

# EVIDENCE FOR SEMICONDUCTION IN APLYSIA NERVE MEMBRANE\*

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Activation by light has been used as a tool by Chalazonitis and Arvanitaki (summarized by Chalazonitis in ref. 1) to explore the hypothesis that nerve membranes behave like semiconductor solids. Data on photoconductance and photopotentials in the pigmented *Aplysia* neuron and in the vitally stained *Septia* axon were consistent with this hypothesis in a general way.<sup>1</sup> The present paper provides additional support for this hypothesis from a new type of kinetic analysis of the experimental data of Chalazonitis.<sup>1</sup>

The question has been asked: What kinetic patterns should be shown by biological reactions that are rate-limited by solid-state conduction? Solution of the pertinent physical and mathematical problems yielded several predictions of kinetic patterns which were different from those that can be derived for the liquid state from ordinary mass action postulates.<sup>2-4</sup> The solid-state theory predicted that a biological reaction which is rate-limited by charge conduction across an activation energy barrier at the surface of a solid should be described by the Elovich equation, which may be written

$$-\frac{dx}{dt} = a \cdot e^{bx}, \quad (1)$$

where  $x$  is the concentration of substrate or reactant,  $t$  is time, and  $a$  and  $b$  are constants. The Elovich equation was found to describe accurately the decay of photogenerated free radicals in eye melanin particles<sup>3</sup> and in bacterial photosynthetic particles.<sup>5</sup> Both systems are particulate in nature, and it has been suspected on other grounds that both involve semiconduction.

In attempting to test the hypothesis of semiconduction in photoactive nerves, Chalazonitis<sup>1</sup> measured electrical resistance across the surface of the neuron of the marine invertebrate *Aplysia* before, during, and after exposure to light. The effects of light were large and were describable by a smooth curve when plotted against time.

If the return of photoactivated electrons from the conducting to the nonconducting state in *Aplysia* nerve membrane involves transfer across an activation energy barrier at the surface of a solid, then the time course of concentration of conduction electrons after exposure to light should conform to the Elovich equation. Since charge carrier concentration in a solid usually is proportional to conductance, conductance as a function of time should also conform to the Elovich equation. The data of Chalazonitis<sup>1</sup> were tested for this possibility.

From the data of Chalazonitis on the decay of resistance of *Aplysia* nerve membrane after exposure to light,<sup>1</sup> a decay curve of conductance was obtained by calculation of reciprocals of membrane resistances. The conductance decay curve was then tested for conformity to the Elovich equation by the plot shown in

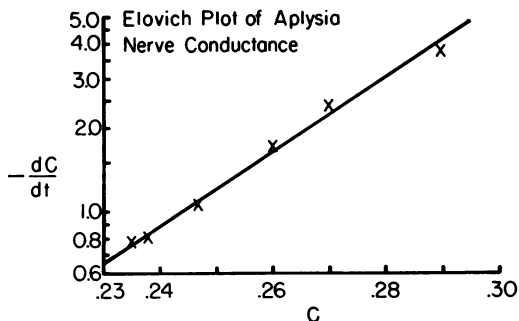


FIG. 1.—A test for Elovich kinetics. The data were taken from Fig. 9 of Chalazonitis,<sup>1</sup> in which the data points represent electrical resistances across the membrane of the photoactive neuron of *Aplysia* at various times after the end of exposure to 18 sec of light with a wavelength of 470–510  $\mu\mu$ , which is the region absorbed by carotenoids.

Membrane conductances were calculated from membrane resistances, and conductance was plotted against time. Slopes ( $-dC/dt$ ) were measured from that curve at various values of conductance ( $C$ ), and a semilog plot of these pairs of values is given above in the figure. Linearity indicates conformity to the Elovich equation as described in ref. 3. ( $-dC/dt$ ) is given in arbitrary units, and  $C$  is given in  $(M\Omega)^{-1}$ .

Figure 1. The close approximations of the data points to a straight line indicate close agreement with the Elovich equation, which supports the concept that one action of light on the *Aplysia* neuron is to transfer charge across an activation energy barrier at the surface of a solid.

Confirmation of this conclusion was sought by a different type of kinetic analysis. In the derivation of the Elovich equation from the hypothesis of charge conduction across a solid biological surface, an approximation that introduces some error was used.<sup>3, 6</sup> A more precise kinetic test for solid-state conduction uses an exact equation derived from the same theory *without* the approximation. The exact equation may be written (ref. 2, equation 57)

$$\frac{1}{v} = A \left[ \frac{B}{x} - 1 \right], \quad (2)$$

where  $x$  is the concentration of substrate or reactant,  $v$  is the velocity of the reaction ( $= -dx/dt$ ),  $A$  is a constant, and  $B$  is a positive constant.

Equation (2) superficially resembles the Lineweaver-Burk equation of Michaelis-Menten enzyme kinetics. The two equations differ by the presence of  $(-1)$  in equation (2) instead of the  $(+1)$  in the equation of Michaelis-Menten kinetics. Hence, the two types of kinetics may be distinguished graphically in a Lineweaver-Burk plot of  $1/v$  versus  $1/x$  by a *negative* intercept on the  $1/v$ -axis for solid-state kinetics and a *positive* intercept for enzyme kinetics. In both cases, the data show linearity in a Lineweaver-Burk plot.

Therefore, if the return of photoactivated electrons from the conducting to the nonconducting state in *Aplysia* nerve membrane involves transfer across a solid

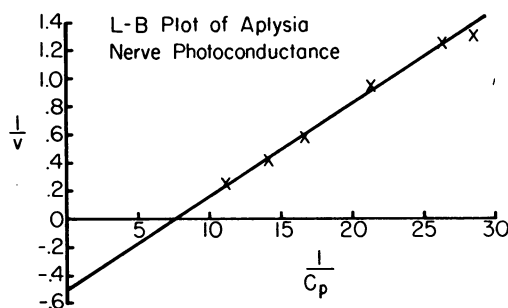


FIG. 2.—Lineweaver-Burk plot of photoconductance of *Aplysia* nerve membrane.  $C_p$  = photoconductance in  $(M\Omega)^{-1}$  of membrane of *Aplysia* neuron;  $v = -dC_p/dt$ , where  $t$  is time. The same data were used as for Fig. 1. The curve of total conductance ( $C$ ) vs. time approached a value of approximately  $22 (M\Omega)^{-1}$  as time increased. Hence,  $22 (M\Omega)^{-1}$  was taken as the value of dark conductance ( $C_d$ ), and was subtracted from all values of total conductance ( $C$ ) to give values of photoconductance ( $C_p$ ), which were used to plot the curve.

surface, the time course of photoconductance as a function of time should yield a linear Lineweaver-Burk plot with a *negative* intercept on the  $1/v$ -axis. The data of Chalazonitis<sup>1</sup> were tested for this possibility.

Total membrane conductances were calculated from resistances as before. In the Elovich plot, it was possible to ignore the obvious fact that the nerve membrane possessed a substantial component of conductance (and hence of charge carrier concentration) *before* exposure to light. For this test, however, mathematics requires that the zero point of the variable  $x$  (conductance or photoelectron concentration) be correctly located. Therefore, we must use only those charge carriers that are generated by light. The simplest approach to quantitation is to assume that total membrane conductance ( $C$ ) in *Aplysia* nerve consists of the sum of two separate components, a dark conductance ( $C_d$ ) which is unaffected by light, and a photoconductance ( $C_p$ ) which is due to charge carriers that become conductive only in light and that decay to the nonconducting state in the dark. The above statements may be written

$$C = C_d + C_p. \quad (3)$$

Values of photoconductance ( $C_p$ ) for *Aplysia* nerve membrane were easily determined from the data of Chalazonitis<sup>1</sup> as described in the legend of Figure 2.

Figure 2 shows that photoconductance in nerve membrane conforms to the prediction derived from solid-state kinetic theory, i.e., a linear Lineweaver-Burk plot with a *negative* intercept on the  $1/v$ -axis. This observation provides additional support for the hypothesis that solid-state processes are involved in photoconduction in the membrane of the *Aplysia* neuron.

\* The opinions and conclusions contained in this report are those of the authors. They are not to be construed as necessarily reflecting the views or the endorsement of the Navy Department.

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