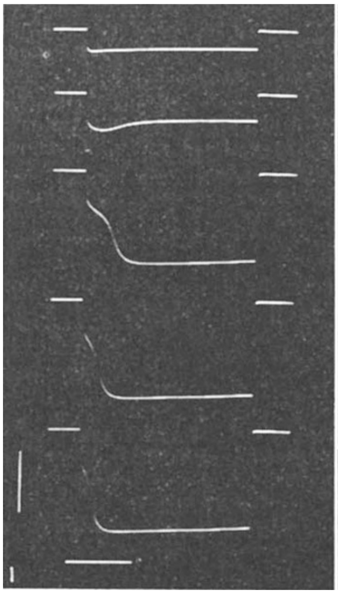
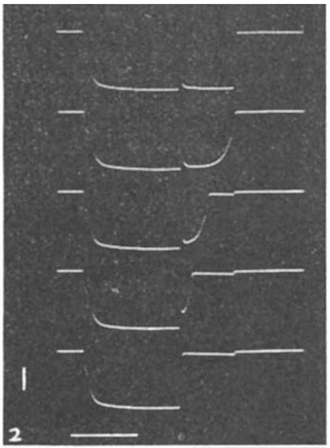
An Anodal Threshold Phenomenon in the Squid Giant Axon

THE action potential of nerve or muscle is an all-or-none response when preceded by a critical decrease in transmembrane potential. Previous investigations[1-3], on the other hand, have indicated that for hyperpolarization by anodal (inward) currents the membrane's properties are a continuous function of current. I wish to report, however, that in a potassium-enriched medium the squid giant axon displays a discontinuous rise in membrane potential for a sufficiently intense anodal current and that this behaviour is, in several respects, similar to that of the action potential.





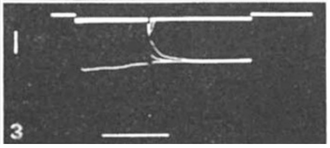


Fig. 1. Changes in transmembrane potential associated with increasing intensities of anodal current. Reading from top to bottom, the current densities (m.amp./cm.^{2}) are 0·079, 0·110, 0·115, 0·120, 0·126, respectively. The vertical and horizontal bars subtend 50 mV. and 50 msec., respectively. Axon No. 1 ; temperature, 21° C.

Fig. 2. Application of short cathodal pulses of increasing (top to bottom) intensities during a suprathreshold response. The vertical and horizontal bars subtend 50 mV. and 50 msec., respectively. Axon No. 2 ; temperature, 22° C.

Fig. 3. Composite record made during repetition (1/sec.) of 130 msec. anodal pulse superposed upon which is a brief anodal pulse (see text for details). The vertical and horizontal bars subtend 50 mV. and 50 msec., respectively. Axon No. 3 ; temperature, 21° C.

The present results were obtained from axons immersed in a solution of 400 mM potassium acetate, 0·6 mM potassium bicarbonate, and sufficient sucrose to maintain tonicity. Fig. 1 shows the change in transmembrane potential recorded at the midpoint of a 17-mm. length of axon across the membrane of which pulses of various intensities of anodal current were passed. A graph of steady-state potential as a function of current consists of two distinct straight lines both extrapolating close to the origin, indicating that for the present medium the threshold change is a discrete decrease in membrane conductance (in the case illustrated the ratio is 0·29 : 1). A long relative refractory period (associated with an increase in conductance relative to that of the resting membrane) follows the 'excited' state : repetitition of the same pulse within a period of less than $1\frac{1}{2}$ min. fails to elicit the suprathreshold response (there is no such refractoriness for subthreshold currents).

That this response represents a discontinuity in the current-voltage (I–V) relationship (when examined with pulses of constant current) and not merely a region of high $\mathrm{d}V/\mathrm{d}I$ is illustrated by Figs. 2 and 3, in which short cathodal and anodal pulses, respectively, superimposed on the main response, are compared.

It can be seen that following the cathodal pulse the potential is stable at only one of two levels—the transition zone is 'forbidden'. (For cathodal currents the steady-state I–V curve contains no discontinuity and it is not possible to abolish a maintained depolarization with a short anodal pulse.) An analogous phenomenon for the normal threshold response (abolition by application of short anodal pulses during the action potential) has been described for the node of Ranvier[4], for the squid axon injected with tetraethylammonium chloride[5], and for cardiac muscle[6].

The converse property is demonstrated by the experiment of Fig. 3, which shows (in a composite record of approximately ten traces) the effect of the repetition (1/sec.) of a 1-msec. anodal pulse superposed midway during a 130-msec. anodal pulse (both pulses were of approximately the same intensity and were not altered during the train). The largest prolonged downward deflexion is the potential recorded during the application of the first pulse of the sequence. The smaller prolonged deflexion is the response to each of the next five pulses—the system is refractory. As the refractoriness subsides, the short pulse becomes adequate to elicit (during the remainder of the long pulse) a suprathreshold response as indicated by the two traces with slow rising phases following the end of the short pulse. This, again, demonstrates that the potential cannot be stabilized in the region between the sub- and suprathreshold levels.

A sufficient condition for the above phenomenon is a concentration of potassium greater than normal irrespective of the presence or absence of calcium, sodium, or of chloride.

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