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On the ionic basis of electrical stimulation.

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In their attempts to develop a physical theory of electrical stimulation, Nernst[1] and A. V. Hill[2] have supposed the current to act by carrying the ions within the tissue against a membrane barrier. The resulting heaping up of the ions at the membrane constitutes the first step in excitation. If we assume, as the work of Loeb[3] shows we have a right to do, that the positive ions are the effective ones, then according to the views of Nernst and of Hill stimulation must occur at the cathode when the current is made. This is a statement of Pflüger's law and is valid for frog tissue, with which Pflüger worked.

A consideration of cases in which Pflüger's law is reversed suggests that a somewhat different and more general picture of the ion mechanism of electrical stimulation is necessary. In the ctenophores Beroe and Mnemiopsis, when the galvanic current is passed through a trough of sea water containing them, the result is a luminescent glow on the anodal side of the animal.[4] This glow occurs on the make and lasts for some seconds during the flow of the current. If an incision is made in the animal transversely with reference to the direction of the flow of the current, then anodal stimulation occurs also at the cut surface. These results mean that galvanic stimulation takes place only at the protoplasm-sea-water surface, and that stimulation is referable to the blocking of positive ions of the sea water at that surface. These ions, therefore, impinge on the protoplasmic membrane from outside. It is a remarkable fact that in ctenophores which consist so largely of included sea water there is no apparent stimulation as a result of internal ionic movements. This conclusion is necessary since stimulation appears only along the surface of the ani-

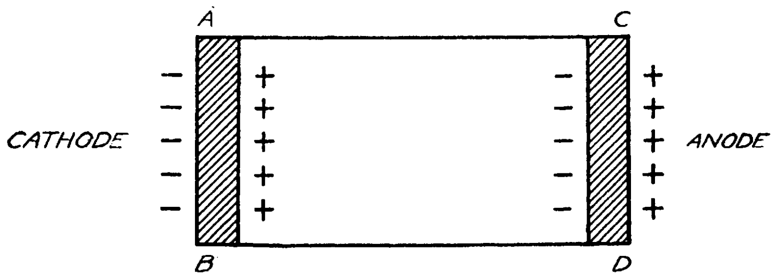
1 Nernst, W., *Arch. f. d. ges. Physiol.*, 1908, cxxii, 275.

2 Hill A. V., *J. Physiol.*, 1910, xl, 190.

3 Loeb, J., *Dynamics of living matter*, New York, 1906, p. 78.

4 Moore, A. R., *Am. J. Physiol.*, 1925, lxxii, 230.

mal next the anode. The situation may be represented by the figure. If stimulation is caused by ions inside the tissue impinging on the membrane, then excitation occurs at A B and is cathodal, *i. e.,* according to Pflüger's law. On the other hand, if ions outside the tissue produce excitation, then the effect is at C D and is anodal, *i. e.,* according to the reversed law of Pflüger. The latter is evidently the situation in ctenophores.



The rectangle A B C D represents the animal or tissue through which the current is passed as indicated by the terms "anode" and "cathode". In consequence, presumably ions would collect as shown on either side of the membranes AB and CD.

Electrical stimulation of the earthworm constitutes another type. Here stimulation occurs at the anode alone when a small current is used, but with stronger current cathodal stimulation takes place simultaneously with that at the anode. Thus at 6 volts a current of .025 ma. produces stimulation only at the anode, but .03 ma. causes excitation of the cathodal region also. Stimulation in the tissues of the earthworm, therefore, takes place as a result of the movement of ions both within and without the tissue, *i. e.,* at both A B and C D in the figure.

There are then three cases as regards the ionic basis of electrical stimulation. (1) The classic case of Pflüger, in which the ions of the tissue stimulated impinge on the membrane from the inside, *i. e.,* at A B, in the region of the cathode. (2) The case of the reversed law of Pflüger, in which the ions in the outside medium alone are effective and produce their action at C D, on the anodal side. (3) Where both types of stimulation occur, both the ions inside and those outside the tissue are effective in causing stimulation, as at A B and C D.