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LAPICQUE'S CANONICAL STRENGTH DURATION CURVE.

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Introduction.

Ever since the study of the strength duration curve was initiated by the researches of Hoorweg and of G. Weiss, numerous investigations have been undertaken to obtain an exact experimental relation between the liminal intensity of a stimulating current, and the duration through which this current flows. The object of most of this work has been to test experimentally some physical theory of excitation, and the excitable tissue usually chosen has been the frog's sciatic nerve. Now with the theoretical aspect we are not here concerned, but the consideration of the tissue employed has given rise to an important generalization due to Lapicque. This investigator has worked upon excitable tissues of very diverse kinds, each of which has its own peculiar strength duration curve, but he claims that if the curve for each tissue is suitably scaled it will coincide with a fixed curve identical for all tissues and called by him "canonical."

The canonical curve relating i and t may be represented within experimental limits by the equation

$$i = a\sqrt{\frac{t+\theta+\sqrt{(t-\theta)^2+0{\cdot}16\theta^2}}{2t}} \qquad \ldots\ldots(1),$$

where i = current, t = time, a = rheobase, and $\theta = 3{\cdot}8$ times the chronaxie.

This equation is not based upon any physical considerations nor is it claimed to have any physical significance, it is purely given as a compact expression from which one may compute the relation which Lapicque has found experimentally. If this relation is true for all excitable tissues then any satisfactory theory of excitation must allow it to be deduced

(approximately at least) from the premises, and this was the chief value to the exact form of the canonical curve, until the last year or so.

Quite recently the investigations of Lapicque and of myself have emphasized a phenomenon demonstrated earlier by Lucas and others [Lucas, 1907–8]. As a result it is quite clear that a muscle may exhibit two strength duration curves of very different time constants (? chronaxies), and the question arises as to their significance. Now according to Lapicque's theory of isochronism, the chronaxie of a muscle fibre is the same as that of its motor nerve provided that the two tissues are in physiological connection, not otherwise. In degeneration, curarization (by curare, not by strychnine), and fatigue, the muscle chronaxie is much prolonged. But of the two excitabilities which may be found in muscle by excitation through fluid electrodes of the "block type" [Rushton, 1930] one has a chronaxie the same as the motor nerve, and the other is very much longer. (The former is called the γ excitability, the latter the α, after Lucas.) In view of the isochronism theory therefore, it might be supposed that the γ fibres are normal fibres in connection with their nerves while the α fibres are physiologically severed. The second part of this suggestion however is not correct. I have made a large number of experiments of different kinds to test whether the α fibres are physiologically normal, and I can find no evidence to the contrary. In brief, the α effect may be obtained from spinal preparations, from those freshly excized, and those after 24 hours' equilibrium with Ringer's fluid [1930]; it was found in all of a dozen different muscles investigated from various parts of the frog, and the isometrical twitch was barely distinguishable from that due to indirect excitation when the two curves were superimposed [1931*a*]; finally the α fibres were shown not only to be supplied by nerves, but to be practically the only fibres that are supplied, for their contraction accounts for nearly all the tension time developed in a maximal twitch excited through the nerve [1932].

It therefore seems to be legitimate to conclude that the α fibres are not abnormal, but this forces us to an important conclusion with regard to the theory of isochronism. For either the α curve is not a "true" strength duration curve from which a "true" chronaxie can be found, or else the great difference between the α chronaxie and that of the nerve which supplies these fibres completely falsifies that theory.

Lapicque accepts the first alternative [1931] and rejects the validity of the α curve on account of the fact that in general it does not fit the canonical curve within the limits of experimental error (which in my experiments are 5 to 7 p.c.). Here now is a new and very important use

for the canonical curve, namely to distinguish true chronaxies from false. For instance, if the chronaxie of a patient be sought clinically (by excitation through the skin after the manner of Bourguignon [1923]), the way to learn whether the value obtained is the "true" one, or whether it is in error by about a hundredfold (as in the case of the α curves) is to map out the whole curve and see whether this is canonical or not. Thus not only in theory but in urgent practice is the canonical curve of the first importance, if we follow Lapicque.

Now neither Lapicque nor anyone else to my knowledge has obtained a strength duration curve from vertebrate skeletal muscle or nerve that follows within even moderate limits the canon at short

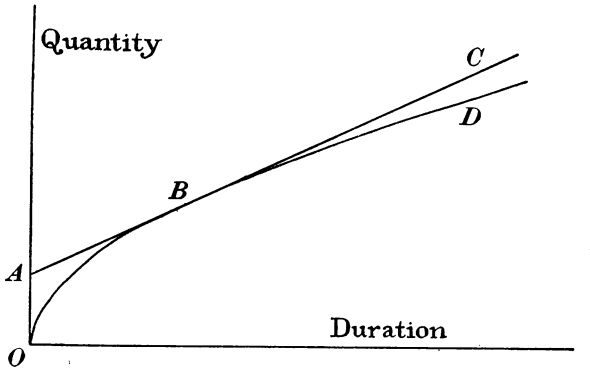

Fig. 1. Quantity-duration curves. *ABC* Weiss straight line. *OBD* Lapicque parabola at short durations.

durations. It is well known that the experimental results of G. Weiss plotted as quantity of electricity against duration, fell approximately upon the straight line *ABC*, Fig. 1. But Lapicque's canonical curve at short durations coincides with the parabola *OBD*[1], hence the results of Weiss were clearly not canonical. As Lapicque points out, the best experimental determinations do not follow the Weiss line exactly but at short durations they drop below it, but they do not drop nearly sufficiently to become canonical. This discrepancy is well appreciated by Lapicque who attributes it to physical imperfections of the stimulating circuit [1926, pp. 89, 116], and who considers that the only reliable curves are those obtained from slowly reacting muscles [p. 97] (*e.g.* snail's foot, frog's stomach, etc.), and in spite of the great physiological

[1] For when t is small compared with θ equation (1) reduces to $i\sqrt{t}=$constant.

difficulty attendant upon obtaining repeatable results from such tissues [p. 77] it is from these that the canon has been formulated.

The chief physical error which is supposed to account for the deviation of the experimental results from the canon in the case of frogs' nerves is inductance. It is certainly a fact that an inductance placed in series with the tissue will cause the current instead of rising abruptly (Fig. 2), to its steady value, to rise gradually along an exponential (broken line), and hence if the current ceases at *AB* after a very short duration, the actual current which has passed *OBA* will only be a fraction of the calculated rectangle *ODCA*. It is clear, then, that inductance, if present to an appreciable extent in this way will account qualitatively at least for the divergence of the experimental results from the canonical curve.

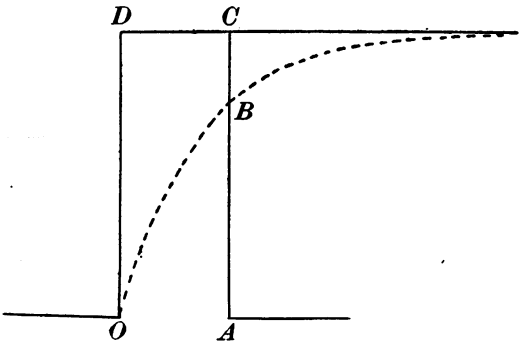

Fig. 2. The effect of inductance upon a "rectangular" stimulus. Ordinates: current, abscissæ: time. *ODCA* non-inductive stimulus, *OBA*, inductive stimulus.

Lapicque, however, describes [p. 296] the care he has taken to avoid inductance by employing resistances of the type "crayons Conté," and with this arrangement it is certainly surprising to learn that inductance produces deviations appreciable still at $0{\cdot}3\sigma$ [p. 215].

But as a matter of fact his method of proving that his circuit is highly inductive is erroneous. In order to test the matter he arranged a double switch so that either the tissue or a ballistic galvanometer could be substituted in the stimulating circuit [p. 111]. In the first case he measured the threshold, in the second (by the fling of the galvanometer) the quantity of current passing, and found that, for short durations, the quantity was much less than that calculated from the product *it* [p. 116]. This shows that when the galvanometer was in the circuit, the circuit was inductive, which was to be expected in view of the inductive nature of the galvanometer. We have no information concerning the inductance

of the circuit when the tissue is substituted, which is in fact the circuit which concerns us. It seems very likely, from its construction, that that circuit was quite non-inductive within experimental limits, and that Lapicque's results, like those of other workers, were essentially accurate —but uncanonical.

In order to test this matter definitely I have attempted to obtain the strength duration curve from the frog's sciatic nerve with a stimulating circuit relatively free from those physical imperfections which might account for the uncanonical nature of the results.

We proceed to a detailed consideration of the apparatus.

Description of apparatus.

Pendulum.

This was the original short range foot-pendulum constructed by Keith Lucas and described by him [Lucas, 1907]. The adjustment of

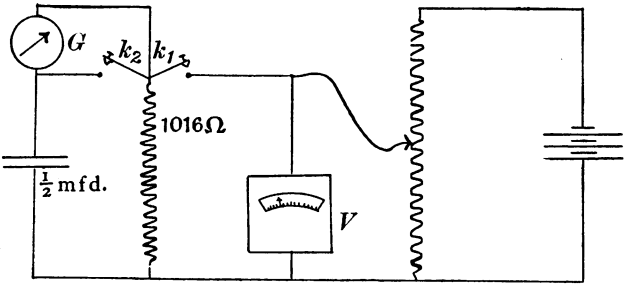

Fig. 3. Circuit for pendulum calibration. k_1, k_2, keys of pendulum; G, ballistic galvanometer; V, voltmeter.

the contacts was controlled by a fine screw and viewed through a micrometer eyepiece, settings could be made to 0·01 mm. Since the speed of the pendulum was about 6 mm. per σ, the error in the setting of the scale could not amount to more than $\pm$ 0·001σ.

With regard to other errors, such as variations of settings of contacts for a fixed position of scale, vibrations of the apparatus and other fortuitous fluctuations in the motion of the arm, we proceed to an experimental investigation from which emerges the remarkable fact that these errors lie within $\pm$ 0·003σ, which may be taken as the limits of accuracy of the instrument.

The method of calibration was similar to that described by Lapicque [1926, p. 335] and Hozawa [1930]. The method differs from Lapicque's

in that his nerve muscle preparation is replaced by a ballistic galvanometer, which could be read to an accuracy 20 times as great as the limits of threshold measurement of a nerve. The method differed from that of Hozawa in using k_2 not as a series key to stop the condenser discharge, but as a short circuit across the galvanometer (Fig. 3) which avoids errors due to leaks in the condenser and adjacent circuit. The condenser was a standard half microfarad with resistance between the plates greater than 10^{10} ohms. The resistance in the discharge circuit was a Ferranti wire-wound non-inductive resistance of 1016 ohms.

Thus if D_o is the galvanometer deflection when k_2 is opened before k_1, D_t is the galvanometer deflection when k_2 is opened at time t after k_1,

$$t = CR \log \frac{D_o}{D_t}$$
$$= 0{\cdot}508 \log \frac{D_o}{D_t} \text{ in } \sigma \qquad \text{.....(2).}$$

When k_2 was left closed and k_1 opened there was no deflection showing that k_2 was an adequate short circuit. The galvanometer deflections could be read correct to 1 mm. of scale, and successive repetitions seldom diverged by more than 2 mm., D_o being always made about 440 mm.

To estimate the error which this divergence produces in the calculated time interval, we obtain from (2) by differentiation

$$\Delta t = -\, 0{\cdot}508 \frac{\Delta D_t}{D_t} \text{ in } \sigma,$$

where Δt = error in interval,

ΔD = error in deflection D_t.

But if $D_t > 200$, $\frac{\Delta D_t}{D_t} < \pm\, 0{\cdot}5$ p.c.

Therefore t alters by less than $\pm\, 0{\cdot}0025\sigma$.

D_t here corresponds to intervals less than $0{\cdot}4\sigma$. It may similarly be shown that the error is less than $\pm\, 0{\cdot}005\sigma$ for intervals less than $0{\cdot}8\sigma$.

It was possible that the calibration curve might alter from day to day to an extent outside the above limits, and to examine this point I made a calibration almost every day for a month. It was found that there was no appreciable change in the curve except for the zero setting. The motion of the lever was uniform, but the exact setting of the steel rods which served as contacts altered from time to time, but never more than $0{\cdot}01\sigma$, and when once the alteration occurred, values remained fixed with the new zero. To take this into account however I made a few observations both before and after each strength duration curve, and thus found the

zero for that case and verified that it had not changed during the experiment.

In view of these observations, we have the rather surprising result that it is possible to regulate the passage of a current within limits of $\pm$ 0·003σ, and even less for very short intervals. Lapicque is very sceptical about the accuracy of pendulums, and I shared his views until the present investigation convinced me of the excellence of this instrument of Lucas's.

The foregoing considerations justify us in regarding the pendulum as accurately repeatable within the specified limits, but they do not justify

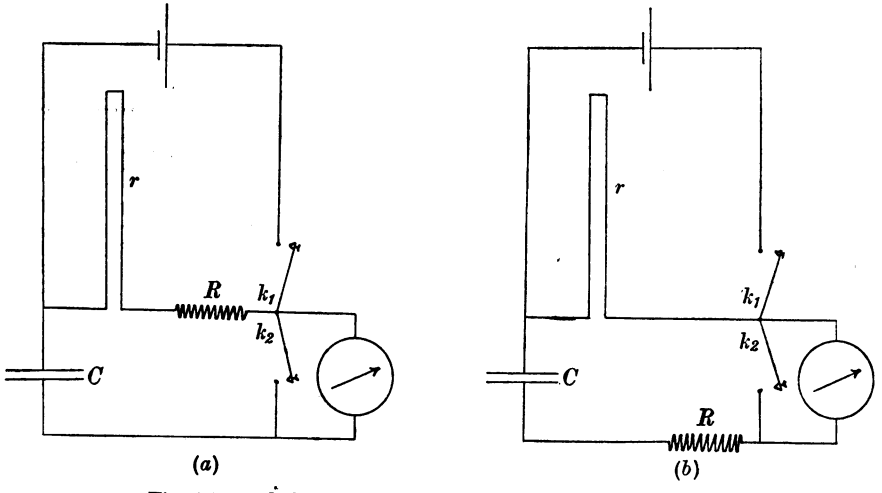

Fig. 4 (*a*) and (*b*). Circuits for estimating effect of inductance on pendulum calibration (see text).

us in accepting the calculated value of t in σ without further discussion. If the standard capacity was not exactly half a microfarad all the results would be altered in the same ratio. Since however (from the canonical equation) this would only be equivalent to altering the temperature of the tissue by a very small amount it does not affect the comparison which is to be made between experiment and canon, and in any case the error in the unit of time will be small. If, however, the resistance is inductive the calculated value t will not be proportional to the interval, but it will be some complicated function of it. It is necessary therefore to estimate the error due to the inductance and if necessary to correct for it. This has been done as follows.

A piece of wire 2 metres long with resistance 20 ohms ran straight

for a metre then doubled on itself and ran back for a metre. The inductance of this is negligible. This resistance is placed as shown at r, Fig. 4 (a) and (b), the 1016 ohms being changed in the two cases as shown at R.

In (a) the current initially flows through R and hence tends to persist owing to inductance when k_1 is opened, and this increases the rate of discharge of the condenser at first. In (b) there is no current initially in R and hence the inductance delays the discharge of the condenser at

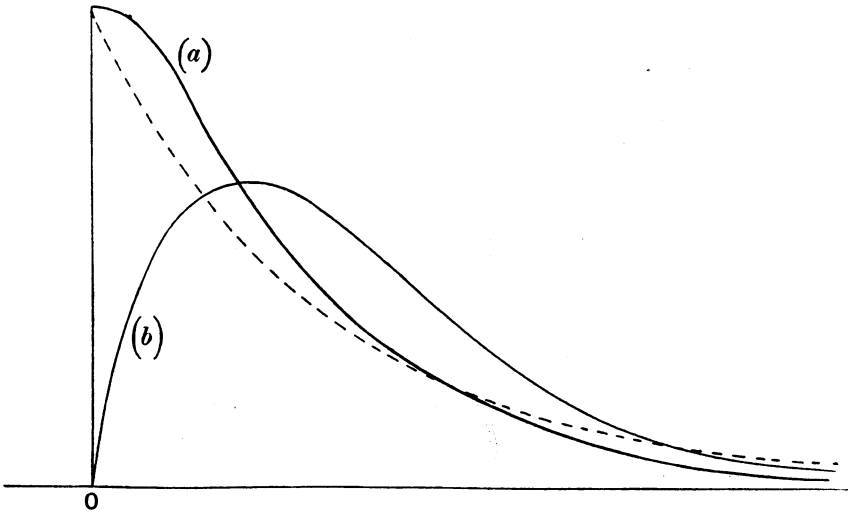

Fig. 5. Current flowing from condenser (ordinates) at various times (abscissæ) after O, the instant when k_1 (Fig. 4) is opened. Curves (a), (b) correspond to R being highly inductive, Fig. 4 a, 4 b respectively; broken curve (exponential) corresponds to R, being non-inductive in either case.

first. The non-inductive case therefore lies initially between these two. Fig. 5 shows current through the condenser plotted against time in the case of (a) and (b) when R is highly inductive. As the inductance diminishes so both these curves approach the broken line, finally to coincide with it in the ideal inductionless case.

Now the fling of the galvanometer which we measure is proportional to the charge remaining on the condenser at the moment when k_2 is opened, which is proportional to the area of the curve in Fig. 5 to the right of the ordinate corresponding to this moment, or to Q_o minus the area to the left of this ordinate since the total area of each curve is Q_o, the initial charge on the condenser.

Thus if the inductance were zero

$$t_a = CR \log \frac{D_o}{D_t} \quad \text{for circuit } (a)$$
$$= t_b = CR \log \frac{D_o}{D_t} \quad \text{for circuit } (b)$$
$$= t = \text{true interval in } \sigma.$$

But since the curves (a) and (b), Fig. 5, deviate from the exponential (broken line) one on either side, initially, we have the relation

$$t_a > t > t_b \qquad \text{.....(3),}$$

or the error in using t_a as the true value of the interval $< (t_a - t_b)$ for small values of t.

The experiment was easily carried out by arranging two switches to transform circuit (a) into (b) and back, so that t_a and t_b could be compared without delay for any setting of the pendulum. It was found that $(t_a - t_b)$ was never more than $0{\cdot}005\sigma$ and hence lay within the limits of error of the apparatus. However, a more exact analysis of the equations for current flow in these two cases shows:

(i) That t_a is a much closer approximation than t_b to the true interval t (as is easily appreciated from Fig. 5).

(ii) That the error in assuming that t_a is the true interval for any setting of the pendulum whatever, is less than $2\,(t_a - t_b)^2$ measured for any one setting of the pendulum (greater than $0{\cdot}1\sigma$), all times being expressed in σ. Thus in the present case, the calibration error due to inductance

$$< 2\,(0{\cdot}005)^2 = 0{\cdot}00005\sigma.$$

As a check upon the method I placed in series with R a very large and heavy self-inductance of about 0·06 henry (calculated from D.C. and A.C. resistance measurements), and measured $(t_a - t_b)$ for values of t_a of about 0·1, 0·4, and $0{\cdot}7\sigma$. The results all agreed in giving

$$(t_a - t_b) = 0{\cdot}067 \pm 0{\cdot}003\sigma.$$

The inductance required by calculation to produce this value is 0·056 $\pm$ 0·003 henry, which is in good enough agreement with 0·06 from direct measurement, since the calculation employed is only strictly true for small inductances.

We may therefore conclude that the expectations from the electrical theory are realized experimentally, and that the calibration of the pendulum by the circuit (a) (which is that originally described, Fig. 3) suffers from no appreciable error due to inductance, and that this instru-

ment, freshly checked with regard to zero error, is accurate to $\pm$ 0·003σ for intervals less than 0·5σ and to $\pm$ 0·006σ for intervals up to 1σ.

Tissue and electrodes.

The tissue investigated was the sciatic nerve of the frog with gastrocnemius attached to serve as index of the efficacy of excitation, the muscle being observed directly. The preparation was sometimes at room temperature and sometimes cooled with ice in order to allow of a more exact examination of the durations short compared with the chronaxie. The electrodes were silver wires freshly coated with chloride electro-

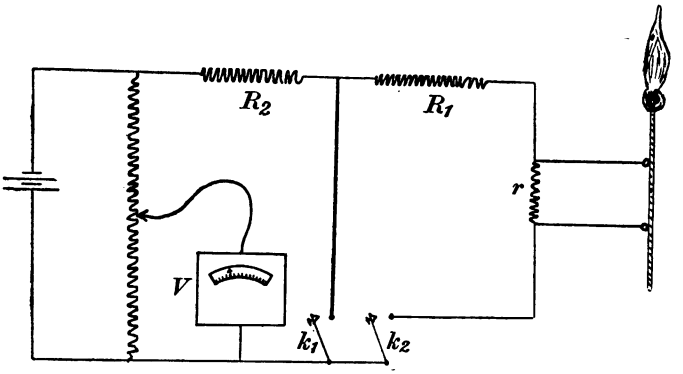

Fig. 6. Stimulating circuit for strength-duration measurements. V, voltmeter; k_1, k_2, keys of pendulum.

lytically. The nerve was placed on these in air in a moist chamber, and excited by a descending current, through 15–20 mm. of its length. The question of the canonical curve is closely related to that of the nature of the electrodes; the form here employed is that which Lapicque recommends.

Stimulating circuit.

Lapicque attributes serious errors to the inductance present in stimulating circuits, and care must be taken to overcome these objections. Consider the circuit Fig. 6 and suppose at first that R_1 alone is inductive, then (as we saw earlier, Fig. 2) when k_1 is opened the current in R_1 (and hence in the nerve) will rise gradually to its final value (curve 1, Fig. 7). If on the other hand R_2 alone is inductive, on opening k_1 the large current which initially flowed through it will tend to persist and only gradually decline, hence the current through the tissue will fall to its final value

(curve 2, Fig. 7). If both R_1 and R_2 are inductive these two tendencies oppose each other and the current in the tissue rises if the ratio

$$\frac{\text{inductance}}{\text{resistance}}, \left(=\frac{L}{R}\right)$$

is greater in the circuit to the right of k_1 than to the left. If the two ratios $\frac{L}{R}$ are equal, a perfect rectangular wave results, behaving as though no inductance at all were present (curve 3, Fig. 7). These statements may easily be verified from the inspection of the well-known equations for current flow in an inductive circuit.

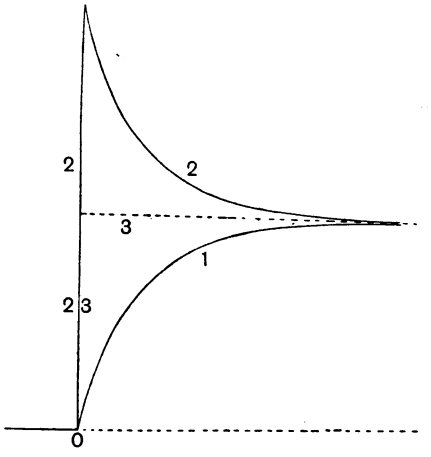

Fig. 7. Current flowing through tissue (ordinates) at various times (abscissæ) after O, the instant when k_1 (Fig. 6) is opened. Curve 1 is when R_1 alone is highly inductive, curve 2 when R_2 alone is. The perfect rectangular curve 3 is when R_1 and R_2 are both inductive to the right extent (see text).

As a result of these considerations it is clearly possible in theory to balance out the effect of inductance entirely by means of a fixed inductance in one half of the circuit and a variable one in the other, but in practice the difficulty is to recognize the balance point. On this account I have not attempted an exact balance, but have employed R_1 and R_2 as non-inductive as possible to reduce the effect of inductance to small dimensions in any case, and have then arranged the rest of the circuit so that the residual inductive effect will act in the direction opposite to that which might explain the uncanonical nature of the observed results. The detailed description will be postponed until these results have been presented.

In the actual circuit used for the experiment, the tissue was shunted

by 200 ohms and R_1, R_2 were each wire-wound non-inductive resistances of 1000 ohms, being the ratio arms of a Wheatstone bridge. Current strengths were varied by a potentiometer and the E.M.F. led off was read directly by an accurate voltmeter. By means of a switch (not shown in the diagram) the pendulum could at any moment be connected to the calibrating circuit (circuit *a*) so that the interval for any setting in case of doubt could be redetermined without delay or shift of setting. The reliability of the pendulum however rendered this hardly necessary.

EXPERIMENT AND RESULTS.

Experiment.

The preparation was set up on the electrodes and allowed to rest (and cool when necessary) for about an hour. During this time the pendulum zero was tested. The rheobase and chronaxie were then taken and thresholds for a number of durations less than the chronaxie obtained. The measurements were then repeated in the reverse order, and when the divergence was small the experiment was considered satisfactory. At the end of the determinations the pendulum zero was again tested.

Results.

All the results that I obtained without exception gave a large divergence from Lapicque's canonical curve at short durations, just as do the results of former workers.

The canonical relation is given by Lapicque in the form quoted on the first page of this paper (1). This may conveniently be developed by Taylor's theorem into the following power series:

$$\frac{i\sqrt{t}}{a} = 1 + 0{\cdot}0046\left(\frac{t}{\tau}\right) + 0{\cdot}0021\left(\frac{t}{\tau}\right)^2 + \ldots \qquad \ldots\ldots(4),$$

where t = duration, τ = chronaxie,

whence it immediately appears that for durations less than τ,

$$i\sqrt{t} = \text{constant (correct to 0·5 p.c.)}.$$

In the following tables the first column gives the duration of the current, the second gives the limits between which the threshold lay, while the third gives the repetition of the measurements in the reverse order. The fourth column gives the threshold calculated from the formula

$$i\sqrt{t} = \text{constant},$$

where the constant is adjusted to fit the results in the neighbourhood of the chronaxie.

At room temperature.

Duration in σ	Threshold: Observed		Calculated
	Frog I		
∞	14 – 13·4	13·4– 13	—
0·175	31 – 30	30 – 29	30·0
0·11	47 – 45	45 – 43	37·6
0·07	65 – 62	63 – 60	47·3
0·032	115 –110	115 –110	70
0·012	>140	>140	116
	Frog II		
∞	5·0– 4·8	5·2– 4·8	—
0·295	11·2– 10·6	11·7– 11·2	11·2
0·175	14·5– 14·0	15·0– 14·5	14·5
0·106	23 – 22	22 – 21	18·7
0·07	32 – 30	31 – 29	23·0
0·035	55 – 50	55 – 50	32·5

Cooled in ice to near zero.

Duration in σ	Threshold: Observed		Calculated
	Frog III		
∞	5·4– 5·0	6·0– 5·6	—
0·98	13·5– 13·0	14·0– 13·5	13·5
0·50	23 – 22	23·5– 22·5	19·3
0·31	36 – 34	36 – 34	24·3
0·195	53 – 50	55 – 52	31
0·12	83 – 78	83 – 79	40
0·08	107 –102	115 –110	47
0·065	>132	>132	53
	Frog IV		
∞	10·5– 10·0	10·5– 10·0	—
0·82	19 – 18	19 – 18	18·5
0·50	27 – 26	28 – 27	24
0·31	40 – 38	40 – 38	30
0·195	62 – 59	60 – 57	38
0·12	92 – 88	94 – 90	49
0·08	>130	>130	59

The threshold measurements are seen to be repeatable usually within the limits of 5 p.c., but the calculated values diverge from these by even a hundred p.c. at the shortest durations with cooled preparations. It is not necessary to add to these examples which are typical of all my observations and which only confirm those of former investigators. The deviation from the canonical formula is progressive and extensive and it merely remains to review the apparatus in order to see whether this can in any way account for the divergence.

Possible errors.

If the inductance of the circuit is to explain the results, we have seen that the ratio $\frac{L}{R}$ must be greater in the circuit to the right of k_1 than to the left, Fig. 6; but actually the reverse is the case. For if the two resistances R_1, R_2 are identical in resistance and inductance, then $\frac{L}{R}$ for the circuit on the right is lowered by the electrode system which is non-inductive, and even capacitative (assuming the tissue shunt non-inductive), whereas in the other circuit the potentiometer is inductively wound on an iron frame. Thus $\frac{L}{R}$ is greatest in the circuit on the left unless this is compensated for by $\frac{L}{R}$ being greater for R_1 than for R_2. This however is not the case for otherwise interchanging R_1 and R_2 would certainly make $\frac{L}{R}$ greatest in the circuit on the left. But in experiments to test this point, R_1 and R_2 could be interchanged by a switch and no alteration of threshold was ever observed even at the shortest durations. Thus the uncanonical results obtain for either position of R_1 and R_2 and hence cannot be explained by inductance, unless it be due to the tissue shunt. But inductance in this shunt will cause it to have a higher equivalent resistance for the shortest durations, and since increasing the shunt resistance was found to lower the threshold, the effect of inductance here also would be to increase the observed discrepancy, not to explain it. Exactly the same result follows from the supposition that the electrodes are polarizable, for that also favours the shortest durations and hence this defect would produce a threshold relatively too low at short durations, whereas what we find is precisely the contrary.

CONCLUSIONS.

The pendulum we have already considered at length, the circuit we have just reviewed, the experimental figures speak for themselves. Whatever may be the case with slow tissues, the frog's sciatic nerve does not fit Lapicque's canonical curve, and hence the canon loses its significance.

We are thus forced back upon the dilemma with which this paper opened. The α fibres are supplied by nerves whose chronaxie is about a hundred times as short as that of the muscle. Either Lapicque's theory of isochronism cannot be accepted or else the α curve is not a "true" strength duration curve from which a "true" chronaxie can be

found. Lapicque accepts the second alternative, and considers that the α curve is false because it does not fit the canonical curve. But in the present paper we have seen that this same objection applies to the strength duration curve of the sciatic nerve, obtained with Lapicque's type of electrodes, and hence all the chronaxies which have hitherto been determined by this method upon this classical tissue are also false. In particular, the experiments from which Lapicque derived his theory of isochronism are to be rejected for there also the sciatic nerve was used, and only a false chronaxie obtained.

It is very far from my wish to minimize the great service that Lapicque has done physiology by pointing out so forcefully that the manifest differences between fast and slowly reacting tissues are essentially mere changes in the unit of time appropriate for each tissue; but when he claims that this phenomenon is mathematically exact [1926, p. 76, footnote], and that the time scale is the only relevant difference between tissues of very varied structure and function, then his theory becomes improbable *a priori*, and untenable experimentally. Lapicque's results with slow tissues accord well with his canonical formula, his results at short durations with skeletal frog's nerves do not. This discrepancy he attempts to explain by inductance; but the present paper shows that inductance is not responsible and that frogs' nerves appear to follow at short durations a curve different from that of slow tissues.

Lapicque's canon is therefore an idea without adequate experimental support. It does not apply to the tissue which allows of the most accurate investigation, it has no theoretical backing or significance, it is not even very easily computed or appreciated mathematically (as compared for instance with the formula of H. and E. Lassalle [1928][1], which is numerically identical with Lapicque's within experimental limits). As a means of extricating the theory of isochronism from the dilemma with which it was faced, the canon is hardly more successful, for, as we have seen, it ends by destroying the validity of the very experiments upon which that theory was based. Thus though Lapicque's qualitative generalization is of great importance, his canon appears to have little utility.

But if Lapicque's canon has lost its significance how shall we tell "true" chronaxies from "false," seeing that such different values may

[1] $i = \frac{a}{\sqrt{2}}\sqrt{\frac{T}{t}+\frac{t}{T}}$, where $T = 7{\cdot}78$ times the chronaxie and the other symbols are as in Lapicque's formula.

be obtained depending upon the electrodes employed? The remedy lies with anyone who cares to suggest a new criterion, but it is difficult to see why one value should be taken in preference to another. It seems to the writer much more satisfactory at this stage to avoid the complications which arise when we imagine that certain values of the chronaxie are "truer" than others. One thing is certain; until we understand more exactly the relation between the nature of the electrodes and the chronaxie obtained by them, it is essential to describe the first when giving an intelligible value for the second, and in this way the chronaxie becomes, not characteristic of the tissue alone, but of the tissue and the electrodes, as Davis insisted in 1922. Lapicque, however, wishes to restrict the term chronaxie to "true" chronaxies, and other values he calls "pseudo-chronaxies" [1931]. This nomenclature seems unfortunate especially since at present there is no method of distinguishing chronaxies from pseudo-chronaxies, but since Lapicque was responsible for the name in the first place it clearly should be used in the sense which he wishes.

It is therefore of practical importance to have a new name to distinguish the time constant of a strength duration curve, quite apart from any theoretical considerations as to the "truth" of this curve, and while realizing that this constant may not suffice to determine the whole curve. Since Keith Lucas used the term Excitation Time in just this sense, it may conveniently be adopted as this characteristic of any strength duration curve whether "true" or not. According to this proposal, therefore, the chronaxie is the particular Excitation Time in the case where the strength duration curve is canonical, or where it satisfies any new criteria which Lapicque may in future suggest.

Summary.

Lapicque has recently insisted that unless the strength duration curve of a tissue coincides with an empirical curve which he calls "canonical," the chronaxie obtained from it will be "false," and may not be used in relation to his theory of isochronism which only applies to "true" chronaxies.

In the present paper it is shown that the chronaxie of the frog's sciatic nerve obtained by Lapicque's method of excitation is "false," for the deviation from the canonical curve is very great at short durations, and this is not due to inductance (as Lapicque supposed when he obtained the same results) for in the present case this and certain other

possible errors have been controlled. Thus Lapicque's definition of a "true" chronaxie apparently destroys the significance of all the work he has done upon the sciatic nerve since there he was only dealing with "false" chronaxies, and in particular this applies to the experiments underlying his theory of isochronism.

Since Lapicque wishes to restrict the name "chronaxie" to "true" chronaxies, it is important to have a new term which can be applied to any strength duration curve "true" or "false." Lucas's "Excitation Time" was used in just this sense and it is proposed that it be adopted.

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