

ON THE NATURE OF ELECTROSENSING IN THE FISH

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ABSTRACT

An evaluative review of the electrosensing literature was carried out with the intention of determining the nature of the electrosensing mechanism and its sensitivity. It was found that the biological data base was weak. It was, however, useful in the development of a mathematical model and mathematical analyses of the sense mechanism and its function. In the course of 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.

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## INTRODUCTION

It has only been a short time 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 that the fish itself generates. With further investigation it was found that this sense is more generally found among fishes than was first thought. Data also appeared indicating that some fish, such as the shark and goldfish, use a passive electrosensing system in that the fish does not seem to generate its own electrical field. Rather, it seems to detect electrical signals, possibly muscle potentials, generated by objects coming into its area.

Although there is now a fairly substantial data base, we find that very little can be applied to the development and understanding of sense mechanism and sensitivity. This is due in part 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. Further, the data base contains very little behavioral data. Thus, there is little information available on system sensitivity and function.

In sum, though there are individual investigators contributing quite useful data to the data base, 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 the data presently available.

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, allows us to interpret much of the data now available. This analysis also provides a specification for tank size,

fish location, and attachments, that will yield valid data in future studies.

Second, 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.

Third, we indicate in the following 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 useable experimental data. A set of equations describing function is developed on the model. These equations are linked to available experimental data. The mathematical model is analysed 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.

#### NATURE OF THE BIOLOGICAL SYSTEM

Both marine and fresh water 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 by the object perturbing the electrical field formed by the electric

generating organ which normally emits a continuous pattern of pulses. The electric field so set up 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 electrical field generating organs and receptor organs. Other weakly electric fish include *Gymnarchus*, an African fish, probably related to the mormyrids, and sternarchid, a South American fish that is probably related to the Gymnotids.

#### Generator Organ

An understanding of the structure and function of the electrical field 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 are derived from the mesoderm (Szabo, 1966), the same type of embryonic tissue as muscle except in the South American family Sternarchidae. The origin of the electrocytes of the sternarchids is the same embryonic tissue from which the neural system is derived, the 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 300-500  $\mu$  in diameter and about 200  $\mu$  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  $\mu$  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 1/5 of the fish's body length. *Gymnarchus*' 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. Some of these are *Eigenmannia*, *Sternopygus*, and the sternarchids. These differences are not absolute, however, and there are species differences in basic rate. The generating organ of the mormyrid *Gnathonemus* for example, is reported (Bennett, 1970) to discharge at frequencies of 30-100 pulses per second (pps). *Gymnarchus* is reported to discharge at a frequency of about 250 pps; *Gymnotus* has a frequency rate of 40-60 pps; *Eigenmannia* emits pulses at a rate of 250-400 pps; *Sternopygus* fires at 60-100 pps; *Steatogenys* emits pulses at 40-60 pps; and *Hypopomus* at 2-20 pps (Hagiwara and Morita, 1963).<sup>1</sup> Sternarchids discharge at

1. Each type of fish has a waveform that is specific to itself. Therefore, although *Gymnotus* and *Steatogenys* have the same frequencies, their waveforms are different. These differences in waveform may be functions of the experimenters' competence in engineering.

rates of 600-2000 pulses per second (Erskine, Howe & Weed, 1966). 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. These circumstances include the presence of another signal with frequency close to the fishes'. For example, Eigenmannia which has an organ discharge rate of 400 pps shifts its frequency 10 to 20 pps when confronted with a 400 pps signal (Larimer & McDonald, 1968). In this context, also, is the observation that Gymnarchus temporarily ceases its discharge entirely when presented with a signal mimicking another Gymnarchus or when startled (Bennett, 1970).<sup>2</sup>

The mechanisms for controlling electric organ output are in the medullary portion of the brain and appear to be 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 synchronously because of one or more compensatory mechanisms in the relay pathway from the pacemaker cells. One mechanism is variation in length of the pathway to the electrocytes. The axons to the more distant electrocytes extend in the straightest possible line but those to the less distant electrocytes follow a circuitous pattern. A second means of maintaining synchronization involve a delay line mechanism whereby the pathways to the electrocytes differ in conduction velocities.

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



A number of investigators have measured the voltage output of the generating organ. Hypopomus is reported to generate a voltage of 8 volts 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 in water is reported to generate a voltage of from 10 to 200 millivolts. 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, we find that inadequate information is given in the reports of voltage measurements of the electric organ output.

Based upon the inadequate information that is reported on voltage measurements and upon measurements that we have made in water, we would suggest ignoring the measurements reported in the literature. 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 reported investigations, that the investigators have been inadvertently loading down 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 the convention for the time being. There is better evidence that there are a number of fish, such as sharks and gold fish, that have good passive electrosensing systems but no active system. These latter fish and passive systems are not considered, as such, in this paper.

Gymnotid receptors. There are two basic types of electroreceptor organs reported in the literature. 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 (low rate spontaneous impulses from the receptor to the brain). 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 the electrical sources moving into the fish's range. The response to a brief stimulus, for example, is acceleration followed by deceleration. The acceleration 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 tubercous 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 tubercous organs differ. They also differ in appearance from mechanoreceptors, i.e., canal organs and free neuromasts. The tubercous organ appears on the skin surface as a single small 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 2,000 ampullary and tubercous organs on a 6 cm. long *Steatogenys*. Most receptors, about 95 percent, are phasic receptors according to Lissmann and Mullinger (1968).

In considering the fine structure of the receptor organs, it can be noted that the ampullary organ has the appearance of a flask with a narrow duct (5-20  $\mu$  in diameter) leading from the skin surface to a cavity (30-40  $\mu$  in diameter) that is located 100-500  $\mu$  within the skin. Embedded in the cavity wall with only a small surface exposed are the sensing cells of the organ. These sensing cells are 10-15  $\mu$  in diameter with each organ containing two to eight of them. Some microvilli 0.8  $\mu$  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.

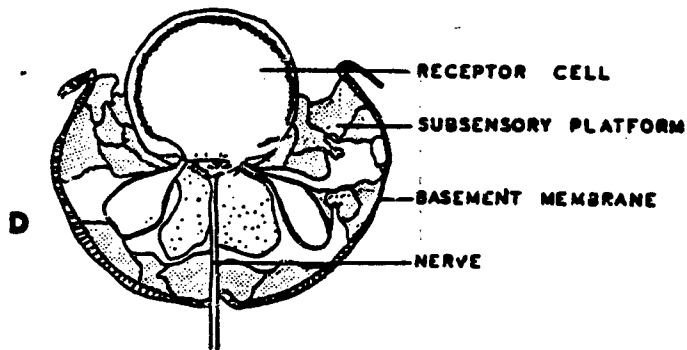
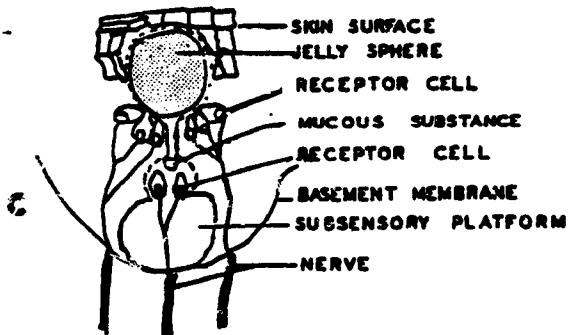
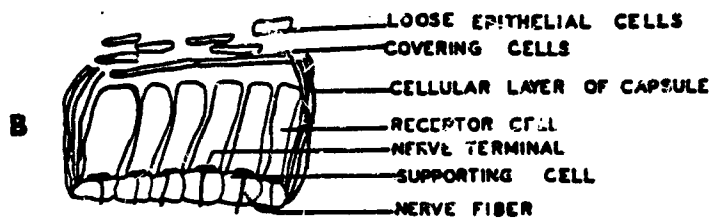
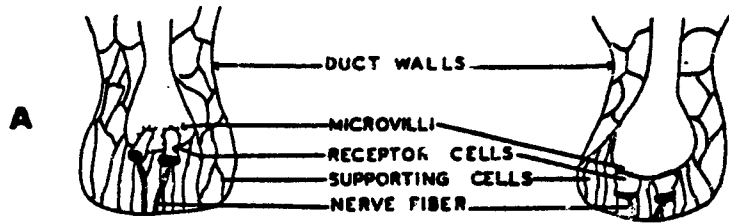


Fig.1 a) Schematic drawing of the two types of ampulla of gymnotids, b) Schematic drawing of the tuberos organ of the gymnotid, c) Schematic drawing of the mormyromast of the mormyrid, d) Schematic drawing of the tuberos organ of the mormyrid.

There are a great many clusters of five to fifteen ampullary receptor cells on the head. On the body there are fewer clusters and they tend to be restricted to 3 bands that extend longitudinally along the fish.<sup>3</sup>

The tuberos organ consists of a bulb shaped invagination of the skin as shown in Fig. 1b. The side of the bulb is composed of 10 to 50 layers of flattened cells for a total thickness of 2-5  $\mu$ . The bottom of the bulb is made up of supporting cells upon which the numerous sensing cells rest. The sensing cells are 25-30  $\mu$  long and project somewhat like rods into the cavity of the bulb. 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  $\mu$  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 to a single nerve which, in most cases, loses its myelin sheath where it passes into the tuberos organ. In a small proportion of the tuberos organs the myelin sheath is retained until the nerve fiber enters the sensory cell. The tuberos organs are randomly distributed on the head, where they are most numerous, and on the anterior half of the body. On the posterior half of the body the tuberos organs are found in four longitudinal bands.

Mormyrid receptors. In Mormyrids, the electroreceptors are referred to as mormyromasts and Knollenorgans (Szabo, 1967). 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 tuberos organ of the gymnotids. Types A and B sensory cells are always separately innervated.

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

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. 1c. 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 tuberos 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 rod like projection, 0.5  $\mu$  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 tuberos 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. 1d. Each complex is a single sensory cell attached to a highly differentiated supporting platform of cells. The organ is innervated by single nerve fiber which is derived from a nerve that appears to

serve many sensory cells.

The sensory cell lies in and almost 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  $\mu$  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. We shall now consider this matter of the receptor organ and system function.

#### System Function, Measurement Technique, and Sensitivity

This section will of necessity be short since there is relatively little data which is acceptable from both a biological and engineering standpoint. Thus, 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 the fish is anesthetized and fixed to a wooden plate in the normal swimming position. The wooden plate is then tilted into the water so that the body is submerged and the head exposed to the air. The regular respiratory movements and oxygenation are maintained by spraying a fine jet of water into the mouth of the fish. The dorsal branch of the lateral line

nerve which lies immediately under the dorsal skin at the head, is then surgically exposed. After desheathing it, 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 to 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 receptors or systems. First, in those cases where anesthesia was used, a question can be raised on the effect of the anesthesia on neural function. Second, the investigators were looking only at the isolated sensor signal under grossly abnormal stimulation conditions. Third, the 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 fourth reason 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. However, he used a small tank which would distort the fishes' field, he did not control impedance within normal limits, & he had extraneous objects in the fishes' field. Clark, Granath, Mincoff & Sachs (1967) used stainless steel electrodes which distorted the fishes' field. Hagiwara, Szabo, Enger & Suga (1965, 1967) all show waveforms 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 experimentors will not offer an explanation for this observation. Mandriota's investigations (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 visibly jerk the fish; shock while studying the function of electrosensing fish.

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 millimeters in diameter in a clay pot but would fail to respond to a glass rod of 0.8 millimeters in diameter in the pot (Lissmann, 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 meet the specifications derived below.

Somewhat akin to this behavioral technique have been a 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 fishes 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 can not be accepted due to deficiencies in engineering.

In sum then, we can conclude very little about sensitivity and system function from the available biological 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 for reasons indicated above, 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 distort the field and seriously effect 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<sup>4</sup>

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

4. The five unnumbered equations used in this section are developed in a later section. They are numbered in the later section as 27a, 27b, 27c, 48, 51, but appear in this order here. Definitions of symbols can be found in the appendix.

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

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

Plotting for different values of L in Fig. 2a we obtain the required cylinder length. Only the positive direction is plotted because the negative direction is identical except 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 5 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 48 of our later development. This equation is

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

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

$$I = \frac{Q L \sigma}{2\epsilon} \left[ \frac{-1}{\left(R^2 + \frac{L^2}{4}\right)^{1/2}} \right]_0^w \quad (1)$$

Equation 1 may be expressed in closed form as

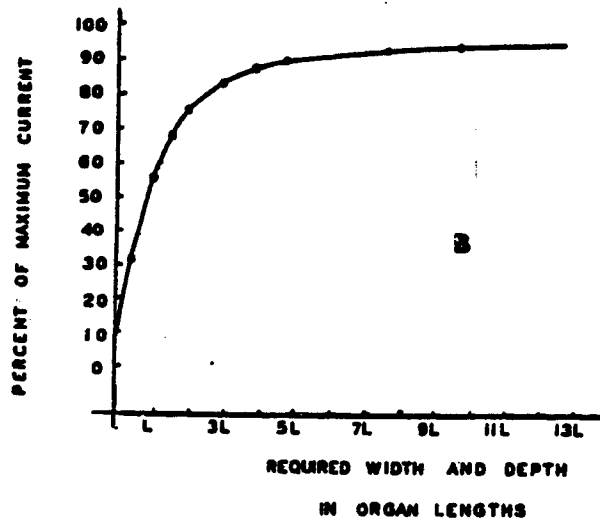
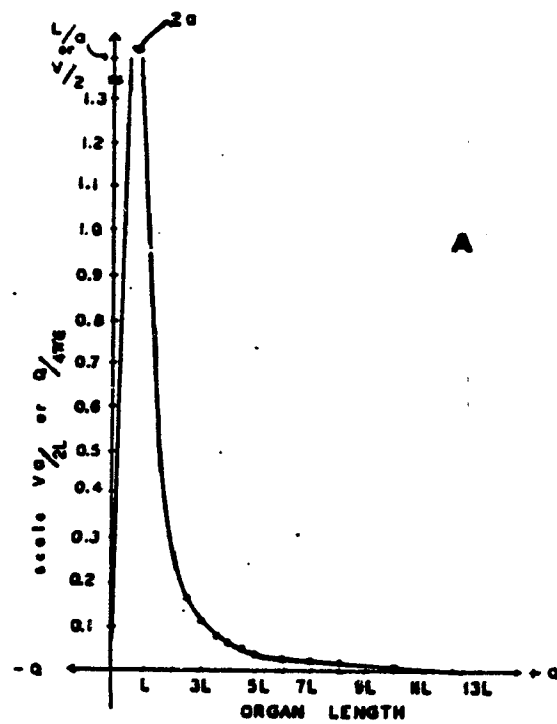


Fig.2 a) This illustrates the potential on the positive side of the dipole electric generating organ. The potential on the negative side is the negative reflection of this. b) This indicates the percent of maximum electric generator current which will flow between the positive and negative ends of the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

$$I = \frac{Q L \sigma}{2 \epsilon} \left[ \frac{2}{L} - \frac{1}{\left( v^2 + \frac{L^2}{4} \right)^{1/2}} \right] \quad (2)$$

The maximum current is expressed in equation 51 of the later development.

It is

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

By letting  $v = \frac{Ln}{2}$  and solving equation 2 for different values of  $n$ , we have obtained a plot of current as a function of width or depth. This plot is shown in Fig. 2b. To obtain 90% of the maximum current requires 5 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 5 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.

## POSSIBLE RECEPTOR MECHANISM AND NEURAL CODING

The possible mechanism discussed below can not 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. The postulating of this mechanism, viewing the electroreceptors and auditory receptors as evolutionary derivations of the same primitive receptor, provides a testable hypothesis of receptor function. It also provides a basis that can be of assistance in determining receptor 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 hair-like sensing cells. Early concepts of pressure waves in the fluid bending the 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 experimentation and theorizing on the inner ear labyrinthine system appear to be 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 our modeling of 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 are due

to electrostatic forces as opposed to ionic current. In his analysis, he points up that dissipative energy loss of an electric field in a dielectric is generally associated with movement of charge carriers. These movements in an electric field result in an effect called polarization. Van Beek (1967) has 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) has indicated that  $P_{mol}$  is related to the macroscopic polarization  $P$  (electric dipole moment per unit volume) and the macroscopic electric field  $E$  by

$$P = N \left( P_{mol} \right) = \chi_e E \quad (3)$$

where  $N$  is the number of molecules per unit volume

$\chi_e$  is the electric susceptibility.

From this and his own experimental data, O'Leary (1970) suggests that a weak electric field in the fluid filled inner ear might be detected by hair cells by the polarization it induces in long-chain filaments of polyatomic molecules in the cilia. Since Van Beer's (1967) studies of dielectric behavior of colloidal solutions indicate that particles such as polystyrene spheres are frequently surrounded by electric double layers when they are dispersed in dilute KCl solutions, it is conceivable that low frequency electric fields polarize the molecules by inducing dipole moments in the

double layers. There is also evidence along this line from Heller, et al (1960) & Saito, et al (1966). Polarization can also occur by a mechanism suggested by Frohlich's observation (1958) that large molecules can have  $\text{CH}_3$ ,  $\text{C=O}$ , or  $\text{OH}$  groups that are in themselves dipolar, but have a net dipole moment of zero due to the vector sum of all the moments. These molecules then behave like nonpolar molecules in that their polarization are of the induced (electronic) type with resonant frequencies in the optical range.

With these two 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

$$F = - m \omega_0^2 x \quad (4)$$

where  $m$  is the mass of the charge

$\omega_0$  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

$$eE = m \omega_0^2 x \quad (5)$$



The induced dipole moment is then defined for one electron as

$$P_{\text{ind}} = ex = \frac{e^2 E}{m \omega_o^2} \quad (6)$$

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

$$P_{\text{ind}} = \frac{e^2}{m} \sum_j \frac{f_j}{\omega_j^2} E \quad (7)$$

$$\text{where } Z = \sum_j f_j$$

Temperature is not a variable in equation 7 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  $kT$ . These quantum limitations are determined by the magnitude of the allowable shifts in energy levels of the molecules caused by the field, considered as a small perturbation, relative to the energy levels of the molecules in the absence of the field.

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  $lkT \approx 4 \times 10^{-14}$  ergs/molecule as suggested by deVries (1949), the corresponding wave number  $1/\lambda$  for an energy transition of  $lkT$

$$hc/\lambda = kT \quad (8)$$

would be  $1/\lambda = 200 \text{ cm}^{-1}$  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  $200 \text{ cm}^{-1}$ .

The occurrence of hyperfine splittings in the Stark effect suggests 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 (the Stark effect). Splittings of about  $10^{-3} \text{ cm}^{-1}$  have been observed from diatomic molecules with field strengths in the range of  $10^2 - 10^3 \text{ v/cm}$ . 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 amplification 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

that is essentially independent of generator output, changing as a function of an environmental stimulus. Qualitative equations can be written for the output frequency of the phasic and tonic organs. These are:

$$F_{\text{phasic}} = \frac{NF_{\text{generator}}}{n} \cdot \left\{ \begin{array}{l} N = 1,2,3,\dots \\ n = 1,2,3,\dots \end{array} \right\} \quad (9)$$

$$F_{\text{tonic}} = F_{\text{resting}} + \frac{\Delta f}{m v} \cdot (\text{stimulus}) \quad (10)$$

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 tuberosus type.

The other useful classification scheme involves 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, Kusano, & Negishi, 1962). The electroreceptors of *Gymnotus* and *Staetogenes* respond with one to six pulses to each generator discharge (Hagiwara & Morita, 1962). 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 field is 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 & Morita, 1962),

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 we can develop a stronger generalization.

Hagiwara and Morita (1962) 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 we can easily extend it to ampullary-tonic receptors with a simple modification. We shall develop below this all encompassing coding scheme since it suggests the nature of the system function.

The threshold model as reported by Hagiwara and Morita (1962) assumes that after a receptor fires, 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.

This will form the basic model on which we will elaborate in order to encompass the different coding mechanisms. First, we will discuss some general properties of biological threshold curves. Then, we will define the relationships between the threshold curve and the electric organ output which are required by the available data. Lastly, we will detail some of the measures which could be made to quantify the threshold function.

It is established in biology that nerves can not fire during or instantaneously after a previous firing. There is also a biological basis for defining the threshold curve as one describing an exponential decay from some value;  $T_{\max}$  the maximum threshold, to  $T_{\min}$  the minimum threshold. In reality, the minimum value probably continues to decay with time. But for situations of repeated sampling, we can approximate it as  $T_{\min}$ , a constant value. 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

$$T = \left[ T_{\max} - T_{\min} \right] e^{-\frac{t}{T_c}} + T_{\min} + S(t) \quad (11)$$

Further, as a very good approximation we could say

$$T_{\max} \approx e^{-\frac{t}{T_c}} + T_{\min} + S(t) \quad (12)$$

The general shape of such a function is shown in Fig 3a. To describe probability coding, we must assume that  $k T_c \gg 1/f$ . 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. 3b.

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  $k T_c \ll 1/f$ . 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. 3c. Again, for phasic coding  $T_{\min}$  must be greater than zero.

As  $k T_c$  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. 4a. They are one and the same. Interpulse interval coding is illustrated in Fig. 4b. It is also interesting that when  $k T_c$  is about two or three times  $1/f$  a combination of probability and number coding can be anticipated. Such coding has been observed for *Sternopygus* (Hagiwara and Morita, 1962).

It should be noted that this model does not account for the observed output of phasic receptors while the generator is between pulses. As has

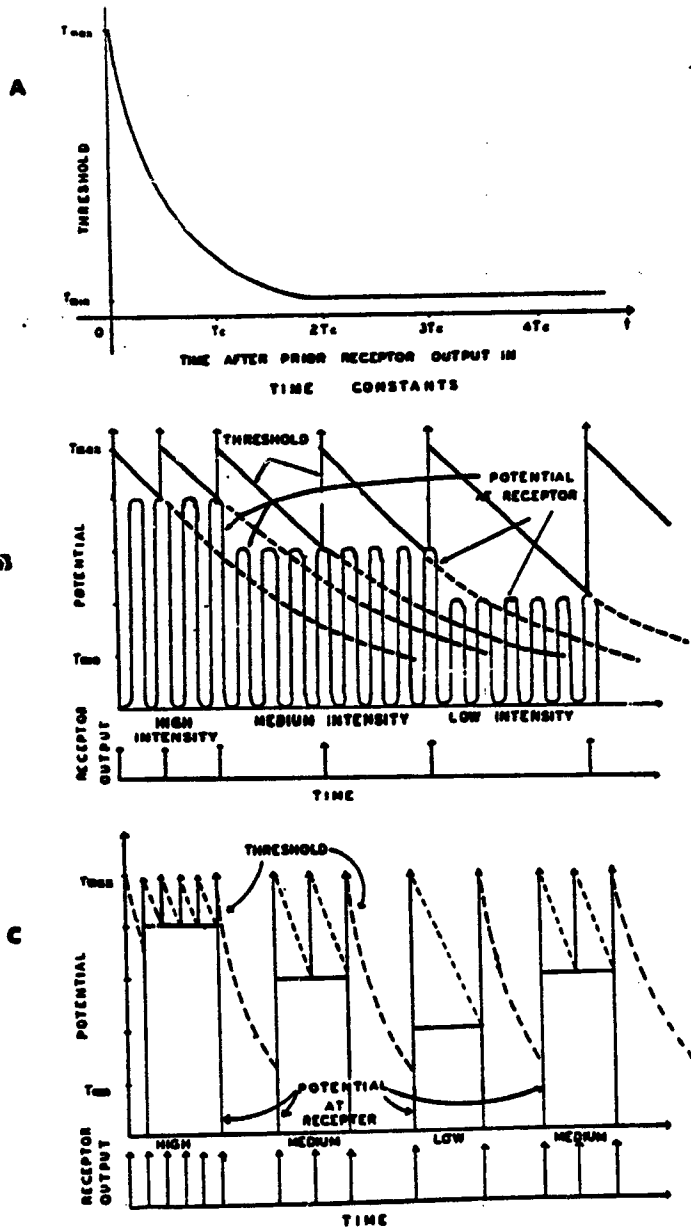


Fig.3 a) This is a mathematical description of the threshold of the receptor to the intensity of the stimulating electrical potential as a function of time following prior receptor output. b) This illustrates the relationship between the electric potential at the receptor, the receptor threshold state, 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. c) This is comparable to case b, 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.

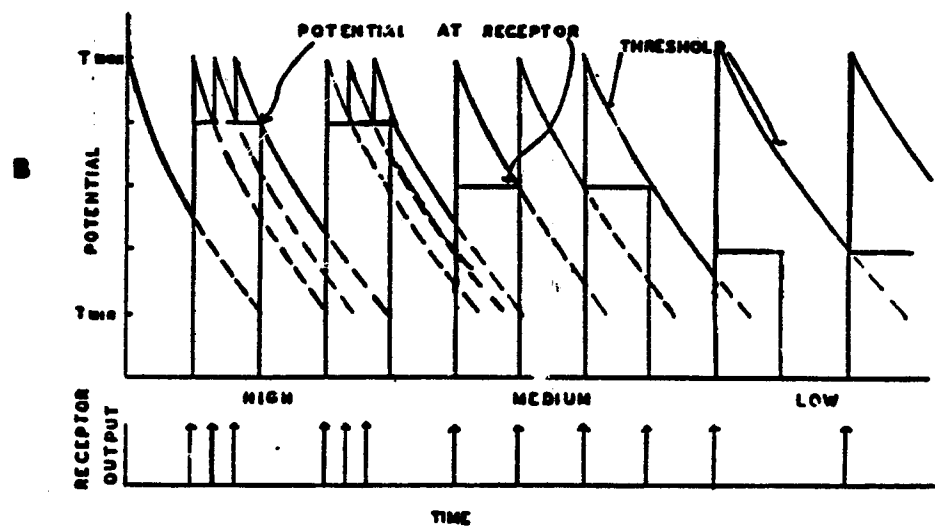
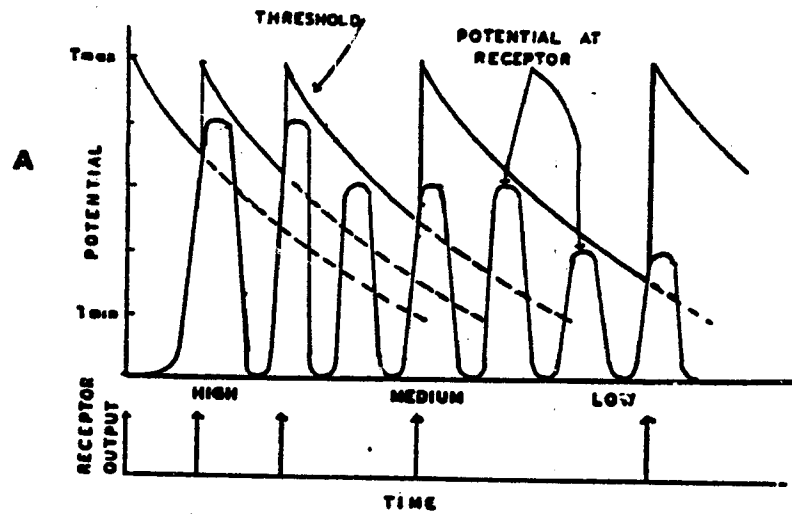


Fig.4 a) This illustrates the relationship between the electric potential at the receptor, the receptor threshold state and receptor output when the generator organ rate is just smaller than the reciprocal of the decay time constant. The output of the electroreceptor in this case is typically referred 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.



been noted previously, there are experimental reports that phasic receptors have an output apparently unrelated to generator output. We do not know if this is due to this not being the best fit model, to our having insufficient data to incorporate those particular observations into the model, the existence of a buffering capability at the receptor, or if the reports report artifacts due to faulty technique.<sup>5</sup> 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 also 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 reasonably test the threshold of the biological system. But by using this method Lissmann & Machin (1958) determined a threshold to potential change of

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

about 0.15  $\mu\text{V}/\text{cm}$ .

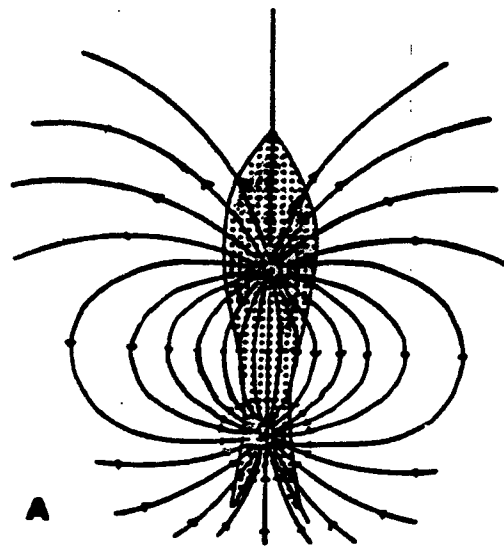
We shall also model the fish as a dipole, but a dipole that differs from the one suggested by investigators such as Lissmann. He suggested that the fish is a head to tail dipole. This suggestion, however, neither fits with the physical location of the electric generating organ as determined anatomically nor with the function 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 toward the head. Thus, we use as our model a dipole field as illustrated in Fig. 5a.

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.

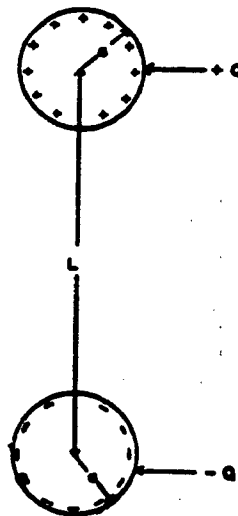
The symbols used are defined in the appendix. The definitions are critical as is the recognition that coordinate transformations are necessary and will be used.

#### Receptor Level

Development. Fig. 5b illustrates a simple dipole. It consists 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



A



B

Fig.5 a) This represents the electric field intensity surrounding the weakly electric fish as indicated by the data of Bullock & Chichibu (1965). b) This illustrates the model used to calculate electric potential, current, and field intensity, due to a fish's electric generating organ. The model consists of two spherical conductors of radius  $a$  separated by an on center distance  $L$ .

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. The electric potential (voltage) is defined to be the increment in work required to move an increment of charge from infinity to a given point in space, or

$$V = \frac{\partial W}{\partial Q} \quad (13)$$

Recall that the fundamental work equation states that work equals the kinetic energy minus the gained potential energy or

$$W = K E - P E \quad (14)$$

If we move a very small charge very very slowly along the line which passes through the two charged spheres, the kinetic energy is essentially zero. The work is the negative of the potential energy. Potential energy is defined by the integral

$$P E = \int_x^y \vec{F} \cdot \hat{dr} \quad (15)$$

where  $\vec{F}$  is the force acting on the test charge as it is moved from  $x$  to  $y$

$\hat{dr}$  is an increment of distance in the path between the points  $x$  and  $y$

The electric force is a conservative force. Thus, if a test charge is acted on by more than one charge, we can determine the potential energy due to each charge and find the total potential energy by addition. In other words if  $P E_n$  represents the potential energy due to the  $n^{\text{th}}$  charge, and if there are

a total of  $N$  charges the total potential energy is

$$P E_{\text{total}} = \sum_{n=1}^N P E_n \quad (16)$$

The potential energy due to a charged sphere can be easily found.

The electric force may be found from Coulomb's Law which states

$$\vec{F} = \frac{Q q_t}{4 \pi \epsilon r^2} \hat{i}_r \quad (17)$$

where  $Q$  is the total charge on the sphere

$q_t$  is the charge of the test charge

$r$  is the distance between the two charges

$\epsilon$  is the dielectric of the media

$\hat{i}_r$  is a vector directed away from the center of the charge  
on a straight line

Using Gauss's Law it can be shown that within the charged conducting sphere there is no electric force. Thus, if the radius of the sphere is  $a$ , the force is

$$F \left\{ |r| < |a| \right\} = 0 \quad (18)$$

If we call the line which passes through the two charges the  $y$  axis, we can find the potential energy at any point on the axis by solving equation 15.

We substitute the force from equation 17 and obtain

$$P E = \int \frac{Q q_t}{4 \pi \epsilon r^2} d r \quad (19)$$

The solution is

$$P E = \frac{Q q_t}{4 \pi \epsilon} \left[ - \frac{1}{r} \right]_{|y+|}^{|y-|} \quad |y+| \geq |a| \quad (20)$$

If we assign the dummy variable  $y-$  for the negative charge, we can solve for the negatively charged sphere

$$P E - = + \frac{Q q_t}{4 \pi \epsilon |y-|} \quad (21)$$

The potential energy for the positively charged sphere is

$$P E + = - \frac{Q q_t}{4 \pi \epsilon |y+|} \quad (22)$$

The total potential energy for the dipole system is

$$P E_{total} = \frac{Q q_t}{4 \pi \epsilon} \left\{ \frac{1}{|y-|} - \frac{1}{|y+|} \right\} \quad (23)$$

If we define a coordinate system as shown in Fig.6, we find that the absolute values of  $y-$  and  $y+$  depend on our location on the  $y$  axis as follows:

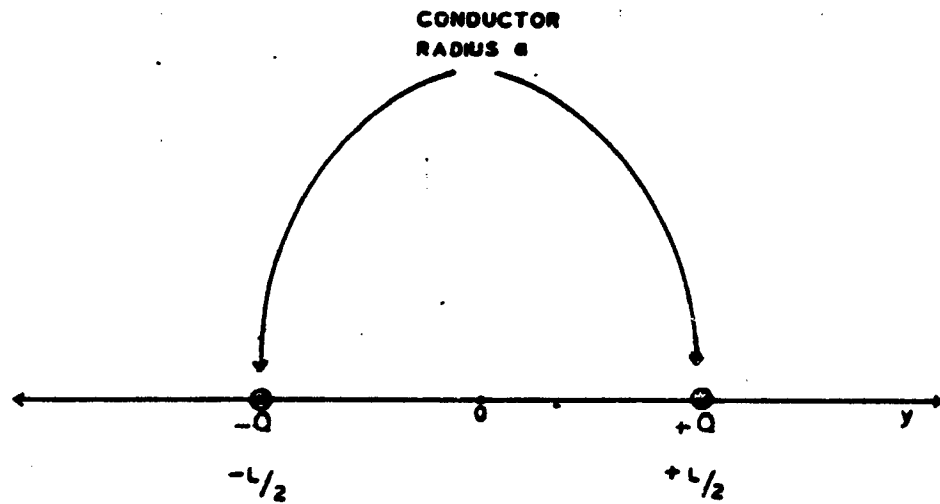


Fig.6 Simplified model which will be used in the study of the electrostatic characteristics of the electric field generated by the fish. The field generating organ is assumed to be composed of two conducting spheres of radius  $a$  separated by a distance  $L$ . For convenience, the origin is taken to be the midpoint between the two conducting spheres.

$$\text{for } y > \frac{L}{2} \quad |y+| = y - \frac{L}{2} \quad (24a)$$

$$|y-| = y + \frac{L}{2} \quad (24b)$$

$$\text{for } \frac{L}{2} > y > -\frac{L}{2} \quad |y+| = \frac{L}{2} - y \quad (24c)$$

$$|y-| = \frac{L}{2} + y \quad (24d)$$

$$\text{for } -\frac{L}{2} > y \quad |y+| = \frac{L}{2} - y \quad (24e)$$

$$|y-| = -\frac{L}{2} - y \quad (24f)$$

The total potential energy can be found from equation 23 and equations 24a to f in each region. Recalling that the kinetic energy is zero and applying equation 13 in terms of the test charge we get:

$$V = \frac{\partial}{\partial q_t} \left\{ - \frac{Q q_t}{4 \pi \epsilon} \left[ \frac{1}{|y-|} - \frac{1}{|y+|} \right] \right\} \quad (25)$$

This yields

$$V = \frac{Q}{4 \pi \epsilon} \left[ \frac{1}{|y+|} - \frac{1}{|y-|} \right] \quad (26)$$



Substituting the appropriate values of  $y+$  and  $y-$  we obtain:

$$\text{for } y > \frac{L}{2} + a \quad V = \frac{Q}{4 \pi \epsilon} \left[ \frac{L}{\left(y - \frac{L}{2}\right)\left(y + \frac{L}{2}\right)} \right] \quad (27a)$$

$$\text{for } \frac{L}{2} - a > y > -\frac{L}{2} + a \quad V = \frac{Q}{4 \pi \epsilon} \left[ \frac{2y}{\left(\frac{L}{2} - y\right)\left(\frac{L}{2} + y\right)} \right] \quad (27b)$$

$$\text{for } -\frac{L}{2} - a > y \quad V = \frac{Q}{4 \pi \epsilon} \left[ \frac{L}{\left(\frac{L}{2} - y\right)\left(\frac{L}{2} + y\right)} \right] \quad (27c)$$

where  $V$  is the absolute voltage ( $V = 0$  at  $y = 0$ ),

$Q$  is the charge on either conductor,

$L$  is the distance between the conductors,

$\epsilon$  is a 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. 6.

Equation 27b 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  $y = \frac{L}{2} - a$  into equation 27b, we find the voltage on the positive sphere to be

$$V (+) = \frac{Q}{4 \pi \epsilon} \frac{L - 2a}{a(L-a)} \quad (28)$$

Substituting  $y = -\frac{L}{2} + a$  into equation 27b we find the voltage on the negative sphere to be

$$V (-) = \frac{Q}{4 \pi \epsilon} \frac{-L + 2a}{a (L - a)} \quad (29)$$

Solving for  $v$  we find

$$v = V (+) - V (-) \quad (30)$$

or

$$v = \frac{Q}{4 \pi \epsilon} \frac{2}{a} \left( \frac{1 - \frac{2a}{L}}{1 - \frac{a}{L}} \right) \quad (31)$$

When  $a/L$  is less than  $1/10$ , equation 31 can be approximated within 5 percent by the relationship

$$v = \frac{Q}{2 \pi \epsilon a} \left( 1 - \frac{a}{L} \right) \quad (32)$$

The capacitance of an object is defined as

$$C = \frac{Q}{V} \quad (33)$$

where  $Q$  is the charge on one symmetric part of the object

$V$  is the voltage across the object.

Determining the capacitance of the dipole from equation 31, it is found to be

$$C = \frac{Q}{V} = 2 \pi \epsilon a \frac{\left(1 - \frac{a}{L}\right)}{\left(1 - \frac{2a}{L}\right)} \quad (34)$$

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

$$C = 2 \pi \epsilon a \left(1 + \frac{a}{L}\right) \quad (35)$$

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 Ohms Law.

$$R = \frac{V}{I} \quad (36)$$

where  $R$  is the resistance

$V$  is the voltage

$I$  is the current

Two equal and opposite charges create an electric field. If we can solve for the magnitude and angle of the electric field  $\vec{E}$ , we can determine the current density  $\vec{J}$  from the relationship

$$\vec{J} = \sigma \vec{E} \quad (37)$$

where  $\vec{J}$  is the current density

$\sigma$  is the conductivity of the media.

Once the current density is known, the current  $I$  can be found from the surface integral

$$I = \int_S \vec{J} \cdot \hat{ds} \quad (38)$$

where the integral is over any closed surface

$\hat{ds}$  is an element of surface taken to have a unit vector located normal to the surface.

The electric field is a vector quantity. Thus, the total field is the vector sum of the field due to the negative charge  $\vec{E}^-$  and the field due to the positive charge  $\vec{E}^+$ . Symbolically we can write

$$\vec{E} = \vec{E}^+ + \vec{E}^- \quad (39)$$

where  $\vec{E}$  is the total field

Due to symmetry, the most convenient surface to use for our current integral is the plane which forms the perpendicular bisector of the line segment joining the two equal and opposite charges. This plane is illustrated in Fig. 7a. The electric field due to the positive charge at any point  $p$  is defined by the equation

$$E^+ = \frac{Q}{4\pi\epsilon D_+^2} \hat{i}_{D^+} \quad (40)$$

where  $D_+$  is the distance between the positive charge and the point p

$\hat{i}_{D_+}$  is a unit vector located in the direction of  $D_+$  away from the positive charge at p.

The electric field due to the negative charge at the same point p is

$$\vec{E}_- = \frac{-Q}{4\pi\epsilon D_-^2} \hat{i}_{D_-} \quad (41)$$

where  $D_-$  is the distance from the negative charge

$\hat{i}_{D_-}$  is a unit vector at p directed by the  $D_-$  line away from the negative charge.

The minus sign in equation 41 is due to the fact that unlike charges attract.

So long as the point p is on a plane which forms the perpendicular bisector of the line segment between the two charges, the distances  $D_+$  and  $D_-$  are equal. They can be found from the equation

$$D_+ = D_- = \left[ R^2 + \frac{L^2}{4} \right]^{1/2} \quad (42)$$

We have defined the y axis to be the line which passes through the two charges. We note that at the point p of Fig.7a, the electrical field due to either charge has both y and radial components. Due to symmetry, however, the radial components cancel each other and the net field in the plane is parallel to the y axis. Also due to symmetry, the y magnitude of the y components are equal. Thus the total electric field is

$$\vec{E}_{\text{total}} = \frac{-2 Q}{4 \pi \epsilon D_+^2} \sin \beta \hat{i}_y \quad (43)$$

We note that  $\beta = \alpha$  because they are opposite angles.  $\sin \alpha$  can be determined from Fig. 7a by

$$\sin \alpha = \sin \beta = \frac{L/2}{D_+} \quad (44)$$

Substituting equation 44 into equation 43

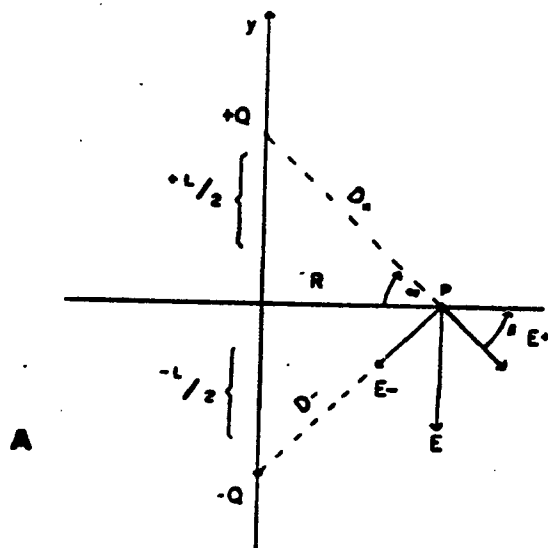
$$\vec{E}_{\text{total}} = \frac{-Q L}{4 \pi \epsilon D_+^3} \hat{i}_y \quad (45)$$

Substituting equation 42 into equation 45, and equation 45 into equation 37 yields

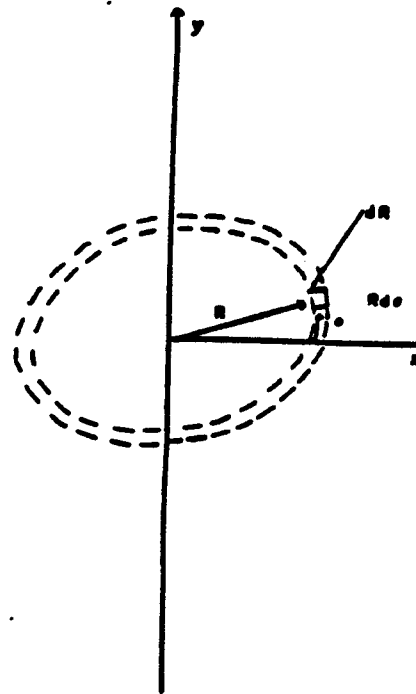
$$\vec{J} = \frac{\sigma Q L}{4 \pi \epsilon \left[ R^2 + \frac{L^2}{4} \right]^{3/2}} \quad (46)$$

The surface of integration is considered to be small ring segments in the x-z plane about the y axis. Fig. 7b illustrates this concept. We note that the electric field is perpendicular to the x-z plane which makes the integral defined by equation 38 easy to evaluate. A surface element for the ring shown in Fig. 7b is

$$ds = R d\phi dR \quad (47)$$



A



B

Fig.7 a) This figure illustrates the relationship between  $E_-$  and  $E_+$  due to the electric fields created by the charges  $Q_-$  and  $Q_+$ , respectively. Note that the vector sum of these two electric fields is parallel to the y axis for any point P in the plane which forms the set of perpendicular bisectors of the two charges. b) This figure indicates the quantities that need be defined in order to evaluate the surface integral required by equation number thirty-eight.

where  $ds$  is the surface element,

$d\phi$  is an increment of angle  $\phi$  which is an angle about the  $y$  axis.

$dR$  is an increment in the distance vector  $R$ .

Substitution of equations 47 and 46 into equation 38, and defining the surface integral, we obtain

$$I = \int_0^L \left( \int_0^{2\pi} \frac{Q L \sigma R}{4 \pi \epsilon \left( R^2 + \frac{L^2}{4} \right)^{3/2}} d\phi \right) dR \quad (48)$$

Solving the inner integral yields

$$I = \int_0^L \frac{Q L \sigma R}{2 \epsilon \left( R^2 + \frac{L^2}{4} \right)^{3/2}} dR \quad (49)$$

Equation 49 can be solved to yield

$$I = \frac{Q L \sigma}{2 \epsilon} \left[ \frac{-1}{\left( R^2 + \frac{L^2}{4} \right)^{1/2}} \right]_0^L \quad (50)$$

In closed form

$$I = \frac{Q \sigma}{\epsilon} \quad (51)$$

We have previously solved for the voltage between the charges in equation 32. Dividing the voltage  $v$  by the current  $I$ , equation 51 yields



the resistance as defined by equation 36

$$R = \frac{V}{I} = \frac{Q(1 - a/l)}{2\pi\epsilon a} \cdot \frac{Q\sigma}{\epsilon} \quad (52)$$

which reduces to

$$R = \frac{1}{2\pi\sigma a} \left(1 - \frac{a}{L}\right) \quad (53)$$

We may now use the derived information. As a first approximation let us assume that 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 fresh water is about  $10^{-3} \Omega^{-1} \text{ m}^{-1}$ . The resistance which loads the generator organ is about 62,000 ohms<sup>6</sup>. The dielectric of fresh water is  $0.707 \times 10^{-9} \text{ fd/m}$ . This means that the capacitance which loads the dipole is 40 pfd. This large resistance and small capacitance indicate that only a small current flows. Thus, an electrostatic approach to the electric fish problem can be justified on electrical grounds as well as on the previously discussed theoretical biological grounds.

Function. Accepting now the 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

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

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. 8a illustrates the problem.

The electric field is defined as the force that would be exerted per unit charge on a small test charge at a given point

$$\vec{E}(p) = \vec{F}(p) / q_t \quad (54)$$

The force on a test charge  $q_t$  due to another charge  $Q$  can be found from Coulomb's Law as

$$\vec{F} = \frac{q_t Q}{4 \pi \epsilon D^2} \hat{i}_D \quad (55)$$

where  $\epsilon$  is the dielectric of the media

$D$  is the distance between the charges

$\hat{i}_D$  is a unit vector directed away from each charge at the charge.

The electric field due to the positive charge in the dipole system is

$$\vec{E}_+ = \frac{Q}{4 \pi \epsilon_w R^2} \hat{i}_R \quad (56)$$

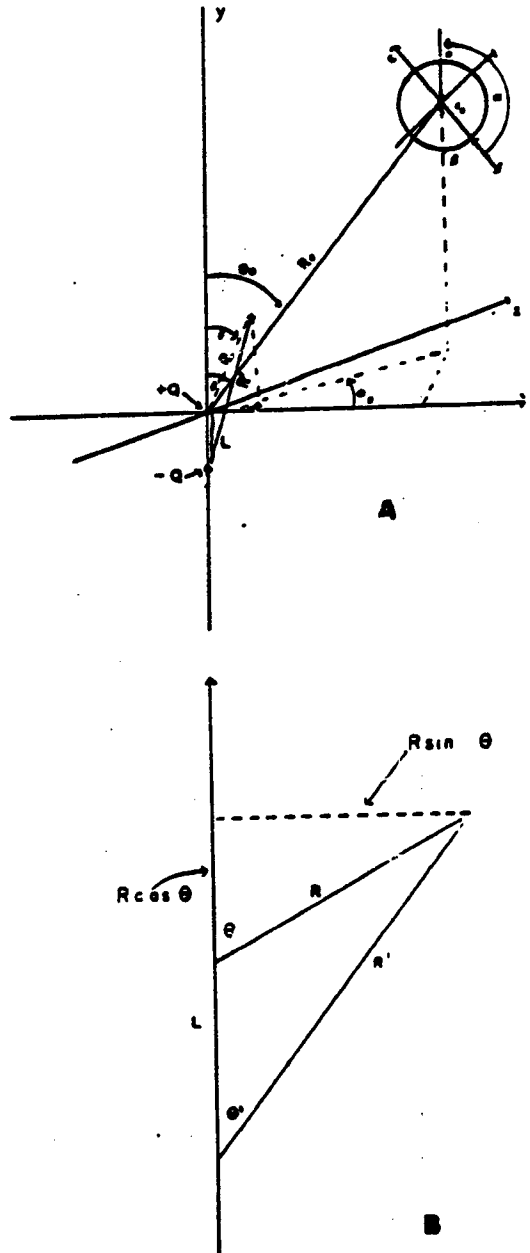


Fig.8 a) This illustrates the variables involved in our model when a spherical perturbing object is present in the model's environment. Note the several coordinate systems that must be considered in the analysis. b) This illustrates the functions required to express  $R'$  and  $\theta'$  in terms of  $R$ ,  $\theta$ , and  $L$ .

The electric field due to the negative charge is

$$\vec{E}_- = \frac{-Q}{4 \pi \epsilon_v R^2} \hat{i}_R \quad (57)$$

The electric field is a vector quantity. Thus, we must perform vector addition in order to determine the total field  $\vec{E}$ . It is easier to determine the components of the field due to each charge and then to add the components. Thus, we will concern ourselves first with the y component and then with the x-z component.

The y component of the electric field due to the positive charge is

$$E_{y+} = |E_+| \cos \theta \quad (58)$$

Likewise the y component of the electric field due to the negative charge is

$$E_y = |\vec{E}_-| \cos \theta' \quad (59)$$

The x-z components of the electric fields are independent of the angle  $\phi$  although the actual x and z components are not. The x-z component of the total electric field will be considered to be the component within the x-z plane at an angle  $\phi$  from the axis. For the positive charge it is

$$E_{x-z} = |\vec{E}_+| \sin \theta \quad (60)$$

and for the negative charge it is

$$E_{x-z} = |\vec{E}_-| \sin \theta' \quad (61)$$

In order to treat these variables by standard mathematical techniques, it is necessary to express  $R'$  in terms of  $R$  and  $\theta$ , and  $\theta'$  in terms of  $R$  and  $\theta$ . Fig. 8b illustrates the factors which will help us do this. Recognizing that  $R'$  is the hypotenuse of a right triangle whose sides are  $R \sin \theta$  and  $L + R \cos \theta$ , we find

$$R' = \left[ R^2 + L^2 + 2 R L \cos \theta \right]^{1/2} \quad (62)$$

and

$$\theta' = \tan^{-1} \frac{R \sin \theta}{L + R \cos \theta} \quad (63)$$

It is useful to note the trigonometric functions for  $\theta'$ . They are

$$\sin \theta' = \frac{R \sin \theta}{\left[ R^2 + L^2 + 2 R L \cos \theta \right]^{1/2}} \quad (64)$$

and

$$\cos \theta' = \frac{L + R \cos \theta}{\left[ R^2 + L^2 + 2 R L \cos \theta \right]^{1/2}} \quad (65)$$

Combining equations 62, 64, and 65 with equations 56 and 57 and substituting into equations 58, 59, 60 and 67 yields

$$E_{y+} = \frac{Q \cos \theta}{4 \pi \epsilon_v R^2} \quad (66)$$

$$E_{y-} = \frac{-Q L + R \cos \theta}{4 \pi \epsilon_v \left[ R^2 + L^2 + 2 R L \cos \theta \right]^{3/2}} \quad (67)$$

$$E_{x-z} + \frac{Q \sin \theta}{4 \pi \epsilon_v R^2} \quad (68)$$

$$E_{x-z} - = \frac{-Q R \sin \theta}{4 \pi \epsilon_v [R^2 + L^2 + 2 R L \cos \theta]^{3/2}} \quad (69)$$

We can now determine the total components of the electric field. The y component of the electric field at any point R,  $\theta$  about the dipole is independent of  $\phi$  and is

$$E_y = \frac{Q}{4 \pi \epsilon_v} \left[ \frac{\cos \theta}{R^2} - \frac{L + R \cos \theta}{R^2 + L^2 + 2 R L \cos \theta} \right]^{3/2} \quad (70)$$

The component of the electric field in the x-z plane is radial and independent of  $\theta$ . It is

$$E_{x-z} = \frac{Q \sin \theta}{4 \pi \epsilon_v} \left[ \frac{1}{R^2} - \frac{R}{R^2 + L^2 + 2 R L \cos \theta} \right]^{3/2} \quad (71)$$

To continue our derivation, we must determine the magnitude  $|\vec{E}|$  and the angle (relative to the y axis)  $\beta$  of the electric field at any point in space. The magnitude may be found from the rules of vector addition as

$$|\vec{E}| = \left[ E_y^2 + E_{x-z}^2 \right]^{1/2} \quad (72)$$