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THE NORMAL PRESENCE OF α AND γ EXCITABILITIES IN THE NERVE-MUSCLE COMPLEX.

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DURING the past twenty years there has been some difference of opinion as to whether the chronaxie of muscle is the same as that of its nerve or quite different. Lucas [1907–8] obtained evidence for the latter conclusion, for he excited a muscle directly with currents of various durations, and found that the strength-duration curve obtained was in general composed of one or more of three types of curve, one being identical with that from nerve, another having a chronaxie several times as great, and a third (with which we are not here concerned) having an extremely short chronaxie. Lapicque [1926], on the contrary, invariably found that the first-mentioned of Lucas's three curves alone was present, and he concluded that the chronaxie of muscle is the same as that of its motor nerve (isochronism). He suggested certain errors in technique which might have accounted for Lucas's results, but did not put his suggestions to the test. In a recent paper [1930] I have attempted to repeat Lucas's results under such conditions that Lapicque's criticisms will not apply, and the results of this investigation confirm Lucas in that they show that there are in fact two excitabilities[1], γ and α in the nerve-muscle complex of which γ is isochronous with nerve, and α has a chronaxie many times longer.

This matter is of importance from two aspects. First the simple technique of chronaxie measurement as set forth and practised by Lapicque and his followers is quite inadmissible if there is more than one excitability present with different chronaxies. For if the rheobase lies on one of the two curves, and the "chronaxie point" lies on the other, a slight relative change in the rheobases of the two component curves will

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[1] In my former paper I used the term α and γ "substances" (following Lucas). I am indebted to Prof. Lapicque for pointing out that the expression might seem to exclude the possibility of the two curves being obtained from a single element by two different modes of excitation (*e.g.* opening and closing). I am therefore substituting his expression "excitability," leaving it an open question whether one or two different structures are involved.

be interpreted as a change in chronaxie of complex tissue. Second, the physiological concept of isochronism and therewith the theory of curarization cannot be maintained in its present form if a nerve can supply the α excitability whose chronaxie is at least twenty times greater.

On account of the importance of these questions, it is desirable to obtain yet further evidence that the presence of the α and γ curves in muscle is normal. The data under discussion have been obtained largely from the sartorius muscle, and Lapicque maintains that this muscle is apt to give anomalous results. I have therefore investigated a number of other muscles from the frog in order to find out whether these also exhibit α and γ curves, for it would obviously be unwise to consider these two curves as the expression of normal nerve-muscle excitabilities if in fact they are merely the peculiarities of a certain anomalous muscle.

CURVES FROM VARIOUS MUSCLES.

The apparatus and procedure were similar to that described in Fig. 6 of the previous paper. In brief the muscles were immersed in Ringer's fluid through which the current flowed, and the stimulus was localized to a certain part of the muscle by concentrating the current under an ebonite block. This was usually placed near the end of the muscle, and the cathode was on the side of the block away from the middle of the muscle. In this way the excitation arose from a place on the muscle not far from its extremity. As may be seen at once from Figs. 1, 2, 5, 7, etc., both α and γ excitabilities may be obtained from all the muscles investigated. These were the following[1]:

1. Tibialis anticus longus.
2. Tibialis anticus brevis.
3. Flex. dig. brev. superfic.
4. Pectoralis (pars abdom.).
5. Semitendonosus.
6. Semimembranosus.
7. Gastrocnemius.
8. Coraco-radialis.
9. Genio-hyoid.
10. Peroneus.
11. Gracilis.
12. Rectus abdominis.

They were selected on account of their size and ease in dissection. No muscle was found which failed to present the two types of excitability, though occasionally the γ curve was present nearly to the exclusion of the α. In such cases it was always possible to increase the proportion of the α by moving the ebonite block further towards the extremity of the muscle. It appears that, in general, the extremities of muscles are relatively deficient in the γ excitability. As is well known, Bourguignon [1923] has compared the chronaxies of many different muscles and drawn interesting conclusions therefrom. No similar comparison of the α curves

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[1] The nomenclature of the muscles is taken from Ecker and Wiedersheim [1896], except that I have called "gastrocnemius" what is there called "plantaris longus."

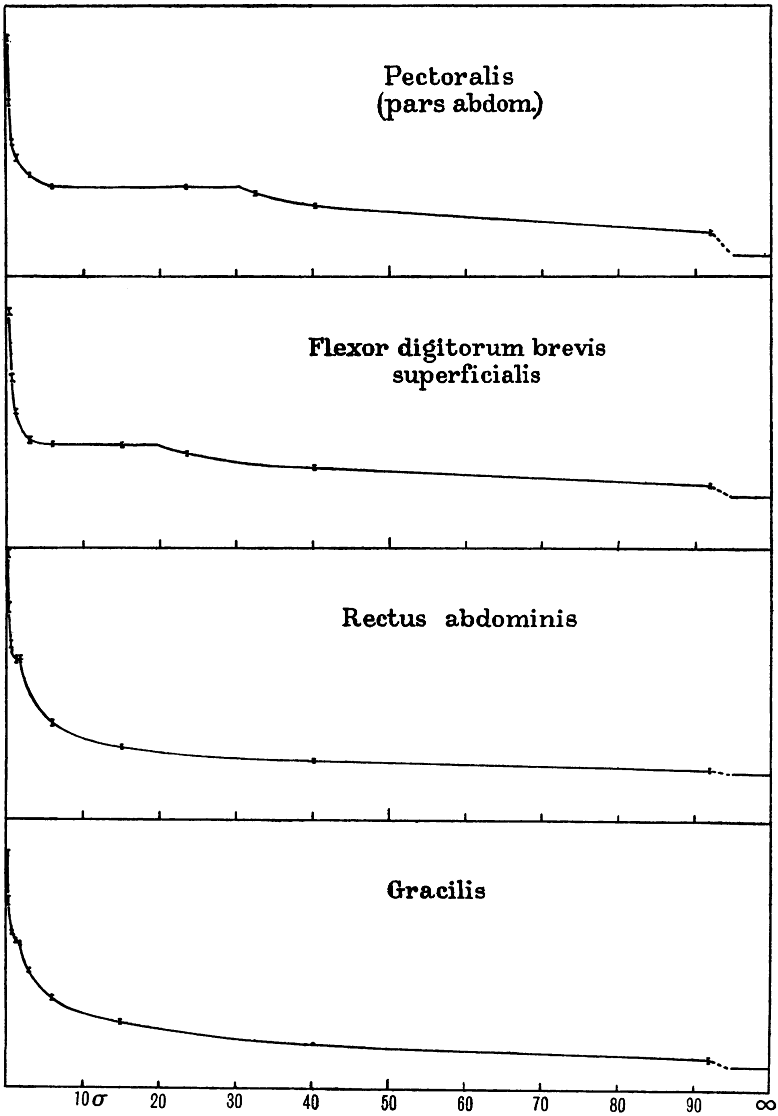

Fig. 1. Strength-duration curves of M. pectoralis (pars abdom.), flexor digitorum brevis superficialis, rectus abdominis, and gracilis. Abscissæ, duration in σ; ordinates, strengths in arbitrary units.

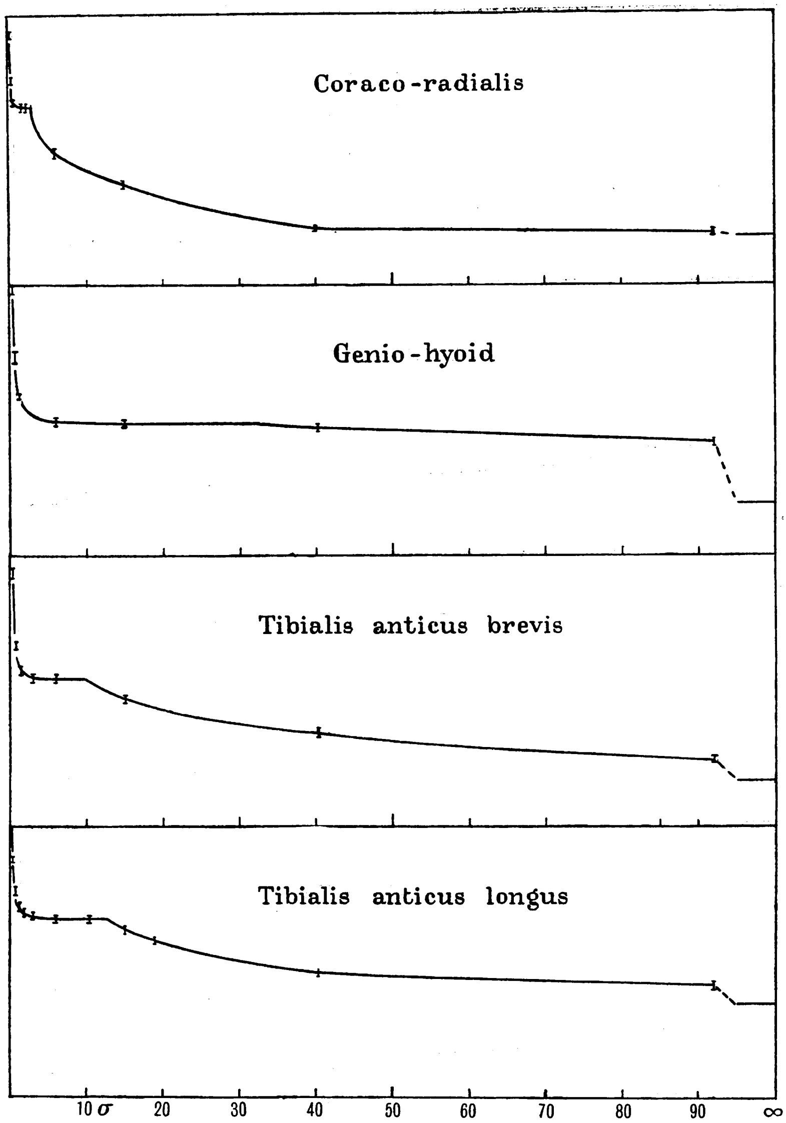

Fig. 2. Strength-duration curves of M. coraco-radialis, genio-hyoid, tibialis anticus brevis, and tibialis anticus longus. Abscissæ, duration in σ; ordinates, strengths in arbitrary units.

in this paper is legitimate. Though in the present arrangement the results may be repeated within experimental limits of 7 p.c., a small alteration in the position of the electrodes often causes changes in the chronaxie of the α excitability as large as the difference between one type of muscle and another. And so, though I would not wish to deny that different muscles may have different typical chronaxies, it must be pointed out that information upon this head cannot be obtained from the present results. In the case of one or two of the muscles investigated it was not found possible to excise them without a certain amount of damage, but there is no reason to suppose that the dual nature of the observed curve was due to any injury. It was found equally in the genio-hyoid and the gastrocnemius, though the first is very delicate and the second robust and easy to excise without injury.

It appears in fact that, whatsoever voluntary muscle is used, it will exhibit the two different excitabilities when treated in the manner described, and hence it is legitimate to conclude that the presence of α and γ is not due to any peculiarity of the sartorius and sterno-cutaneous investigated in the previous paper, but is a property of all striated muscles.

STIMULATION BY CONDENSERS.

Though Lapicque and his school have sometimes used brief constant currents (rectangular pulses) as stimuli for strength-duration investigations, the method of condenser discharges (exponential pulses) has been found by them to be more convenient and hence has been more commonly employed. The question naturally arises as to whether the α and γ curves obtained by the former method, as just described, also present themselves in the latter case.

It will be recalled that Lucas was originally led to his investigation of "the excitable substances in muscle" by the observation that the sartorius muscle when stimulated in its middle region by condenser discharges exhibited a double "energy minimum," *i.e.* at two definite rates of discharge the energy required for a threshold excitation was less than that required for other rates of discharge. Lucas's energy-capacity curves [1906–7] show a marked discontinuity, and so we might expect that the corresponding voltage-capacity curves would also show a discontinuity.

This expectation was confirmed in experiments upon the sartorius, gastrocnemius, semimembranosus and peroneus muscles, using the block type of electrode previously described. The electrical circuit was of the usual form where the condenser is discharged through the tissue by opening a contact mechanically. The resistance of the discharge circuit was measured directly before and after the experiment by the alternating current bridge method (1000 cycles) with telephone detection of the balance point, and the two results agreed to 2 p.c. Now the rate of discharge is characterized by the product of the capacity and the effective resistance through which the discharge flows, and according to Lapicque, $\frac{3}{8}\,CR$ gives the duration of an equally effective constant current whose strength is the same as the initial discharge current when this is twice the rheobase. Thus in Fig. 3 the abscissae are scaled to represent not capacity, but $\frac{3}{8}\,CR$, and hence should give strength-capacity curves quantitatively comparable with the strength-duration curves in this paper.

The strength-capacity curves in Fig. 3 exhibit kinks of the same kind as with rectangular waves, but the discontinuities are not generally so conspicuous with condenser discharges as with constant currents. The curves from the peroneus and the sartorius show the break obviously. In the results from the gastrocnemius, two curves are superimposed. The set of points A, here represented with a kink, when plotted alone allows of a single perfectly smooth curve to be drawn through it. At the time of obtaining the results, however, it was plotted in logarithms (see Fig. 9). In this representation it is seen at a glance that the curve A is obviously composed of two parts, and I therefore sought to obtain physiological confirmation of the duality. A shift of the cathode towards the peripheral extremity of the muscle gave a strength capacity curve with no break even with the logarithmic representation (B, Fig. 9), and this, when the ordinates are suitably reduced, is seen in Fig. 3 to coincide with the former curve exactly in its lower range, but to deviate abruptly at the point $\frac{3}{8}\,CR = 2{\cdot}7\,\sigma$. It is exactly here that the kink occurs in the logarithmic representation.

In the results from the semimembranosus muscle, strength-duration curves (circles) were also obtained from the preparation with electrodes unaltered. Of these curves the lower pair is taken with the cathode on the side of the block nearer the centre of the muscle. This exhibits mainly a γ curve with an α portion at long durations. The other pair (whose ordinates have been doubled for clearness of the figure) was obtained by reversing the current, and, as usual, the α excitability was much more prominent. A γ portion was present in both these portions also, but only at a duration shorter than here represented. It is obvious that the two curves of each pair by no means coincide, nor can they be made to do so by any uniform alteration of scale, for the strength-capacity curves do not

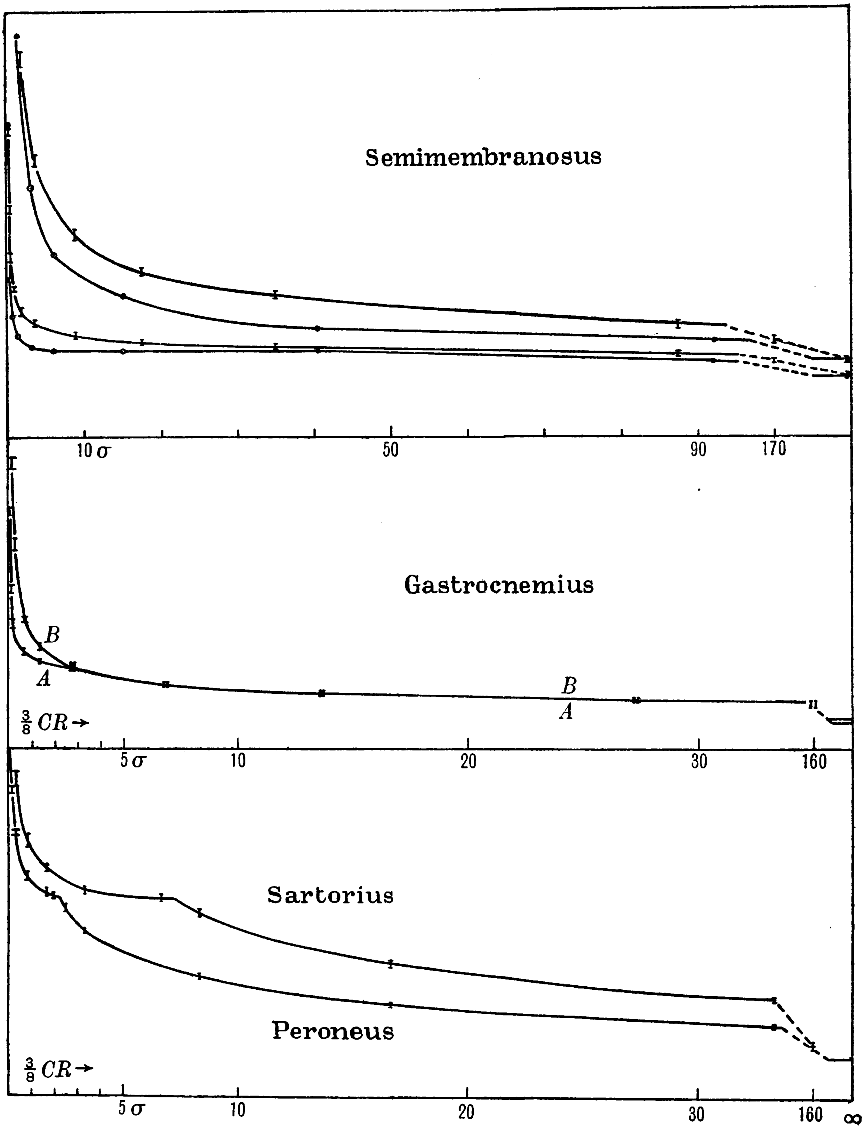

Fig. 3. Condenser discharges; strength-capacity curves of M. semimembranosus, gastrocnemius, sartorius and peroneus. Also strength-duration curves for semimembranosus (circles). Ordinates $\frac{3}{8}$ *CR* in σ.

turn up from the rheobase nearly so suddenly as do the strength-duration curves. This difference accounts for the greater difficulty in obtaining kinks in the strength-capacity curves, for it is easily seen from the figure just considered, that if the α pair and the γ pair are superimposed by any suitable scaling of ordinates, the α and γ strength-duration curves (circles) will meet far more obtusely than will the α and γ strength-capacity curves.

One is inclined to ask why it is that the strength-capacity curves exhibit this difference from the strength-duration curves, but might it not legitimately be countered why the two should be similar? It is not easy to appreciate intuitively the essential points of comparison between constant currents of different durations and condenser discharges of different rates, but if we assume that the tissue resembles a condenser with resistance in series and in parallel, then it is not difficult to calculate the limiting strength-duration and strength-capacity curves, such that a certain fixed charge is attained by this condenser.

The strength-duration relation is

$$E=A/(1-e^{-t/\alpha});$$

the strength-capacity relation is

$$E=A\ (\alpha/\beta)^{\alpha/(\alpha-\beta)};$$

where A = rheobase; α = time constant of tissue ($=CR$ term); β = time constant of condenser discharge.

When E is plotted against t on the one hand and against β on the other, it is found that the two curves resemble closely the corresponding physiological curves, and in particular that the former rises much more sharply from the rheobase. It is therefore not unreasonable to attribute the difference in the experimental curves to the physics of the system as indicated by the simplified condenser model.

A practical consequence of this difference between the curves with rectangular and exponential waves is that the former is greatly preferable in circumstances where the detection of a kink in the curve is important.

FURTHER EVIDENCE FOR KINKS IN CURVES.

Since the presence of the two excitable substances is detected by discontinuities in the slopes of the curves, it is naturally important to be satisfied that these kinks are not due to errors. In the former paper certain methods of confirmation were given, *e.g.* variation of threshold with angle or comparison of supposedly complex curves with the primaries if they can be obtained alone. Neither of these methods is easily applicable unless the muscle is very regular, and so in the majority of muscles certain other tests must be applied. Often the two curves meet at an angle so obtuse that discontinuity is well marked and no further satisfaction is required than that the observations are repeatable within the recorded limits. When, however, the curves meet at a duration of 30σ or more, there may be such a small angle between the horizontal γ rheobase and the slowly falling α portion that the kink is not very obvious, and some further confirmation of the supposed discontinuity would not seem out of place. In such cases the break is illustrated more accurately and convincingly by plotting in logarithms, a form of representation which is discussed at the end of this paper, but it is also possible to obtain certain fresh physiological data which will clearly demonstrate some change of function coincident with the questioned kink in the curve.

Two methods will be described:

(*a*) Latent period;
(*b*) Double contraction.

(*a*) *Latent period.*

The circuits are shown diagrammatically in Fig. 4. The Lucas pendulum was fitted with three keys. K_1 and K_2 are arranged as usual to send

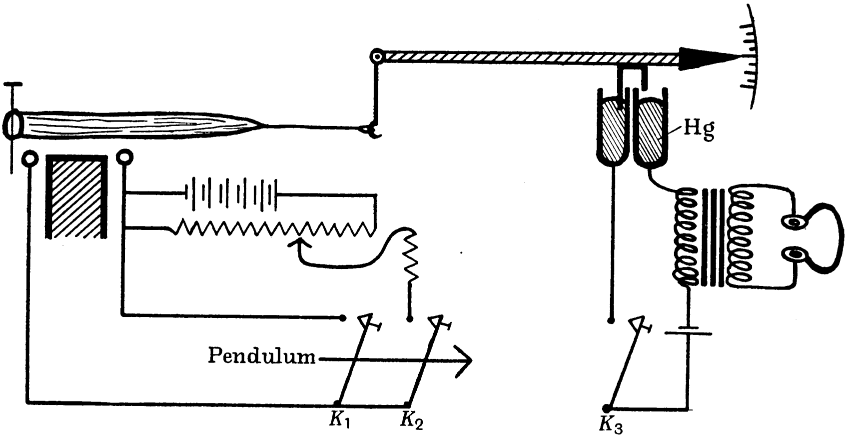

Fig. 4. Circuit diagram for latent period experiment.

a rectangular wave into the tissue. K_3 is in quite a separate circuit including a 6-volt accumulator, the primary of an inductorium and a mercury contact in connection with a light torsion lever. As is easily appreciated from the figure, a contraction of the muscle depresses the lever, and thus causes the amalgamated copper wire to dip into the two mercury cups thereby completing this portion of the circuit. The secondary of the inductorium was connected to a telephone headpiece, and thus when the muscle contracted a loud click was heard as the mercury contact was made, provided that K_3 was still closed. By arranging K_3 to be opened at shorter and shorter intervals after K_1K_2 a point would be reached at which the click was no longer heard. This of course is when K_3

was opened just before the mercury contact was made. The setting of K_3 now gives the instant when the contraction had developed sufficiently to cause a certain fixed small movement of the lever. The experimental procedure was therefore as follows. The muscle was set up and the block placed in such a position as to cause the α and γ curves to meet at a duration of more than 10σ. If a preliminary determination of the strength-duration curve showed that this condition had not been obtained, the block was shifted and a redetermination made. When this was satisfactory the main experiment began, the results of one of which are shown in Fig. 5.

K_1K_2 were set at an interval corresponding to $0{\cdot}5\sigma$ and the threshold sought, using as index both the smallest visible movement of the lever, and also the presence of a click in the telephones when K_3 was short-circuited (by a key not shown in the figure). The two criteria usually gave the same result. On the γ curve the difference was certainly less than 1 p.c., and on the α curve the smallest movement occurred at about 2 p.c. below the threshold for a click. Just adequate threshold stimuli were then sent in and the interval between K_1 and K_3 adjusted so that a position was obtained where a click was heard, but which when diminished by 2 or 3σ abolished the click. The threshold was finally redetermined as a check upon the stability of the preparation and then the K_1K_2 interval was increased to 1σ and the whole set of measurements repeated. This was continued with a number of different intervals as may be seen from Fig. 5, which shows the strength-duration curve plotted in the usual manner, and also the interval between K_1 and K_3 plotted on a vertical time scale equal to the horizontal time scale. The upper limits of the experimental "points" on this second curve represent instants when a click was heard, the lower limits represent instants when no click was heard, thus the interval between the start of the stimulus and the make of the mercury contact is given by the ordinate of some place on the experimental "point." One practical difficulty arises in dealing with a threshold excitation in this way. Clearly when a click is heard it signifies that K_3 opened after the mercury contact was made, but when no click is heard it may mean either that K_3 has opened too early or that the threshold has altered slightly and the stimulus become just subthreshold. To distinguish between these two possibilities without further stimulation, use was made of the fact that an amalgamated point, in equilibrium very close above the mercury surface, remains after immersion in contact with that surface due to surface tension. Hence when no click was heard it was merely necessary to note that there was a click on closing K_3 again to be satisfied that there had been a contraction. Then of course the point was lifted from the mercury surface before the next observation was made.

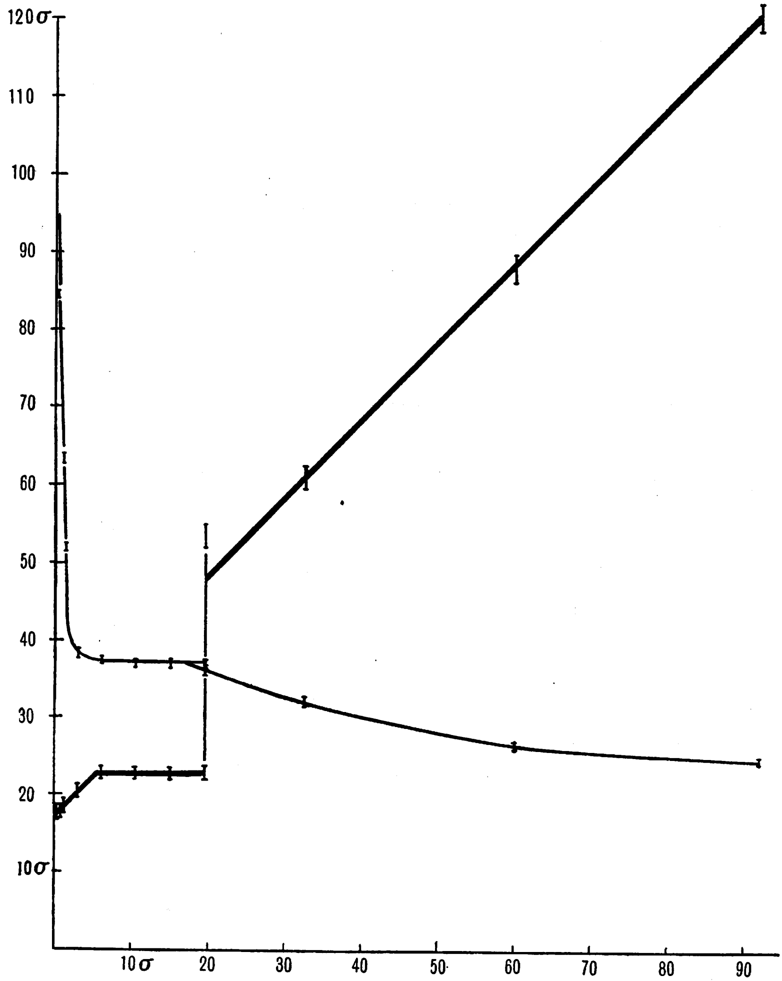

Fig. 5. Strength-duration curve of M. semimembranosus and latent period curve (heavy line). Abscissæ, duration in σ; ordinates, strengths in arbitrary units and latent period in σ. For each duration the stimulus was the ordinate of the strength-duration curve, and the corresponding latent period, the ordinate of the other curve.

Turning now to the experimental results (Fig. 5), the strength-duration curve is seen to fall rapidly for the first 3σ, reach a horizontal plateau (γ rheobase) at some point before 6σ, to continue horizontal until after 15σ and then to fall again (α curve) before 20σ and continue to fall at least until 90σ. It is such a curve as this whose dual nature might be contested. Is the accuracy of the points sufficient to warrant the conclusion of discontinuity in the region 15–20σ? On this head the evidence supplied by the latent period curve (heavy line) is very definite. This is seen to rise at 45° for the first 3·5σ, then run horizontal to 15–20σ, then jump suddenly to a point some 25σ above, and thereafter continue to rise at 45°. I have made experiments upon the sartorius, gastrocnemius, and semimembranosus muscles and in all of these the same relation has been observed between the two curves. Namely, when the strength-duration curve is falling (whether α or γ), the latent period is rising at 45°; when the γ curve is running horizontally, so is the latent period curve; when the γ curve changes to α there is a great jump in the latent period curve, and this jump is more pronounced the greater the abscissa at which the γ and α curves meet. In this way it has been possible to demonstrate the presence of a kink occurring as late as 100σ, for although in this case the α curve was represented by a single experimental point, the latent period at this point jumped about 100σ, showing very emphatically a change of function.

It is a matter of interest to consider why the latent period curve is composed of four straight lines, one at 45°, one horizontal, one vertical, and a second at 45°, and why these correspond to specific regions of the complex strength-duration curve. The interpretation is easy.

If a muscle is excited by a threshold stimulus greater than the rheobase, then (by definition) the threshold will not be reached until the moment when the stimulus ceases and the impulse will start at this instant [Bishop, 1927]. If the movement of the muscle lever occurred simultaneously with the starting of the impulse, then the interval between K_1 and K_3 would be the same as the interval K_1K_2, or, plotted as in Fig. 5, the latent period curve would be a straight line at 45° passing through the origin (since both time scales are equal). Since, however, there is a certain delay between excitation and making of the mercury contact, this 45° line will not pass through the origin but will cut the vertical axis at an interval corresponding to this delay.

This 45° course of the line obtains, however, only so long as the stimulus lies above the rheobase. Down to this point the impulse starts at the instant before the threshold stimulus stops. When, however, we employ durations longer than the γ utilization period (about 3·5σ in present example), the impulse no longer waits until the stimulus ceases but arises at the end of the utilization period no matter how long the stimulus persists. Thus the latent period curve runs at first at 45°, but when the duration of stimulus attains the utilization period, it suddenly turns and runs horizontally. This horizontal line will continue so long as the threshold lies above the γ rheobase, but as soon as an α point is found below it, the impulse can no longer arise at the end of the γ utilization period, and will not be elicited until the α stimulus ceases. The conditions are exactly the same whether we are on the sloping part of the α curve or the γ. Thus in the α region too the latent period curve is a straight line at 45° and if the delay period for α were the same as for γ, the 45° line should be a continuation of the γ 45° line, with a gap. Actually the delay period for α is always greater than for γ (by an amount which varies with the preparation), a fact which makes the discontinuity we are observing the more pronounced, and which is easily explained.

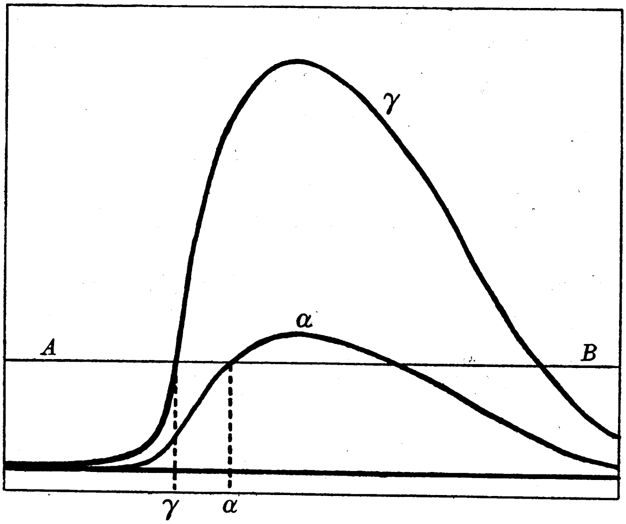

Fig. 6. Diagrammatic time tracing of α and γ contractions.

One property of the γ excitability which usually distinguishes it from α is that the most excitable elements are connected to a great many muscle fibres. In this way a certain strength of stimulus which gives no contraction will when increased by 1 p.c. cause quite a large contraction. The α excitability gives only a small movement in these circumstances, and hence the two excitabilities can usually (but not invariably) be distinguished by observing the size of threshold contraction. This was indicated earlier when the threshold was measured both by the movement of the lever and by the click in the telephones. In the present case the threshold contraction for γ was certainly much larger than that for α, so that the two may diagrammatically be represented as in the time tracing (Fig. 6). If the line AB represents the amount of contraction required to make the mercury contact, it is at once obvious why the delay in the α contact is much longer than the γ delay and why it varies considerably.

In Fig. 5 the latent period corresponding to the shortest duration on the α curve appears to be too long, for the point lies well above the 45° line. This is probably due to the fact that at this point special care was taken not to exceed the α threshold by more than 1 p.c. so as still to lie below the γ rheobase; consequently the mercury contact was not made till near the maximum of the contraction, in contrast to the other α points where the stimuli exceeded the threshold by 2 or 3 p.c. and hence the contact was made earlier in the course of the contraction.

At the duration 20σ (Fig. 5) two points are given on each curve. The threshold here is just below the γ rheobase and the latent period corresponding is about 50σ. An increase of 2 p.c. in current strength, however, attained the γ rheobase, and here a much larger contraction resulted and the latent period dropped 30σ to the other value shown. Thus a change from γ to α is shown not only by a change in the slope of the curve but by the difference in the size of the contraction and the jump of the latent period.

It is obvious that the method here employed is quite unsuited for an accurate estimation of the true latent period, but it is absolutely adequate for the matter in hand. Within the experimental limits of a few σ, the latent period curve is in complete accord with our expectations; the simplicity of its form makes it easy to recognize a chance erroneous point, and the manifest jump coincident with the junction of γ and α leaves the dual nature of such strength-duration curves incontestible.

(*b*) *Double contraction.*

In the foregoing section it has been shown that the threshold γ contraction occurs considerably before the threshold α contraction in cases where the two curves meet at an abscissa of 20σ or more. This suggests the possibility of obtaining a double contraction from a single rectangular wave due to the different latent periods of the two excitabilities. Three examples of this are shown in Fig. 7, together with the corresponding strength-duration curves, upon which the crosses A, B, C, indicate the strength and duration of the stimuli employed.

I. *Gastrocnemius.*

The first stimulus A is seen to lie above the γ threshold but below the α curve.

The third stimulus *B* lies above the α curve but below the γ rheobase.

The second stimulus *C* lies above both α and γ curves.

Thus contraction of *A* is a γ contraction, *B* is an α contraction and *C* is a contraction of γ and α. The tracing shows that *C* is obviously compounded of *A* and *B*.

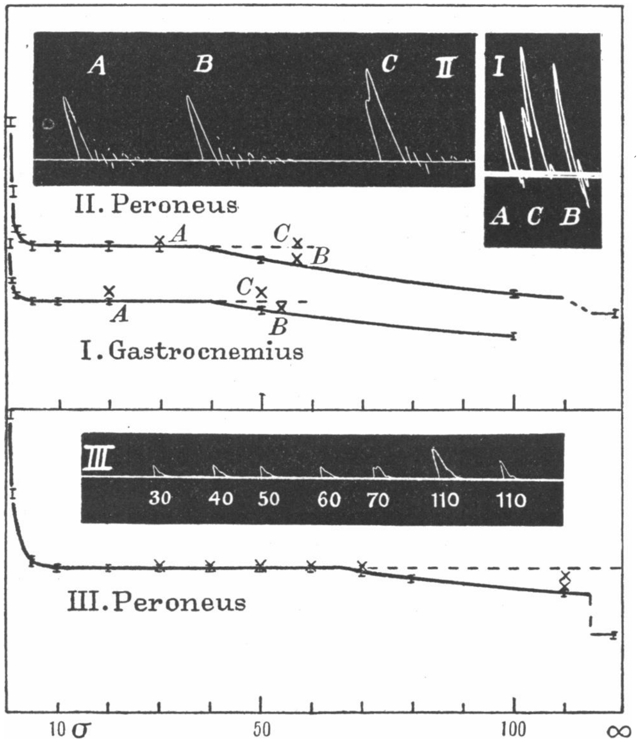

Fig. 7. **Double contractions. Contraction curves from gastrocnemius and peroneus muscles produced by stimuli of strength and duration shown by crosses on adjacent curves. Abscissæ in σ.**

II. *Peroneus.*

The case here is exactly as in I.

III. *Peroneus.*

The contractions here were only just threshold, as shown by crosses on the strength-duration curve. It is seen that the rheobase produces the same form of contraction however long it lasts (30–60σ) until at 70σ

the α appears below the γ curve. At this point a double contraction results. At 110σ two different current strengths below the γ rheobase give single-peaked contractions.

The true form of these curves was somewhat distorted by the undamped tension lever used, whose natural period (as may be seen from I and II) was not very remote from that of the double contractions recorded. It is very unlikely, however, that the double contractions are simply of instrumental origin, for they could never be obtained by any magnitude of contraction involving only α or only γ, but appeared at once as soon as the stimulus exceeded the thresholds of both excitabilities. Moreover, the relative prominence of the two contractions could be varied at will by selecting a stimulus which lay near the threshold for one and well above that for the other, a thing which would be difficult to explain on the grounds of lever resonance to a single simple twitch.

Lucas [1917] in his experiments on *Astacus* used the method of double contraction to demonstrate the discontinuity in his strength-duration curve, but in that case the two contractions were of different kinds. In the present instance the α excitability, though of much greater chronaxie than the γ, does not appear to give an appreciably slower contraction, and seems to be an exception to Lapicque's generalization that contraction rate is more or less proportional to chronaxie[1].

In this paper we set out to learn whether the α and γ curves formerly obtained from the sartorius were of normal occurrence in voluntary muscles. It has been shown that in every one of the dozen different muscles investigated these two excitabilities are to be found. Sometimes the strength-duration curves show an obvious kink, and there is no further question, but sometimes the kink is less obvious and confirmation is useful. Three methods have been employed. By shifting the electrode block the proportion of α and γ can be changed so that the new curve shows clearly a kink, either by itself, or at least when viewed in conjunction with the former curve (cf. Gastrocnemius, Fig. 3). By measuring the latent period for threshold excitations of various durations, a great discontinuity is found coincident with the suspected kink in the strength-duration curves. A tracing of the contraction shows a double peak only when the stimulus is a current whose strength and duration is represented by a point lying above both α and γ curves. And though these last two methods will only apply when the strength-duration curve is almost

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[1] The approximate identity of the α and γ contraction curves has been verified by the use of an isometric lever of period some nine times as short as the duration of a twitch.

exclusively γ, yet it is just in these circumstances that the confirmation is most needed.

As a result of these observations, I think that we may conclude that by the use of large electrodes of the block type, α and γ curves may be obtained from any voluntary muscle in the frog.

METHODS OF PLOTTING THE STRENGTH-DURATION RELATION.

The representation of the relation between strength of exciting current and the duration necessary to attain a threshold excitation is useful in two connections. There is the obvious value as representing the result of a determination in a graphical manner, at once appreciated very much more readily than a table of figures. But no less important is a graphic representation during the actual experiment. If a curve shows no irregularities it may be drawn with some accuracy if only a few points are determined, but if there are kinks it becomes at once essential first to investigate whether the kink is the expression of some physiological discontinuity or merely a chance error, and second, in the event of its being found to be significant, to determine accurately the whole neighbouring region of the curve. It is obvious that a detailed appreciation of the irregularities of a curve cannot be obtained unless the curve be plotted during the actual investigation, and it will often happen, when this is not done, and a curve is constructed later from the numerical data of a previous experiment, that the results are found to be doubtful. A point slightly displaced might be significant or merely a chance error; a single new point determined in a critical region would have settled the matter beyond dispute. For this reason it is important to plot the points as they are determined. This procedure, moreover, has an advantage of a different kind. In order to obtain reproducible results it is necessary to avoid applying stimuli which are excessively numerous or much above the threshold. In other words it is well to have a good idea of the probable position of a point on the curve before determining it. It may then be obtained with a minimum of erroneous trials. This might be criticized on psychological grounds, but, working with limits of 5 p.c., the presence or absence of a twitch is so definite that the observer's imagination can hardly influence the results. Thus the graphic representation of the experimental points as they are determined has the additional advantage that it allows a closer guess at the probable position of the next point.

Turning then to the question of the particular form of curve to be employed, we should consider the two uses of this representation. For a record of the experimental results the curve should be illustrative of the important features (*e.g.* experimental limits, change in form of the curve, kinks, etc.). For use during the actual experiment it should also admit of a fairly accurate extrapolation from point to point, and should not require any elaborate computations to obtain the required functions.

Of the many forms of representation which are possible, four will here be mentioned. They are all discussed in Lapicque's book [1926], and may be tabulated as follows:

Plot vertically	Plot horizontally	
i	t	This is the usual strength-duration curve.
it	t	Quantity-duration curve, the Weiss-Hoorweg line.
i^2t	t	Energy-duration curve (cf. Hermann, energy minimum).
$\log i$	$\log t$	Lapicque, *loc. cit.* p. 152.

The strength-duration curve has directness and familiarity to commend it. The objections are that, even with the most favourable scaling, the curve is nearly vertical at short durations, which makes it difficult to appreciate both the form of the curve in this region and the limits of experimental error. When two curves are plotted for comparison it is very hard to distinguish them in the "vertical" region or to find which "points" belong to which. It is also difficult even with some practice to tell how two such curves would compare when scaled to the same rheobase (which is in fact what one usually wants to know). But when two different curves such as α and γ are both to be represented on the same scale, matters become acute. The γ curves often have chronaxies of $0{\cdot}2\sigma$, and hence cannot be adequately represented on a scale of less than 5 mm. for 1σ. But the α curve, which, though indubitably present, often does not appear until a duration of 50σ, seldom reaches its rheobase by 100σ (using the block electrode system I have generally employed). The graph must therefore be half a metre or more in extent, which is obviously impossible for publication purposes. Moreover, the kink in the curve in this case seems so small, due to the large scaling, that one is apt to overlook it altogether or at least to minimize it, since the angle at which two curves meet is what actually strikes the eye. In view of these considerations it is seen that, though the strength-duration curve is adequate for the representation of a single simple curve suitably scaled, it fails to illustrate clearly the more complex conditions which further analysis reveals.

The quantity-duration curve is recommended by Lapicque as a representation which shows up experimental errors. For general purposes, however, I do not think that it is better than the strength-duration curve. It has the advantage of being clearer at short durations and it is certainly easier to anticipate points during an investigation if they all lie on the Weiss-Hoorweg line. But against this, each point requires a small calculation, the α curve does not lie upon the Weiss line, but approaches rather the Nernst parabola ($it = k\sqrt{t}$), and in addition a kink in the curve is obscured by this method of plotting, since the divergence of angle though significant is very small. In addition, all the scaling objections which applied to the strength-duration curve enter equally here.

The energy-duration curve has practically no advantages over the foregoing. Many of the objections are emphasized, some new ones enter, and the one advantage, relating to the energy minimum, is shared equally by the next method to be considered.

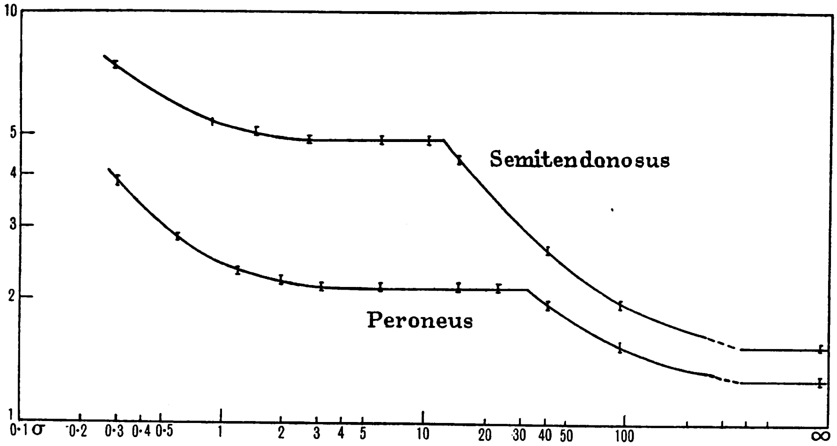

Fig. 8. Logarithmic plotting of strength-duration relation of semitendonosus and the peroneus shown in II, Fig. 7. Ordinates, log (strength); abscissæ, log (durations) in σ at half scale.

Double logarithmic scale.

The most satisfactory method of plotting that I have found is on paper graduated in logarithms on both axes. On the horizontal axis the scale 1 to 10 occupies $2\frac{1}{2}$ inches, on the vertical axis 1 to 10 occupies 5 inches. Such a scale can easily be constructed from the long and short scales of a 5-inch slide rule, etc. In this way the intensity axis has a range of 1 to 100 and the time ranges from 0·1 σ to 1 sec. on a sheet of 10 × 10 inches.

It is sometimes objected to logarithmic plotting that it distorts the results and is often employed to give a spurious accuracy by reducing the errors to vanishing point. This objection does not hold if care is taken to epresent the magnitude of the experimental errors on the new scale, and if it is remembered in comparing small deviations on the graph that at the left of the scale they are insignificant, whereas six decades to the right, a miss is as good as a mile, or at least a micron is as good as a metre.

Now plotted in this way the strength-duration curve can be very well

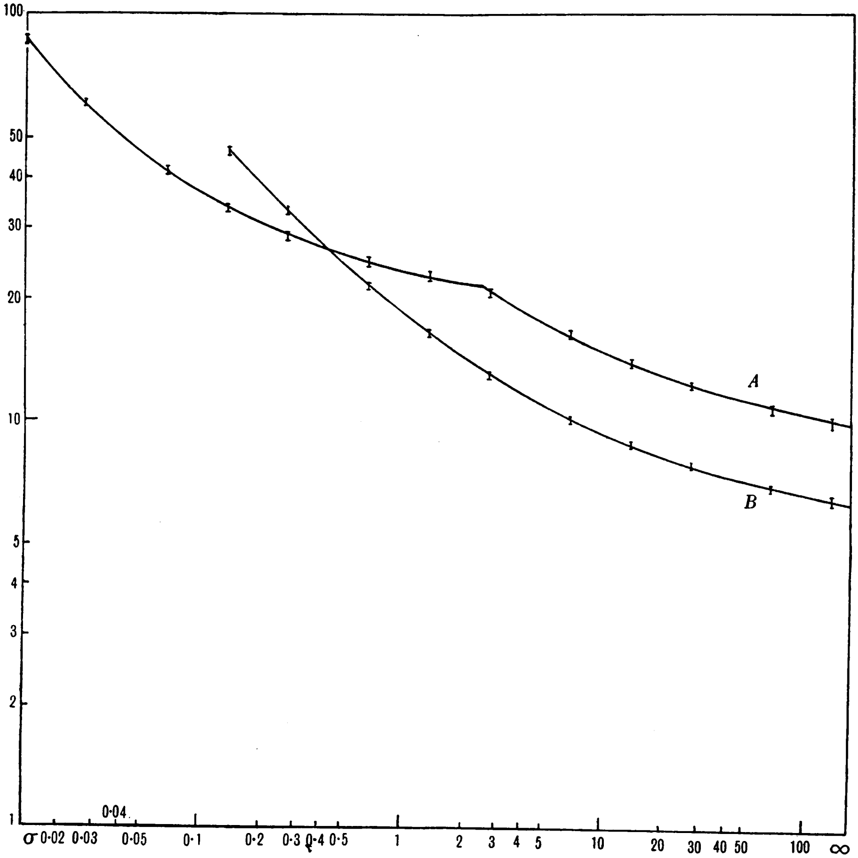

Fig. 9. Logarithmic plotting of strength-capacity relation from the gastrocnemius in Fig. 3. Ordinates, log (strength); abscissæ, log ($\frac{3}{8}$ *CR*) in σ at half scale.

represented. The horizontal limits of error are negligible, except at the shortest durations, and the vertical limits, being always about 5 p.c., are always a line of about 0·1 inch. An instance of this form of plotting is given in Fig. 8, where results are obtained from the semitendonosus and the peroneus. The data from the latter are identically that of Fig. 7 (II), and it is obvious how clearly the discontinuity between α and γ stands out in comparison with the former method, especially when it is noted that there is no experimental point where the two curves meet. In fact, when the results are represented logarithmically there is hardly any need for the corroborative evidence of the double contraction. Wherever it occurs the discontinuity is clearly seen by this method of plotting except in the event of it falling in the neighbourhood of 0·3σ. In this region the two curves appear to become tangential, and hence there *is* no kink between them to be brought out by any method of plotting.

The smallness of the curvature of the logarithmic relation makes it easy to anticipate the next point in an investigation, and as a routine it is usually safe to extrapolate linearly; this gives a strength a little below threshold, which can then be attained in about two 5 p.c. steps.

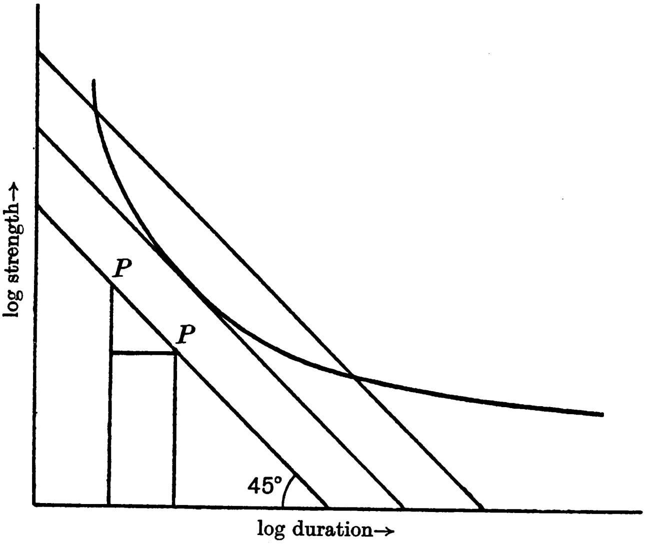

Fig. 10. Diagrammatic logarithmic plotting of strength-duration relation.

In comparing several curves on the same graph, the logarithmic method allows of greater clearness than any of the others considered; and has the considerable advantage that a change in rheobase without change in the time relations merely causes the curve to be shifted parallel to itself in a vertical direction. Thus in Fig. 9, which represents the strength-capacity results on the gastrocnemius shown in Fig. 3, we can see at a glance, not only that one curve is simple and the other complex, but also that the simple curve will coincide with the α portion of the other when shifted vertically, and hence that the two α curves will coincide when suitably scaled (as is seen to be the case in Fig. 3). Finally the energy minimum is easily found from the logarithmic curves, being the point where the tangent lies at 45° to the axes (gradient $= -1$). For, if P (Fig. 10) is any point moving along a 45° line it is clear that in changing its position it increases its x by as much as it decreases its y, hence $x + y =$ constant on that line. But $x = \log t$, $y = 2 \log i$ (because of the double scale), hence

$$\log t + 2 \log i = \text{const.} = \log i^2t.$$

Hence

$$\text{energy} = \text{constant}.$$

45° lines therefore are lines of constant energy and are also the lines demanded by Nernst's equation $i^2t =$ const. It is thus clear that the point of minimum energy is at that place where the curve has reached the 45° line nearest the origin, *i.e.* when the 45° line is tangent to the curve.

It thus appears that the logarithmic plotting in the manner described has most of the advantages and not many of the defects of the methods considered, and is hence to be recommended both in obtaining and in representing the strength-duration relation.

SUMMARY.

The present investigation was undertaken to learn whether the α and γ excitabilities in the strength-duration curves of muscle, demonstrated in a recent publication, are of general occurrence or due to certain particulars of preparation and the technique there employed. As a result we may conclude that:

(*a*) The two excitabilities are not confined to the sartorius and sternocutaneous muscles previously investigated, for they may be equally obtained in a dozen other muscles from the frog.

(*b*) The relative prominence of α to γ may nearly always be increased by causing the cathode to lie nearer the extremity of the muscle.

(*c*) When γ is present nearly to the exclusion of α, the presence of the latter may be confirmed by the very considerable change in the latent period of contraction which occurs at the point where the threshold changes from γ to α, and also by the double-peaked contraction curve which can be obtained from a single stimulus.

(*d*) When condenser discharges are used as stimuli the strength-capacity curves also show α and γ portions, but the kinks are generally not so obvious as in the case of brief constant currents.

(*e*) The strength-duration relation is very conveniently expressed by plotting in logarithms. The question of the relative advantages of certain methods of plotting is discussed.

In conclusion I should like to express my indebtedness to Prof. Bronk for his help and encouragement during the present work.

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