GALVANOTROPISM IN THE EARTHWORM.

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In a former paper Kellogg and the writer have described the effects of a galvanic current on the body positions of *Lumbricus terrestris*.[1] When the current flows transversely through such an animal or piece of one, the muscles respond by unilateral contraction on the cathodal side. The result is to bring the ends of the worm toward the cathode, thus forming a U with the median part nearest the anode.

It is not, however, necessary to have the worm submerged in the water to show galvanotropism, as the following experiment proves. A worm is put on a glass plate and the current is applied transversely through the middle of the animal by means of non-polarizable electrodes.[2] When the momentary effects of the make-shock have subsided, the head and tail actively bend toward the cathodal side although the current itself does not act directly on either end.[3] This result is shown in Fig. 1. If, now, the nerve cord is cut at a distance of a centimeter or so on either side of the locus of application of the electrodes, then the position of the part lying beyond the cut is unaffected by the action of the current. This proves that the impulses to galvanotropic bending are carried by the nerve cord and suggests that the primary action of the current is on the elements of the nerve cord.

[1] Moore, A. R., and Kellogg, F. M., *Biol. Bull.*, 1916, xxx, 131.

[2] The non-polarizable electrodes are modifications of the Schafer type. The tubes are filled with Ringer's solution and both ends are plugged with absorbent cotton. The current is obtained from a single storage cell yielding a current of 2 volts 0.1 milliampere.

[3] This experiment proves that galvanotropic orientation in the earthworm is not the result of cataphoresis of head and tail. Hence the hypothesis recently advanced by Hyman and Bellamy (Hyman, L. H., and Bellamy, A. N., *Biol. Bull.*, 1922, xliii, 313) is eliminated from consideration.

If the electrodes are placed on two opposite sides of the worm the bending of head and tail is to the cathode, as in Fig. 1; if the current is sent through the animal dorsoventrally the bending is in the dorsoventral plane, the ends of the body bending dorsally or ventrally, depending upon whether the cathode is applied respectively to the dorsal or ventral side.

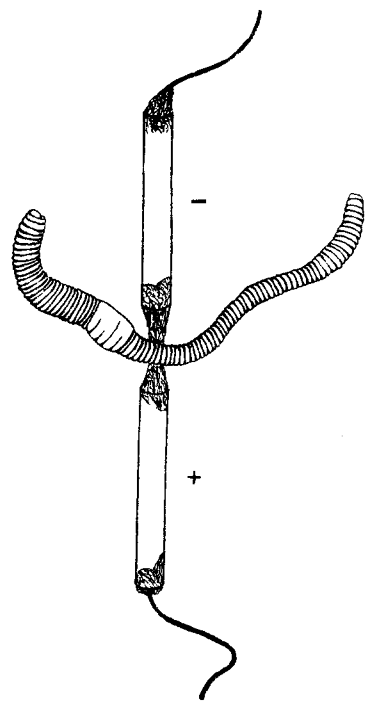

FIG. 1. A worm lying on a glass plate. The galvanic current is flowing across the animal from the ends of the modified Schafer electrodes. The sign of each electrode is indicated at the side. The worm bends both head and tail to the cathodal side.

In these experiments the current does not act directly on the ends of the animal, the parts which show the greatest displacement in orientation, but only on a few ganglia of the median segments. The differential muscle tonus, which causes bending to the cathode, is the consequence of impulses carried from the nervous elements situated in the path of the current and presumably acted upon by it. It is to be noted that conduction of the impulses occurs equally well in the direction of either head or tail, and therefore the conducting mechanism does not exhibit polarity. This is in marked contrast to the phenomenon of forward conduction associated with the homostrophic reflex.[4]

Further evidence of the muscle tension theory of galvanotropism is furnished by experiments in which the current flows through the animal longitudinally from head to tail or the reverse. The experiments were carried out by putting the worm into a narrow trough made of paraffin. The trough was filled with tap water sufficient to cover the worm, so that the length of the column of water was 12 cm. and the cross-section was 3 sq. cm. Non-polarizable electrodes made of pads of absorbent cotton were placed at either end of the trough. The current furnished by a single storage cell was of 2 volts, 0.1 milliampere strength. In such an arrangement, if the current flows through the worm with the cathode at the head of the animal (cathodal galvanotropism), contraction of the circular musculature follows and the worm is extended to its extreme length. When the current is reversed so that the anode is at the head (anodal galvanotropism), the longitudinal muscles contract, shortening the worm during the flow of the current.

The same results are obtained if the worm is taken out of the trough and the current applied by putting the electrodes directly to the ends of the worm. Also, pieces of worm of convenient length may be used and the same results as to tonus of muscle groups obtained.

What structures are involved in these galvanotropic reactions? The influence of the cutaneous receptors can be eliminated by means of magnesium anesthesia. If this is done the reactions of the worm to the constant current are the same as in the normal worm. That the action of the current on the nerve cord alone is responsible for the galvanotropic effects described can be further demonstrated in the following way. Let a piece of worm about 2 cm. long be prepared by making first a longitudinal dorsal slit through the myodermal sheath and then removing the intestine. This leaves the muscle

[4] Moore, A. R., *J. Gen. Physiol.*, 1922–23, v, 327.

sheath and the nerve cord with connections intact. Such a preparation reacts to the current in characteristic fashion, exhibiting polarity when subjected to the longitudinal flow of the current, and unilateral muscle tone when reacting to the transverse current. If, now, the cord be removed, the tonus effects which were characteristic before have disappeared, and the same reaction is elicited whether the anode or cathode is at the anterior end of the piece. In other words, removal of the nerve cord has destroyed the galvanic polarity of the piece and left only a muscle preparation.

Since the essential action of the current is on the nerve cord, the next question is as to which elements in the cord are the seats of that action. The cord is composed of motor neurons and their fibers and dendrites. The well known fact that the axis cylinder is not stimulated by the constant current, renders it improbable that nerve fibers are the loci of action of the galvanic current. We may therefore regard the ganglion cell as the structure acted upon by the current. In fact, Loeb and Maxwell have made this assumption in their analysis of galvanotropism in *Palæmonetes*.[5]

The fact that the current causes contraction of the circular muscles only, when the cathode is at the anterior end of the animal, while with the anode at the head the longitudinal muscles alone react, must be referred to differences in the respective motor neurons relative to the direction of the galvanic current. Nernst and Barratt[6] regard the action of the electric current on nervous structures as due to the transport of ions and the subsequent blocking of them by membranes. As a result, one region of the cell has a higher concentration of a given ion than any other part of the same cell. How, then, can an electric current flowing in one direction affect one group of neurons and not a second group, while the reversed current stimulates the second group of neurons and not the first? The simplest supposition is that the ganglion cells are asymmetric with reference to the direction of the current flow and that their different orientations in space are responsible for their different reactions to the galvanic current. Such a mechanism may be visualized in the following way (Fig. 2). The usual form of the ganglion cell is approximately oval with the

[5] Loeb, J., and Maxwell, S. S., *Arch. ges. Physiol.*, 1896, lxiii, 121.
[6] Nernst, W., and Barratt, J. O. W., *Z. Electrochem.*, 1904, x, 664.

axon or fiber growing out of one end or pole. The opposite pole may or may not be provided with dendrites. Any plane cutting the cell at right angles to the long axis of the cell, *i.e.* in equatorial section, is symmetrical with respect to the axis and therefore does not offer apparent possibilities of asymmetry. But the axonal pole is different in form from its opposite pole. In other words, the cell is asymmetrical with regard to its two poles. Suppose that in order for stimulation to take place the concentration of positive ions must increase at the axonal pole of the ganglion cell but that a similar increase at the opposite pole would not lead to excitation.[7] Then if all the motor ganglion cells of the circular muscles were inclined with the axonal pole toward the anterior end of the animal, and all the ganglion cells of the longitudinal musculature were inclined with the axonal poles directed posteriorly, the necessary conditions for the galvanotropic phenomena would have been fulfilled. A diagrammatic representation of this arrangement shown in Fig. 2 makes it clear that cathodal galvanotropism would involve stimulation solely of the neurons of circular musculature, and anodal galvanotropism would involve stimulation of the neurons of longitudinal musculature alone. A transverse current (x to y in Fig. 2) would stimulate ganglion cells, the axonal poles of which are oriented toward the cathode. Suppose that in the diagram x represents the cathode, then neurons oriented as 1 and 4 would alone respond. The result would be contraction of both circular and longitudinal muscles on the cathodal side. The foregoing hypothesis is based on the assumption that there is a direct correspondence between anatomic and dynamic polarity. As a matter of fact, there is evidence for the soundness of this view in the reactions of the ciliate protozoa to the galvanic current as, for example, in the case of paramecia.

Further evidence of the rôle of the nerve cord in galvanotropism is brought out by the following experiment. Instead of subjecting the entire worm to the action of the current in the galvanic trough, let the posterior two-thirds or three-fourths of the body be held up out of the water during the flow of the current. This can be done by

[7] It would serve our purpose just as well to suppose that stimulation is the result of an opposite set of conditions; namely, excitation results from a heaping up of positive ions at the antiaxonal pole.

holding the tail with a pair of forceps. If, now, the anterior part of the body which remains under water and is therefore subject to the action of the current, is directed head toward the cathode, extreme extension of the entire animal follows as a result of contraction of the circular muscles. This reaction in no way differs from the one shown in cathodal galvanotropism as before described. If, next, the worm is rotated so that the head is directed toward the anode, the longitudinal muscles contract and the worm shortens. This reaction is often so

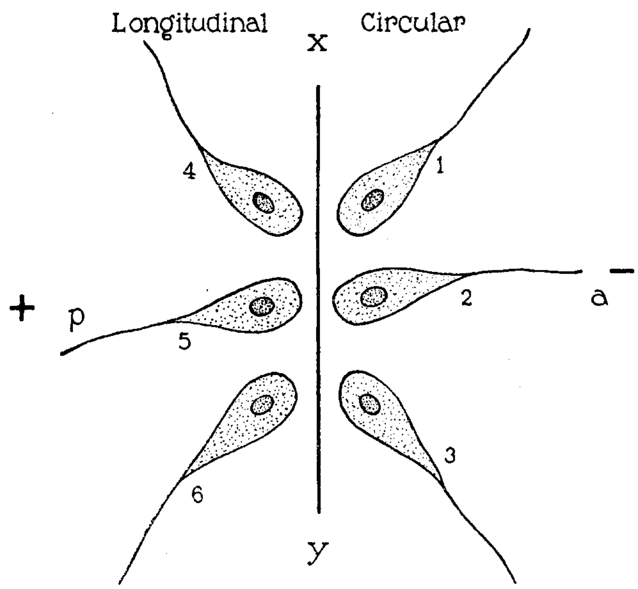

FIG. 2. Scheme showing orientation of motor ganglion cells in a ganglion. *a* denotes anterior, *p* posterior. "Longitudinal" and "circular" refer to the type of musculature innervated by the neurons figured underneath. For the sake of clearness a septum is shown drawn through the center of the ganglion, and all the ganglion cells of the circular muscles are assembled on the anterior side, while those of longitudinal musculature are put on the posterior side of the septum. In nature there is, of course, no such separation. When the current is flowing as figured, with the cathode anterior, stimulation of the neurons of circular musculature alone can take place.

strong as to cause the worm to be pulled entirely out of the trough. The result, as far as muscle tone is concerned, is identical to that observed in ordinary anodal galvanotropism.

The significant fact in these experiments is that the entire worm responds to the direction of flow of the current although only a few of the ganglia in the anterior segments are directly acted upon by the current. This proves that motor neurons of the same type of function, as for example, those of the circular muscles, are linked longitudinally by conducting tissue, as shown in the diagram of Fig. 3, so that stimulation of the ganglion cells of one type in a few anterior segments involves excitation of all the neurons of that type in the

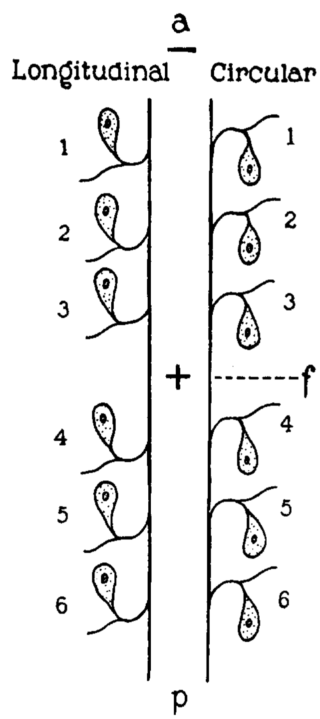

FIG. 3. Diagram showing arrangement for linear conduction of impulses between neurons having the same function. Each neuron represents a ganglion in the nerve cord. The signs are the same as in Fig. 2. With the current flowing as indicated, only ganglion cells 1, 2, and 3 of the neurons of circular musculature will be directly stimulated, but the excitation of these cells will be communicated by linear conduction to "circular" 4, 5, and 6, through the conducting fiber, *f*.

cord. The connections must, however, be strictly linear since conduction across the cord would render impossible the unilateral effects of the transverse action of the galvanic current.