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Excitability of Slowly Reacting Muscle.

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Much attention has been given recently to the alpha excitability of Lucas¹ in the striated muscle of the frog. This excitability which gives rise to a strength-duration curve which approaches closely to its rheobase only with durations of about 200 m.sec. has been the subject of debate by Rushton,² Lapique³ and others because its time scale is so long that it does not satisfy such generalizations from experiment as Lapique's theory of isochronism,⁴ while at the same time the same tissue will give results satisfying these generalizations if a different method of stimulation is adopted. In slowly reacting muscle, similar low excitabilities are measured by any of the usual methods, but, as these correspond with the slowness of the other reactions of the muscle, the validity of their strength-duration curves with long-time scales has not been questioned. For this reason the data on these tissues are well suited to providing an answer to the question as to whether the same excitatory mechanism can be postulated in the slow tissues as in the highly excitable ones such as the frog's sciatic nerve.

It has been shown⁵ that the high excitabilities and the few low excitabilities which have been studied are adequately represented by assuming that the local excitatory process is given by

$$\frac{dp}{dt} = KV - kp \quad (1)$$

where p is the excitatory state, V is the stimulus, and k and K are constants, and that there is an independent and much faster process which appears with respect to the process of Equation (1) to be complete for all but very short stimuli and to raise or lower the threshold from a constant value h to $h \pm \alpha V$ where α is a constant.

¹ Lucas, K., *J. Physiol.*, 1906, **35**, 103; 1907, **36**, 113.

² Rushton, W. A. H., *J. Physiol.*, 1930, **70**, 317; 1931, **72**, 265; 1932, **74**, 231; 1932, **75**, 161, 445.

³ Lapique, L., *J. Physiol.*, 1931, **73**, 189, 219.

⁴ Lapique, L., *L'excitabilité en fonction du temps*, Paris, Les Presses Universitaires de France, 1926.

⁵ Blair, H. A., *J. Gen. Physiol.*, 1932, **15**, 709, 731; **16**, 165, 177; 1934, **18**, 125; 1935, **18**, 755; *Am. J. Physiol.*, 1935, **112**, 277.

According to this hypothesis the data of rectangular currents are representable by

$$\log \frac{V}{V-R} = kt + \log \frac{K + k\alpha}{K} \quad (2)$$

and those for condenser discharges by

$$\frac{V}{R} = (crk)^{\frac{1}{crk-1}} \quad (3)$$

R being in either case the rheobase and c and r being the capacity and the resistance, respectively, of the condenser circuit.

Data by Bonnardel and Goudchaux⁶ on the ventral muscle band of the leech provide a means of testing these equations as they include both strength-duration and voltage-capacity curves. Some of the data are assumed by the authors to be mixed curves including more than one excitability because the energies of the stimuli have double minima. These cases are avoided, the simple curves only being considered.

The method of applying these equations has been given previously.⁵ In the upper part of Table I are 3 typical strength-duration curves as measured and as calculated according to Equation (2). These measured values are either single sets or the means of several determinations on the same preparation as indicated in the legend. The constants k and $K + k\alpha/K$ are given also in the legend for each case. It will be observed that Equation (2) fits these examples quite well.

In the lower part of Table I similar examples of voltage-capacity data are given as measured and as calculated according to Equation (3). The calculated values in Set F are slightly low for the larger capacities but as this divergence does not occur in the other curves it is probably not significant.

Since these 6 curves are representative of sets of large numbers of determinations which are quite consistent among themselves it seems possible to conclude that the excitatory process in these muscles is adequately represented by Equation (1) along with the faster process whose presence is shown by the constant $K + k\alpha/K$. With these data this faster process is always complete as is evidenced by the fact that Equation (2) is valid even with the shortest stimuli.

It is pointed out by Bonnardel and Goudchaux⁶ (p. 220) that their mixed curves, *i. e.*, the data giving 2 energy minima, indicate that these muscles have a number of excitabilities analogous to the

⁶ Bonnardel, R., and Goudchaux, S., *Arch. internat. physiol.*, 1935, **41**, 201.

TABLE I.
Strength-Duration and Voltage-Capacity Curves of the Ventral Muscle Band of the Leech.

Duration m. sec.	A		B		C	
	Obs. volts	Calc.	Obs. volts	Calc.	Obs. volts	Calc.
∞	10	10	7.5	7.5	12	12
100	17	17	13	13.1	20.5	19.0
80	19.8	20	15	15.1	23	21.8
60	24.3	23.5	18.5	18.3	27	26.1
40	30	31.1	25	24.7	34	34.7
30	37	38.1	29.5	30.5	43	43.3
25					48	49.4
20	48	50.3	41	41.0	54	58.1
15					71	70.7
10	77.5	76.9	67.5	67.5	93	95.3

Capacity mfd.	D		E		F	
	Obs. volts	Calc.	Obs. volts	Calc.	Obs. volts	Calc.
∞	9.5	9.5	6.5	6.5	7	7
9.5	19.5	20.1	11.5	10.4	12.4	10.7
5	27	27.1	13	13.4	15.3	13.5
3.5	31.2	32.8	18	18.0	19.7	17.8
2.5	38	40.3	22	21.6	22.5	21.2
2.0	43.5	46.5	27	26.4	27.3	24.4
1.5	56	57.0	37	36.9	37.3	35.5
1.0	74.2	76.5	50.5	49.7	48.6	47.0
0.8			60	62.1	56.4	55.6
0.7	97.5	99.5				
0.6			74	73.8	69.2	69.3
0.5			85	85.3	79.4	80.2
0.4					94.5	96.9

A. Observed voltages: the means of determinations 4 and 5, p. 216.⁶

$$k = 8.30; \log_{10} \frac{K + ka}{K} = 0.024.$$

B. Observed voltages: the first set of the experiment of June 8, p. 212.

$$k = 8.09; \log_{10} \frac{K + ka}{K} = 0.016.$$

C. Observed voltages: the fourth set of the experiment of May 25, p. 212.

$$k = 9.57; \log_{10} \frac{K + ka}{K} = 0.017.$$

D. Observed voltages: the means of the first and second sets, p. 206. $k = 14.0$.

E. Observed voltages: the third set, p. 207. $k = 14.95$.

F. Observed voltages: the means of all sets, p. 208. $k = 17.7$.

The resistance of the condenser circuit, $r = 13,000$ ohms.

Ag-AgCl wire electrodes were used in all cases, the preparation being suspended in air at room temperature, 15°-24° C.

Lucas excitabilities in the skeletal muscles of frogs and toads. The writer has shown recently⁷ that the energy minimum for condenser stimuli is at $e = 2.718$ rheobases and that at this point $crk = 1$ (Equation 3). Therefore k can be evaluated, approximately, without any further data than the minimal capacity and the resistance.

⁷ Blair, H. A., *J. Gen. Physiol.*, 1936, in press.

Applying this to the mixed condenser curves (p. 219) of Bonnardel and Goudchaux⁶ the upper minimum is with a capacity of about 1 mfd. Therefore $k = 1/1 \times 10^{-6} \times 13 \times 10^3 = 77$,* approximately, which is 5 to 9 times as great as those in Table I.† These excitabilities are not greatly different but with other data (p. 218) 2 curves have their higher minima at about 0.1 and 0.5 mfd., respectively, giving $k = 700$ * and 150, approximately. These values are considerably greater than those in Table I but the data are not very extensive and their validity is not so certain as that of the others (p. 219, data above).

It is concluded from these considerations that the excitatory process in the slowly reacting muscle of the leech is of the same type as that occurring in highly excitable tissue⁵ and that while the excitability as usually determined is about 10 there are others considerably greater. It is not established that these higher excitabilities are from nerves but it does not seem likely that the muscle itself would show such a range with wire electrodes.

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Parabiotic Twins as a Means of Determining Cellular Individuality.*

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It has been shown¹ that a division of species-specific substances of the erythrocytes of Pearlneck (*Spilopelia chinensis*), not present in those of Ring dove (*Streptopelia risoria*), is found in the progeny of male hybrids backcrossed to Ring dove. Individual differences in the cells of these backcross birds make reasonable the conclusion that many different heritable cellular components distinguish Pearlneck from Ring dove. It seemed opportune to test whether or not

* Condenser chronaxie is $2/k = 0.026$ sec. and 0.0028 sec., respectively.

† The lower minima in these mixed curves are not well defined but it is indicated that they correspond to excitabilities like those of the simple curves in Table I.

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¹ Irwin, M. R., and Cole, L. J., *J. Exp. Zool.*, in press.