

THE MECHANISM OF OBJECT LOCATION IN
GYMNARCHUS NILOTICUS AND SIMILAR FISH

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INTRODUCTION

Present observations suggest a correlation between the electrical discharges emitted by certain species of fish and their sensory perception.

The theory postulated for this mechanism of perception implies that the potential distribution over the surface of the fish is detected by a series of receptors; this information is then interpreted to indicate the position of objects with a conductivity differing from that of water (Lissmann, 1951, 1958). Although the theory is supported both by morphological and physiological evidence, the quantitative physical aspects appear to involve an unusually high degree of electrical sensitivity on the part of the fish.

The present paper examines the implications of the theory on a quantitative basis.

THE SENSITIVITY OF *GYMNARCHUS NILOTICUS*
TO SMALL DIRECT CURRENTS

It has been shown (Lissmann, 1958) that *Gymnarchus niloticus* gives a response (in the form of a sudden movement) when a magnet or an electrified insulator is moved outside the tank. Quantitative experiments have been made to measure the threshold of the response, both to a moving magnet and to a moving electrostatic charge.

A small bar magnet held perpendicularly to the wall of the tank was moved by hand in a vertical direction. A single downward sweep produced a response in the fish if the movement was sufficiently rapid and the distance between the fish and the magnet sufficiently small. With the particular magnet used a response could be elicited at a velocity of about 3 m./sec. when the fish was about 50 cm. from the magnet. The same magnet was then mounted at this distance from a deflexion magnetometer; this gave the value of the magnetic field at the fish. The results are evaluated in Appendix I, where it is shown that a potential gradient of $0.03 \mu\text{V./cm.}$ is induced in the water.

Next, an electrostatic charge was moved horizontally just in front of the glass of the tank: again the fish responded if the charge and the velocity were sufficiently high and the distance from the face of the tank sufficiently small. For the electrostatic charge a small aluminium cylinder (a 35 mm. film can) was mounted on an insulated handle, and charged from a Wimshurst machine. The voltage of the

machine was stabilized and measured approximately by letting a continuous stream of sparks flow across a ball-ended spark gap of known spacing. With a voltage of about 60 kV. (spark gap of 4 cm.) a response could be elicited from a fish 50 cm. from the tank face if the velocity of the charge was 3 m./sec. In Appendix I it is shown that this is equivalent to a potential gradient of about $0.04 \mu\text{V./cm.}$ in the water near the fish.

DISCUSSION OF THE DIRECT CURRENT SENSITIVITY
OF *GYMNARCHUS NILOTICUS*

From the experiments of the previous section it appears that *Gymnarchus* detects potential gradients of the order of $0.03 \mu\text{V./cm.}$ in the surrounding water. This represents a total voltage from head to tail of about $1 \mu\text{V.}$, and a current density in the fish of about $2 \times 10^{-5} \mu\text{A./cm.}^2$. It was not possible to investigate by these simple techniques the variation of sensitivity with the relative orientation of the fish and the field; the experiments serve merely to establish its order of magnitude.

Table I compares the sensitivity of *Gymnarchus* with that of other fish, giving values of current densities at which responses were noted.

TABLE I

Species	Current density ($\mu\text{A./cm.}^2$)	Source
<i>Phoxinus phoxinus</i> (minnow)	10	Scheminzki (1931)
<i>Cyprinus carpio</i> (carp)	60	Adler (1932)
<i>C. auratus</i> (goldfish)	16	Regnart (1931)
<i>Parasilurus asotus</i> (catfish)	8	Abe (1935)
<i>Gasterosteus aculeatus</i> (stickleback)	110	Johnson (personal communication)
<i>Gymnarchus niloticus</i>	2×10^{-5}	Present authors

It is clear that the sensitivity of *Gymnarchus* is of an entirely different order of magnitude to that of the other fish. This has three important consequences:

(1) Mechanisms of object location involving the detection of minute direct currents become theoretically possible.

(2) The mechanism of perception of electric currents in *Gymnarchus* is likely to be more specifically developed than in most other fish.

(3) Experimental artefacts due to spurious electric currents are likely to be troublesome.

(1) and (2) will be discussed later: some of the implications of (3) will now be considered.

Parker & van Heusen (1917) have shown that currents flow between different parts of a metallic rod immersed in water. They attributed the currents to electrolytic cells formed of the base metal and traces of impurities on its surface. They also found that currents of the order of a few microamperes could be produced in this way: they demonstrated that catfish (*Amiurus nebulosus*) responded to these

currents when metallic rods were brought close to them. It appears from other experiments described in the paper that current densities of the order of several $\mu\text{A./cm.}^2$ are needed to evoke a response from the catfish. This agrees with the findings of Abe (1935). *Gymnarchus*, with a sensitivity of at least 10,000 times this value, is likely to be even more responsive to currents generated in this manner.

It is suggested, therefore, that experiments with *Gymnarchus* using metallic electrodes or isolated metallic bodies in contact with the water may well be invalidated by the response of the fish to the small direct currents caused by surface impurities. Thus the response of *Gymnarchus* to the external closing of a circuit between two immersed electrodes (Lissmann, 1951, 1958), the 'trapping' of a fish by an arrangement of copper wires, and the operation of a metallic strip or wire as a punishment device (Lissmann, 1958) can be explained in this way. If currents of the same order of magnitude as those observed by Parker & van Heusen (1917) were set up by these metallic bodies, the current density over nearly the whole aquarium would be greater than the critical value for a response by *Gymnarchus*. The effects would, of course, be maximal close to the metal. Grundfest (1957) reports that gymnotids reacted to metallic conductors near their skin: this is probably a manifestation of the same effect.

It is impossible to be certain that metallic objects do not influence *Gymnarchus* by locally 'short-circuiting' the electric field set up by its own emissions, but this effect is likely to be much smaller than the one described above.

It seems, then, that critical conclusions should only be drawn from experiments in which there are no metallic objects in contact with the water of the aquarium.

RESPONSE TO A STATIONARY MAGNET

Gymnotus carapo can be trained to feed when a stationary permanent magnet is mounted just outside its aquarium and not to feed when the magnet is removed (Lissmann, 1958). A fish swimming through the magnetic field will have currents induced in it in exactly the same manner as currents are induced in a stationary fish by moving a magnet. With the magnet used the field 20 cm. away was about 10 oersted, so that a fish moving at 10 cm./sec. could generate current densities as high as $10^{-4} \mu\text{A./cm.}^2$. While no definite figures about the sensitivity of *G. carapo* are available, it seems likely from the results on *Gymnarchus niloticus* that currents of this magnitude could readily be perceived, and could be used as the basis for a training experiment.

THE LOCATION OF OBJECTS BY ELECTRIC FISH

The remarkable ability of *Gymnarchus* to avoid obstacles has been noted and attributed to the perception of disturbances to its electric field (Lissmann, 1951). Now that its extremely high sensitivity to direct currents has been shown, it is necessary to re-examine certain apparently unlikely mechanisms for locating objects by means of direct currents. For completeness one non-electric mechanism will also be considered.

(1) Dijkgraaf (1934, 1947) has indicated how objects can be located by most fish by the use of the pressure-detecting function of the lateral line organs. The distribution of water pressure over the surface of a swimming fish depends on the velocity of the fish relative to the water and upon its shape. A nearby obstacle will change the flow pattern of water round the fish, and consequently change the pressure distribution on its surface. On this theory a fish should be incapable of detecting the difference between rigid objects which are geometrically identical, even when made of different material.

(2) The movement of water near a swimming fish will generate small potentials in the earth's magnetic field. Attention was first drawn to this by Thornton (1931), who suggested it as a mechanism by which a fish could locate moving objects such as other fish. He did not perceive, however, that the mechanism could be extended to the detection of stationary objects. For every flow pattern of water there will be a corresponding potential distribution around the fish, the water streamlines coinciding with the electrical equipotentials (Appendix II). A change in the water flow-pattern caused by a stationary object will change the potential distribution around the fish: this effect could be detected and used to locate the object. It can be shown (Appendix II) that the conductivity of the object does not affect the potential distribution, and hence this mechanism again cannot differentiate between geometrically identical objects.

(3) Electric fish emit impulses which set up a flow-pattern of electric current in the surrounding water. Any object with a conductivity different from that of the water will distort this pattern, and hence change the potential distribution around the fish. This change can be used to locate the object. With this mechanism it will be possible to distinguish between geometrically identical objects with differing electrical conductivities. Conversely, it will not be possible to distinguish between dissimilar objects which modify the current distribution in a similar way.

By a series of experiments described later, it has been shown that *Gymnarchus* can distinguish between geometrically identical objects if they have different electrical conductivities, and cannot distinguish between objects which, although geometrically identical and with similar electrical effects, have different internal arrangements.

It is thus clear that in this fish mechanism (3) must play a significant part in the location of objects. The other two cannot be ruled out, but seem unlikely on the following grounds.

(a) The differential sensitivity required of the receptors (i.e. least detectable change of pressure \div ambient pressure for mechanism (1), and least detectable change of potential \div ambient potential for (2) and (3)) is of the same order for the three mechanisms. (3) operates while the fish is stationary, being unaffected by velocity, while (1) and (2) require the fish to be moving. Since in *Gymnarchus* mechanisms (1) and (2) offer no obvious advantages over (3), it does not seem likely that they play any major role in the location of objects.

(b) Mechanism (2) depends on the orientation of the fish to the earth's magnetic field. In the equatorial regions where these electric fish originate, the field is

predominantly horizontal, so that large differences might be expected in the potentials developed depending on whether the fish was swimming north to south or east to west.

THE LOCATION OF OBJECTS BY DISTORTION OF
THE FISH'S OWN ELECTRIC FIELD

The conclusions of the previous section, taken together with the experimental results given later, make it clear that *Gymnarchus* can detect objects by the distortions they cause in the potential distribution which the fish itself sets up in the water.

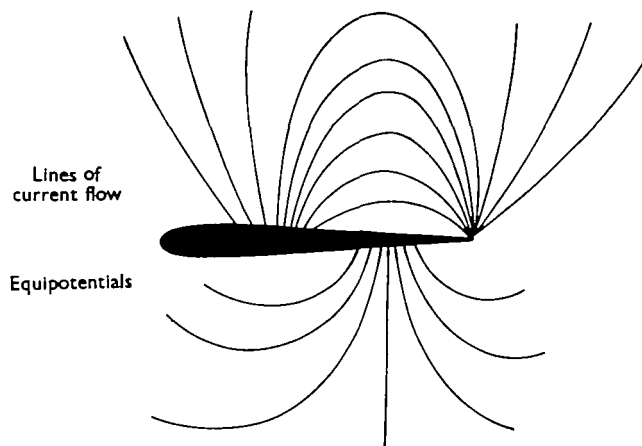


Fig. 1. The electric field around a fish.

For a stationary fish in an infinitely large tank the lines of current flow and the equipotentials are similar to Fig. 1, and correspond approximately to those of a dipole source of current. When an object of a conductivity lower than that of the surrounding water is brought near, the pattern becomes like Fig. 2*a*, while for an object of higher conductivity Fig. 2*b* applies. The distribution of potential around the fish is altered, and therefore the pattern of stimuli received by any electrical receptors on the surface of the fish will be modified. The suggestion that mormyromast-type structures are electrical receptors has been put forward by Lissmann (1958); these structures are situated in the skin and communicate with the surface by jelly-filled canals. The arguments presented here are based on the assumption that these structures are in fact electrical receptors.

In an attempt to find how the potential distribution around a fish would change in the presence of perturbing objects, a model experiment was set up (see Appendix V). A voltage was applied to an electrolytic tank at two points to simulate the dipole field of a fish. The potential in the tank was sampled by pick-up electrodes arranged around these points in the shape of the body of the fish. With delicate and protracted measurements it was possible to locate a large insulating object a few centimetres away from the probe electrodes. However, with any

apparatus of only moderate complexity it was impossible to detect changes in the potential distribution for small and remote objects which could easily be detected by *Gymnarchus*. Some results are, however, quoted later.

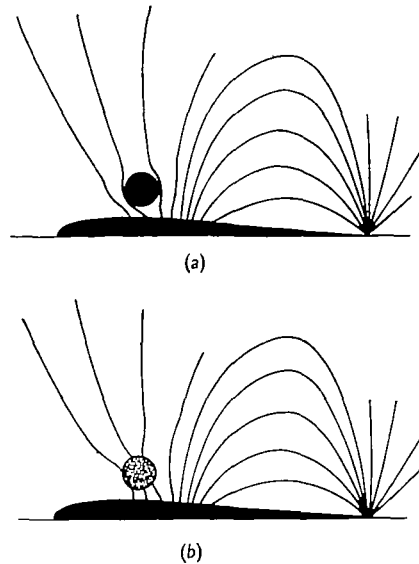


Fig. 2. The electric field in the presence of an object (a) of low conductivity, (b) of high conductivity.

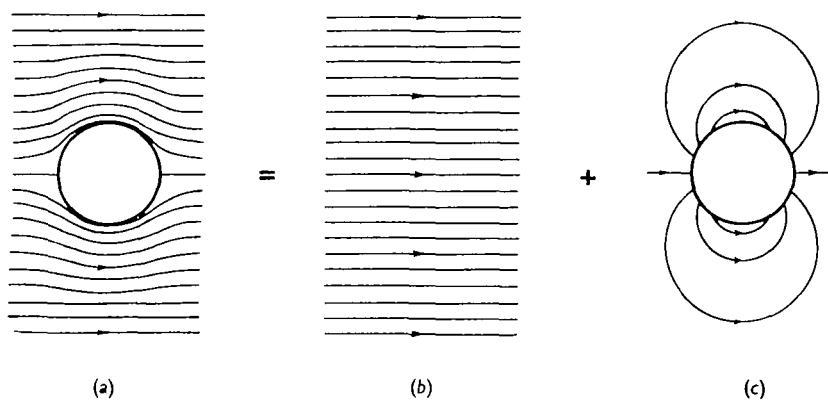


Fig. 3. The resolution of: (a) the field in the presence of an object into (b) the original field and (c) a perturbing field.

A theoretical approach to the problem was next undertaken along the following lines. The field round the fish in the presence of an object can be split up into the original field in the absence of the object, and a perturbing field. This process is illustrated in Fig. 3. The potential at a given point on the body of the fish in the absence of the object is due to the original field; the *change of potential* caused by the object is equal to the *potential* due to the perturbing field. If the

the perturbing field can be calculated the pattern of *potential changes* around the body can be derived and hence the sensitivity of the electrical receptors can be assessed.

For objects of certain shapes in a dipole field the perturbing field can readily be calculated since this field is the same as that of an 'image' dipole within the object (Maxwell, 1873). The calculation is carried out in Appendix III for a cylindrical object in a two-dimensional dipole field; this approximates to the conditions obtaining in the experiments described later. The results of the calculation show that the image in the cylinder is a current dipole of moment M' given by

$$\frac{M'}{M} = \left\{ a^2 \frac{\sigma_0 - \sigma}{\sigma_0 + \sigma} \right\} \left\{ \frac{1}{r_1 r_2} \right\},$$

where a is the radius of the cylinder, σ its electrical conductivity, σ_0 the conductivity of the water, M the moment of the current dipole due to the fish, r_1, r_2 are the distances from the centre of the cylinder to the poles of the original dipole.

The term $\left\{ a^2 \frac{\sigma_0 - \sigma}{\sigma_0 + \sigma} \right\}$ is a characteristic of the object only: it will be termed the 'imprimence'* of the cylinder. It is positive if $\sigma < \sigma_0$ and negative if $\sigma > \sigma_0$. For a perfectly insulating cylinder, the imprimence is equal to a^2 , while for a perfect conductor it equals $-a^2$.

The second term of the equation for M' , i.e. $(1/r_1 r_2)$, depends on the position of the object relative to the fish. For any relative position of the fish (idealized to a dipole) and the cylinder the moment and inclination of the image dipole can be calculated. Assuming that the fish has approximately the same conductivity as the water and that it does not appreciably distort the perturbing field (i.e. does not produce an image of the image), the potential distribution around the fish due to the perturbing field can be calculated.

The effect of the perturbing field on the receptors depends upon the resistance of the jelly-filled canals of the mormyromasts relative to the resistance of the tissue between their proximal ends. It is shown in Appendix IV that when the canal resistance is very high the receptors in effect measure potential. When the canal resistance is very low, the receptors will measure the second derivative of the potential (i.e. the rate of change of potential gradient) around the body of the fish.

The perturbing field due to an object in various positions near a fish has been computed. Before describing the results the assumptions on which the calculation is based will be re-stated: (1) the problem may be treated two-dimensionally; (2) the fish is equivalent to a current dipole; (3) the conductivity of the fish is equal to that of the water. These approximations are not entirely valid for the actual fish; however, the calculations will serve to illustrate qualitatively the effect of objects on the receptor system. In addition, at least the order of magnitude of the perturbation will be indicated.

* In the absence of a suitable word to describe quantitatively the effect of an object on an electric field, the word 'imprimence' has been coined. It is derived from 'imprint' ('something that impresses or imprints') with an ending denoting quantitative measure (cf. 'capacitance'). The use of this coined word avoids the subjective implications of such words as 'electrical perceptibility' or 'visibility'.

The computations have been carried out for a 'fish' of 50 cm. length, and of the general shape of *Gymnarchus*. For simplicity, however, the nose has been drawn elliptical. An insulated cylinder 5 cm. in diameter (i.e. with an imprudence of 6.25 cm.²) is taken as the object; for other values of imprudence the results may be scaled linearly. Results are given for five positions, designated A-E in Fig. 4.

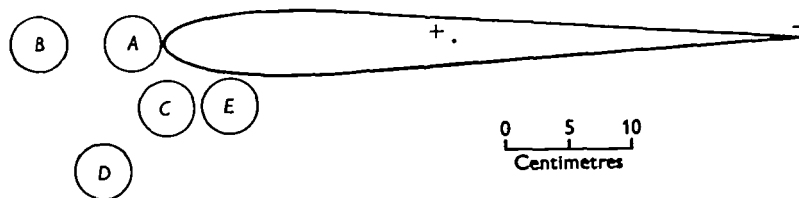


Fig. 4. The position of objects around the model fish.

The strength of the current dipole of the fish has been chosen so that the potentials correspond approximately with those observed in the actual fish (Lissmann, 1951).

Two sets of results are given: (1) for the potential, and (2) for the second derivative of the potential around the surface of the fish. These correspond to the two extremes of relative resistance in the receptor system.

In Fig. 5 the *change of potential* around the fish due to the presence of the object is shown for five positions of the latter. For comparison the *potential* around the fish in the absence of the object is shown to the same scale in Fig. 6.

Fig. 7 shows the *change of second derivative of potential* due to the object. The *second derivative of potential* in the absence of the object is shown in Fig. 8. The large central peak in Fig. 8 is to a great extent artificial and due to the small radius of curvature at the elliptical nose. The peak will be less marked at the nose of an actual fish, since this is flatter than a true ellipse.

The curve *W* shows the *change of potential* (Fig. 5) and the *change of the second derivative of potential* (Fig. 7) which is caused by a 6 cm. displacement of the tail of the fish to the left.

The results lead to the following conclusions:

(a) A characteristic disturbance occurs in both the potential and its second derivative around the point on the surface of the fish nearest to the object.

(b) The changes of potential are slowly varying and extend over almost the whole of the surface of the fish, while the changes of second derivative are much sharper and more closely confined to the part of the fish nearest to the object.

(c) In the second derivative mode the greatest sensitivity is obtained in the 'head-on' position.

(d) In the 'head-on' position the width of the peak of second derivative gives information about range: at short ranges a sharp peak flanked by troughs is produced, while at larger ranges the peak is broader. No such discrimination is available in the potential mode.

(e) For the second derivative mode the *changes* in stimulation of the receptors due to the presence of the object are of the same order of magnitude as the *total*

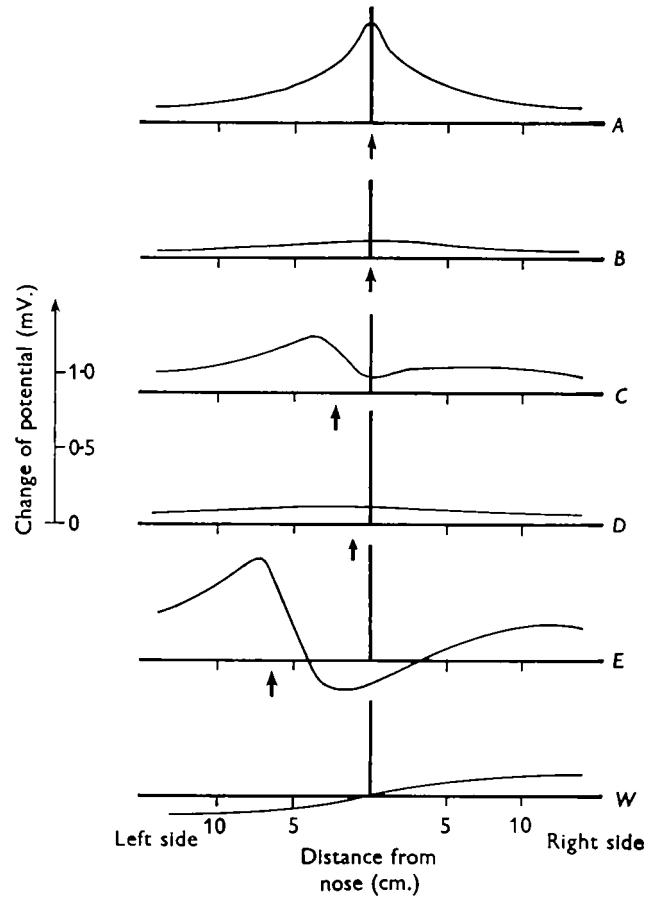


Fig. 5. The change of potential around the model fish due to the presence of an object.

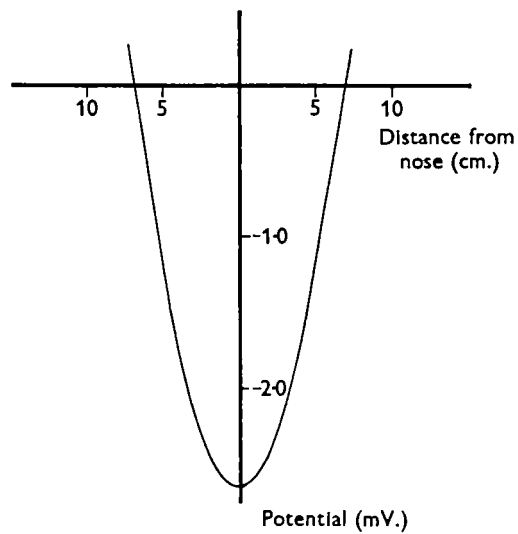


Fig. 6. The potential around the model fish in the absence of an object.

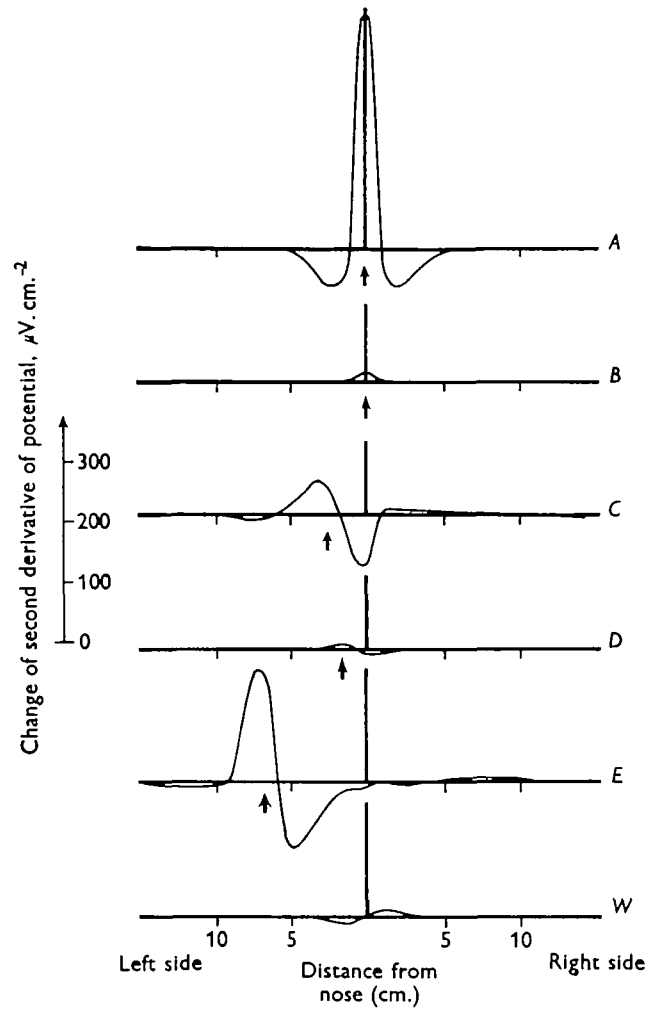


Fig. 7. The change of second derivative of potential around the model fish in the presence of an object.

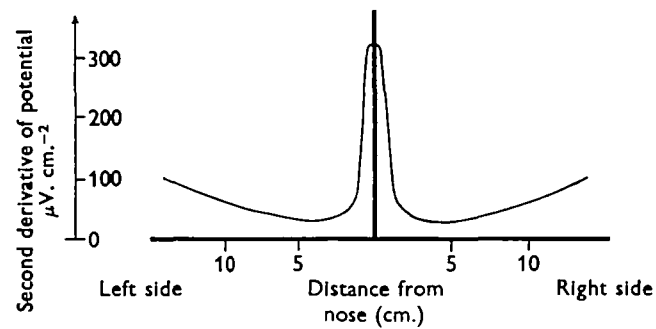


Fig. 8. The second derivative of potential around the model fish in the absence of an object.

stimulation they receive in the absence of the object. For the potential mode the changes are about one-fifth of the total stimulation.

(f) Movement of the tail of the fish produces relatively smaller changes of stimulation for the second derivative mode than for the potential mode.

It is clear that the second-derivative mode is capable of the greater location accuracy, and is less disturbed by tail movements. Furthermore, relatively greater changes of stimulation of the receptors are produced by operation in the second-derivative mode. The sensitivity required of the receptors is considered in more detail in a later Section.

EXPERIMENTAL PROGRAMME

The experimental work consisted of a series of training experiments using *Gymnarchus*, and was designed to test the validity of the theory given earlier.

Four sets of experiments were made:

- (1) To test whether the fish could distinguish between objects which were geometrically and optically similar but of different electrical conductivity.
- (2) To test whether the fish could distinguish between externally similar objects of similar electrical conductivity but of different chemical composition.
- (3) To test whether the fish could distinguish between objects of similar 'imprimence' but of different internal construction.
- (4) To determine the object of minimum imprimence which could be detected by the fish.

MATERIAL AND METHOD

The training experiments were performed with two specimens of *Gymnarchus*, 52 and 54 cm. in length. Most of the tests were carried out on one of these fish, and the crucial observations checked on the other. The experimental tank measured 120 × 75 × 45 cm., and the water in it was kept at a temperature between 25° and 28° C. The experiments were conducted under ordinary laboratory conditions.

The objects to which the fish were trained were bacteriological filter candles (Berkefeld Filters). These are cylindrical porous pots 15 cm. long and of an outside diameter of 5 cm. The walls, which enclose the lower end, are about 1 cm. thick; the inner cavity has a capacity of about 80 cm.³. The porcelain top of the filter candle was cut off and replaced with a large cork to which the filter was fixed by means of 'Araldite'. This cork had a central hole of the same dimension as the diameter of the cavity in the pot; it could be closed by a rubber bung. The rim of the cork was provided with a peg which could be clamped into a wooden fork on a lever arm, so that two such pots could be dipped simultaneously into the aquarium (Fig. 9). This was always done when the fish was at the far end of the aquarium and facing away from the training site.

This type of object was selected because:

- (i) It was found that when such porous pots were placed in water and all the air evacuated from the pores by means of a filter pump, their imprimence was very

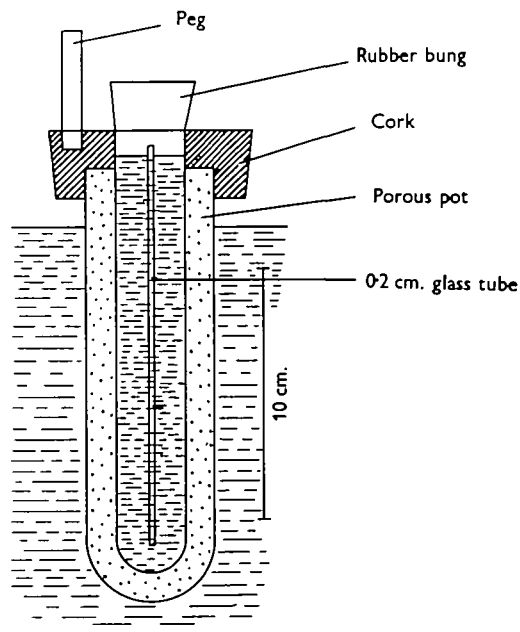
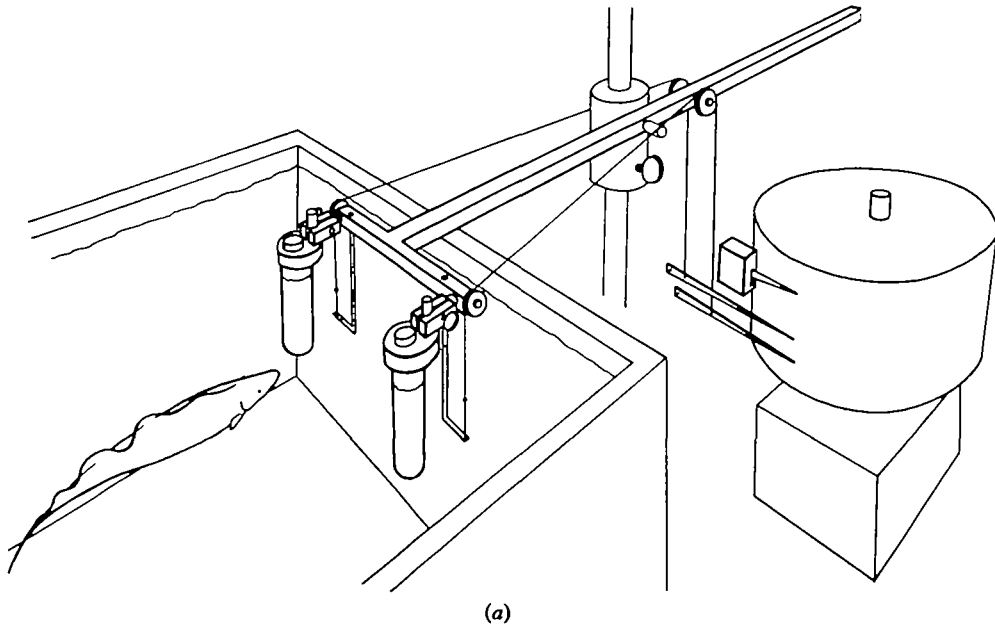


Fig. 9. (a) Experimental set-up for conditioning experiments.
 (b) Section through porous pot.

low: notably the very porous 'Nordtmayer' Filters caused very little distortion of a uniform field in an electrolytic tank.

(ii) The presence of a cavity in the pot allowed the inclusion of objects and solutions of varying electrical conductivity and chemical composition.

(iii) The pots were sufficiently strong to withstand the vicious attacks by the fish to which they were exposed during the training experiments.

The training method was of the reward-punishment type. The reward consisted of small pieces of fish, usually one-sixth of a medium-sized minnow. This food was dipped into the tank simultaneously with the porous pot and behind it. It was sewn through with a thread which extended from a Perspex rod fixed to the lever arm holding the pot to a small writing lever writing on a smoked drum (Fig. 9). When the fish accepted the food the pull on the thread recorded on the smoked drum the instant of acceptance. The records also show the instant of presentation and withdrawal of the pots (Fig. 10). Occasionally anomalous records were obtained; this was due mainly to two causes: (i) on some rare occasions the fish bit through the thread holding the food, in which case the tension on the writing lever collapsed suddenly and the subsequent withdrawal of the pot was not recorded; (ii) during presentation of a negative stimulus the more violent attacks by the fish, which were directed against the pot, shook the apparatus to such an extent that acceptance of food was simulated on the record; in actual fact the food was ignored by the fish on these occasions. The automatic recording of the reactions of the fish allowed the experimenter to withdraw in critical tests, thereby reducing the chance of subjective assessment or unconscious signalling.

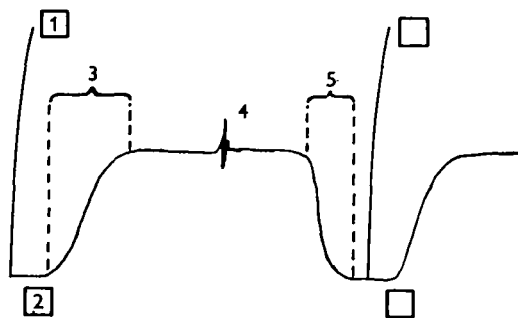


Fig. 10. Diagram of a record in the training experiments. 1, no. of trial in experimental series; 2, type of stimulus; 3, immersion of porous pot and food; 4, acceptance of food; 5, withdrawal of porous pot.

Punishment consisted in chasing away the fish when it approached the food: this was done by immersing a wide wire fork into the water above the fish (see p. 453); in the later stages of this work this punishment was not always sufficient and on occasions the fish had to be knocked gently on the snout with one end of this wire fork.

In some trials the fish had to choose between two porous pots and two sources of food dipped simultaneously into the tank; in another set of experiments the

choice had to be made successively in response to the same pot the contents of which could be altered at will. In the latter case each trial was terminated on presentation of a negative stimulus either after punishment following an attempt to secure the food (noted as incorrect response), or after the fish did not attempt to take the food within a previously determined period of time, which was never less than 30 sec. This was noted as a correct response. Conversely, on presentation of a positive stimulus the trial was ended either as soon as the food had been taken (correct response), or when the fish had refused to accept it within the same period of time (incorrect response).

The order of presentation of the various conditioning stimuli and their position (right or left) was determined by the toss of a coin. Care was exercised to eliminate temperature differences which might be associated with the conditioning stimuli.

QUALITATIVE EXPERIMENTS

In a preliminary series of experiments the fish was trained to distinguish between a porous pot F_1 filled with aquarium water, which represented the positive stimulus, and another pot F_2 , saturated and filled with paraffin wax, representing the negative stimulus. Both were offered simultaneously with the food reward behind each. The position of the two pots was varied at random between the right and left corners of the aquarium.

TABLE 2

Trial no.	Position of F_1W	Reaction	Time taken (sec.)
1	R.	+	12
2	L.	+	8
3	L.	+	8
4	R.	+	10
5	R.	+	8
6	L.	+	10
7	R.	+	10
8	R.	+	8
9	R.	+	5
10	L.	+	10
11	R.	+	12
12	L.	+	12
13	L.	+	18
14	L.	+	10

{ 3 hr.
break

F_1W = positive stimulus (porous pot (F_1) filled with aquarium water).
 F_2P = negative stimulus (porous pot (F_2) filled with paraffin wax).

After an exploratory period, during which the training technique was developed, the fish clearly distinguished between the two pots, and towards the end of the training period accepted the food near the pot F_1 , usually within 5 to 12 sec. of presentation. An example of one day's trials is given in Table 2.

The variation in the reaction time can be attributed to various causes, but it seems to be partly due to the fact that the fish equally often approached the pot F_2

(negative stimulus) first, before retreating and turning to the other corner where the food was taken behind F_1 . It is difficult to state with any degree of accuracy the distance at which the negative stimulus appeared to be recognized, but after a preceding trial which involved punishment the approach was more careful and the point of decision seemed to lie about 20–30 cm. from F_2 . With successive trials without punishment the range became gradually closer, but F_2 was rarely approached closer than 5–10 cm., whereas F_1 was frequently touched with the snout both before and after the food had been taken.

Although the two porous pots used in these experiments were superficially similar, they were clearly not identical, and the conclusion that discrimination was accomplished on the basis of the electrical conductivity of the contents cannot be accepted as decisive, unless other senses, notably optical and chemical, can be ruled out. However, when F_1 was replaced by another similar pot F_3 , also filled with aquarium water, the fish (without further training) accepted the food behind it without hesitation in five successive trials within an experimental series. Therefore it appears that no optical clues of F_1 were involved in the positive reactions. Moreover, the aquarium water in either of these pots could be replaced with tap water without altering the reactions, and it can be assumed that chemical stimuli from the aquarium water in the pots played no role in these experiments.

TABLE 3

Trial no.	Position of F_1	Contents of F_1	Reaction	Duration of trial (sec.)
1	R.	W	+	15
2	L.	W	+	18
3	R.	W	+	12
4	R.	A	–	180
5	R.	W	+	12
6	L.	W	+	8
7	L.	A	–	180
8	L.	W	+	20

W=aquarium water; A=air; R. and L.=right and left positions of F_1 .

That the water-filled pots do not merely represent neutral signals which are differentiated from the negative signals of the wax-filled pot F_2 but represent positive signals, could be demonstrated by emptying the water from F_1 and replacing it with air. This air-filled pot F_1 was now presented simultaneously with the wax-filled pot F_2 . Such trials were interspersed with others in which F_1 remained filled with aquarium water. As can be seen from Table 3 the air-filled pot F_1 now represents a negative stimulus, and although the fish repeatedly approached both pots in these experiments, it always retreated and did not attempt to secure the food within the 3 min. that these trials lasted.

Although this negative reaction towards an air-filled porous pot, which had never been associated with punishment, strongly suggests that no chemical associations are involved, it may perhaps be contended that a novel feature in the aquarium—possibly with strange acoustic properties—could be held responsible for the negative behaviour of the fish. To rule out such objections and to exclude any subtle optical and geometrical differences between two pots, it was decided to use only one single pot, and to present it *successively* offering different conditioning stimuli inside it.

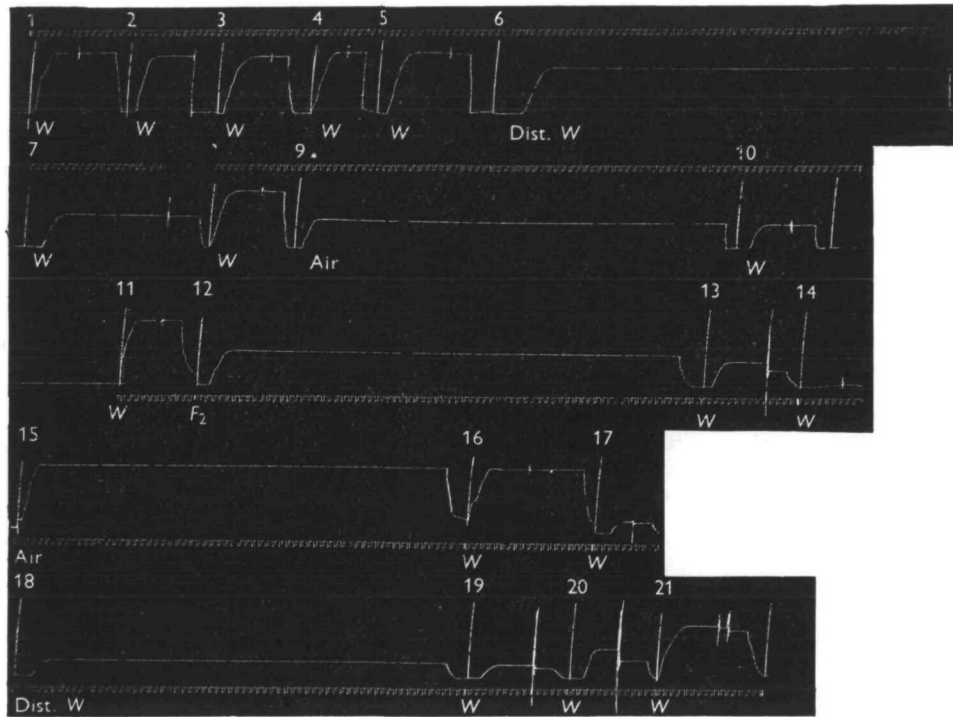


Fig. 11. Record of trials with a fish trained to aquarium water (W = positive stimulus) and paraffin wax (F_2 = negative stimulus) in a porous pot. Note that without further training a negative response is also obtained to air and to distilled water in the porous pot. Time marker = 1 sec.

The conclusions of the previous series of experiments, in which the stimuli were presented simultaneously, were fully confirmed in this way, i.e. the food was now taken within a few seconds when pot F_1 was filled with either aquarium water or tap water, and it was refused within the 60 sec. (later reduced to 30 sec.) after the presentation of a negative stimulus. The negative stimulus to which the fish had been originally trained was the wax-filled pot F_2 ; without additional training, a negative reaction was also obtained with F_1 , if it was filled with air or glass-distilled water which had an electrical conductivity of less than $20\mu\text{mhos/cm}$. (Fig. 11). The exchange between the distilled water inside the pot and the aquarium water outside

appears to be negligible within the duration of the experiment (30 sec.). Even after the pot had been left in the aquarium for 60 sec. the conductivity of the distilled water inside was found to be $30\mu\text{mhos/cm.}$, indicating an interchange of 3% of the pot's volume in this time.

However, it is known that taste receptors are capable of discriminating between tap water and distilled water with a high degree of accuracy (e.g. Liljestrand & Zottermann, 1954). To exclude the possibility that the small interchange of water during the experiment might affect the result the following experiment was carried out. The porous pot F_1 was filled with aquarium water; into this was immersed a glass tube of 2.5 cm. diameter which approximately fitted the central cavity. Again, without additional training, presentation of such a pot evoked negative responses, just as did paraffin wax, air or distilled water. In view of these observations, which were confirmed with both specimens of *Gymnarchus*, it seems hard to avoid the conclusion that the negative stimulus to which these fish have been trained can be attributed to the insulating properties of the contents of the porous pot.

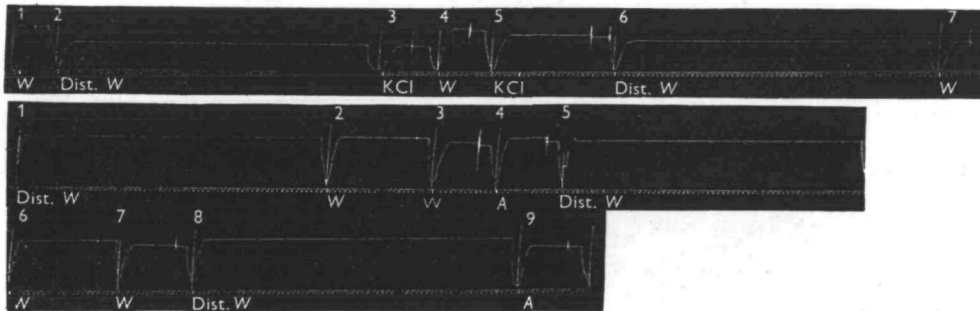


Fig. 12. Record of trials with a fish trained to aquarium water (W = positive stimulus) and distilled water (dist. W . = negative stimulus). Note that, without further training, the positive reaction is also given to KCl and acetic acid (A) solutions if their electrical conductivities approximate to that of the aquarium water. Time marker = 1 sec.

The converse experiment, namely the demonstration that the electrical conductivity and not the presence of any particular ions in the aquarium or tap water represents the positive conditioning stimulus, was carried out by adding various pure solutions to distilled water in the porous pot until the conductivity of the contents approximated to that of the aquarium water. Fig. 12 shows that positive reactions were obtained to solutions of either KCl or acetic acid with conductivities approximately equal to that of the aquarium water.

These results seem to suggest:

- (1) That *Gymnarchus* can distinguish between objects which are geometrically and optically identical but which are of different electrical conductivity.
- (2) That *Gymnarchus* cannot distinguish between externally identical objects of similar electrical conductivity but of different chemical composition.

QUANTITATIVE EXPERIMENTS

It has been shown in the previous section that *Gymnarchus*, trained to the two extremes (i.e. paraffin wax and aquarium water in a porous pot), will behave towards solutions as if they were aquarium water, provided that their electrical conductivity is approximately that of aquarium water. It was noticed, however, that the behaviour of the fish changed when more dilute solutions of KCl were used. Thus, as long as the conductivity was of the order of $1000\mu\text{mhos/cm.}$ (conductivity of aquarium water = $980\mu\text{mhos/cm.}$), the behaviour was indistinguishable from that towards aquarium water, but when trials with solutions of 130 and $260\mu\text{mhos/cm.}$ were introduced into a series in which aquarium water had to be distinguished from distilled water, the fish hardly ever accepted the food. On the rare occasions when it did so, this happened after much hesitation just before the 60 sec. trial period had elapsed. On the other hand, it was noted that when trials were conducted in

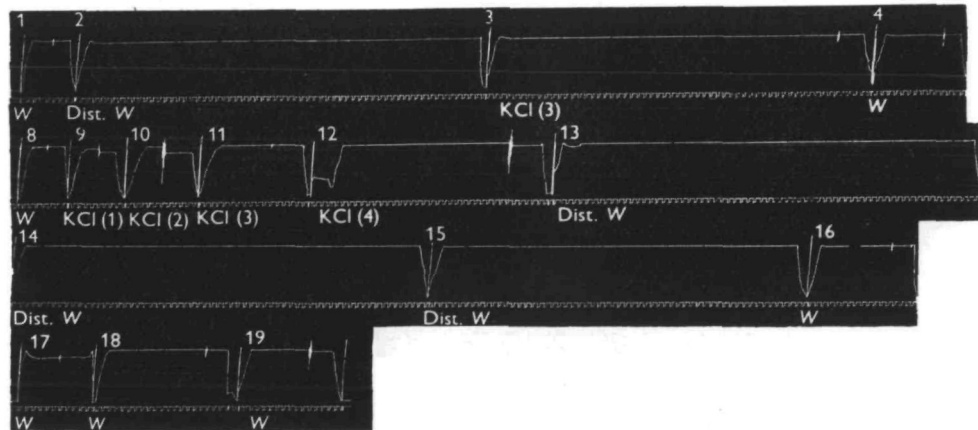


Fig. 13. Record of trials with a fish trained to aquarium water (W = positive stimulus) and to distilled water (dist. W = negative stimulus) responding to KCl solutions of various strengths. Electrical conductivity of KCl (1)— $1000\mu\text{mhos/cm.}$; KCl (2)— $500\mu\text{mhos/cm.}$; KCl (3)— $260\mu\text{mhos/cm.}$; KCl (4)— $140\mu\text{mhos/cm.}$

rapid succession with gradually decreasing concentrations of KCl solutions the fish was more ready to accept the food even at these lower concentrations. The example in Fig. 13 shows the positive reactions in successive trials towards aquarium water and KCl solutions of a conductivity of 1000, 500, 260 and $140\mu\text{mhos/cm.}$, presented in that order. It will be seen from this record that the fish showed progressively more hesitation, and that it refused the food in the three succeeding trials with distilled water, although still hungry and ready to feed, as can be seen from the four following positive responses towards aquarium water.

The regularity in the increase of the reaction time in this record may, in part, be considered as fortuitous, but the increase does suggest that *Gymnarchus*, given sufficient time, is capable of detecting smaller differences in the electrical conductivity of the contents of the porous pot than has become apparent in the quali-

tative experiments described earlier. In order to obtain information about the degree of sensitivity of *Gymnarchus*, a series of training experiments was undertaken in which the fish had to distinguish between mixtures, in different proportions, of aquarium water and distilled water. In Table 4 are summarized the results of training experiments in which the fish (previously trained to distinguish between

TABLE 4

Stimulus	No. of trials	Response		
		Correct	Incorrect	
<i>W</i>	58	52	6	
75 % dist. <i>W</i>	39	27	12	
	97	79	18	$P < 0.1\%$
<i>W</i>	8	8	0	
50 % dist. <i>W</i>	7	4	3	
	15	12	3	$P < 0.1\%$
<i>W</i>	58	54	4	
25 % dist. <i>W</i>	50	31	19	
	108	85	23	$P < 0.1\%$
<i>W</i>	18	12	6	
12.5 % dist. <i>W</i>	4	2	2	
	22	14	8	$P = 25\%$

Positive stimulus = (*W*) aquarium water.
 Negative stimulus = (% dist. *W*) = aquarium water + % distilled water.

aquarium water and distilled water) had to distinguish between aquarium water and aquarium water containing 75, 50, 25 and 12.5% of distilled water included in the pot. In each series training was continued until at least ten successive positive responses were achieved. It is clear from these results that *Gymnarchus* can at least distinguish aquarium water from 75% aquarium water + 25% distilled water. Insufficient data are available in this series for lower dilutions of aquarium water (87.5% *W.* + 12.5% dist. *W.*), but the general impression—borne out by later experiments—suggests that even these finer differences can be appreciated.

The conclusion that discrimination was achieved in these experiments by the ability of the fish to sense the electrical conductivity of the solutions and not their chemical composition was supported by a further series of training experiments in which the fish had to differentiate between a porous pot filled with aquarium water and the same pot with aquarium water which also contained centrally placed glass tubes of varying diameters.

A fish, trained to respond negatively to distilled water and positively to aquarium water, also responded negatively, without further training, to aquarium water which contained a glass tube of 2.5 or 2.3 cm. diameter (and occasionally also to tubes of 1.9 and 1.5 cm. diameter), whereas to a tube of 0.9 cm. diameter a positive response was usually given. With further training, however, finer discriminations could be demonstrated. The results of all training experiments to glass tubes of 0.9, 0.6, 0.4, 0.2 and 0.08 cm. are summarized in Table 5.

TABLE 5

Stimulus	No. of trials	Response		
		Correct	Incorrect	
<i>W</i>	34	33	1	$P < 0.1\%$
<i>W</i> + 0.9 cm.	38	26	16	
	62	55	17	
<i>W</i>	47	43	4	$P < 0.1\%$
<i>W</i> + 0.6 cm.	49	33	16	
	96	76	20	
<i>W</i>	38	35	3	$P < 0.1\%$
<i>W</i> + 0.4 cm.	39	22	17	
	77	57	20	
<i>W</i>	167	134	33	$P < 0.1\%$
<i>W</i> + 0.2 cm.	151	69	82	
	318	203	115	
<i>W</i>	49	35	14	$P = 60\%$
<i>W</i> + 0.08 cm.	47	16	31	
	96	51	45	

Positive stimulus = (*W*) aquarium water.

Negative stimulus = (*W* + *x* cm.) aquarium water + glass tubes of varying diameter.

Although it is clear that under such experimental conditions *Gymnarchus* can detect at a distance a glass tube of 0.2 cm. diameter, a closer examination of the records suggests that (i) the performance of the fish is somewhat variable from day to day; (ii) the fish does not remember from one day to the next the more difficult discriminations.

This table, therefore, does not present a completely true picture of the powers of learning and discrimination. In a short test series proportionately more mistakes will be recorded. If two short test series, performed on different days, are added up, the proportion of correct to incorrect reactions would be lower than in a single consecutive series of the same number of trials.

Moreover, in a number of instances the trials were started with the easier task (0.9 cm. tubes) and then made progressively more difficult by reducing the diameter. The learning acquired in the earlier trials was clearly of influence on the later, more difficult, trials.

It is, possible, however, to perform more than 100 trials with a hungry fish in one session. A continuous series of trials with 0.6, 0.35 and 0.2 cm. diameter glass tubes was therefore undertaken in the course of one day during which one may assume that the conditions were more or less constant. The results, summarized in Table 6, show a progressive worsening of the responses with decreasing diameter and they also show that, whereas the responses towards aquarium water remain significantly correct, there is a marked deterioration in the number of correct responses towards the negative stimulus with decreasing diameter of the glass tubes.

Attempts to investigate the ability of the fish to distinguish between two glass tubes of different diameter presented inside the porous pot filled with aquarium water have been undertaken, but have not been pursued to the limits of discrimination.

TABLE 6

Stimulus	No. of trials	Response		
		Correct	Incorrect	
<i>W</i>	7	7	0	
<i>W</i> +0.9 cm.	6	3	3	$P=3\%$
	13	10	3	
<i>W</i>	8	8	0	
<i>W</i> +0.6 cm.	10	7	3	$P=0.1\%$
	18	15	3	
<i>W</i>	21	19	2	
<i>W</i> +0.4 cm.	19	12	7	$P<0.1\%$
	40	31	9	
<i>W</i>	20	15	5	
<i>W</i> +0.2 cm.	14	6	8	$P=14\%$
	34	21	13	

Positive stimulus = (*W*) aquarium water.

Negative stimulus = (*W*+*x* cm.) aquarium water + glass tubes of varying diameter.

TABLE 7

Positive stimulus, 0.9 cm. diam. tube	Negative stimulus 1.5 cm. diam. tube
Responses 20 correct; 0 incorrect	Responses 17 correct; 6 incorrect

An example of such an experimental series in which the fish had to distinguish between a glass tube of 0.9 cm. diameter and another of 1.5 cm. are given in Table 7.

If the theory given earlier is correct, the fish should be incapable of distinguishing between a pot containing a glass tube and one containing a water mixture, provided that the mixture is adjusted so that the imprimences are equal in the two cases.

Accordingly, a fish trained to respond positively to a 0.9 cm. glass tube and negatively to a 1.5 cm. tube was presented with various water mixtures introduced into a series of trials with glass tubes. The results are shown in Fig. 14.

It will be seen that both 75 and 50% aquarium water evoke positive reactions, while 40% gives a negative reaction. The corresponding imprimences are shown in Table 8. Thus in terms of imprimence values the boundary between positive and negative reaction lies between 0.2 and 0.6 for glass tubes and between 0.5 and 0.7 for water mixtures. In view of the approximations made in the theory there is little point in attempting to define the boundary more accurately, and the measure of agreement in the results is considered adequate.

TABLE 8

Stimulus	Imprimence, cm. ²	Reaction
0.9 cm. tube	0.2	+
1.5 cm. tube	0.6	-
75% aquarium water	0.2	+
50% aquarium water	0.5	+
40% aquarium water	0.7	-

It must be remembered that in all these experiments:

(i) The fish has no means of simultaneous comparison of the two conditioning stimuli and must remember the differences from one trial to the next. Experiments using two externally identical pots with different contents presented simultaneously became inconclusive at fine levels of discrimination, presumably because the impriments of the pots themselves differed.

(ii) The fish must recognize the differences of the stimuli through the 1 cm. thick walls of the pot, i.e. the impriment of the pot is added to that of the stimulus in all cases. Furthermore, the conditions under which these experiments were performed were not ideal and various extraneous noises and vibrations clearly influenced the behaviour of the fish.

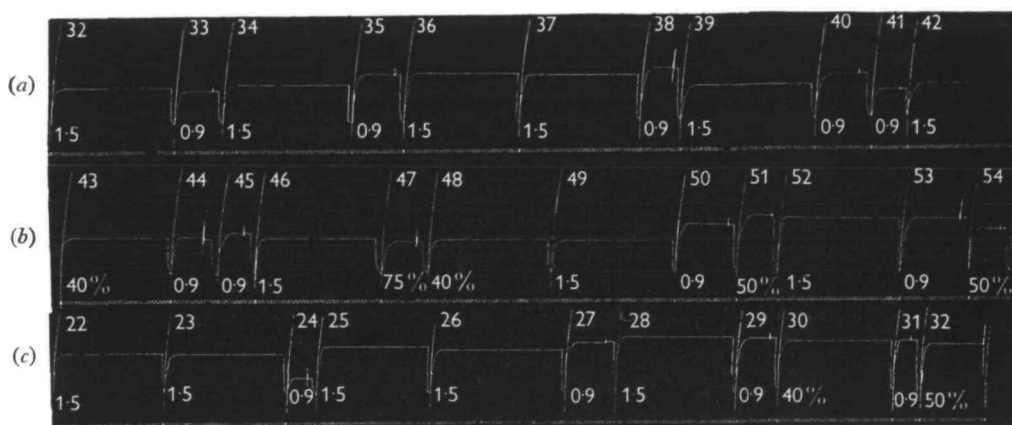


Fig. 14. Record of trials with a fish trained to distinguish a glass tube of 0.9 cm. diameter in a porous pot (0.9 = positive stimulus) from another tube of 1.5 cm. (1.5 = negative stimulus). This fish also responds positively to a mixture of 50% aquarium water + 50% distilled water, and negatively to 40% aquarium water + 60% distilled water. Records (a) and (b) consecutive series; (c) 2 days later. Time marker = 1 sec.

Despite these limitations the general inference from these quantitative experiments is: (1) that *Gymnarchus* cannot distinguish between objects of similar impriment but of different internal construction; (2) that the object of minimum impriment which can be detected by the fish is represented by a glass tube about 0.2 cm. in diameter.

Further tests are, however, needed to establish discrimination thresholds for the whole receptive range.

CRITICAL CONSIDERATIONS OF THE METHOD AND GENERAL OBSERVATIONS ON LEARNING AND BEHAVIOUR IN *GYMNARCHUS NILOTICUS*

From time to time in the course of this work the authors had doubts about the validity of the observed results. The delicate reactions of the fish towards external stimuli gave rise to suspicion. For example, the porous pots were clamped to the

lever arm by wooden screws. These screws, when tightened, sometimes produced a squeak in the middle of an experiment. In cases when a weak negative stimulus was presented and the fish hovered near the pot this sound almost invariably led to a sudden attempt to secure the food. After this defect in the apparatus had been eliminated, the same response could be evoked by the slightest touch with the tip of a finger on the slate wall of the aquarium near the pot. The question therefore arose as to whether the responses of the fish were guided or assisted by unconscious signals supplied by the experimenter. This appeared unlikely, because on a few occasions it happened that in a long experimental series with correct responses a single 'mistake' was accounted for by the fact that the experimenter had forgotten to include a glass tube in the pot. This became apparent only after the fish had been mistakenly punished and the bung removed from the pot. After such treatment it was found useful to guide the suspicious fish back to the training site during the next positive stimulus by lightly touching the wall of the aquarium.

In most experiments the fish could have seen only part of the face of the experimenter. Although its indifference to all but the most violent optical stimuli makes it unlikely that it could have received any visual clues, a number of tests were made during which the experimenter was completely out of sight; the reactions of the fish, recorded on the smoked drum, were unaltered. Moreover, violent movements of arm and hand, holding the punishment device above the training site, neither prevented nor delayed the acceptance of food on presentation of a positive stimulus.

Furthermore, in the series of experiments in which *Gymnarchus* had to discriminate between glass tubes of different diameters, trials were undertaken in which the 'experimenter' behind a screen, according to the toss of a coin, included one or the other of the two glass tubes into the porous pot. This was then closed with a rubber bung and passed to the 'handler' who performed the experiment not knowing the diameter, and who then reported back to the 'experimenter' his conclusions by observing the behaviour of the fish. An example of the results of one such test series is given in Table 9. The statistical significance obtained in such tests dispelled all doubts about the validity of the experimental results.

No general conclusions about the learning process in *Gymnarchus* can be drawn from these experiments, since they were performed on only two specimens and involved frequent re-training. It was noted, however, that in the early stages of training there appeared for a number of days a significant number of 'correct' responses during the first six to twelve trials, after which the performance would completely deteriorate. Whether this can be related to the method and number of punishments involved appears uncertain. After punishment the fish usually retreated to the far corner of the tank. Early in the training period the approach in the next trial was undertaken with much caution, often tail first with the tip apparently performing exploratory movements. In the series when different stimuli were presented successively the fish, on presentation of a negative stimulus, first

TABLE 9

No. of trial	Tube diameter known to Experimenter	Tube diameter, reported by Handler
1	1.5	1.5
2	0.9	0.9
3	0.9	0.9
4	1.5	0.9*
5	1.5	1.5
6	0.9	0.9
7	1.5	1.5
8	1.5	1.5
9	0.9	0.9
10	0.9	0.9
11	1.5	1.5
12	0.9	0.9
13	0.9	0.9

* Mistake.

approached the training site and then retreated. Often, however, notably after a number of negative stimuli had been presented in succession, an aggressive mood developed. This usually took the form of a few lateral oscillations, followed by a sudden charge against the pot. Sometimes such attacks were also noted when the usual time of presentation of the stimulus (30 sec.) was extended. An attack also usually took place as soon as the withdrawal of the pot was begun. As can be seen from the records, the withdrawal had to be performed smartly to avoid damage to the pot.

It has been mentioned that *Gymnarchus* does not seem to remember the finer discriminations from one day to the next. On the other hand, evidence is on record that a fish trained to distinguish aquarium water from distilled water in a porous pot showed signs that it remembered this training over a period of four months. When the training was re-started after this interval, the first eight trials gave correct responses; after punishment in the ninth trial very few further mistakes occurred in this series.

THE SECOND DERIVATIVE MODE AS THE MOST PROBABLE MECHANISM; LIMITS OF DETECTION

In a previous section it was shown that a receptor system operating in the second derivative mode gives better discrimination in angle and range than one using the potential mode. Furthermore, from the approximate values of the relevant resistances calculated in Appendix IV, it seems clear that the second derivative mode is the more likely one in *Gymnarchus*. In both modes the receptors have to detect changes in an already existing stimulus; in the typical case in Figs. 5-8 the object changes the existing potential by 15%, while the second derivative of potential changes by 130% for the same object. If the Weber-Fechner Law applies to the receptors, the second derivative mode is clearly capable of higher sensitivity. This mode is also less affected by movements of the tail of the fish.

One point against the second derivative mode is that the actual currents flowing in the receptors are very much smaller than for the potential mode. It is therefore necessary to investigate whether these very small currents are detectable amongst the random fluctuations or 'noise' inherent in every detector system.

The conditioned reflex experiments have demonstrated that *Gymnarchus* can just detect whether a porous pot containing aquarium water also contains a 0.2 cm. diameter glass tube (impermeance of 0.01 cm.²). From Fig. 7, drawn for an impermeance of 6.25 cm.², it can be calculated that in the most favourable ('head-on') case the fish must be able to detect a change of about 0.6 μV.cm.⁻². The standing value of the second derivative as shown in Fig. 8 is about 300 μV.cm.⁻², so that the relative change (i.e. Weber fraction) is about 0.2%. The thresholds observed in other sense organs are in general higher than 1%, so the detection of this small change would probably present great difficulty. However, as we have noted earlier, the large standing value of second derivative is somewhat artificial and is not likely to be so large in the actual fish. A fairer comparison would be with the object in position C; here the change which must be detected is about 0.3 μV.cm.⁻² in a standing value of 25 μV.cm.⁻², i.e. about 1%.

To find the change of current in the receptors, the results of Appendix IV are used, together with the approximate value for the inter-mormyromast resistance calculated there. The change of current is then 0.01 μμA. during each pulse, or a mean value (for 1 msec. pulses at 300 c./s.) of 0.003 μμA. It is these currents which must be compared with the noise currents in the receptor circuit.

The R.M.S. noise current in a circuit of total resistance R is given by

$$i_{\text{R.M.S.}} = \sqrt{\frac{4KT\Delta f}{R}},$$

where K is Boltzmann's constant, T is the absolute temperature and Δf is the 'bandwidth' of the receptor system, i.e. the frequency range over which the receptors operate. For the resistance in a mormyromast circuit ($\sim 300 \text{ k}\Omega$) the noise current $i_{\text{R.M.S.}}$ equals $\frac{1}{2}\sqrt{\Delta f} \mu\mu\text{A.}$

The probable bandwidth of the receptor system must be carefully considered. It is usually necessary in problems of this type to consider the law of the detector element—whether linear, square law, etc. In the present case the detector will inevitably be linear for small changes of input, due to the presence of the large standing input. With such a linear system there is no restriction on the bandwidth of the system; it can be made indefinitely small. As the bandwidth is reduced the noise current will decrease, while the current due to the signal will remain the same. The individual pulses will gradually lose their shape, and eventually their identity. Since no information is carried by the pulse nature of the signal, this is of no importance. The reduction of bandwidth to Δf is equivalent to an integration of the signal over a time τ given by $\tau = 1/(2\pi\Delta f)$ and thus the reduction of noise is achieved only at the expense of a long response time.

In addition to temporal integration, the noise can be reduced by spatial integration, i.e. by averaging (possibly in the C.N.S.) the response of many neighbouring

receptors. If n receptors are thus averaged, the noise can be reduced by a factor of \sqrt{n} . With both temporal and spatial integration the R.M.S. noise current is given by

$$i_{\text{R.M.S.}} = \frac{I}{4\sqrt{n}} \sqrt{\frac{1}{2\pi n\tau}} \mu\mu\text{A.}$$

There is an optimum value for n depending on the structure of the field pattern due to a typical object. If too many receptors are averaged, the pattern of stimulation of the type shown in Fig. 7 is blurred, with consequent loss of directional accuracy. From that figure it is clear that averaging can be carried out over a strip about 1 cm. wide without much loss of information: in such a strip there may be about 5000 receptors. With this value of n , the noise current becomes

$$i_{\text{R.M.S.}} = \frac{0.0015}{\sqrt{\tau}} \mu\mu\text{A.}$$

For this current to be smaller than the mean value of the change in current due to the presence of the object (estimated above as $0.003 \mu\mu\text{A.}$), τ must be greater than about $\frac{1}{4}$ sec. Such an integration time would not unduly limit the usefulness of the locating mechanism.

Spatial and temporal integration are not unknown in other sense organs (de Vries, 1956), so that their assumption in the present case is plausible. Indeed, some form of temporal integration is essential if the output from the receptors is transmitted along their nerves in the usual way. Without temporal integration it is not possible to transmit information about the amplitude of 1 msec. pulses at 300 c./s. by means of impulses in the sensory nerve where the maximum repetition frequency is of the order of 500 c./s.

Two other mechanisms can be employed to improve the signal-to-noise ratio for the receptor system as a whole. By swimming to and fro near the object the fish may 'scan' the area, giving a field pattern which sweeps over the receptors in a readily identifiable way. This gives an effective increase of integration time, since the information from the receptors may be collected over the time of one whole 'scan'. Furthermore, the small relative change in stimulus would be much more readily detected since several comparisons could be made in a short time.

The other mechanism involves inhibition of the receptors between transmitted pulses. For a 1 msec. pulse with a repetition rate of 300/sec., an improvement of signal-to-noise ratio by a factor of about $\sqrt{3}$ would be obtained in this way. This 'blanking' would have to take place before the point at which temporal integration occurred; there seems no obvious mechanism for carrying this out. Since the signal-to-noise ratio is improved by a relatively small factor, it is unlikely that any very complicated mechanism would be evolved to give 'blanking' of the receptors.

From the point of view of the threshold of object detection the characteristics of the pulses emitted by the fish have little effect. If no 'blanking' takes place only the mean value of the transmitted current affects the threshold. The duration and frequency of the pulses may be dictated by the physiology of the electric organs and possibly by the characteristics of the integration mechanism in the receptors.

COMPARISON OF THE THRESHOLD OF OBJECT DETECTION
WITH THE DIRECT CURRENT SENSITIVITY

If the fish is exposed to a uniform electric field, the distribution of potential around it is determined only by the shape of the fish. The second derivative of potential reaches a maximum at the nose: for the model fish of Fig. 4 this is $1.3E$ volts cm.^{-2} , where E is the uniform potential gradient. Assuming that the same receptors are responsible both for object location and for sensitivity to small direct currents, the threshold for the two effects may be compared.

In an earlier section the threshold for direct currents was established as about $0.04\mu\text{V./cm.}$ The maximum value of the second derivative of potential is thus $0.05\mu\text{V.cm.}^{-2}$. For the detection of objects it was shown that the threshold involved the detection of a change of $0.3\text{--}0.6\mu\text{V.cm.}^{-2}$. In view of the approximate nature of the theory and in view of the experimental accuracy an agreement within an order of magnitude may be considered satisfactory. We may conclude, then, that it is not unreasonable to assume that the same receptors are acting in both cases.

SUMMARY

1. Experiments with moving electrostatic and magnetic fields show that *Gymnarchus niloticus* is sensitive to a potential gradient of about $0.03\mu\text{V./cm.}$
2. Alternative explanations of some previous experiments are given in terms of this high d.c. sensitivity.
3. An explanation in similar terms is given of experiments in which *Gymnotus carapo* is trained to detect a stationary magnet.
4. The mechanisms available for the location of objects by electric fish are reviewed. It is concluded from the results of a critical experiment (described in a succeeding section) that *Gymnarchus niloticus* can detect objects by the disturbance of its own electric field in the water.
5. The approximate theory of this method of object location is derived. The effect on the receptors of the perturbing field due to an object depends on the electrical properties of the receptors: in the extreme cases the stimulation of the receptors is proportional either to the potential or to its second derivative. Graphs are given showing the effect of an object on the potential and on its second derivative around the surface of the fish.
6. Experiments are described using *Gymnarchus niloticus* which (a) confirm that the mechanism of object location employs electric field distortion; (b) indicate the limits of the sensitivity of the fish.
7. The second derivative mode appears to be the most probable one operating in *Gymnarchus*. The experimentally determined limits of detection are discussed in relation to the random noise in the receptor circuit: it is concluded that both spatial and temporal integration are likely to be employed.
8. The thresholds for object location and for response to direct currents are compared: it is concluded that the same receptors are probably operating in both cases.

The authors are indebted to Elisabeth Machin for much help with the mathematics and computation.

APPENDIX I. THE CALCULATION OF THE CURRENTS INDUCED
BY MOVING ELECTROSTATIC AND MAGNETIC FIELDS

In this Appendix estimates will be made of the current which can be detected by *Gymnarchus niloticus* when moving electrostatic or magnetic fields are generated outside its tank. Since the calculations are intended only to establish the order of magnitude of the effects, the approximations which will be made are not unjustified.

Electrostatic case

It is at first sight not apparent how the movement of an electrostatic charge outside the tank can affect the fish, which is virtually immersed in a perfectly conducting medium. The explanation can best be given in the following terms. When a positive charge is placed in front of the tank, an electric field exists momentarily in the water (i.e. for about $\frac{1}{100}$ μ sec.). This causes a current to flow, and negative and positive charges to build up on the front and back faces respectively of the tank. The electric field due to this separation of charge is just equal and opposite in the water to the applied field; therefore no further current flows. The distribution of charge on the water/glass interface at the front of the tank is called the 'induced charge'; it is equal in magnitude and opposite in sign to the charge placed outside the tank.

The explanation of the effect can now be given in terms of this induced charge. Referring to Fig. 15, when the test charge is at *A*, there is a distribution of induced charge *A'* with a maximum density opposite *A*, falling off outwards. If the test charge now moves to *B*, the induced charge must appear as *B'*. The movement of induced charge from *A'* to *B'* must be through the water, so that currents will flow along such paths as *p*, *q*, *r*.

Hence the calculation involves the following steps:

- (a) Describe the distribution of induced charge *A'*.
- (b) Let it move with a velocity equal to that of the test charge.
- (c) Calculate the current which thereby flows in the water at the appropriate distance from the front face.

This calculation cannot be solved analytically, but involves numerical integration. This has been done, but it was thought more suitable to present here an approximate calculation which illustrates more clearly the physical principles, and which gives a result only slightly different from that of the more detailed analysis.

The density of induced charge falls off as $1/d^3$ (Fig. 16); 90% of the induced charge is confined within a radius $1.8a$ of the point *P*. Without serious error we may consider all the induced charge confined within a square of side $2a$ centred on *P* (Fig. 16). The charge density is then $-q/4a^2$. If the test charge moves sideways a distance dx , the charge on *AA'D'D* disappears, and an equivalent charge appears on *BB'C'C*. A charge dq , given by

$$dq = 2a dx \left(-\frac{q}{4a^2} \right) = -\frac{qdx}{2a},$$

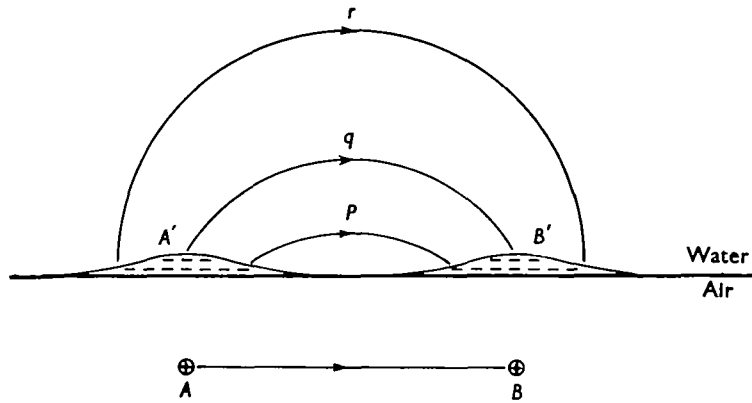


Fig. 15. The induced charge due to a moving test charge.

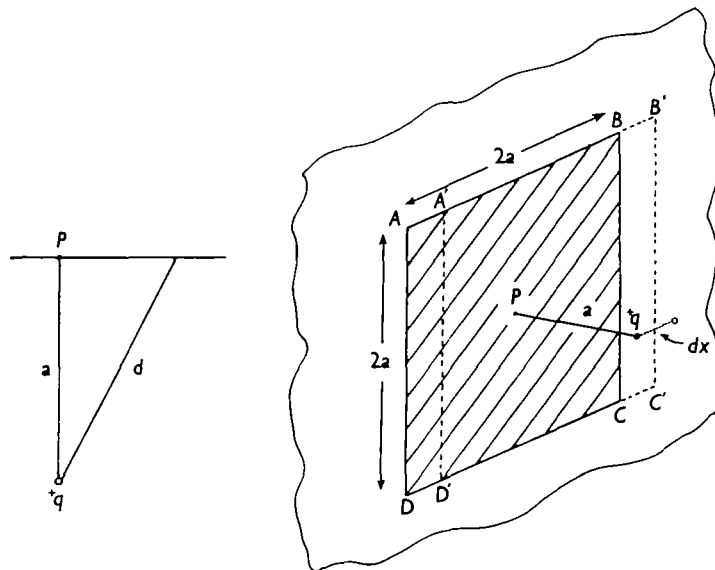


Fig. 16. The geometry of the electrostatic problem.

is thus transferred a distance $2a$. The current flowing from one edge of the square to the other is then given by

$$i = \frac{dq}{dt} = -\frac{q}{2a} \frac{dx}{dt} = -\frac{q}{2a} v,$$

where v is the sideways velocity of the test charge. This flow of current will spread into the tank in the manner shown in Fig. 17, and the current density at a point R within the water can be calculated.

If $d \gg a$, the lines of current flow will correspond to a current dipole of strength M given by

$$M = 2ai = \frac{qv}{2a} 2a = qv.$$

The current density J in the water at the point R is given by

$$J = \frac{M}{4\pi d^3} = \frac{qv}{4\pi d^3}.$$

In the experiment described in the text, a body of capacity approximately 2 e.s.u. was charged to a voltage of 60 kV. (200 e.s.u.) from a Wimshurst machine. The charge was thus 400 e.s.u. The velocity with which the charge was moved in front of the tank was about 3 m./sec.; a positive reaction could still be obtained from the fish when it was 50 cm. from the tank wall.

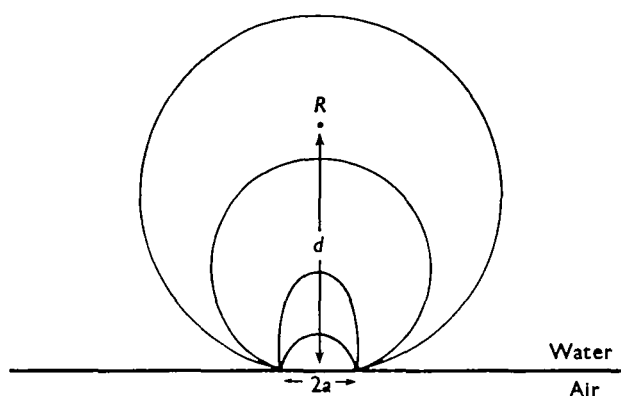


Fig. 17. The spread of current due to the movement of induced charge.

If we assume that the conductivity of the fish is not very different from that of the water, the current density in the fish will be given by the last equation as 0.08 e.s.u., or about $2 \times 10^{-5} \mu\text{A./cm.}^2$. If the full calculation is carried out without any of the simplifying assumptions made above, a current density of about half this value, i.e. $10^{-5} \mu\text{A./cm.}^2$ is obtained.

Putting in a value of $500 \mu\text{mhos/cm.}$ for the conductivity of the fish, the potential gradient along it becomes $0.04 \mu\text{V./cm.}$; for a fish 50 cm. long this represents a total head-to-tail voltage of about $1 \mu\text{V.}$

Magnetic case

The potential gradient induced in a conductor of unit permeability by a magnetic field H sweeping through it at a velocity v is equal to Hv . In the present experiments, a small bar magnet moved at 3 m./sec. elicited a reaction from a fish 50 cm. away. At this distance, the field was shown by a deflexion magnetometer to be about 0.01 oersted. Hence the potential gradient is equal to 3 e.m.u., or $0.03 \mu\text{V./cm.}$

The very satisfactory correspondence between this figure and the one ($0.04 \mu\text{V./cm.}$) obtained for the electrostatic case must be regarded as fortuitous, since the approximations made in the calculations will inevitably introduce errors of much greater magnitude.

APPENDIX II. THE POTENTIAL INDUCED IN A FLUID WHICH
MOVES IN A MAGNETIC FIELD

The potential gradient, i.e. electric field, induced at any point in a moving fluid is proportional to $vH \sin \theta$, where v is the local velocity of the fluid, H is the magnetic field and θ the angle between them. The direction of the induced electric field is at right angles to both the velocity and magnetic field vectors.

An electric equipotential is a line along which there is no component of electric field; we may therefore identify equipotentials with lines in the fluid *perpendicular* to which there is no component of fluid velocity. Such lines are, of course, the streamlines of the fluid flow. It is clear then that all streamlines must also be electrical equipotentials; the spacing of the lines for equal increments of potential will not necessarily be the same as the spacing of the streamlines.

Since any obstacle to the flow will have one streamline coincident with its boundary, this boundary will also be an equipotential. No current will flow in the obstacle whatever its conductivity; the conductivity of an obstacle therefore cannot affect the potential distribution in the fluid in any way.

APPENDIX III. THE CALCULATION OF THE PERTURBING FIELD BY
THE METHOD OF IMAGES

The theory of images in conducting media can best be treated by analogy with electrostatics. It is well known (e.g. Harnwell, 1938) that the equipotentials in a continuous conducting medium are identical with those in free space, and that the lines of current flow coincide with the lines of electrostatic force. The equations of electrostatics can be applied to the conduction case, provided that we substitute for the electrostatic quantities the analogous quantities for conduction. These substitutions are:

Electric induction— $4\pi \times$ current density
Permittivity—Conductivity

The image theory will be developed using electrostatic terminology, and at the end of the calculation the results will be transformed into those appropriate to the conduction case.

The calculation of the perturbing field due to an object of arbitrary shape in a specified field configuration is intractable, so an idealized situation, approximating to the actual one but simpler to analyse, must be used. Since only the order of magnitude of the perturbing field is required the errors introduced by the approximations are not likely to be significant.

In the experiments with *Gymnarchus niloticus* the field of the fish approximated to that of a dipole; the depth of the tank was of the same order as the length of the dipole. Cylindrical objects of about half this length were used. In these circumstances it is a reasonable approximation to treat the problem two-dimensionally. The fish is represented by a line dipole, and the object by an infinite cylinder.

Smythe (1950) gives the image of a line charge in a dielectric cylinder. If a single

charge q is situated at a distance b from the centre of a cylinder of radius a , two images are present:

- (a) q' at a distance a^2/b from the centre of the cylinder along the radius from q ;
- (b) $-q'$ at the centre of the cylinder.

Here q' is given by

$$q' = q \frac{\epsilon_0 - \epsilon}{\epsilon_0 + \epsilon},$$

where ϵ_0 and ϵ are the permittivities of the surrounding medium and the cylinder respectively. When a dipole is reflected in the cylinder, the two charges at the centre cancel out, leaving the image also as a dipole. This is illustrated in Fig. 18. From the geometry of the figure it follows that the length l' of the image dipole is given by

$$l' = \frac{a^2 l}{r_1 r_2},$$

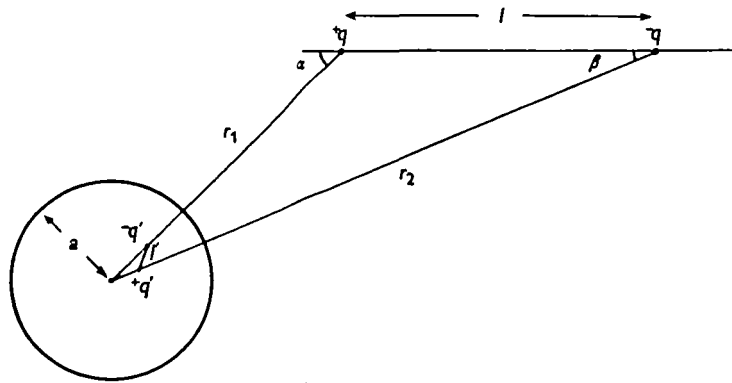


Fig. 18. The image of a dipole in a dielectric cylinder,

and its inclination γ to the original dipole axis by

$$\gamma = \alpha + \beta.$$

The moment M' of the image dipole is thus given by

$$M' = q'l' = q \frac{\epsilon_0 - \epsilon}{\epsilon_0 + \epsilon} \frac{a^2 l}{r_1 r_2} = \frac{M}{r_1 r_2} a^2 \frac{\epsilon_0 - \epsilon}{\epsilon_0 + \epsilon},$$

where M is the moment of the original dipole.

Substituting σ , the conductivity, for ϵ , the permittivity, it follows that:

The image of a current dipole of moment M in a cylinder of radius a is itself a dipole of moment M' at an angle γ to the original dipole axis, where

$$M' = \frac{M}{r_1 r_2} a^2 \frac{\sigma_0 - \sigma}{\sigma_0 + \sigma} \quad \text{and} \quad \gamma = \alpha + \beta.$$

Here σ_0 = conductivity of surrounding medium; σ = conductivity of cylinder; r_1, r_2 = distances from centre of cylinder to the poles of the original dipole; α, β = angles to the axis of the lines joining the poles of the original dipole and the centre of the cylinder.

APPENDIX IV. THE EFFECT OF MORMYROMAST RESISTANCE

The electric currents flowing into any mormyromast will depend not only on the distribution of potential in the neighbouring water, but also on the relative resistances of the jelly-filled canals and the intervening tissue. The situation may be represented in the one-dimensional case by the equivalent circuit of Fig. 19.

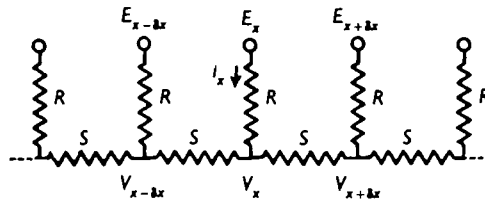


Fig. 19. The equivalent circuit of the receptor system.

Here R is the resistance of the jelly-filled canals and S is the resistance of the tissue between their proximal ends. The terminals are 'sampling probes' at the same potential E as the surrounding water. If V is the potential at the proximal end of R , and i is the current flowing in it, then

$$i = \frac{V_x - V_{x-\delta x}}{S} + \frac{V_x - V_{x+\delta x}}{S} = -\frac{(\delta x)^2}{S} \frac{d^2 V}{dx^2}.$$

Furthermore,

$$i = \frac{E - V}{R}.$$

From these equations

$$Si - R \frac{d^2 i}{dx^2} (\delta x)^2 = -\frac{d^2 E}{dx^2} (\delta x)^2.$$

The full solution of this equation must be expressed in terms of Fourier series, but the two extreme cases will be considered.

(a) $R = 0$. Here

$$i = -\frac{1}{S} \frac{d^2 E}{dx^2} (\delta x)^2.$$

(b) $S = 0$. Here

$$R \frac{d^2 i}{dx^2} = \frac{d^2 E}{dx^2} \quad \text{or} \quad i = \frac{E - C_1}{R},$$

where C_1 is the mean potential inside the fish.

Thus when the resistance of the jelly-filled canals is low, the current in them (i.e. the stimulus to the receptor at the proximal end) will be proportional to the second derivative of the potential in the neighbourhood. If, on the other hand, the tissue resistance is low, the current (i.e. stimulus) will be proportional to the local potential.

It can be shown that, if

$$\frac{S}{R} \gg \frac{1}{E} \frac{d^2 E}{dx^2} (\delta x)^2,$$

the receptor system will operate effectively in the 'second derivative' mode, while if

$$\frac{S}{R} \ll \frac{1}{E} \frac{d^2E}{dx^2} (\delta x)^2$$

it will operate in the 'potential' mode.

In *Staetogenys elegans* the jelly-filled canals were found to be about 0.1 mm. long and 0.02 mm. diameter; if the conductivity of the contents is the same as that of the slime measured by Thornton (1931) they would have a resistance of about 300 kΩ. Assuming a similar value for *Gymnarchus*, the value of S corresponding to operation in the two modes can be calculated. From Figs. 5-8, $\frac{1}{E} \frac{d^2E}{dx^2}$ is of the order of 0.1 cm.⁻²; furthermore, δx , the distance between neighbouring mormyromasts, is of the order of 0.2 mm. From the inequalities given above, the operation will be in either the potential or second derivative mode, depending on whether S , the tissue resistance, is much smaller or much greater than 15 ohms.

A very rough value for S may be obtained by considering the proximal ends of the mormyromasts as spheres of 0.1 mm. diameter embedded in material with a conductivity of 2000 μmhos/cm. (the value given by Thornton (1931) for fish skin). This gives a value for S of about 10,000 ohms, indicating that the second derivative mode is the most likely one.

APPENDIX V. MODEL EXPERIMENT USING AN ELECTROLYTIC TANK ANALOGUE

A full-scale electrolytic tank analogue of *Gymnarchus niloticus* was set up in order to measure the changes of potential produced by objects.

Electrodes representing (i) the transmitting dipole (two carbon rods) and (ii) the receptors around the nose (25 silver-tipped wires) were mounted in the appropriate positions on a Perspex sheet. The electrodes were immersed in a shallow tank of tap water.

The equipment could be operated in either the 'potential' or 'second derivative' mode. The circuits for these two modes are shown in Figs. 20a and 20b. A ganged multi-way switch selected the appropriate electrodes for connexion to the circuit.

A wax-filled pot of the type used for the conditioning experiments with *Gymnarchus* could be mounted in various positions relative to the 'nose'.

Readings either of potential or of its second difference were taken for each position of the switch, both with and without the object present. The difference between the two sets of readings gave the effect due to the object.

The experimental results are shown in Fig. 21. They agree in general shape with the theoretical results of Figs. 5 and 7, but it is clear that the experimental errors are too large for the method to be of much value.

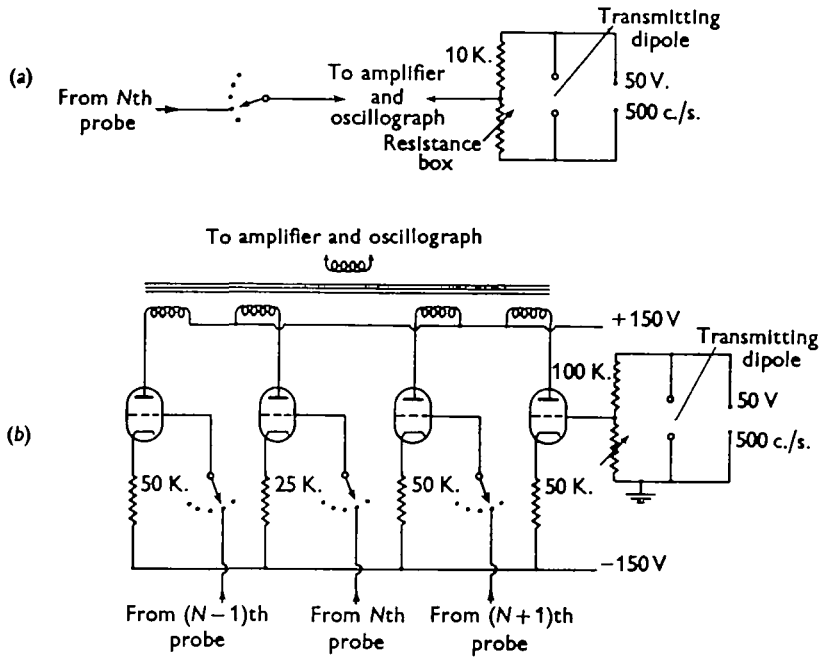


Fig. 20. Circuit of the electrolytic tank analogue: (a) potential mode, (b) second derivative mode.

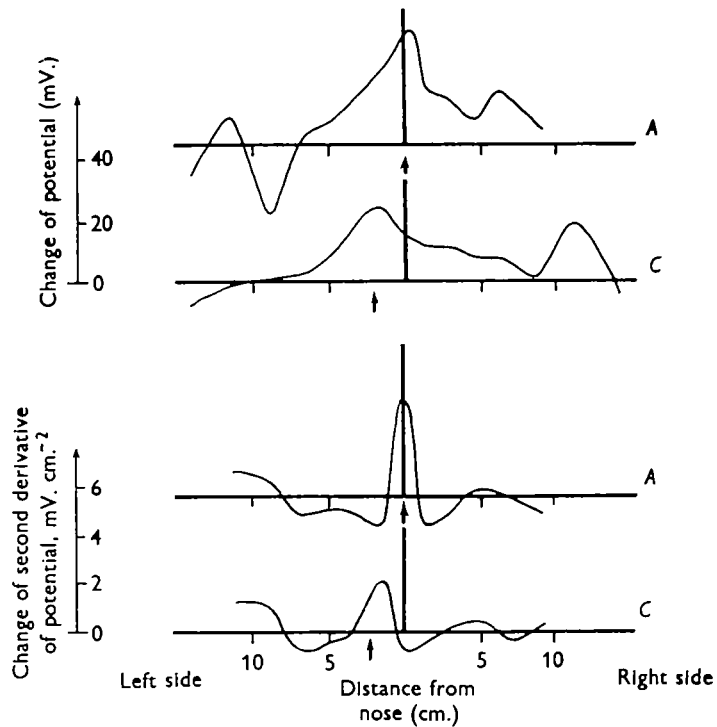


Fig. 21. The change of potential and its second derivative due to the presence of an object. A and C denote pot positions similar to A and C of Fig. 4.

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