field. Splittings of about 10^{-3} cm^{-1} have been observed from diatomic molecules with field strengths in the range of 10^2–10^3 v/cm. Smaller "hyperfine" splittings were then predicted theoretically and observed using high resolution spectrometers.

Based upon the foregoing, transduction in the hair cell can be viewed as a quantum amplication process that is modulated by the average microscopic polarization of an ensemble of long-chain molecules associated with the cilia. This development suggests, accepting it for the electric fish sensor, that the electric sensor would need protection from mechanical stimuli. Both mechanical and electrical stimuli might be detected by this molecular effect in the electrical sensor because mechanical forces should also affect the microscopic polarization of long-chain molecules. The bending or shearing of cilia that contain long-chain molecules could result in a change in the net dipole moment and should also be detected by a transduction mechanism that was sensitive to microscopic polarization. The structure of the fishes' receptor organs suggests that there is such protection. This would be necessary to minimize noise in the system.

If we are correct in suggesting that this is the type of receptor mechanism that is used by the fish for electrosensing, then it would provide a basis for accepting the qualitative statements on the high sensitivity of the fishes' electrosensors. Lacking well-controlled behavioral data on sensitivity, we would hesitate though to conclude that the fish is as sensitive as this analysis suggests.

We have now considered the structure and function of the generator organ and receptor organ. Now we shall look at the next level of the nervous system. We shall consider the coding of nerve impulses by the receptor organ, its transmission toward the brain, and the implications of the coding in understanding the electrosensing function and sensitivity.

Coding

As has been noted earlier, the literature is encumbered with multiple classification schemes for electroreceptors. This has the potential for confusion and does little to increase our understanding of receptor function. For example, one scheme is based on external physical appearance, e.g. small, medium, and large mormyromasts, another on total configuration, e.g. ampullary and tuberous, and there are other crude classification schemes.

Two somewhat more useful schemes also exist. One is used by almost everyone who discusses electroreceptors. In this scheme, the output of the receptor is related to the output of the generating organ. The electroreceptors are said to be either phasic or tonic. Phasic receptors respond (give an output) at some integer division of the generator frequency with a string of from one to *n* pulses. Tonic receptors maintain a steady output that is essentially independent of generator output, changing as a function of an environmental stimulus.

There is a general relationship between the physical classification scheme discussed in an earlier section and the tonic-phasic scheme just described. Receptors fit for the most part into two classes: tonic receptors that are sensitive to low frequency stimuli and are of the ampullary type, and phasic receptors which are sensitive to high frequencies and are of the tuberous type. The other useful classification scheme involved the apparent coding employed by the electroreceptor for transmission of information to the brain.

One fish, *Hypopomus*, has electroreceptors which respond to each discharge of the electric organ with a succession of short pulses. Each "pulse train" contains eight or more pulses (Hagiwara et al., 1962). The electroreceptors of *Gymnotus* and *Steatogenes* respond with one to six pulses to each generator discharge (Hagiwara and Morita, 1963). Some studies indicate that the number of pulses in each train can be related to the potential near the receptor. This has been referred to as "number coding."

In another weakly electric fish, *Eigenmannia*, each organ discharge does not produce a receptor output. If the fishes' electrical fields are distorted though, we find that the receptor output is at most one impulse per generator organ discharge. If we decrease the distortion we find the receptor output to be one impulse per every two generator organ discharges and so on. In other words, the chance that a receptor will fire is related to the stimulus intensity acting on it. This type of coding is called "probability" coding (Hagiwara and Morita, 1963).

Another fish, *Sternopygus*, was thoroughly studied by Bullock and Chichibu (1965). They found fibers that carry one impulse per organ discharge. They noted a phase or time relationship with the intensity of the stimulus. This is referred to as "phase" or "latency" coding. They also found other nerve fibers that maintained a rhythmical firing out of phase with the electric organ discharge. The frequency of these receptors changed as a function of the intensity of the electric field near the receptor. This type of coding is frequency coding and is characteristic of ampullary organs.

As a weak generalization, it appears that ampullary receptors give tonic responses with frequency coded information and tuberous receptors give phasic responses with either number, phase, latency, probability or frequency coded information; but a strong generalization can be developed.

Hagiwara and Morita (1963) suggest a model for probability coding based on an assumed nerve threshold. By making certain assumptions about the threshold curve, we have extended their model to encompass all coding schemes proposed to date. Their model was originally developed for tuberous-phasic receptors, but it can be extended to ampullary-tonic receptors with a simple modification as we now show.

The threshold model as reported by Hagiwara and Morita (1963) assumes after a receptor fires that the threshold resets to some high value. The threshold then begins to decay until the intensity at the receptor is equal to or momentarily exceeds the threshold. At this point, the receptor fires, and the threshold resets.

It is established in biology that nerves do not fire during or instantaneously after a previous firing. There is also a biological basis for defining the threshold curve as an exponential decay from some value: $T_{\max}$ the maximum threshold to $T_{\min}$ the minimum threshold. Finally, it is probable that the threshold curve shifts as a function of the needs of the fish. Such shifts, if understood, could be modeled by changing $T_{\min}$, $T_{\max}$, or the exponential time constant T_c.

With these facts in mind, we can describe the threshold function for time after each firing as

$$T = [T_{\max} - T_{\min}]\, e^{-t/T_c} + T_{\min}. \tag{8}$$

Further, as a very good approximation we could say

$$T \approx T_{\max}\, e^{-t/T_c} + T_{\min}. \tag{9}$$

To describe probability coding, we must assume that $4\,T_c \gg 1/f$. In such cases, the electric organ can discharge several times without firing the nerve. The number of times it must discharge before activating the nerve is a function of the stimulus potential relative to the threshold. The higher the potential the sooner the nerve will fire. This is illustrated in Fig. 3 A.

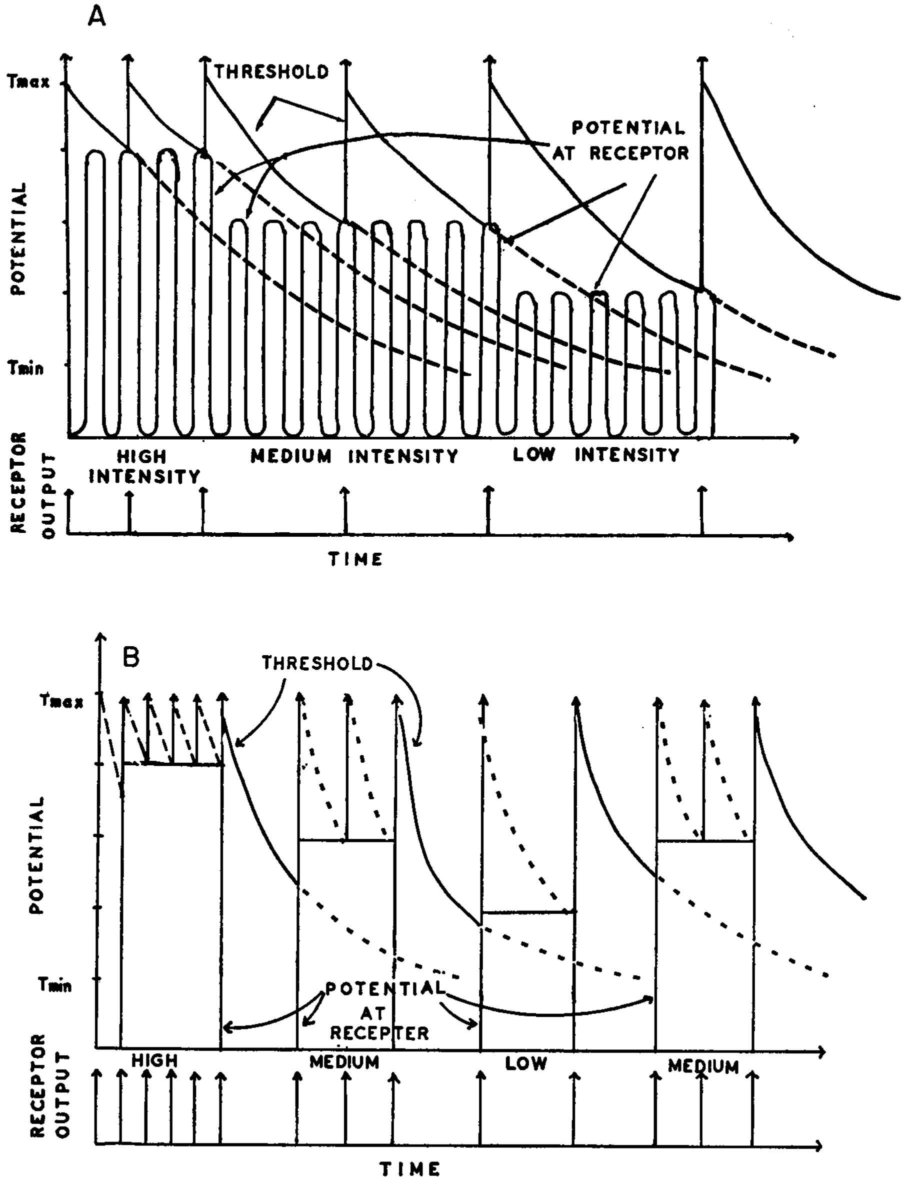

FIGURE 3 (A) This illustrates the relationship between the electric potential at the receptor, the receptor threshold state, and receptor output when the receptor threshold decay time constant is greater than the repetition rate of the electric generating organ. In this case the apparent coding is commonly referred to as probability or frequency coding. (B) This is comparable to case A, but the decay time constant is much less than the duration of the electric organ output. In this case the output of the electroreceptor is said to be pulse count coding.

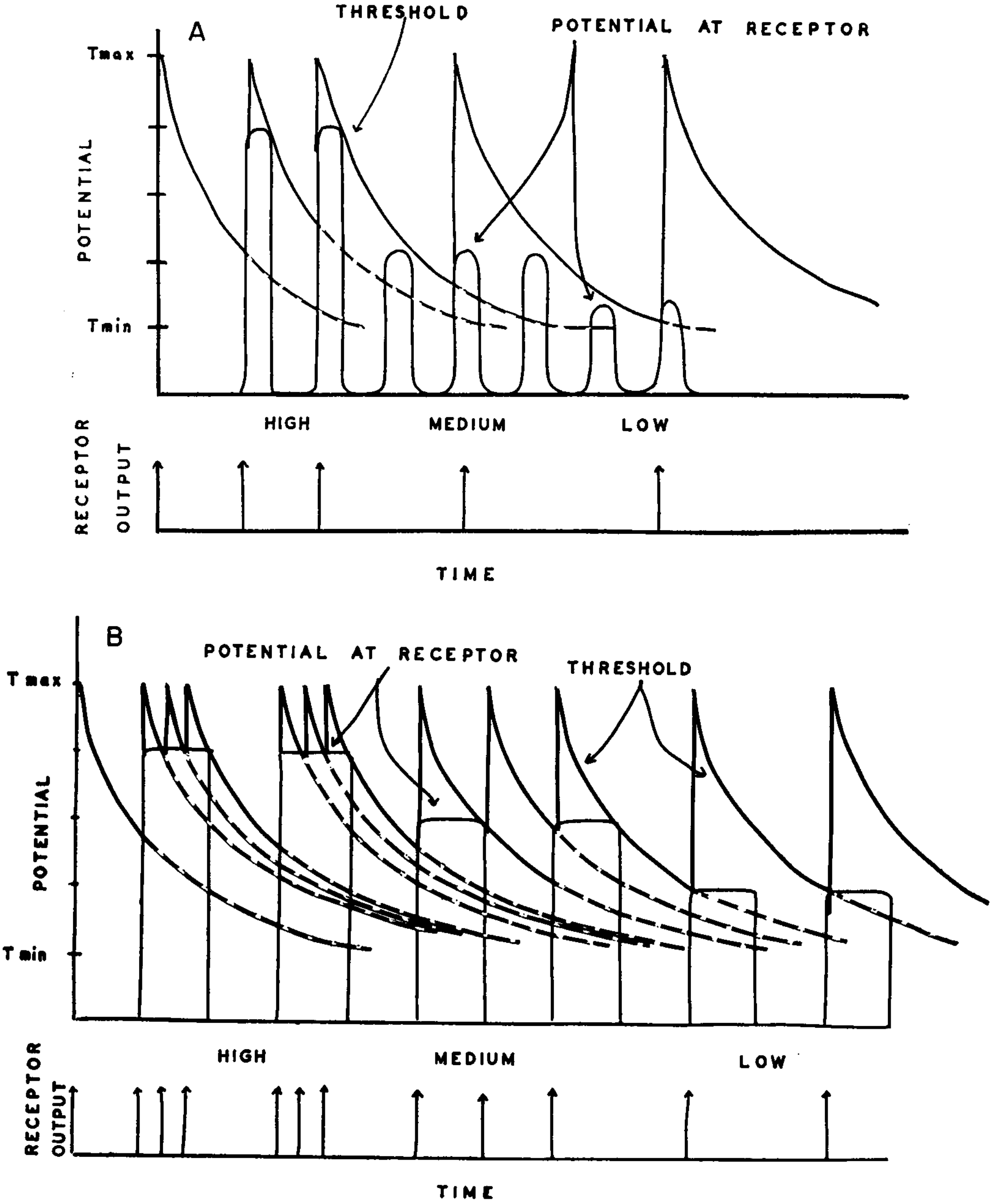

FIGURE 4 (A) This illustrates the relationship between the electric potential at the receptor, the receptor threshold state, and receptor output when the generator organ rate is is just smaller than the reciprocal of the decay time constant. The output of the electroreceptor in this case is typically referred to as phasic or latency coding. (B) This illustrates the relationship between the electric potential at the receptor, the receptor threshold state, and receptor output when the generator organ rate is just larger than the reciprocal of the decay time constant. The output of the electroreceptor in this case is typically referred to as interpulse interval coding.

We can also see that phasic coding requires $T_{min} > 0$. If T_{min} were zero, the sensor would reset independently of the electric organ and one form of tonic coding would be observed.

To describe number coding we must assume that $4\ T_c \ll 1/f$. In such cases the electric organ will cause the receptor to fire more than once each time it discharges. The number of times the receptor will fire is proportional to the intensity at the receptor as illustrated in Fig. 3 B. Again, for phasic coding T_{min} must be greater than zero.

As $4\ T_c$ becomes approximately the same as $1/f$, several interesting possibilities occur: phasic coding, latency coding, and interpulse interval coding. Phase and latency coding are illustrated in Fig. 4 A. They are one and the same. Interpulse interval coding is illustrated in Fig. 4 B. It is also interesting that when $4\ T_c$ is about 2 or 3 times $1/f$ a combination of probability and number coding can be anticipated. Such coding has been observed for *Sternopygus* (Hagiwara and Morita, 1963).

This model does not account for the observed output of phasic receptors while the generator is between pulses. As has been noted previously, there are reports that phasic receptors have an output apparently unrelated to generator output. We do not know if this is due to an error in the model, insufficient data to incorporate particular observations into the model, the existence of a buffering capability at the receptor, or if the reports report artifacts due to faulty technique;[5] but whichever is the case, the utility of the model is not affected. It can usefully be used as a unifying framework for studies of threshold, sensitivity, and response time across all weakly electric fish. With such a framework, sensitivity could be well defined experimentally and the mechanism of the sense better understood.

MODEL: DEVELOPMENT, FUNCTION, AND SENSITIVITY

In outline, the fishes' sensing system appears to function as follows: the generating organ emits an intermittent electric potential or current. This results in an electric (dipole-like) field in the water surrounding the fish. Objects within the environment and the environmental boundaries distort the electric field. This distortion causes a change in the electric field near the fish which we shall refer to as the stimulus. The receptors measure the electric field or properties of it thereby providing information that is processed by the fish's nervous system.

This system model generally agrees with data reported by Lissmann (1963) from conditioned response experiments. In his experiments, *Gymnarchus* was trained to respond to changes in the conductivity of objects placed in a sealed container. Positive reinforcement was a food reward, and negative reinforcement or punishment was the insertion of a metallic object into the fish's tank. This punishment was probably not sufficient to test reasonably the threshold of the biological system. But by using this method Lissmann and Machin (1958) determined a threshold to potential change of about 0.15 μv/cm.

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[5] If T_{min} were below the mechanical noise level, phasic receptors would appear to be tonic receptors.

We shall also model the fish as a dipole, but a dipole that differs from the one suggested by investigators such as Lissmann. He suggested that the fish is a head-to-tail dipole. This suggestion, however, neither fits with the physical location of the electric generating organ as determined anatomically nor with the data reported by Bullock and Chichibu (1965). As noted in an earlier section, the electric generating organ has been found to be located near the tail in most if not all weakly electric fish. Bullock and Chichibu (1965) observed the zero potential plane to be perpendicular to the fish and found it located approximately one-quarter of the way toward the head measuring from the tail. Thus, we use as our model a dipole field located in the rear half of the fish.

We will develop a simplified model of the receptor and then discuss system function. We will use the dipole concept described above as well as the hypothesis on sensor function derived from above. Through the development of a set of equations and a computer analysis, we will obtain an approximate solution for the response of the receptors due to perturbations caused by an object in the field. Through this, we will determine critical variables in the sense function and quantify their effect. With the information so derived, we will consider the practical implications of the sense.

The symbols used in the following development are defined in Symbols. The definitions are critical as is the recognition that coordinate transformations are necessary and will be used.

Receptor Level

Development. Consider a simple dipole consisting of two conducting spheres of radius a separated by a distance L. One sphere is positively charged to a total charge of $+Q$. The other sphere is negatively charged to a total charge of $-Q$. We will assume that a is much less than L. When this is the case, the charge on each sphere can be assumed to be evenly distributed about the surface.

We assign a coordinate system as shown in Fig. 5, where the y axis passes through the centers of both spheres, with its origin at the center between the spheres. For such a coordinate system, the potential v can be expressed in three regions as:

$$\text{for} \quad y > \frac{L}{2} + a, \qquad V = \frac{Q}{4\pi\epsilon}\left[\frac{L}{\left(y - \frac{L}{2}\right)\left(y + \frac{L}{2}\right)}\right]; \qquad (10\,a)$$

$$\text{for} \quad \frac{L}{2} - a > y > -\frac{L}{2} + a, \qquad V = \frac{Q}{4\pi\epsilon}\left[\frac{2y}{\left(\frac{L}{2} - y\right)\left(\frac{L}{2} + y\right)}\right]; \qquad (10\,b)$$

$$\text{for} \quad -\frac{L}{2} - a > y, \qquad V = \frac{Q}{4\pi\epsilon}\left[\frac{L}{\left(\frac{L}{2} - y\right)\left(\frac{L}{2} + y\right)}\right]; \qquad (10\,c)$$

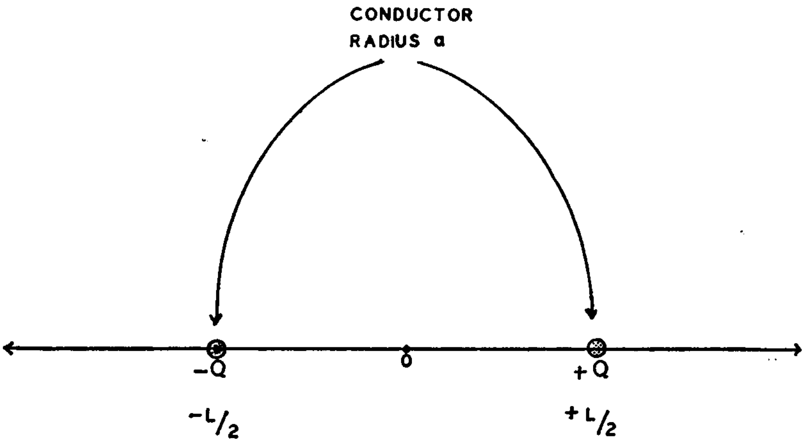

FIGURE 5 Simplified model which will be used in the study of the electrostatic characteristics of the electric field generated by the fish. The field generating organ is assumed to be composed of two conducting spheres of radius *a* separated by a distance *L*. For convenience, the origin is taken to be the midpoint between the two conducting spheres.

where V is the absolute voltage ($V \mid \infty \mid = 0$), Q is the charge on either conductor, L is the distance between the conductors, ϵ is the constant known as the dielectric, y is a continuous variable representing an absolute scale with 0 being located between the positive and negative charge as indicated in Fig. 5.

Equation 10 *b* can now be employed to find the relative voltage between the two spheres. This is the voltage which should be measured in the laboratory.

Let us define v to be the relative voltage between two spheres. We note that v is the value of the voltage at the positive sphere minus the value of the voltage at the negative sphere. By substituting $y = L/2 - a$ into equation 10 *b*, we find the voltage on the positive sphere to be

$$V(+) = \frac{Q}{4\pi\epsilon} \frac{L - 2a}{a(L - a)}. \tag{11}$$

Substituting $y = -L/2 + a$ into equation 10 *b* we find the voltage on the negative sphere to be

$$V(-) = \frac{Q}{4\pi\epsilon} \frac{-L + 2a}{a(L - a)}. \tag{12}$$

Solving for v we find

$$v = V(+) - V(-), \tag{13}$$

or

$$v = \frac{Q}{4\pi\epsilon} \frac{2}{a} \frac{\left(1 - \frac{2a}{L}\right)}{\left(1 - \frac{a}{L}\right)}. \tag{14}$$

When a/L is less than $1/10$, equation 14 can be approximated within 5% by the relationship

$$v = \frac{Q}{2\pi\epsilon a}\left(1 - \frac{a}{L}\right). \tag{15}$$

The capacitance of an object is defined as

$$C = \frac{Q}{V}, \tag{16}$$

where Q is the charge on one symmetric part of the object and V is the voltage across the object. Substituting equation 15 into equation 16 yields:

$$C = \frac{Q}{v} = 2\pi\epsilon a \frac{\left(1 - \frac{a}{L}\right)}{\left(1 - \frac{2a}{L}\right)}. \tag{17}$$

This may be approximated within 5% for a/L less than $1/10$ as

$$C = 2\pi\epsilon a\left(1 + \frac{a}{L}\right). \tag{18}$$

It is useful to determine the resistance of the dipole we have just considered. Since we have already evaluated the voltage between the charges, if we can find an expression for the current that flows between the two points, we can solve for the resistance from Ohm's law.

The current I for the dipole may be found by evaluating the surface integral shown in equation 19, where $d\phi$ is an increment of angle ϕ which is an angle about the y axis, and dR is an increment in the distance vector R.

$$I = \int_0^\infty \left[\int_0^{2\pi} \frac{QL\sigma R}{4\pi\epsilon\left(R^2 + \frac{L^2}{4}\right)^{3/2}}\, d\phi\right] dR, \tag{19}$$

which yields:

$$I = \frac{Q\sigma}{\epsilon}. \tag{20}$$

We have previously solved for the voltage between the charges in equation 15. Dividing the voltage v by the current I, equation 20 yields the resistance:

$$R = \frac{1}{2\pi\sigma a}\left(1 - \frac{a}{L}\right). \tag{21}$$

As a first approximation let us assume the radius of each charged sphere a is 1 cm and that the length of the generator organ L is 10 cm. The conductivity of freshwater is about $10^{-3}\ \Omega^{-1}\ \mathrm{m}^{-1}$, thus the resistance which loads the generator organ is about 62,000 Ω.[6] The dielectric of freshwater is 0.707×10^{-9} F/m. This means that the capacitance which loads the dipole is approximately 40 pF. This large resistance and small capacitance indicates that only a small current flows. Thus, an electrostatic approach is suitable for a first model of the electric fish.

Function. Accepting for now an electrostatic model, we will consider the effect of an intruding object on an individual receptor. As a simplification the intruding object will be assumed to be a sphere. Such an object moving into the fish's field will modify the potentials along the fish's surface. To obtain a solution for these modifications, we will first consider the electric field produced by the dipole generator organ undisturbed by the perturbating object. We will calculate its magnitude at an arbitrary point p. We will then consider the effect at point p of a perturbating object located in a uniform field. Then we will transform the perturbation portion of our solution back to the original coordinate system.

Once we have obtained an appropriate solution, we will assume and fix certain variables. Then we will study the nature of the fishes classification techniques by plotting our results for given receptors along the fish. It should be noted that this analysis is three dimensional and although not conceptually difficult, it is somewhat complex. Fig. 6 illustrates the problem.

The magnitude of the electric field expressed in terms of the coordinate system is (Bohn, 1963):

$$|\mathbf{E}| = \frac{Q}{4\pi\epsilon_w R^2}\left[1 - \frac{2R^2(R + L\cos\theta)}{(R^2+L^2+2RL\cos\theta)^{3/2}} + \frac{R^4}{(R^2+L^2+2RL\cos\theta)^2}\right]^{1/2}, \quad (22)$$

and the angle relative to the projected y axis is:

$$\beta = \tan^{-1}\left\{\frac{\sin\theta[(R^2+L^2+2RL\cos\theta)^{3/2} - R^3]}{(R^2+L^2+2RL\cos\theta)^{3/2}\cos\theta - R^2 + L + R^3\cos\theta}\right\}. \quad (23)$$

These rather complicated equations completely describe the electric field due to the dipole in a continuous media of dielectric ϵ_w.

To obtain a first approximation of the perturbation due to a sphere of radius r at a location R_0, ϕ_0, θ_0, relative to the dipole coordinates, we assume that the sphere is located in a uniform field of strength E_0 at an angle β relative to a line parallel to the y dipole axis through the sphere center. We will further assume that the value of this field is the value of the dipole field at the center of the sphere, disregarding the effect of the sphere. If the sphere is small relative to the dipole length or if it is very small

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[6] In a practical model, the resistance loading of the generator can be controlled by the choice of generator electrode size.

relative to the separation between the dipole and the sphere, the assumption will permit a solution within acceptable limits. The equations which describe the electric field due to the dipole could be simplified to a good approximation if the separation between the dipole and the object sphere is more than 10 dipole lengths. Since the biological data is not adequate, we do not know the range of the electric sense. Consequently, we will not approximate the field at this point.

Assuming a uniform field (without the perturbation) and expressing the potential in terms of the coordinate system centered at the object we obtain[7]

$$U_0 = -E_0 \rho \cos \alpha. \tag{24}$$

The surface charge on the perturbating sphere is exactly like a dipole. Thus, the potential is of the form

$$U_x = \frac{A \cos \alpha}{\rho^2}, \tag{25}$$

where A is a constant to be determined from the boundary conditions. Finally the potential inside the sphere is of the same form as the potential due to the original field or

$$U_L = -B\rho \cos \alpha, \tag{26}$$

where B is a constant to be determined from the boundary conditions. The potential outside the sphere is the sum of U_0 and U_x or

$$U_{\text{total}} = -E_0 \rho \cos \alpha + \frac{A \cos \alpha}{\rho^2}. \tag{27}$$

The electrostatic boundary conditions require that when $\rho = r$

$$-\epsilon_w \frac{\partial U_{\text{total}}}{\partial \rho} = -\epsilon_x \frac{\partial U_I}{\partial \rho}, \tag{28}$$

and that when $\rho = r$

$$U_{\text{total}} = U_I. \tag{29}$$

Substituting equations 26 and 27 into equation 29 yields

$$E_0 r^3 - A = B r^3. \tag{30}$$

Substituting equations 26 and 27 into equation 28 yields

$$\epsilon_w E_0 + 2A\epsilon_w = r^3 \epsilon_x B. \tag{31}$$

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[7] We employ the boundary condition approach to this solution because it provides greater insight than the solution of Laplace's equation.

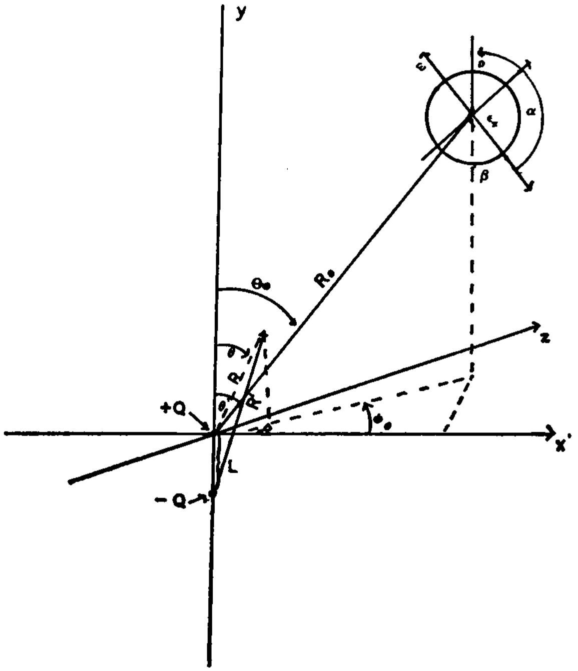

Figure 6 This illustrates the variables involved in our model when a spherical perturbing object is present in the model's environment. Note the several coordinate systems that must be considered in the analysis.

We can solve for A or B in equation 30 and 31 to find

$$B = \frac{3\epsilon_w}{\epsilon_x + 2\epsilon_w} E_0, \tag{32}$$

and

$$A = \frac{\epsilon_x - \epsilon_w}{\epsilon_x + 2\epsilon_w} r^3 E_0. \tag{33}$$

The potential U_0 was assumed to be the potential due to the dipole. We have an accurate expression for this field. The potential within the sphere does not effect the potential near the dipole. The critical term is the potential U_x which is the approximate modification of the dipole field due to the spherical object. Substituting equation 33 into equation 25 yields

$$U_x = \frac{\epsilon_x - \epsilon_w}{\epsilon_x - 2\epsilon_w} \frac{r^3}{\rho^2} |E_0| \cos \alpha, \tag{34}$$

the perturbation potential.

We recall the value of E_0 to be the value of equation 22 when $R = R_0$ and when

$\theta = \theta_0$ or

$$E_0 = \frac{Q}{4\pi\epsilon_w R_0^2}\left[1 - \frac{2R_0^2(R_0 - L\cos\theta_0)}{(R_0^2 + L^2 + 2R_0^2\cos\theta_0)^{3/2}} + \frac{R_0^4}{(R_0^2 + L^2 + 2R_0 L\cos\theta_0)^2}\right]^{1/2}, \quad (35)$$

and we recall that α is measured relative to an angle β which is equation 23 evaluated at R_0, θ_0, or

$$\beta = \tan^{-1}\left\{\frac{\sin\theta_0[(R_0^2 + L^2 + 2R_0 L\cos\theta_0)^{3/2} - R_0^3]}{(R_0^2 + L^2 + 2R_0 L\cos\theta_0)^{3/2}\cos\theta_0 - R_0^2 L + R_0^3\cos\theta_0}\right\}. \quad (36)$$

To complete our analysis, we must express ρ and α in terms of R, θ, ϕ, R_0, and θ_0. In reduced form this is:

$$\rho = \{R^2 + R_0^2 - 2\,RR_0[\cos\theta_0\cos\theta - \sin\theta_0\sin\theta\cos(\phi - \phi_0)]\}^{1/2} \quad (37)$$

We can solve for α in terms of R, θ, θ_0, β, and ρ. This is

$$\alpha = 360° - \left[\sin^{-1}\frac{R\sin(\theta - \theta_0)}{\rho}\right] - \theta_0 - \beta. \quad (38)$$

We now have a multitude of equations but they provide a basis for a computer study of the effect of the variables. Thus, we will review the salient ones and group them in an orderly fashion for computer study.

Sensitivity. The magnitude of the electric field at any point in space can be found from equation 22 when $R = R_0$ and $\theta = \theta_0$. Equation 22 becomes equation 35 which is assumed linear throughout the perturbation. The magnitude of the electric field is

$$E_0 = \frac{Q}{4\pi\epsilon_w R_0^2}\left[1 - \frac{2R_0^2(R_0 + L\cos\theta_0)}{(R_0^2 + L^2 + R_0 L\cos\theta_0)^{3/2}} + \frac{R_0^4}{(R_0^2 + L^2 + 2R_0 L\cos\theta_0)^2}\right\}^{1/2}. \quad (39)$$

The angle of this field relative to the y axis in the R_0 -y axis plane is given by equation 23 which for $R = R_0$, $\theta = \theta_0$ becomes

$$\beta = \tan^{-1}\left\{\frac{\sin\theta_0[(R_0^2 + L^2 + 2R_0 L\cos\theta_0)^{3/2} - R_0^3]}{(R_0^2 + L^2 + 2R_0 L\cos\theta_0)^{3/2}\cos\theta_0 - R_0^2 L + R_0^3\cos\theta_0}\right\}. \quad (40)$$

This field creates a perturbation field in a remote object of radius r and dielectric ϵ_x. The potential of the perturbation field is given by equation 34 which is

$$U_x = \frac{\epsilon_x - \epsilon_w}{\epsilon_x + 2\epsilon_w}\frac{r^3}{\rho^2}E_0\cos\alpha. \quad (41)$$

Unfortunately, ρ and α are in terms of a secondary coordinate system. Our primary coordinate system is R, θ, ϕ. Equation 37 expresses ρ in terms of R, R_0, θ, θ_0, ϕ, and ϕ_0. This is the first place where the perturbation angle ϕ_0 is important. The expression for ρ is

$$\rho = \{R^2 + R_0^2 - 2RR_0[\cos\theta_0 \cos\theta - \sin\theta \sin\theta_0 \cos(\phi - \phi_0)]\}^{1/2}. \quad (42)$$

The angle α can be expressed in terms of R, R_0, θ, θ_0, ϕ, and ϕ_0. It is simpler, however, to express it as

$$\alpha = 360° - \left[\sin^{-1}\left(\frac{R \sin(\theta - \theta_0)}{\rho}\right)\right] - \theta_0 - \beta. \quad (43)$$

The undistorted potential about the fish due to the dipole alone, expressed in this coordinate system, is (Bohn, 1968):

$$U_0 = \frac{Q}{4\pi\epsilon_w}\left[\frac{1}{R} - \frac{1}{(R^2 + L^2 + 2RL\cos\theta)^{1/2}}\right]. \quad (44)$$

Speaking anthropomorphically, the fish knows U_0, R, L, θ, ϕ, Q, and $4\pi\epsilon_w$. It must determine R_0, θ_0, ϕ_0, r, and $4\pi\epsilon_x$. To find these variables, it makes an analysis of the potential function $U_0 + U_x$. Exactly how this analysis is made is unknown.

As an approach to determine how the fish might operate, we shall find the ratio U_x/U_0 at different points along the fish for different values of ϵ_x, r, R_0, θ_0, and $(\phi - \phi_0)$. The equations are rather complex, and require computer analysis. Thus a Fortran computer program was written which manipulates and evaluates the desired variables. In the computer program, certain variables have been assigned values for reasons that are discussed below.

The distances about the model can be normalized with respect to generator organ length. This normalization is effected by assigning the generator organ length as 1 m. Thus, range, perturbating object size, and electroreceptor locations are all discussed in terms of generator organ lengths. The dielectric of the perturbating object has been expressed in terms of the dielectric of water. In other words the analysis is in terms of ϵ_w/ϵ_x rather than ϵ_x or ϵ_w themselves.

The fish is defined as a cylinder 2 times as long as the electric generator organ, with a radius 0.2 times the generator length. Six longitudinal bands of 11 receptors are assigned along the length of the cylinder. Three bands, each band 15° apart, are located on each side of the fish. The center band on each side is assumed to be in the same plane as the center of the perturbing object and the axis of the cylinder. These dimension ratios and receptor locations were assigned based on actual fish dimensions. They do not, however, represent the physical structure of a specific weakly electric fish.

The computer program analysed various combinations of four factors: (*a*) the ratio of ϵ_w/ϵ_x or the ratio of the dielectric constant of water to the dielectric constant of the object, (*b*) the distance in generator lengths from the center of the cylinder to the center of the perturbing object, (*c*) the angle in radians formed by the cylinder axis and the vector from the cylinder center to the center of the perturbing object, and (*d*) the radius of the perturbing object in generator lengths.

With each combination of the above factors, the program had the computer manipulate and print out values of three variables that describe receptor position and also the associated ratio of perturbation potential to free field potential. The three variables were manipulated to show the effect on the perceived potential ratio. These variables are defined as: R, the line segment from the center of the cylinder to the receptor on the cylinder surface; θ, the angle formed by the intersection of line segment R and the cylinder axis; $\phi - \phi_0$, the angle defined by the intersection of the plane passing through the center of the object and cylinder axis and the plane passing through the cylinder axis and a band of eleven receptors on the fish's surface. In the actual printout, this angle was taken for each of six receptors defined by the same radius r and angle θ to find (U_x/U_0) the ratio of the potential due to the perturbation and that due to the dipole effect in the free field.

The following are the primary conclusions from the computer analysis of the electrostatic model: (*a*) the value of the signal (disturbance/free field) is the same at receptors 15° above and below the receptors on the plane defined by the cylinder axis, receptor band, and center of the perturbing object. (*b*) The magnitude of the signal is largest in most circumstances at the head end of the simulated fish. (This may explain the high concentration of electroreceptors on the head of the actual fish.) (*c*) The magnitude of the signal is smallest at the cylinder surface closest to the two poles of the generator dipole.

Assuming the fish can detect a signal of 1 ppm (humans can detect sounds 1 millionth normal speech loudness) the fish can easily detect objects of dielectric 0.1 times water whose radius is 0.1 generator organ lengths, at distances to the side of six generator lengths. It would have difficulties at 10 lengths or for dielectrics of 0.5 or 5 times water.[8]

With the assumed sensitivity, the fish could detect objects of dielectric 0.1 water, assuming that object radius is 0.1 generator organ lengths at 10 electric organ lengths if approached from front or rear. Objects of dielectric 10 times water could be detected at a considerable angle from the direct front or rear approaches at 10 lengths.

An indication of required receptor sensitivity for the detection of objects of dielectric 10 times water and 0.1 water with a radius of one organ length is given in Table I. The analysis shows that the signal is about twice as large for dielectrics 10 times water as it is for objects with dielectrics 0.1 times water.

This model of the electric sense and our analysis to date leaves many questions unanswered. We have not considered the perturbation of either the dipole potential

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[8] The dielectric of water is approximately 81, plastics are about 8, air is about 1, and metals would be extremely high, virtually infinite in many cases.

TABLE I

RECEPTOR SENSITIVITY

Detection distance	Receptor discrimination
1 length	1 part/1000
10 lengths	1 part/10,000
100 lengths	1 part/1,000,000
1000 lengths	1 part/100,000,000
10,000 lengths	1 part/10^{10}

or the object potential due to the fish's body. We can anticipate that such a perturbation exists. We have not evaluated the effects of changes in the model geometry, and we have not considered the importance of the time-varying potentials which are generated by electric fish. We are now extending our current model to include the perturbation due to the fish's body, the time-varying signal generated by the electrocyte, and the interactions resulting from relative motion between the fish and the external object. The model presented is an attempt to obtain order-of-magnitude approximations of the characteristics and range of the electric sense. It meets this objective.

System Level

It is likely that the fish can use inhibitory and facilitating circuits, possibly in the manner used by the mammal, to sharpen the aforementioned data from the receptor, extract signal from noise, and classify multiple incoming signals. In essence, it might function as a system at the receptor level with interactions among receptors and at the whole organism level involving the receptors, generator, and brain. For example, there is evidence that a plot of receptor potential along a band of receptors would yield, for a single perturbing object, a unimodel curve (Hagiwara and Morita, 1963). We suggest as a possibility for consideration that the configuration of the curve is a function of the over-all impedance of the perturbing object, defining impedance as the sum of the resistance and the reactance of the object. The reactance of an object is given by

$$X = 2\pi FL + \frac{1}{2\pi FC}, \qquad (45)$$

where X is reactance, F is frequency, L is the inductance in henrys of the object under observation, and C is the capacitance in farads of the object under observation.

As may be seen, by operating as a system by coordinating the generator and receptor function, the fish by changing generator frequency can induce a lower or higher over-all effective impedance in the object. If an object had an impedance very similar to that of water, the fish could enhance its discrimination and classification ability by varying its frequency; making the object create a greater or lesser potential gradient at the receptor. Thus, if the fish was trying to locate a certain object, it could adjust its frequency to optimize its detection of the object. Using this system approach it would also be possible for the fish to sense differences in objects that have the same exterior physical appearance. This would be done through varying the frequency and sensing and comparing the changes in the reactance of the objects. At least some species of fish seem to be using the foregoing system approach. In the earlier discussion of the available biological data, it was noted that a generator frequency shifting technique was used.

There also appear to be mechanisms that can be used to optimize detection and classification of one stationary object among several stationary objects or a moving object among stationary objects. For example, to detect a moving object several scans could be carried out, stored, and compared. In this way, stationary objects in the field would be nulled and only objects of changing impedance or location would be perceived.

CONCLUSION

Although there is a fairly substantial data base, we find that very little can be applied to the development of an understanding of sense mechanism and sensitivity. This is in part due to the fact that pioneering data in this area, as it is in most areas, tend to have faults no matter how competent the investigators. One of the prime deficiencies in the reported work is the use of a tank of inadequate size or with extraneous objects in the field. These distort the field and seriously affect the data obtained. Further, the data base contains very little behavioral data.

Thus, we undertook several tasks to provide a basis to assess the fishes' electrosensing mechanism and capability, using the data presently available.

Through limited experimental work with electrical fields, sensors, and objects in various size bodies of water we have gathered data which, when taken with the mathematical analysis, provide a specification for tank size, fish location, and attachments, that will yield valid data in future studies. We found that for experimental results to be considered valid there should be at least five electric organ lengths of water surrounding the fish. For free swimming experiments, it would be best to have at least 10 electric organ lengths about the fish. When the fish must be restrained near the surface, 10 organ lengths of water in all other directions should be the minimum. It should also be noted that to simulate infinity in research, the tank must be connected to earth ground and made to conduct. This does not seem to have been done in past research.

We have suggested as a working hypothesis an electrosensor mechanism. This hypothesis is subject to test and thereby may provide the means for collapsing the current multiple crude categorizations of the receptor that is so typical of a new area of investigation. The hypothesis may also provide a basis for analyzing higher interactions in the fishes' nervous system and thereby increase our understanding of the sense.

We have also, through quantitative analysis, shown the linkage among the various neural coding schemes suggested for the fish and have shown their essential identity.

We have also developed a mathematical model of the fish based upon the usable experimental data. A set of equations describing function was developed on the model and these equations linked to available experimental data. The mathematical model was analyzed by a computer to ascertain the sensitivity of the fish at the receptor and to determine the effects of manipulating a number of variables. These variables included fish size, object size, object electrical characteristics, object distance from the fish, direction and angle of the object from the fish's axis, etc. From the computer analysis, we determined the sensitivity to various perturbing objects under a variety of conditions and found the fish to be quite sensitive particularly in certain directions.

Sondra Feld and Rodman Messenger, Jr. have made contributions to this project that we wish to acknowledge.

This investigation was sponsored by the office of Naval Research.

Received for publication 14 January 1972 and in revised form 16 May 1972.

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