EXCITATION THEORIES OF RASHEVSKY AND HILL

BY FRANKLIN OFFNER

(*From the Department of Physiology, University of Chicago, Chicago*)

(Accepted for publication, April 23, 1937)

Blair (1932) proposed the equation

$$dp/dt = KI - kp \tag{1}$$

to describe the change of the excitatory process of nerve, p, under the action of a current I. K and k are constants, and action results when p exceeds some threshold value h. The equation fits extensive experimental data but is quite unable to account for the anodic excitation at break and for non-excitation by slowly rising currents. Rashevsky (1933) added a parallel equation for an inhibitory process, or threshold rise,

$$de/dt = KI - k(e - e_o) \tag{2}$$

$$di/dt = MI - m(i - i_o) \tag{3}$$

where K, k, M, and m are constants, e the excitatory process, and i the inhibitory one. Action results when $e \geqq i$; and for $m << k$ and $K/k \leqq M/m$ ($\therefore M << K$), the negative process, that is, slower than the positive one, these equations satisfy the two phenomena not covered by Blair's treatment as well as those which are. These equations can also be given a physical interpretation in terms of the migration of two antagonistic ions, e and i representing their respective concentrations.

Hill (1936) proposed another set of equations, based on Blair's equation for the excitatory process but assuming that the negative one, or threshold rise, is a function of the magnitude of the excitatory process at any instant rather than of the magnitude of the stimulating current—as assumed by Rashevsky. The differential equations he implies are[1]

[1] I have substituted k' for Hill's k to avoid confusion with Rashevsky's.

$$dV/dt = bI - (V - V_o)/k' \tag{4}$$

$$dU/dt = \beta(V - V_o) - (U - U_o)/\lambda \tag{5}$$

where V is the excitatory process, U the threshold, and b, k', β, and λ constants, with $\lambda >> k'$. Action occurs when V equals or exceeds U.

Though Hill's equations describe a physical picture of inhibition or accommodation somewhat different from Rashevsky's, it can be shown that both treatments lead to identical equations for strength—duration curves obtained with any form of stimulating current varying as an arbitrary function of time.

Integration of (4) and (5) gives respectively

$$V = V_o + be^{-t/k'} \int_{\theta=0}^{\theta=t} Ie^{\theta/k'}\, d\theta \tag{6}$$

$$U = U_o + \beta e^{-t/\lambda} \int_{\theta=0}^{\theta=t} (V_\theta - V_o)e^{\theta/\lambda}\, d\theta \tag{7}$$

where V_θ is the instantaneous value of V at time θ. Substitution of (6) in (7), with appropriate change in the argument and interchanging the limits of integration gives, after some rearrangement,

$$U = U_o + \beta b[k'\lambda/(k' - \lambda)]\left[e^{-t/k'} \int_{\theta=0}^{\theta=t} Ie^{\theta/k'}\, d\theta - e^{-t/\lambda} \int_{\theta=0}^{\theta=t} Ie^{\theta/\lambda}\, d\theta\right] \tag{8}$$

Equations (6) and (8) give for the condition that at time t, $V = U$ and, therefore, action occurs:

$$[(\lambda - k')/\beta\lambda k' + 1]e^{-t/k'} \int_{\theta=0}^{\theta=t} Ie^{\theta/k'}\, d\theta = (U_o - V_o)(\lambda - k')/b\beta\lambda k' + e^{-t/\lambda} \int_{\theta=0}^{\theta=t} Ie^{\theta/\lambda}\, d\theta \tag{9}$$

Solution of Rashevsky's equations (2) and (3) gives,

$$e = e_o + Ke^{-kt} \int_{\theta=0}^{\theta=t} Ie^{k\theta}\, d\theta \tag{10}$$

$$i = i_o + Me^{-mt} \int_{\theta=0}^{\theta=t} Ie^{m\theta}\, d\theta \tag{11}$$

and again for the condition that at time t, $e = i$ and action occurs,

$$(K/M)e^{-kt} \int_{\theta=0}^{\theta=t} Ie^{k\theta} d\theta = (i_o - e_o)/M + e^{-mt} \int_{\theta=0}^{\theta=t} Ie^{m\theta} d\theta \qquad (12)$$

Equation (12) for the strength—duration relationship derived from Rashevsky's theory is identical with the parallel equation (9) derived from Hill's, provided

$$K/M = (\lambda - k')/\beta\lambda k' + 1; (i_o - e_o)/M = (U_o - V_o)(\lambda - k')/b\beta\lambda k'; \quad k = 1/k'; m = 1/\lambda \qquad (13)$$

Assuming with Hill a "normal accommodation," is equivalent to putting $\beta = 1/\lambda$ (Hill) or $K/M = k/m$ (Rashevsky). Relationships (13) then become

$$(i_o - e_o)/M = (U_o - V_o)(\lambda - k')/bk'; k = 1/k'; m = 1/\lambda \qquad (14)$$

Thus any prediction as to excitation by any arbitrary current form deduced on the basis of one theory can, by suitable choice of constants, be exactly duplicated by the other, and it becomes impossible to distinguish between the theories by any such experiments.

I wish to express my appreciation to Dr. R. W. Gerard who suggested this investigation.

REFERENCES

Blair, H. A., *J. Gen. Physiol.*, 1932, **15**, 709.
Hill, A. V., *Proc. Roy. Soc. London, Series B*, 1936, **119**, 305.
Rashevsky, N., *Protoplasma*, 1933, **20**, 42.