

ON GALVANOTROPISM AND OSCILLOTAXIS IN FISH

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(With Eight Text-figures)

INTRODUCTION

HERMANN (1885) found that small fish (and fish embryos) and other animals such as tadpoles in a direct current (D.C.) field of a certain density, direct themselves parallel to the current lines, with their heads towards the anode (galvanotropism). On reversing the current all these animals turn 180° and the fish swim to the other electrode (galvanotaxis). This has been confirmed by Blasius & Schweizer (1893), Nagel (1894-5), Scheminzky (1924*a*) and others. When a fish is turned round in a field, so that it faces the cathode, it becomes excited and shows swimming movements and tremors of the body and tail. This occurs with normal as well as with spinal animals (Hermann, 1886; Hermann & Matthias, 1894). Destruction of the spinal cord abolishes all these phenomena.

Several explanations have been given for galvanotropism. The earlier authors were of the opinion that the position parallel with the current lines, with the head towards the anode, is the location in which the animal is stimulated least, the fish having moved around until it got into this position (Hermann, 1886; Nagel, 1894-5). Loeb & Maxwell (1896) and Loeb & Garry (1896-7), who worked on crayfish and on *Amblystoma*, assume that the D.C. stimulates nerve cells having a certain position in the central nervous system (C.N.S.) and so causes an orientation of the animal, which makes movements towards the anode more easy, towards the cathode more difficult. Breuer (1905) observed, in fish held at right angles to the current lines in a D.C. field, a bending of the head and the tail towards the anode. This reaction was abolished by destruction of the spinal cord and is, according to him, caused by a stimulation of structures in the cord. He thinks that this reaction alone cannot explain the galvanotropism, but that the movement of the head towards the anode and the moving of the tail into a position parallel with the current lines is governed by the labyrinths. Scheminzky (1924*b*) supports this view, as he could not demonstrate galvanotropism in trout embryos at an age at which the labyrinths were still undeveloped.

Scheminzky (1924*a*) described a phenomenon, comparable with galvanotropism, for fish in an alternating current (A.C.) field. The animal tends to take a position

at right angles to the current lines, parallel with the electrodes. He called this "oscillotaxis".

Since none of the explanations of galvanotropism mentioned above are very satisfactory, the following experiments were performed to get a better insight into its mechanism.

METHOD

A homogeneous electric field was obtained by conducting a current through the water in a trough 50 cm. long, 18 cm. wide and 14 cm. deep, by electrodes of zinc as large as the ends of the trough. The D.C. was obtained from a motor generator. Though this current usually has slight irregularities (ripple), it has been found by Blasius & Schweizer (1893) and by Scheminzky (1924*a*) that the effect of a field made with this current is the same as that obtained by a current supplied by a storage battery. The A.C. used was obtained from the municipal lines and had a frequency of 50 cycles. A potentiometer enabled us to get the potential desired. All these experiments were performed on goldfish (*Carassius auratus*), having a length of 8-12 cm.

ARE THE LABYRINTHS AND THE LATERAL-LINE ORGAN NECESSARY FOR GALVANOTROPISM?

The main evidence for the necessity of the labyrinths for galvanotropism is the parallel development in fish embryos of galvanotropism and of the labyrinths (Scheminzky, 1924*b*). However, it is possible that at about the same time other structures or mechanisms develop, which are necessary for galvanotropism. To investigate this, the effect of removal of the labyrinths upon galvanotropism was studied in mature fish. The acoustic nerve was transected by a method described by Parker (1903): a sharp and narrow scalpel (cataract knife) was inserted into the skull and so directed that it transected the n. octavus. A fish, thus operated bilaterally, assumed at rest almost the normal position, but when swimming swiftly the animal rotated round all its axes.

In a field of 1-3 δ (1 δ = 1 μ A. per mm.²) normal and operated animals showed a distinct galvanotropism. On reversal of the current both kinds of animals turn 180° and swim swiftly towards the new anode (galvanotropism and galvanotaxis). The normal animal reaches the anode more quickly than the operated one. We will discuss the possible explanation for this later.

As it is possible that the lateral-line organ is stimulated in a D.C. field, the nerve supply of this organ was destroyed in fish in which the acoustic nerves had previously been transected. The lateral-line organ is innervated by two nerves, the lateral nerve supplying the part of this organ in the body, and the facial nerve innervating the cranial part. Parker (1903) also described methods of transecting these nerves. The transection of the facial nerve is performed in a way similar to that of the acoustic nerve, and the lateral nerve can be cut directly posterior to the operculum. After transection of these nerves the fish still showed a distinct galvanotropism in the D.C. field. The autopsies of these animals showed that the nerves (VII, VIII

and the lateral nerves) had been really transected. Thus we must conclude that galvanotropism is a reaction independent of the labyrinths or the lateral-line organ; therefore we have to look for other mechanisms to explain this phenomenon.

THE GALVANOTROPIC REFLEX

A fish, fixed in a D.C. field at right angles to the current lines, bends its tail towards the anode (Breuer, 1905). This reaction is shown in Fig. 1 in a fish in which the spinal cord has been transected directly posterior of the head 4 days previously. The animal was fixed in the normal position in the D.C. field (2.5δ) by a band directly posterior to the operculum, leaving the hindpart of the body and the tail free to move. By rotating the animal round a vertical axis the fish was given various positions in the field with regard to the current lines. As long as the



Fig. 1. A fish in which the spinal cord was transected 4 days previously is illustrated in several positions with regard to the current lines in a D.C. field. The strength of the field is 2.5δ . Each picture has been taken 10 sec. after closing the current. The lines in the background indicate the direction of the current lines. The cross indicates the positive electrode.

animal is parallel with the current lines, no curving of the body and tail occurs, but when the fish is brought into other positions, the body and tail bend towards the anode. Each of the pictures of Fig. 1 was made 10 sec. after closing the current.

This reaction was recorded by fastening a thread to the tail of a spinal fish fixed in a D.C. field, at right angles to the current lines. The thread was led over pulleys to a muscle lever writing on a smoked drum (Fig. 2). To avoid the contraction of the whole musculature on switching the current on or off, the potential was increased and decreased in the course of a few seconds. The contraction lasted all the time (about 20 sec.) the current was conducted through the tank. The deflexion diminishes during this time; the contraction is not smooth.

As Breuer had reported we found that the destruction of the spinal cord abolishes this reaction. Chemical narcosis produced the same effect as destruction of the cord. When a fish is put in a 3% ethyl alcohol solution it is narcotized in about 10 min. During this time the reaction to D.C. diminished and at last disappeared; on putting the animal back in ordinary water the reaction reappears after some time. These experiments prove that the reaction in the D.C. field is not caused by a direct action of the current on the muscles or on the motor nerves, and that the spinal cord must be intact and functioning to obtain it. It is likely that such a reaction is a reflex. However, to prove this we have to demonstrate that the impulses causing the reaction start in the periphery of the body, and not somewhere in the central nervous system (C.N.S.) as has been assumed by Loeb & Maxwell (1896) and later by Breuer (1905).

To obtain the reaction it is not necessary to bring the whole animal in the field, but it is sufficient to apply the current (potential of 4–6 V.) locally, placing a pair of electrodes (silver chloride plated silver plates of 10 mm. length and 2 mm. width) symmetrically upon the two sides of the body. For instance, placing the electrodes symmetrically on the skin of the abdomen, parallel with and ventral to the lateral line (Fig. 3), a bending of the body towards the side of the anode is evoked. A cut was made through the body wall, parallel and dorsal to one of the electrodes, of a fish in which this reaction had been demonstrated, the cut being sewed up afterwards (Fig. 3). On making the electrode on the operated side positive, the body remained straight during the passing of the current. A muscle contraction occurred

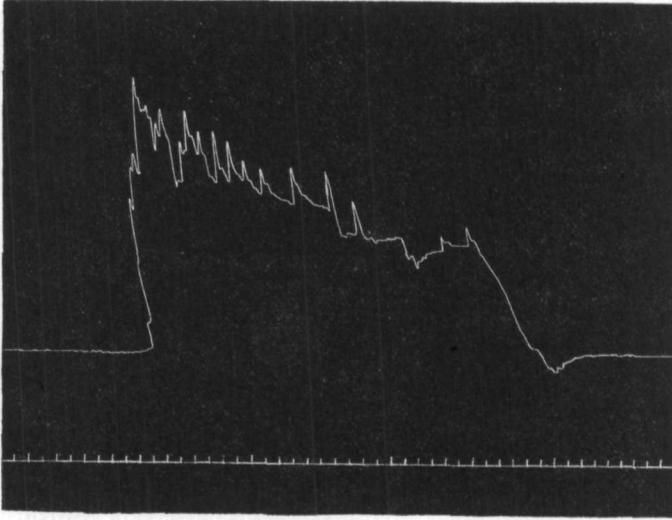


Fig. 2. Record of the reaction of a spinal fish (9 cm. body length) fixed at right angles to the current lines in a D.C. field of 2.5 δ density. The current is increased in the course of some seconds to avoid the contraction of the animal on switching the current on at once, is then kept unchanged for about 20 sec., and then decreased slowly again. Time is 1 sec.

only on closing the current. When the electrode on the uninjured side is made positive, however, the body of the animal curves to that side as long as the current passes. As the operation will not greatly affect the current lines in the animal and thus in the cord it must be concluded that the reaction in the D.C. field is not caused by an action of the current on the spinal cord directly, but that the transection prevented the transport of impulses from the periphery, where they are evoked, towards the C.N.S.

The stimulating effect of the positive pole is local; upon placing the anode 1–2 mm. ventral to the cut in the body wall no reaction is seen during the passing of the current but as soon as the anode is dorsal of the cut the reaction occurs. The cathode does not seem to cause any reaction during the passing of the current.

It must be concluded that the above-mentioned reaction is a reflex; the impulses arise in the periphery and the spinal cord has to be intact and functioning. We will

call this and similar reflexes caused by the passing of a D.C. a "galvanotropic reflex (G.R.)", since it is the basis of galvanotropism as we will discuss later.

The reflex is restricted to the stimulated segments and perhaps to the adjoining ones. Using the small silver electrodes and placing them symmetrically on both sides of the body at different levels, the body bends exclusively near the stimulated place (Fig. 4).

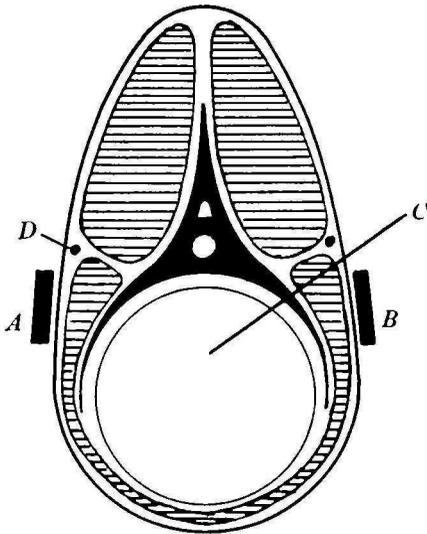
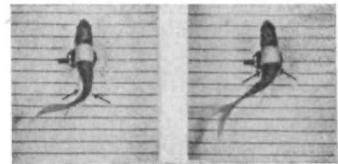


Fig. 3



A B

Fig. 4

Fig. 3. Position of the small electrodes, causing the reaction to the passing of a current in a transverse direction. *A* and *B* are the right and the left electrodes, *C* the location and direction of the cut abolishing the reaction on making the electrode *B* positive, and *D* is the n. lateralis.

Fig. 4. Reaction of a spinal fish to a current applied locally by a pair of small electrodes placed symmetrically on both sides of the body. The place of the electrodes is indicated by arrows. The potential difference between the electrodes is 6 V. The electrode on the left side is positive. In picture *A* the electrodes are placed on a more caudal level of the body than in *B*. It is clear that the curving in *A* takes place on a lower level than in *B*.

OTHER MANIFESTATIONS OF THE GALVANOTROPIC REFLEX

We have discussed the reaction of a fish in a D.C. field of transverse direction. A similar reflex can be obtained by bringing the animal in a homogeneous field of dorso-ventral direction (1-3δ). A spinal fish bends its body and tail towards the anode again, thus dorsalwards when the dorsal electrode is the anode and ventralwards in a field of the reverse direction. As the bending in the dorso-ventral direction is restricted, the movements of this reaction are small. The reaction is a bilateral one and not only bends the body in a dorso-ventral direction, but at the same time stiffens it. This can be shown in the following way. The body and tail of a fish, fixed on its side in the water, curve down by gravity. On establishing a D.C. field in the water in dorso-ventral or ventro-dorsal direction, this curvature is straightened out. To obtain this the fish has to be situated quite symmetrically

in the field, otherwise a mixture of this reaction and the galvanotropic reflex in the transverse field occurs and the body is bent in the transverse plane.

The galvanotropic reflex in the dorso-ventral field can be demonstrated also by applying a current with small electrodes, one placed on the ventral surface of the fish, the other on the back; not symmetrically, but a few mm. to one side of the median plane (Fig. 5). In this way the reflex is evoked only unilaterally, and the body not only bends in the dorso-ventral plane towards the anode but it curves in the transverse plane also, because the muscles contract only on one side. Since bending in this plane is easier, the curving in the transverse plane is much larger

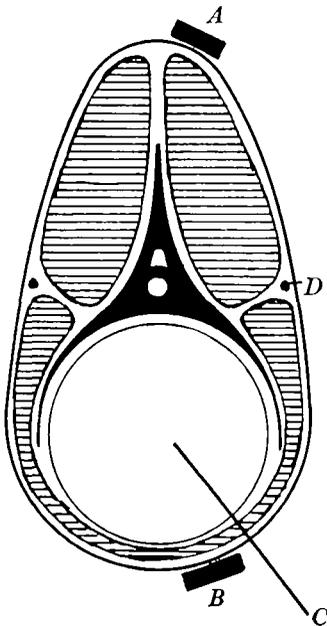


Fig. 5

Fig. 5. Position of the small electrodes causing a unilateral reaction to a current in a dorso-ventral direction. *A* and *B* are the dorsal and the ventral electrodes, *C* the location and direction of the cut abolishing the reflex on making the electrode *B* positive, and *D* is the n. lateralis.

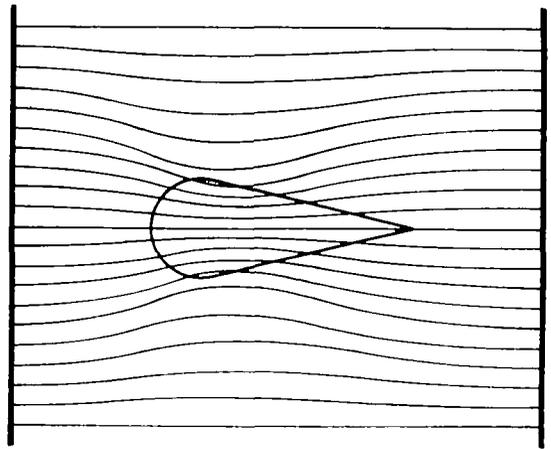


Fig. 6

Fig. 6. Diagram of the current lines for a fish in fresh water in which a D.C. field has been made.

than in the sagittal one, thus making the reaction more obvious. This bending in the transverse plane is obtained in either direction of the current, as is to be expected. After making a cut through the body wall dorsal of the ventral electrode (Fig. 5), the reaction on making this electrode positive is abolished again, proving its reflex nature. Furthermore, when the body bends ventralwards in a homogeneous field of dorso-ventral direction, the contraction must be confined to the ventral muscles of the body; otherwise the much stronger muscles of the back would bend the body dorsalwards.

The third main position of the animal in relation to the field, namely, that in which the fish is parallel to the current lines, will now be considered. It has been known for a long time that a normal or spinal fish fixed in an ascending field ($1-3\delta$)

shows an unrest of the body and tail. It can be shown in the same way as was described for an animal in a dorso-ventral field, that a fish is stiffened in the ascending field. The destruction of the spinal cord abolishes these reactions. In a descending field of the same strength the fish is more quiet and remains more relaxed. These phenomena have usually been explained by the assumption that the ascending current has an exciting and irritability increasing effect on the spinal cord, whereas the descending field has the opposite effect. However, it seems possible that a larger or smaller part of the contractions (and stiffness) in the ascending field are reflex contractions caused by a bilateral galvanotropic reflex. We have seen that a D.C. field of such a direction that it makes the surface of the body and tail positive with respect to the interior causes a galvanotropic reflex. In an ascending field, because of the wedge shape of the body and tail, the surface of this part of the animal becomes positive in relation to the interior. At first sight it looks as if the angle at which the current lines hit the surface of the fish is very small; however, as the electrical resistance of the animal is much smaller than that of the surrounding water, a concentration of the current lines occurs, by which the angle is increased (Fig. 6). When the fish is not brought into a homogeneous ascending field, but instead the current is supplied by two electrodes about 5 cm. apart and parallel with and 1–2 cm. away from the surface on one side of the body and tail, a unilateral reaction is evoked bending the tail in a transverse direction. In this case also the majority of the current lines hit the surface of the animal at a small angle. Thus it is possible that in an ascending homogeneous field the structures involved in the galvanotropic reflex are stimulated and that the unrest of the animal is partly caused by a form of the galvanotropic reflex.

In some of the muscles of the fins, reactions could be obtained, comparable with the galvanotropic reflex. The pectoral fin is abducted and rotated ventralwards when a small anode (some mm. square) is placed in front of the insertion of this fin (potential difference 4–6 V.). The fin stays in this position as long as the current passes. This reaction again is abolished by destruction of the spinal cord. It matters very little where we place the cathode as long as the anode is located in front of the insertion of the pectoral fin. Under the skin at this place is located the muscle causing this movement of the fin. Using higher stimulating potentials the place from which this reaction can be evoked spreads, and it can be obtained from a place posterior to the insertion of the fin. However, the place where the muscle causing this movement is located is the spot where the reaction can be obtained with the least potential. By placing the anode on other regions of the skin, no other movement of the pectoral fin is seen during the passing of the current. As the spinal cord has to be intact to obtain this reaction, and as the impulses are evoked at the periphery, this phenomenon also must be considered as a reflex. The reflex is evoked also in a homogeneous descending field (1–2δ) and in a dorso-ventral field when the anode is ventral.

When a small electrode is placed in front or alongside of the dorsal fin, this fin is erected as long as the current passes (stimulating potential 4–6 V.). This is again the place where the muscles causing this position are located. The reverse position

of the fin could not be obtained by placing the anode on other parts of the back. In a homogeneous field ($1-2\delta$) in dorso-ventral direction, the dorsal fin was erected only when the anode was on the dorsal side. The ascending field also caused an erection of the fin. The transverse field did not cause any reaction in this fin.

The anal fin is extended when a small anode is placed in front of it or alongside. It is extended in a dorso-ventral homogeneous field when the anode is ventral; often it is extended in the ascending field.

The pelvic fin sometimes was abducted when a small anode was placed in front of it; the same movement was in a number of cases obtained in a homogeneous ascending field as well as in a dorso-ventral field when the anode was ventral.

THE LOCALIZATION OF THE STRUCTURES STIMULATED DURING THE GALVANOTROPIC REFLEX

The skin, containing many sensory end-organs, was considered the most likely place in which the structures stimulated in the galvanotropic reflex are situated. However a galvanotropic reflex was obtained after removing the skin on both sides of the body of the animal. When besides this the fins are clipped off no skin is left in nervous connexion with the cord of a spinal animal. Although this is a serious injury the procedure changed the galvanotropic reflex very little, if at all, in a number of cases. Neither do the impulses arise in the abdominal organs (e.g. swimming bladder), as evisceration does not abolish the reflex. Brushing the lining of the body cavity of an eviscerated fish with a 5% cocaine solution does not change the reflex either. The galvanotropic reflex was observed very clearly in a fish to which all the aforesaid procedures had been applied. The structures in which the impulses for this reflex arise seem thus to be located somewhere in the body wall.

Is it possible to indicate more precisely in which tissue of the body wall these structures are situated? The possibility of excluding the peripheral nerves and the bones as the place where the impulses for the galvanotropic reflex are started is given by the fins, which contain these two tissues, but no muscles. We tried in vain to obtain a certain constant position of the dorsal fin during the passing of a D.C. (4-6 V.) applied to the fin locally. The three main directions of the current in the fin were tried out but without result. Only on making and breaking the current were movements observed. Thus it is unlikely that the structures stimulated in the galvanotropic reflex are situated in the bones, or that they are the peripheral nerves. Though no reflexes were obtained during the passing of a D.C. through the fin, it is easy to evoke regularly certain attitudes of the fins by applying the current to the fin muscles, as we described above. This indicates that the structures stimulated in the galvanotropic reflex are situated in the muscular tissue. It is unlikely that the sensory nerve fibres in the muscle are stimulated, as the passing of the current through the fin did not cause reflexly a certain position of the fin. The muscle (or tendon) probably contains some structure (sensory nerve ending), which is oriented in a certain direction and which can be stimulated by a D.C. flowing in a certain direction with regard to the situation of this structure.

The galvanotropic reflex resembles in certain respects the myotatic reflexes of the higher animals. In both cases the reflex impulses are evoked in the muscle and the reflex is more or less confined to the muscle in which these impulses are evoked. This last is shown very clearly in the muscles of the fins, but it holds true for the body musculature too. On placing the anode on the left side of a fish, thus stimulating the structures in the muscle on that side, a contraction of the muscles on the left side occurred, bending the body towards the anode. When the anode is placed on the ventral side of the animal, the ventral musculature contracts, etc.

THE MECHANISM OF GALVANOTROPISM

When a D.C. field is made at the moment that a freely swimming fish is at right angles to the current lines, a galvanotropic reflex is evoked by which the animal becomes concave on the side of the anode. The linear movements of the fish will now be impossible and the animal will swim in a curve until it is parallel with the current lines with its head towards the anode. Then the curving of the body by the galvanotropic reflex ceases. This position is the only one in which the fish can move, as in any other position the galvanotropic reflex is evoked, which automatically brings the animal back to its former position. Thus it is clear that the animal must always reach the anode sooner or later (galvanotaxis), though this electrode has no particular attraction for the animal.

When the fish is parallel with the current lines with its head towards the cathode at the moment that the field is made, the animal sometimes swims for a short time towards the cathode. It seems that the animal swims with difficulty, which is conceivable since the fish probably receives strong stimuli causing reflex contractions (unrest and stiffness of body and tail). As soon as the animal leaves the position parallel with the current lines, however, the galvanotropic reflex bends it and the fish turns automatically towards the anode.

The conditions for galvanotropism are: the galvanotropic reflex, and the possibility of swimming. It was found that the normal position is favourable for galvanotropism, since in this position the steering effect of the galvanotropic reflex is maximal. A fish without functioning labyrinths (and lateral-line organ) shows galvanotropism, as the galvanotropic reflex can be elicited in such an animal and it can swim. The animal is handicapped only by the fact that it does not always stay in the normal position. This may be the reason why a labyrinthless fish reaches the anode somewhat later than a normal one, as we stated before. It is possible that the impulses causing the galvanotropic reflex at the same time cause swimming movements in a normal fish; however, much more effective in this respect is the strong stimulus of making or reversing the field suddenly. This causes swift swimming movements and explains why a much more distinct galvanotropism is seen on making the field suddenly than upon increasing the current gradually. The sudden making of a field can even in a spinal fish cause movements by which the animal is propelled for a short distance through the water, and since this animal can perform the galvanotropic reflex it sometimes shows galvanotropism under these circumstances.

ON OSCILLOTAXIS

Scheminzky (1924*a*) found that fish in an A.C. field tend to take a position at right angles to the current lines; he called this phenomenon "oscillotaxis". We too saw that a goldfish in an A.C. field (0.25–0.75δ) often takes this position, though this reaction is not nearly as usual as the galvanotropism.

A spinal fish fixed in an A.C. field bends its body when the animal is in certain positions with regard to the current lines. In Fig. 7 A–E, a goldfish is shown in five positions in an A.C. field of 0.5δ. When making an angle of 45° with the current lines the body and tail curve towards that electrode to which the tail pointed before. In the positions parallel with and at right angles to the current lines the body stays

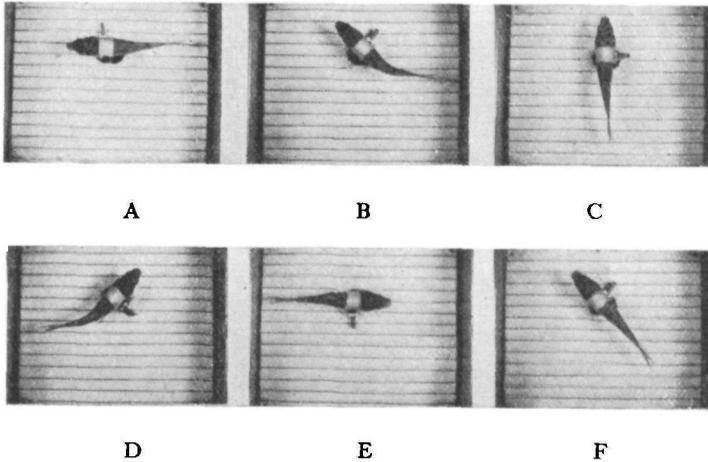


Fig. 7. A fish in which the spinal cord was transected 2 days previously is illustrated in several positions with regard to the current lines in an A.C. field. The strength of the field in A, B, C, D and E is 0.5δ, in F it is 1.5δ. The lines in the background indicate the direction of the current lines.

straight. As the two electrodes in an A.C. field are symmetrical, another explanation is necessary for the bending of a fish, making an angle of 45° with the current lines, than the one given in the case of the galvanotropism. The posterior part of a fish is wedge-shaped, and so the body wall on one side of the animal has a different position with regard to the current lines than the other, as can be seen in Fig. 8. From this diagram it follows that the current lines hit the side that contracts in the reaction in the A.C. field at a larger angle than the other. Thus any structure in the body wall stimulated by the A.C. causing either directly or reflexly¹ a contraction of its muscles has a different position with regard to the current lines on the two sides of the animal. This may account for the difference in contraction on the two sides of the fish in a weak A.C. field. On making the field stronger, the muscles on both sides will finally contract maximally, and the curvature of the body is straightened out, as

¹ It has been found that in fish in which the spinal cord has been destroyed this reaction still can be elicited. It is possible, however, that in the intact animal the reaction is caused reflexly in a weaker field than the one that is necessary for direct stimulation (see van Harrevel, A. (1937), *Arch. néerl. Physiol.* **22**, 84).

then the reaction is symmetrical. In Fig. 7 F is shown the same fish as in Fig. 7 A-E, but now in a field of 1.5δ . The animal, though fixed in a position at an angle of 45° to the current lines, remains straight in a field of this strength.

When an A.C. field is made at the moment that a fish is swimming at 45° to the current lines, the curving of the body described above will steer the animal into a position parallel to the electrodes. When this position is reached, the bending is straightened out. Deviations from this position cause the curving of the body again by which the fish, when it swims, is brought back automatically into the position parallel with the electrodes. As in galvanotropism, the conditions for oscillotaxis are the bending of the body and tail in the A.C. field and the swimming movements.

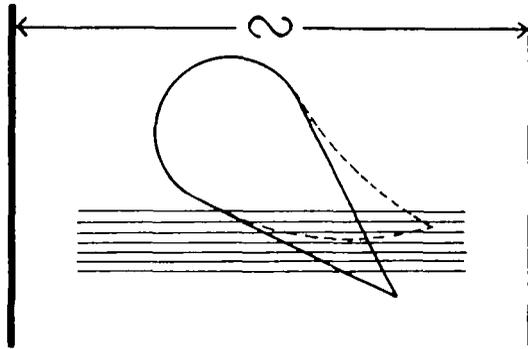


Fig. 8. Diagram of the current lines for a fish fixed in an A.C. field at an angle of 45° to the current lines. With the dotted lines is indicated the bending of the animal in this position in the field. The horizontal lines are current lines.

SUMMARY

A spinal fish bends with the concave side towards the anode in a D.C. field of transverse direction. This reaction, which lasts as long as the current passes, is shown to be a reflex (*galvanotropic reflex*). Other manifestations of this reflex have been found. In a field of dorso-ventral direction the animal is bent in the sagittal plane towards the anode. The unrest of body and tail in an ascending field in the longitudinal direction of the fish may be caused partly by the same reflex. The same reflex has also been found in some of the fin muscles. The structures (sensory end-organs) stimulated during the galvanotropic reflex are situated in the muscles (or tendons).

Galvanotropism has been demonstrated in fish in which the labyrinths and the lateral-line organs have been eliminated by the transection of their nerves.

The mechanism of galvanotropism is discussed and this phenomenon is found to be based on the galvanotropic reflex and the ability of the animal to swim.

A fish placed at 45° to the current lines in an A.C. field shows a curving of the body and tail. This is explained by the wedge shape of the fish body and tail, by which the two sides of the animal have a different angle with the current lines, and thus are differently stimulated. The mechanism of oscillotaxis is discussed in relation to this reaction.

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