

the intensity of the stimulating light (*cf.*, Fig. 1, A and B). Dark adaptation also modifies the discharge frequency, *i. e.*, the end organ responds to a stimulating light of given intensity with an initial frequency which is greater the longer the eye has been in the dark.

The short pause following the initial burst of impulses, observable in Fig. 1A, is a characteristic response of the completely dark adapted eye to light of high intensity. This "silent period" is absent if the eye is not completely dark adapted, or if the intensity of the stimulus is low. The discharge then consists of an unbroken succession of impulses regularly decreasing in frequency (*cf.*, Fig. 1B).

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Time-Intensity Relations for the Stimulation of Tissue by Electric Currents.

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Justification is felt in advancing a new analysis of the time-intensity relations for electrical stimulation as it is much simpler mathematically than any existing general analysis and therefore more useful in planning and co-relating experiments while at the same time it fits, as well or better, the experimental data of the Lapicques.

The derivations are based on the following hypotheses: (a) The rate of growth of the local excitatory process whose magnitude is designated by p is proportional to the applied voltage. (b) The tissue has a reaction toward normal at a rate proportional to p . (c) When p reaches a liminal value h excitation is accomplished.* The differential equation expressing (a) and (b) is,

$$\frac{dp}{dt} = KV - kp$$

where V is the applied voltage, K and k are constants.

For direct current a solution is,

$$kt = \log \frac{KV}{KV - kh} = \log \frac{V}{V - R}$$

when the rheobase, R , is substituted for kh . All the direct current data in Lapicque's book³ fit the equation,

* h is probably in general a function of the voltage, *e. g.*, when C is not zero with direct currents.

$$\log \frac{V}{V-R} = kt + C$$

very well, C being usually positive. With the newer data of Lapicque,^{1, 2} the fit is as good, C being positive sometimes, sometimes negative, frequently zero. The new data indicate that C depends on the type of electrodes used.

In the following examples of the agreement of the equation with Lapicque's data the values marked with asterisk were used to calculate the constants.

Helix-nerve muscle, ³ page 214. $k = 10.24$. $C = .0636$.						
t secs.	.014	.021	.036	.057	.086	∞
V obs.	*8.2	6.4	5.0	*4.0	3.5	3.1
V calc.	8.2	6.5	4.9	4.0	3.5	3.1
Frog-sartorius, fluid electrodes, ¹ page 206. $k = 292.3$. $C = 0$.						
t secs.	.001	.002	.003	.005	.010	.020
V obs.	*4.5	3.2	2.45	2.3	2.2	2.2
V calc.	4.5	3.0	2.5	2.3	2.2	2.2

The second example is typical for fluid electrodes in that $C = 0$, or is small. This was also pointed out by Lapicque.¹ He derived, at one time,⁴ an expression equivalent to the above equation using a leaky condenser model. He did not include C , so discarded the equation on account of the poor agreement with experiment.

Chronaxie is given by,

$$T = \frac{1}{k} (\log 2 - C)$$

For condenser discharges the solution is,

$$p = \frac{Kq_0r}{crk-1} \left\{ e^{\frac{-t}{cr}} - e^{-kt} \right\}$$

where q_0 , c , are the initial charge and the capacity, respectively, of the condenser, and r is the series resistance. This equation has a maximum when

$$t = \frac{cr}{1 - crk} \times \log \frac{1}{crk}$$

This is the predicted *durée utile* of the discharge. The following example is from Lapicque's data :

¹ Lapicque, L., *J. Physiol.*, 1931, **73**, 189.

² Lapicque, L., *J. Physiol.*, 1931, **73**, 219.

³ Lapicque, L., *L'excitabilité en Fonction du temps*. Presses Universitaires, Paris, 1926.

⁴ Lapicque, L., *J. Physiol., Path. gen.*, 1907, **9**, 622.

Frog sciatic-gastrocnemius,⁵ page 701. $k = 298.4$.

durée obs. secs.	*.00181	*.00154	.00135	.00093	.00063
durée cal. secs.	.00181	.00154	.00147	.00091	.000602

The general equation for condenser stimulation is

$$h = Kq_0r \frac{erk}{1 - erk}$$

For chronaxie,

$$T_c = \frac{2}{k} \log 2$$

The relation of direct current chronaxie to cr is,

$$T = \frac{\log 2 - C}{2} cr$$

When $C = 0$, which is probably the ideal case,

$$T = cr \frac{\log 2}{2} = .3466 cr$$

This is close to Lapicque's mean value from experiment, 0.37 cr .

The summation of condenser stimuli gives

$$h = \frac{Kq_0re^{-\frac{t}{cr}}}{erk - 1} \left\{ \frac{1}{\theta} + \frac{1}{\theta} + \frac{1}{\theta^2} + \dots + \frac{1}{\theta^{n-2}} \right\}$$

where $\theta = e^{kt}$ and t is the duration of each stimulus as well as the interval between them. A similar expression derived by Lapicque from other considerations fitted the experiments of the Chauchards.⁶

For currents of linear and exponential rise solutions are easily obtained but there is no data suitable to test them.

For alternating current the solution is

$$p = \frac{KV_0}{k^2 + w^2} \left\{ k \sin wt - w \cos wt + we^{-kt} \right\}$$

when the applied voltage is $V = V_0 \sin wt$. The transient term we^{-kt} may account for the twitch observed at voltages lower than those required for tetanus. Neglecting the transient term the maxima of the equation are given by,

$$p = \frac{KV_0}{k^2 + w^2}$$

which equals h when the stimuli are adequate. When w is large compared to k ,

$$V_0 = \frac{h}{K} w$$

⁵ Lapicque, L., *Compt. rend Soc. Biol.*, 1907, **62**, 701.

⁶ Evans, C. Lovatt, *Recent Advances in Physiology* (4th ed.). 1930.

This conclusion that the applied voltage may be proportional to the frequency at high frequencies has been reached through experiment also.⁷ The second to last equation fits new experimental data using frequencies from 400 to 40,000. K and k change, however, although particular values apply to large frequency ranges.

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The Thoracic Window.

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Direct observations of activity in the lungs and heart have always been complicated by the fact that artificial respiration has been required to keep the animal alive. The results of the observations were often vitiated by the lung movements and consequent difficulty of maintaining a focus when microscopic observations were made.

Hall¹ described a method in which the isolated lung was studied by transillumination. The method was complicated and observations were limited to a rather short survival period. Later, Wearn² developed a much simpler method in which the animal was not exposed to excessive surgery. The tip of a lower lobe of the lung was used. Illumination was secured by a light directed through the diaphragm. Observations were made through the thinned thoracic wall. Intratracheal insufflation was used. The field for observation was definitely limited to a small area in the lowest portion of the lung.

The thoracic window is another method of making direct observations not only of the lungs and heart grossly, but also microscopically. Artificial respiration is not needed. The animal (cat or rabbit) is thoroughly anesthetized. An oval section of skin is removed from the anterior aspect of the chest. The skin remaining on the thorax is separated from the underlying muscles. Artificial respiration is begun when the chest is opened. Several ribs are resected on each side at a point about midway between the sternum and vertebral column. After removal of the ribs and sternum

⁷ Asher, Leon, *Skand. Arch.*, 1923, **43**, 6.

¹ Hall, Harry L., *Am. J. Physiol.*, 1925, **72**, 446.

² Wearn, J. T., Ernstene, A. C., and Bromer, A. W., *Am. J. Physiol.*, 1928, **85**, 410.