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the cell, and when reformed the reverse should occur. A relation between carbohydrate metabolism and potassium interchanges has, in fact, been already noted (for example, by Verzar) and is here rationally interpreted.

With the above membrane the potential changes with varying external solutions can also be readily understood, previous explanations assuming chloride impermeability being demonstrably incorrect.

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Sept. 1.

Action Potentials Recorded from Inside a Nerve Fibre

NERVOUS messages are invariably associated with an electrical change known as the action potential. This potential is generally believed to arise at a membrane which is situated between the axoplasm and the external medium. If this theory is correct, it should be possible to record the action potential between an electrode inside a nerve fibre and the conducting fluid outside it. Most nerve fibres are too small for this to be tested directly, but we have recently succeeded in inserting micro-electrodes into the giant axons of squids (*Loligo forbesi*)[1].

The following method was used. A 500 μ axon was partially dissected from the first stellar nerve and cut half through with sharp scissors. A fine cannula was pushed through the cut and tied into the axon with a thread of silk. The cannula was mounted with the axon hanging from it in sea water. The upper part of the axon was illuminated from behind and could be observed from the front and side by means of a system of mirrors and a microscope; the lower part was insulated by oil and could be stimulated electrically. Action potentials were recorded by connecting one amplifier lead to the sea water outside the axon and the other to a micro-electrode which

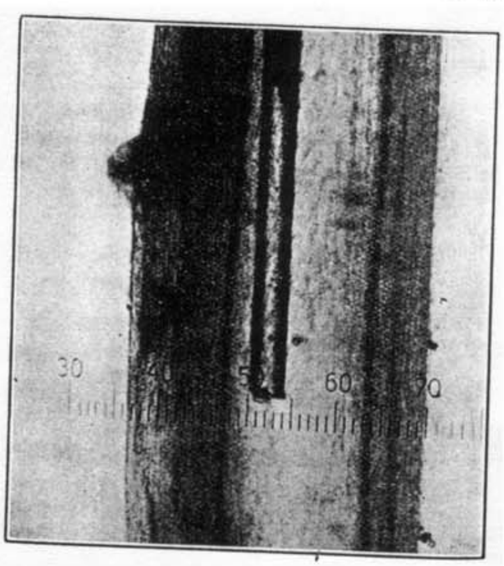

Fig. 1.
PHOTOMICROGRAPH OF ELECTRODE INSIDE GIANT AXON. 1 SCALE DIVISION = 33 μ.

was lowered through the cannula into the intact nerve beneath it. The micro-electrode consisted of a glass tube about 100 μ in diameter and 10–20 mm. in length; the end of the tube was filled with sea water, and electrical contact with this was made by a 20 μ silver wire which was coated with silver chloride at the tip. Fig. 1 is a photograph of an electrode

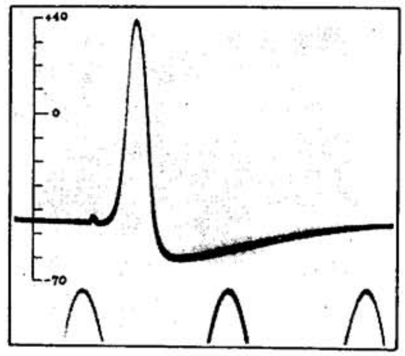

Fig. 2.
ACTION POTENTIAL RECORDED BETWEEN INSIDE AND OUTSIDE OF AXON. TIME MARKER, 500 CYCLES/SEC. THE VERTICAL SCALE INDICATES THE POTENTIAL OF THE INTERNAL ELECTRODE IN MILLIVOLTS, THE SEA WATER OUTSIDE BEING TAKEN AT ZERO POTENTIAL.

inside the living axon. The giant axon shows as a clear space and is surrounded by the small fibres and connective tissue which make up the rest of the nerve trunk. The silver wire can be seen inside the electrode and about 1 mm. from its tip. A small action potential was recorded from the upper end of the axon and this gradually increased as the electrode was lowered, until it reached a constant amplitude of 80–95 mv. at a distance of about 10 mm. from the cannula. In this region the axon appeared to be in a completely normal condition, for it survived and transmitted impulses for several hours. Experiments with external electrodes showed that the action potential was conducted for at least a centimetre past the tip of the micro-electrode.

These results are important for two reasons. In the first place they prove that the action potential arises at the surface, and in the second, they give the absolute magnitude of the action potential as about 90 mv. at 20° C. Previous measurements have always been made with external electrodes and give values which are reduced by the short-circuiting effect of the fluid outside the nerve fibre.

The potential difference recorded between the interior and exterior of the resting fibre is about 50 mv. The potential difference across the membrane may be greater than this, because there may be a junction potential between the axoplasm and the sea water in the tip of the electrode. This potential cannot be estimated, because the anions inside the nerve fibre have not been identified.

We wish to express our indebtedness to Mr. J. Z. Young, whose discovery of the giant axon in *Loligo* made this work possible.

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August 26.

[1] Young, J. Z., *Proc. Roy. Soc.*, B, 121, 319 (1936).

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